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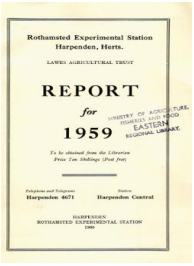
Full Table of Content



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INFECTIOUS DISEASES OF THE HONEYBEE

By

L. Bailey

Research at Rothamsted on infectious and other diseases of the honeybee began in 1934, and was supported by a yearly grant of £250 for the first 3 years from the British Beekeepers Association and an equal sum from the Agricultural Research Council, together with contributions from private individuals. The grants were primarily for work on diseases of honeybee larvae—brood diseases—incidence of which in England and Wales was causing concern. This review is of the research done at Rothamsted since then on infectious diseases of honeybees, and of relevant work elsewhere. There are infections of honeybees other than those mentioned below, but they are of less significance or incidence in England and Wales, and consequently have not been specially studied at Rothamsted. H. L. A. Tarr began the research: his work was mainly on the natural history of Bacillus larvae, established by White (1907) as the cause of American foul brood disease (AFB), and on the etiology of European foul brood disease (EFB).

American four brood disease

Sturtevant (1924), finding that reducing sugars, particularly in concentrations over 2 or 3%, inhibited germination of spores and vegetative growth *in vitro* of *Bacillus larvae*, suggested that this is why only sealed larvae, which have consumed all their food and the sugar it contains, become diseased. Tarr (1938a), however, found that spores germinated in a liquid medium of minced chicken embryo with concentrations of reducing sugars up to 12·5%. Furthermore, even small numbers of spores (100–140) sometimes would germinate in his medium. Lochhead (1933) also found that a few spores germinated below the surface of semi-solid media of entirely different constitution to Tarr's, and it seems possible, therefore, that spores germinate best in a critical, reduced-oxygen tension. Previously, Sturtevant (1932) found only large inocula of spores germinated *in vitro* and thought that this may explain why small doses fail to cause disease in bee colonies: a few larvae infected when 4–5 days old died in his experiments, but only when inoculated with massive doses of about 10 million spores each.

Tarr (1937a) showed that spores were necessary to infect larvae: vegetative cells, even in massive doses, did not infect. Unlike Sturtevant, however, he could not cause AFB by inoculating the food of 4–5-day-old larvae. He infected larvae more successfully by spraying them with spores than by feeding their colonies spores in syrup, and he noted young larvae seemed more susceptible. Subsequently Woodrow (1942) found one spore enough to cause disease provided the infected larva was younger than 1 day old: larvae

https://doi.org/10.23637/ERADOC-1-92

older than 2 days were immune. On this basis it is difficult to explain why only sealed larvae die of disease, particularly as spores germinate within 24 hours after entering the larval mid-gut (Woodrow & Holst, 1942). Furthermore, the vegetative rods do not grow much in unsealed larvae (Maassen, 1908), and may even diminish in numbers shortly after larvae are sealed (Holst, 1946). *Bacillus larvae* may not grow much in the larval intestine, as this is probably too anaerobic, or bacterial growth quickly makes it so (see EFB section below), particularly perhaps in the most rapid growth phase of the larva which starts on the 3rd day after hatching (Nelson, 1924). Larvae may ultimately be killed during a critical phase of pupation by the toxic enzymes that Patel & Gochnauer (1959) found in remains of larvae dead of AFB, and which may be liberated by *B. larvae* as it grows. The relatively few bacteria in the larvae then could invade the dead tissues, proliferate and sporulate.

Shortly after Haseman & Childers (1944) found that sulphonamide drugs effectively suppressed signs of AFB, experiments were made at Rothamsted to test the value of such treatment. Milne (1947) summarised his investigations and confirmed the effectiveness of sulphonamides in allaying disease, but emphasised that treatment was impermanent, because dormant spores of *Bacillus larvae*, now known to stay viable for at least 33 years (Haseman, 1959), can develop once the drug is exhausted. In view of the lessening of the disease in England and Wales since the implementation of the Foul Brood Disease of Bees Order of 1942, which enforces destruction of known diseased colonies, use of sulphonamides was not considered advisable, and work on chemotherapy of brood diseases was suspended at Rothamsted. Work continued abroad, however, principally in Canada and the United States: oxytetracycline (Terramycin) was found by Katznelson & Jamieson (1952b) to be an effective antibiotic, but it has the same limitations as sulphonamides. There is still controversy, even in countries where use of drugs is permissible, about the desirability of their use in preference to destroying diseased colonies.

European foul brood disease

Tarr began investigations at Rothamsted on EFB when there was considerable confusion, not only about the etiology of the disease, but even about its existence. He worked first on *Bacillus alvei*, a bacterium commonly present in remains of larvae that have died of the disease and was, at the time, usually considered the cause. Burnside & Foster (1935) described *Bacillus para-alvei* as an organism similar to *B. alvei* and causing a disease similar to EFB. Tarr (1936a) found that *B. alvei* and *B. para-alvei* were biochemically indistinguishable; their differences, which were slight, were solely morphological. Davis & Tarr (1936) also found *Streptococcus apis* (another organism often present in diseased larvae) was indistinguishable from *Streptococcus liquefaciens* or *Streptococcus glycerinaceus* (all now classified as *Streptococcus faecalis*: see Bergey's *Manual of Determinative Bacteriology*, 6th ed.). This was apparently independent of Hucker (1932), who had already identified *A. apis* as *S. liquefaciens* by cultural and serological tests. At first Tarr (1936b) thought *A. apis* or *B. alvei* were able to cause EFB: he

https://doi.org/10.23637/ERADOC-1-92

found that disease sometimes developed after larvae had their food inoculated with pure cultures of either organism and were incubated without nurse bees for 4 days at 35° before being returned to their parent colony. It seems likely that EFB was endemic in the experimental colonies he used, and this may have made results unreliable, but it is also possible that signs similar to those of EFB were induced in the inoculated larvae whose resistance was lowered by starvation (see below). Later, Tarr (1937b) realised, as had White (1912), that another organism always seemed to occur in diseased larvae, particularly in the early stages of their infection. It was hardly distinguishable morphologically from *S. apis*, but its presence was suspected when attempts to make cultures *in vitro* from larvae, apparently containing very large numbers of *S. apis*, failed. Tarr (1938b) attempted to cultivate the organism, which he now recognised as *Bacillus pluton* White, on a variety of media without success. However, he confirmed many observations of White (1912, 1920).

Thus Tarr usefully clarified the complicated bacteriology of EFB, and his eventual confirmation of White's original observations, which previously had not been accepted or had been considerably modified, encouraged continuation of work with the principal fundamental aim of cultivation, *in vitro*, of *Bacillus pluton*. Meanwhile Burri (1943) introduced further complications by claiming to identify *B. pluton* as a dissociant form of *Bacterium eurydice* White, another organism commonly plentiful in larvae with EFB. Miss E. Kops at Rothamsted could not verify Burris' observations (*Rep. Rothamst. exp. Sta.* for 1947) but found *B. eurydice* to be pleomorphic and in some conditions to resemble *B. pluton* morphologically. Miss Kops and Miss H. Finegan tested a wide variety of media and conditions for cultivation of *B. pluton*, but all were unsatisfactory. Later, attempts were renewed with the co-operation of Professor L. P. Garrod (St. Bartholomew's Hospital), and field trials with one of his isolates indicated the possibility that *B. pluton* could be cultivated as an anaerobe (*Rep. Rothamst. exp. Sta.* for 1954). A medium was eventually developed at Rothamsted which gave satisfactory growth of *B. pluton* in anaerobic conditions (Bailey, 1957a), and the first experiments made with pure cultures showed it to be the primary pathogen in EFB (Bailey, 1957b, 1957c). As the organism does not form spores, it was decided that *Streptococcus pluton* (White), suggested by Gubler (1954), was a more appropriate name. Apart from low oxygen tension, the major critical requirements of *S. pluton* for growth *in vitro* are a high ratio of potassium to sodium, unidentified constituents of certain yeast extracts, high inorganic phosphate concentration, and CO_2.

Unlike *Bacillus larvae* (the cause of AFB), *Streptococcus pluton* develops abundantly in the larval mid-gut, suggesting that the mid-gut is virtually anaerobic, which may explain the feeble development of *B. larvae* in growing larvae. *S. pluton* apparently weakens larvae directly by depriving them of food (Bailey, 1959a), which enables secondary invaders to develop abundantly and help kill the larvae. Typically, *Bacterium eurydice* is the first of these to develop, as it is commonly present in bee colonies, living normally, apparently harmlessly, in the anterior parts of the alimentary tract of adult

https://doi.org/10.23637/ERADOC-1-92

bees (*Reps. Rothamst. exp. Sta.* for 1957, 1958). Other secondary invaders, such as *Streptococcus faecalis*, which seems common in cases of EFB in continental Europe, but not now in Britain, are probably picked up from outside sources by foraging bees. *Bacillus alvei* is not always present, but tends to become established in endemically infected colonies: it seems to be the last of the secondary invaders, developing in larvae that have died (Bailey, 1959b).

Tests with sulphonamides against EFB were made at Rothamsted in 1946 and appeared ineffective. Various antibiotics, however, particularly streptomycin and oxytetracycline, were found by Katznelson *et al.* (1952) to be effective, and their use has become common in North America and Europe. Growth of *Streptococcus pluton* is completely inhibited *in vitro* by penicillin G (concentration 10^{-7}–10^{-9}); oxytetracyclin (10^{-5}–10^{-7}) and streptomycin (10^{-4}–10^{-6}) (*Rep. Rothamst. exp. Sta.* for 1958). Despite the great efficiency of penicillin G *in vitro*, it is ineffective *in vivo*, against both AFB and EFB, and probably because it is unstable, particularly at pH values about 4·0, such as occur in honey and larval food. Dormant cells of *S. pluton* are now known to remain viable for over a year, however, and they probably become well distributed within bee colonies from some infected larvae, which, nevertheless, survive. Such larvae void very many bacteria in their faeces before pupation (Bailey, 1959a). Thus, treatment with antibiotics has, fundamentally, the same disadvantages with EFB as with AFB—continued application of drugs is needed until dormant bacteria have been eliminated by consumption of contaminated food and cleaning of combs by adult bees, but there can be no certainty of when this has been achieved.

Acarine disease

After the mite, *Acarapis woodi* (Rennie), was discovered by Rennie *et al.* (1921), it quickly acquired the reputation of being very destructive to adult bees, because it was considered to cause the " Isle of Wight disease ", from which many colonies of honeybees were alleged to have died in the British Isles from 1906 until shortly after the time *A. woodi* was discovered. Accordingly, the limited research at first possible at Rothamsted on adult bee infections was aimed at improved remedial measures, particularly as surveys between 1941 and 1944 (Butler, 1945) showed 20% of colonies infected and widely distributed in England and Wales. It had already been shown elsewhere that careful application of the vapour from Frow's mixture (nitrobenzene, safrol and petrol), or from burning sulphur, killed mites with no apparent damage to the bees. Butler (1941) also found terpineol vapour effective in laboratory tests. Later, more extensive field and laboratory trials were made with a variety of fumigants, including newer acaricides applied as smokes and reported effective by continental workers (Bailey & Carlisle, 1956). Briefly, Frow's mixture was found effective when applied in cold autumn weather, but infested bees eventually died in winter earlier than is normal. Thus, although the chances of heavy infestations recurring next season can be decreased, even if not eliminated, treated colonies are more likely than uninfested ones to die in the late winter because their numbers are abnormally low. Newer

https://doi.org/10.23637/ERADOC-1-92

acaricides of the di-(*p*-chlorophenyl) methyl carbinol ("Dimite") type are convenient for spring or summer use and are more effective than sulphur fumes. Repeated applications are necessary, however, unless they are used in warm weather, but then the colonies may be damaged because the smoke over-excites the bees.

Acarapis woodi achieved its bad reputation without any quantitative observations or experimental evidence about the pathology and epidemiology of infestation. Accordingly, since 1951, records were kept at Rothamsted of infestation and mortality of colonies that were not treated, and these showed that infestations in endemically infested hives are usually suppressed naturally. The proportion of total colonies examined that was detectably infested was similar to that found in the national surveys made in 1941–44, but most were only lightly infested, and when colonies found infested at any one time were graded according to the degree of infestation the numbers in each group fell exponentially as the degree of infestation increased. Few colonies ever had more than 30% of their bees infested during any one season. Obvious damage to colonies was found only with these heavy infestations, and then only in late winter: the very few with more than 75% bees infested usually die about March (Bailey, 1958). The effect of infestation on the life of individuals is slight and difficult to detect in summer bees. Queenlessness and inactivity of colonies in poor seasons are principal factors causing increased infestations (Bailey & Lee, 1959).

Thus, heavy infestation is the consequence of events unfavourable to colony development: it may be more common after several poor seasons, when the bees are kept alive by artificial feeding. On this basis, the apparent close association of mite infestation with "Isle of Wight disease" (Rennie *et al.*, 1921) may be reinterpreted. This disease probably had no single cause; rather, the name included a wide variety of debilities with similar signs (Rennie, 1923). Heavy mite infestation may well have resulted from, not caused, these various ailments, which on some occasions at least, including those of Rennie's investigations, occurred in very poor seasons. From its known wide distribution, *Acarapis woodi* was probably endemic in honeybees before the days of the "Isle of Wight disease": it has been found in *Apis mellifera* in most parts of Europe, including Sardinia and Mallorca, in Russia and in South America. It also occurs in *Apis indica* in India (Sardar Singh, 1956) and in *Apis mellifera adansoni* in the Belgian Congo (Benoit, 1959). Its apparent absence from Scandinavia, North America, Australia and New Zealand (Jeffree, 1959) seems remarkable, therefore, and deserves study.

As heavy infestation by *Acarapis woodi* is usually symptomatic of a poor economy, treatment, however successful in killing mites, may not be expected to produce a striking response in colony development. The value, therefore, of treatments that are directed solely against mites needs careful consideration, particularly as present methods have some detrimental effect on bees.

Nosema disease

In a survey in 1941–44 (Butler, 1945) adult bees infected with *Nosema apis* Zander were detected in about 5% of colonies widely

https://doi.org/10.23637/ERADOC-1-92 *pp 6*

distributed in England and Wales in April and May, the period when an acute peak of infection occurs in endemically infected colonies. This annual epidemic had been reported from Switzerland (Morgenthaler, 1939) and was confirmed at Rothamsted (*Rep. Rothamst. exp. Sta.* for 1939/45). Widespread infection of colonies at Rothamsted was first noticed in 1946, and from 1947 to 1950 Hassanein studied the natural history and pathology of the infection. Earlier workers showed that heavy artificial infection in autumn killed colonies in winter (White, 1919; Morgenthaler, 1941); that infected queens soon become unable to produce eggs (Fyg, 1945) and that hypopharyngeal glands of infected bees become prematurely atrophied (Lotmar, 1936). Hassanein (1951, 1952a) confirmed the last two observations, and found that brood-rearing was lessened in naturally infected colonies in spring, presumably because infected bees produced less hypopharyngeal brood-food, and that infected bees began foraging earlier and had shorter lives than uninfected individuals (Hassanein, 1953). There was plenty of experimental evidence, therefore, that infection with *N. apis* was pathological—more so, to individual bees, apparently, than infestation with *Acarapis woodi*.

Endemically infected but otherwise normal colonies are rarely obviously affected, however; this follows from the extent to which infection is naturally suppressed in such colonies during the summer. Burnside and Revell (1948) considered that increased temperature of the cluster, as brood-rearing increased, could account for the suppression of infection, and they confirmed results of Lotmar (1943a) showing that temperatures over 35° suppressed development of the parasite in individual, caged bees. An alternative explanation was that transmission of parasites to newly emerging bees, which are free of infection, ceases in summer when bees fly freely and defaecate outside the hive, and this was tested by experiments at Rothamsted in which bees were transferred to uncontaminated combs in early summer (Bailey, 1955a, 1955b). This treatment usually lowered infection to undetectable levels with no recurrence the next year. It seemed reasonable to suppose, therefore, that infection normally persisted in summer as faecal contamination deposited on combs the previous winter, and the decline of infection in summer reflected fewer spores left on combs to infect new bees. Recent experiments (Bailey, 1959c) showed that artificially infected bees, introduced to endemically infected colonies in summer when infection was naturally diminishing, all developed similar numbers of spores to those in naturally infected bees in spring when natural infection was high. Thus, high temperature seems to be unimportant, and the amount of infection on combs seems fundamental to the natural history of infection.

Means of decontaminating combs were developed: the best found was fumigation, at normal temperatures, with fumes of formaldehyde for empty combs, or with vapour of acetic acid for combs with food in them. The effectiveness of acetic acid was confirmed by beekeeping institutes abroad (Gavrilov, 1957; Jordan, 1957; Lunder, 1957). At Rothamsted almost all the bees were transferred to such combs in early summer 1954, and the percentage of colonies with detectable infection fell from between 50 and 90 to 7 the following spring (*Rep. Rothamst. exp. Sta.* for 1955). Many

https://doi.org/10.23637/ERADOC-1-92

colonies were also treated with fumagillin (see below), which may have helped, but there was no significant difference between colonies that received both treatments and those only fumigated (Bailey 1955b). These experiments were made in a poor season when infection locally, and generally in England and Wales, rose from 10 or 20 to 35 or 40% of colonies (Min. of Agric., Fish. & Food, 1956). Absolute elimination of infection seems unlikely by the methods employed, but keeping levels of infection low would be acceptable provided this could be done cheaply. Fumigating spare combs only, before re-use, has so far proved inadequate, but at Rothamsted colonies are handled more often than in normal beekeeping, and the seasons since the trial have been very poor. Nevertheless, this simplified method has some value, because the numbers of potential parasites are decreased; the susceptibility of wax-moths, particularly their eggs, and *Streptococcus pluton* to the same treatment (*Reps. Rothamst. exp. Sta.* for 1955, 1958) gives it added value.

Direct evidence of the effect of manipulation on infection of colonies was obtained (*Rep. Rothamst. exp. Sta.* for 1958) when infection increased significantly in colonies inspected monthly in winter. A similar but smaller effect may be expected in summer, and the high levels of infection of package bees from the southern states of the United States (Reinhart, 1942; Farrar, 1947) may derive from the handling they undergo followed by their long journeys. Infected samples of bees received for diagnosis about April and May by the National Agricultural Advisory Service have risen from the 1941–44 level of about 5% to approximately 20% since about 1953. This may not be entirely attributable to poor weather: there is no doubt that transportation of bees, mainly to orchards in spring and to heather in autumn, is more frequent now than during and shortly after the war of 1939–46, and transportation seems an important cause of high levels of infection (Bailey 1955a). Commercial beekeepers have considerably higher infection in their colonies than have beekeepers in general (unpublished data, Min. of Agric., Fish. & Food) and probably transport their bees more.

After the discovery of the striking effect of fumagillin in suppressing infection by *Nosema apis* (Katznelson & Jamieson, 1952a) field trials were made with it at Rothamsted. Feeding fumagillin in autumn prevented or retarded development of infection the following winter (Bailey, 1953a, 1955b). Results were not wholly satisfactory: infection was apparently always checked or diminished by treatment, but absolute elimination seemed unlikely. Repeated autumn application may eventually succeed: spring treatment alleviates the immediate acute infection, but comb contamination is less likely to be decreased.

It is necessary to consider the value of possible treatments and the circumstances in which they are applied. The degree of infection in spring with *Nosema apis* reflects to some extent the degree to which other circumstances of honeybees were unfavourable the year before. Lotmar (1943b) found a significant positive correlation between wet summers and the degree of infection the next year, and the only striking fall of infection in England and Wales in recent years was after the unusually good season of 1955 (Min. of Agric., Fish. & Food, 1956, 1957, 1958). In poor seasons the natural

https://doi.org/10.23637/ERADOC-1-92

cleaning of combs is probably decreased, because brood rearing and nectar gathering is diminished and defaecation by infected bees in the hive may be more frequent than in good seasons. Colonies should not be disturbed in poor seasons, and drug treatment seems most useful at the end of such seasons. Comb changing would be most likely to eliminate infection in good seasons.

More fundamental studies of infection in individual bees show that the parasite is first established at the anterior and posterior ends of the ventriculus, usually mostly at the anterior end, with a region of minimal infection centrally (Bailey, 1955c). The last region has many cytoplasmic granules of calcium phosphate which disappear when infection penetrates the cells. Their presence may, therefore, initially inhibit growth and development of *Nosema apis*. Infection soon disappears from bees fed syrup containing fumagillin, leaving apparently normal cells except at the anterior end of the ventriculus, where infection persists even after continuous drug treatment for several weeks (Bailey, 1953b).

Amoeba disease

Malpighamoeba mellificae Prell was studied at Rothamsted first by Hassanein (1952b), who confirmed that an annual epidemic, similar in character to that of *Nosema apis*, occurs in adult bees of endemically infected colonies. This annual epidemic appears to have the same explanation as that of *Nosema apis*; transference of infected colonies to non-contaminated combs in early summer eliminated infection, and transference of combs from infected to uninfected colonies in autumn introduced infection which became epidemic the following spring (Bailey, 1957d). Cysts of *M. mellificae* on combs were killed as readily as spores of *N. apis* by vapour of acetic acid, but fumagillin did not affect the development of *M. mellificae* in infected bees (Bailey, 1955d).

The incidence of infection with *Malpighamoeba mellificae* in England and Wales was less than 1% in 1941–44 (Butler, 1945), but in recent years it has risen to about 3%. The rise is coincident with that of *Nosema apis* mentioned above, and seems likely to be for similar reasons. Infection is restricted to the south-east of England, however, particularly near London (Min. of Agric., Fish. & Food, 1956, 1957, 1958), which is strikingly similar to infection reported from Denmark, where most is near Copenhagen (Fredskild, 1955). The reason for this is not clear, but bees may be examined and disturbed more frequently in urban than rural regions. Much more disturbance seems necessary to maintain abnormally high levels of infection by *M. mellificae* than by *N. apis*, as the cyst stage of the former does not appear until 3 weeks after infection (Fyg, 1932; Hassanein, 1952b), so that in summer, infected bees will be foragers that are almost at the end of their lives before they become infective. Infective spores of *N. apis* form after 10 days or less—well within the life span of the bee in summer.

Paralysis

Results of experiments by Burnside (1933) made it appear that adult bees with " paralysis "—dark, greasy-looking, virtually hairless bees, with sprawled legs and wings—had an infectious disease

https://doi.org/10.23637/ERADOC-1-92

that was transmitted directly between them. Butler (1943) made similar laboratory tests with the same results, but at the same time he pointed out that a variety of diseases, some non-infectious, and various poisons may produce similar signs. Burnside (1945) made further controlled laboratory experiments which seemed to show that the infectious disease was caused by a filterable virus. About 2% of samples of bees sent to the National Agricultural Advisory Service annually from England and Wales are diagnosed as paralysis, but the proportion that are of the infectious variety is unknown.

Conclusions

The common infections of the adult honeybee are not principal factors limiting the survival and growth of endemically infected colonies that are otherwise normal. But they tend to reach serious proportions when such colonies suffer set-backs. The set-backs are sometimes adventitious, but they are often imposed or aggravated by beekeeping practices. The increasing knowledge of the natural histories of adult bee infections should help to mitigate these actions. An understanding of the striking annual epidemic of EFB, which usually occurs in endemically infected colonies, should produce similar advantages. More epidemiological studies of AFB may be helpful, even though natural control of this disease, once present, seems poor.

Devising prophylactic measures depends on fundamental knowledge of the natural history of the infection concerned. Direct therapy may often be improved and evaluated by such information. Accordingly, the accumulation of fundamental knowledge remains the primary purpose of research on diseases of the honeybee at Rothamsted.

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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

https://doi.org/10.23637/ERADOC-1-92

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,

https://doi.org/10.23637/ERADOC-1-92

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 lifespan. 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

https://doi.org/10.23637/ERADOC-1-92

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.

https://doi.org/10.23637/ERADOC-1-92

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

https://doi.org/10.23637/ERADOC-1-92

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;

https://doi.org/10.23637/ERADOC-1-92

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 ex-

https://doi.org/10.23637/ERADOC-1-92 *pp 20*

perimentally (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

https://doi.org/10.23637/ERADOC-1-92

TABLE 1

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

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

https://doi.org/10.23637/ERADOC-1-92 pp 22

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

https://doi.org/10.23637/ERADOC-1-92 *pp 23*

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

https://doi.org/10.23637/ERADOC-1-92 *pp 24*

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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THE EXHAUSTION LAND SITE

An Account of Experiments made before and during the Period of Soil Exhaustion

By

R. G. Warren & A. E. Johnston

The Exhaustion Land site is a strip of 2½ acres of arable land at the north end of Hoosfield and derived its name from the unmanured cereal cropping which began in 1902 to measure the residual effects of manures that had been applied in previous experiments. From 1852 to 1902 Lawes and Gilbert used the site for a succession of three experiments. The first, which lasted only 4 years, was a test of the Lois Weedon system of husbandry and was followed by a 20-year wheat experiment consisting of a few of the Broadbalk fertiliser treatments. In the last 26 years before the exhaustion period began there was a manurial experiment on potatoes.

The "Lois Weedon" Plots at Rothamsted, 1852–55

In 1849, during an agricultural depression, the Rev. Samuel Smith promised, in a pamphlet entitled *A Word in Season to the Farmer*, a profit of £4–£6/acre to those who adopted his system of growing wheat year after year without manure. The system, devised and employed by Mr. Smith on the heavy land portion of his 12-acre farm at Lois Weedon, Towcester, Northants, was not continuous wheat as on Broadbalk (until 1925), but was a succession of wheat and fallow strips across the field so that only half the area was in wheat each year. Each strip was 3 feet wide, was sown with three widely spaced rows of wheat at the low seed rate of 1–2 pecks (15–30 lb.)/acre and was cropped and fallowed in alternate years. An essential feature of the system was the intensive cultivation of the strips when they were in fallow, during which the subsoil was broken up and allowed to weather before it was mixed with the surface soil. The results from this system of growing wheat on the heavy land part of the Lois Weedon farm are summarised by Mr. Smith in his book *Lois Weedon Husbandry* (London, James Ridgway, 1856):

> "The ten years' average from this moiety of the acre has been thirty-four bushels; a very high average on any plan from a whole acre. And here, too, therefore, the proverb holds good —The half is more than the whole."

Lawes is most widely known in connexion with superphosphate and experiments testing the effects of different manures on individual crops grown continuously on the same land. However, Lawes and Gilbert were also interested in crop rotations, and in 1851 they began preparations for some "Lois Weedon" plots at Rothamsted on the site at the north end of Hoosfield. At the same time they also started on 1 acre of land adjoining the "Lois Weedon" plots a com-

https://doi.org/10.23637/ERADOC-1-92

parison of wheat after fallow for which normal methods of cultivation were to be used and the crop grown without manure. This comparison developed into a long-term experiment, known as the Alternate Wheat and Fallow Experiment. On the " Lois Weedon " plots Lawes and Gilbert followed the operational details as published by Mr. Smith. The fallow strips were, in fact, trenched to 14 or 15 inches.

The " Lois Weedon " plots failed to give the good results that Mr. Smith obtained on his own farm. Not only were yields lower than on the Alternate Wheat and Fallow Experiment but also lower than those of the continuously cropped unmanured plot on Broadbalk. The " Lois Weedon " experiment on Hoosfield was ended after the harvest of 1855. During the course of the experiment half the land had been trenched once and the other half twice.

Winter Wheat Experiment 1856–74

Lawes and Gilbert were sure that the low yields on the " Lois Weedon " plots at Rothamsted were caused by the low seed rate prescribed for the system, but nevertheless they began a search for the reasons that would explain the success of the system at Lois Weedon and the failure at Rothamsted. Smith suggested that a deficiency of minerals was one of the causes of the failure on Hoosfield at Rothamsted, but Lawes and Gilbert thought that the amount of assimilable nitrogen in the soil was more important. Broadbalk up to this time had demonstrated the greater importance of nitrogen for wheat. To confirm this for the Hoosfield soil they started in 1856 to test some of the Broadbalk manurial treatments on the site of the Lois Weedon strips. There were four plots, each containing an equal proportion of the trenched fallow and stubble ground, and the four treatments selected were unmanured, ammonium salts only, minerals only and ammonium salts with minerals; the fertiliser rates were the same as those of plots 5, 10 and 16 on Broadbalk, 1855. The land was prepared in the autumn of 1855 in the normal way, manures including the ammonium salts were applied in the autumn, and winter wheat sown at about 2 bushels/acre. On the north side of the plots there was another unmanured strip. This was narrower than each of the four plots and later formed part of plots 1 and 2 of the potato experiment, 1876–1901.

The results of the first year of this wheat experiment were similar to those for the comparable plots on Broadbalk and led Lawes and Gilbert to make the following statement in their account of the Lois Weedon System (*J. R. agric. Soc.* **17** (1st Series), 1856, p. 591):

> " Hundreds of other experiments, and the whole range of recorded agricultural experience, conspire to show, that in ordinarily cropped and cultivated soils, the available mineral supplies are generally in excess relatively to the available supply of nitrogen of the soil and season, in the case of the wheat crop: in fact that, excepting in cases of very special and unusual exhaustion of the mineral or soil-proper constituents, the direct supply of them by manure for wheat does not increase the crop in any practicable and agricultural degree, unless there be a liberal provision of *available and assimilable nitrogen in the soil.*"

https://doi.org/10.23637/ERADOC-1-92

The results showed that a supply of " available " nitrogen was more important than deep cultivation on the Hoosfield soil but did not explain the success of the system at Lois Weedon. Lawes and Gilbert never offered a satisfactory solution to this problem, for they drew no conclusions from their figures for total nitrogen in the soil and did not supply any figures to indicate the amount of " assimilable " nitrogen in the soil. It can be said now that, as the land at Lois Weedon had been old grassland it probably contained more " available " nitrogen than the Rothamsted soil. The turf had been pared off and used on other land for root crops, but the remaining soil evidently contained ample mineralisable nitrogen, because Smith made the following comment in his book:

> " This fresh-broken up land for several years produced over-luxuriant crops and very frequently the usual evil results."

The wheat experiment on Hoosfield continued until 1874. The results for the first 6 years (*J. R. agric. Soc.* **25** (2nd Series), 1864, p. 449) continued to resemble those on Broadbalk, but in later years the yields of wheat in the Hoosfield experiment were lower and the response to nitrogen less. The average yields for 5-year periods from 1856 to 1870 for Hoosfield and Broadbalk are given in Table 1.

TABLE 1

Yields of wheat on Hoosfield and Broadbalk, 1856–70

Five-year averages of dressed grain, bushels/acre

Years	Treatment							
	Unmanured		Ammonium salts		Minerals		Ammonium salts and minerals	
	H *	B	H	B	H	B	H	B
1856–60 ...	16	16	29	24	18	20	37	36
1861–65 ...	10	15	18	28	14	16	36	42
1866–70 ...	10	13	13	24	13	15	20	32

Fertiliser Dressings per acre:

Ammonium salts—
200 lb. ammonium sulphate
200 lb. ammonium chloride

Minerals—
200 lb. potassium sulphate †
100 lb. sodium sulphate
100 lb. magnesium sulphate
Superphosphate prepared from 200 lb. calcined bone and 150 lb. sulphuric acid.

* H = Hoosfield; B = Broadbalk.

† 300 lb. potassium sulphate, 200 lb. sodium sulphate in the three years 1856–58; the quantities were then reduced as they were on Broadbalk.

Lawes and Gilbert did not comment on the difference between the behaviour of the Broadbalk and Hoosfield wheat plots during the years 1861–70. A note in the record book of the Hoosfield experiment, however, stating that the land was very foul with weeds in 1870, may partially explain the lower yields. The site was fallowed in 1871 and 1872 and was again cropped with wheat in 1873 and in 1874, the first of the two crops was unmanured. For the 1874 crop the minerals were not given and the ammonium salts were *withheld until the spring* and then applied at only *half the usual rate.*

https://doi.org/10.23637/ERADOC-1-92

The yields were higher than those on the corresponding plots on Broadbalk and the response to nitrogen greater. It is worth noting here that the time of applying ammonium salts on Broadbalk, except Plot 15, was changed from autumn to spring for the 1878 crop and altered again for the 1884 crop to a divided dressing, part being given in autumn and part in spring. Starting in 1873, Plot 15 received all its ammonium salts in spring, then for the 1878 crop all the nitrogen was applied in autumn, the current practice. The Hoosfield experiment ended with the 1874 crop, and the land was fallowed in 1875.

Potato Experiment 1876–1901

In 1873, after a virulent attack of potato disease in the previous year, a special committee of the Council of the Royal Agricultural Society initiated investigations on the potato crop. As a part of these investigations a questionnaire on the cultivation of the crop was sent to leading growers. In the report on the questionnaire by Jenkins (*J. R. agric. Soc.* **10** (2nd Series), 1874, p. 475) one feature which must have interested Lawes and Gilbert was the considerable variation in the manuring of the crop, though many growers did use farmyard manure. A few years earlier Voelcker had published the results of several experiments on the manuring of potatoes in the *Journal of the Royal Agricultural Society* [**3** (2nd series), 1867, 500; **6** (2nd Series), 1870, 392; **7** (2nd Series), 1871, 365]. Voelcker concluded that good crops of potatoes could be grown on light land comparatively cheaply by using fertilisers consisting of ammonium sulphate, superphosphate and potassium sulphate. On heavy land " in good agricultural condition " he considered that ammonium sulphate could be omitted or less used and that, on this type of land, sodium nitrate may be more effective than ammonium sulphate.

Lawes and Gilbert began their manurial experiment on potatoes in 1876, and although one of the objects was to find whether the type of manuring was related to the amount of disease in the crop, the main purpose of the experiment was to obtain information on the nutrient requirements of the potato crop. The wheat site was extended about 12 links on the north side to make the fifth strip nearly the same width as the remainder, and the five strips were then halved. The new plot numbers of the potato experiment and the corresponding wheat plot numbers, together with the manurial treatments, are shown opposite one another in Table 2.

TABLE 2

Wheat Experiment	Potato Experiment	
Plot 1 (P, K, Na, Mg)	Plot 9 (P)	Plot 10 (P, K, Na, Mg)
2 (N, P, K, Na, Mg)	7 (N, P, K, Na, Mg)	8 (N*, P, K, Na, Mg)
3 (N)	5 (N)	6 (N*)
4 (O)	3 (dung, P)	4 (dung, N*, P)
5 (O)	1 (O)	2 (dung)

N = Ammonium salts.
N* = Sodium nitrate.

The fertiliser treatments from the wheat were continued in the potato experiment, and new treatments with farmyard manure and sodium nitrate were added.

https://doi.org/10.23637/ERADOC-1-92

The results of the first 12 years of the experiment were given in a lecture by Gilbert at the Royal Agricultural College, Cirencester, in 1888 and published in the *Agricultural student gazette*, New Series, **4**, part 2. The average yields during the first and second 6-year periods are given in Table 3, together with the average yields during the remaining years of the experiment, 1888–1901.

TABLE 3

Average annual yields of potatoes grown continuously on Hoosfield 1876–1901

Plot	Treatment	Years 1876–81	1882–87	1888–1901
1	Unmanured	2·28	1·69	0·84
5	N	2·51	2·07	1·19
6	N*	3·20	2·04	1·69
9	P	3·98	3·35	1·91
10	P, K, Na, Mg	4·14	3·39	2·17
7	N, P, K, Na, Mg	7·52	5·94	4·12
8	N*, P, K, Na, Mg	7·78	5·52	4·38
2	F.Y.M.§	5·23	3·05	1·48
3	F.Y.M., P †	5·58	4·25	4·62
4	F.Y.M., N*, P ‡	7·11	4·01	4·74

Fertiliser rates per acre:

N	200 lb. ammonium sulphate + 200 lb. ammonium chloride
N*	550 lb. sodium nitrate
P	1876–1896 3½ cwt. of superphosphate 1897–1901 400 lb. basic slag
K	300 lb. potassium sulphate
Na	100 lb. sodium sulphate
Mg	100 lb. magnesium sulphate
F.Y.M.	Farmyard manure 14 tons

§ 1876–81, farmyard manure: 1882–1901, unmanured.
† 1876–82, farmyard manure and superphosphate, 1883–1901, farmyard only.
‡ 1876–81, farmyard manure, sodium nitrate and superphosphate; 1882, farmyard manure and superphosphate: 1883–1901, farmyard manure only.

Yields from different treatments must be compared only in the same period, as the variety of potato grown changed during the experiment. Changes were also made in the three farmyard manure treatments. Further, in this experiment with only a few plots and with each treatment represented by one plot, the results from the single nutrient tests (plots 5, 6 and 9) do not give useful information on the requirements of the potato crop. It is also necessary to mention that the yields of plot 9 (P) may be misleading, at least for the early years, because it received P and K fertilisers each year during the preceding experiment on wheat. The wheat crops probably used not more than one-quarter of the added K and left appreciable residues in the soil. The best information is derived from comparing the yields on the plot which received minerals only (10) with those of plots that had minerals and nitrogen (7 and 8) or had farmyard manure (2, 3 and 4). In the first 6 years of the experiment the full complement of fertilisers gave yields above the average for the country and above the yield obtained by farmyard

https://doi.org/10.23637/ERADOC-1-92 *pp 32*

manure alone. Both forms of fertiliser nitrogen, ammonium sulphate and sodium nitrate, at 86 lb. N/acre on plots 7 and 8 did equally well and produced about 3·5 tons more tubers per acre than the minerals alone (plot 10). The yields on the three farmyard manure plots for the same period indicate that the farmyard manure contained much less available nitrogen than was supplied by the complete fertiliser treatments. Adding superphosphate to the farmyard manure increased the yield by only ⅓ ton, whereas adding superphosphate and sodium nitrate gave nearly 2 tons more tubers per acre. Although the experiment showed that the 14 tons of farmyard manure was more deficient in nitrogen than phosphorus, it provided no evidence on the potassium status of the manure. In the second 6-year period the complete fertilisers continued to give higher yields than farmyard manure, but in the last 14 years the average yield from farmyard manure was 0·4 ton/acre more than from the complete fertilisers.

The determination of the amounts of nitrogen, phosphorus and potassium in agricultural crops was an important part of Lawes' and Gilbert's investigations. The large differences they found between the N, P and K contents of a crop and the amounts in the manures applied to the crop led them to make single plot tests to measure the effect of the unused nutrients on succeeding crops. In several of their experiments (e.g., Broadbalk, Hoosfield barley and Park Grass) a manurial treatment was discontinued but the land was cropped as usual. The three farmyard manure treatments in the Hoosfield potato experiment were modified to produce further information on the effect of residues, and they published several papers on the valuation of unexhausted manure, their principal concern being with the cash value of manurial residues from different feeding-stuffs. In the last paper (*J. R. agric. Soc.* 8 (3rd Series), 1897, 674) they gave the following conclusions from the Rothamsted experiments on the effect of manurial residues on succeeding crops:

> 1. Heavy and repeated dressings of organic manures must be given before effective residues are built up in the soil. Plant nutrients are released only slowly from the residues, more slowly in heavy soils than in light ones. Three-quarters of the increased yield of barley given by the farmyard manure comes from nitrogen in the residues.
> 2. The use of inorganic N fertilisers over long periods may give residual effects because the crop residues left in the soil are increased. For wheat the effect is small.
> 3. A considerable portion of the P and K added as fertilisers is fixed in the soil and is only slowly available to subsequent crops.

The Exhaustion Land Experiment 1902–58

After Lawes died in 1900 and Gilbert in 1901, Hall decided to end the potato experiment because the physical condition of the soil that had not received farmyard manure was poor and unsuitable for potatoes.

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At the end of the wheat and potato experiments the plots on the Exhaustion Land site had received the following treatments:

Number of dressings each plot received, 1856–1901*

Plot no.	1	2	3	4	5	6	7	8	9	10
Treatment:										
Farmyard manure	—	6	26	26	—	—	—	—	—	—
PK	—	—	—	—	—	—	42	42	17	42
P	—	—	7	7	—	—	—	—	25	—
N	—	—	—	6	44	44	44	44	—	—

Average dressing per acre: farmyard manure 14 tons, superphosphate 3 cwt., ammonium salts 3½ cwt. or sodium nitrate 5 cwt., potassium sulphate 2½ cwt.

* The number of dressings given in *Proc. Fertil. Soc.* 1956, No. 37, have been corrected here to allow for the omission of N in 1 year and PK in 3 years.

The amounts of nitrogen, phosphorus and potassium removed in the wheat and potato crops cannot be estimated precisely, because only a few of the crops were analysed, but a large part of the P and K applied was left in the soil.

After the potato experiment the site was cropped from 1902 to 1940 without manure to measure the duration of the residual effects of the previous manures. The crops were cereals, mainly barley, except on plots 5–10, where there was a soil inoculation trial on clover, 1905–11. The yields of the cereals were recorded regularly only till 1922. Beginning in 1941 the cereals received 2½ cwt./acre of ammonium sulphate each year, and from 1949 the yields were again recorded. Table 4 gives the yields of cereals for three periods, 1902–4, 1917–22 and 1949–53. In 1902, the first year after manuring had ended, barley yielded well (28–34 cwt. grain/acre) on the plots that had previously received farmyard manure or N fertilisers, and the residues from these treatments increased yield by 18 cwt. and 14 cwt. of grain/acre over the unmanured plots. Only the farmyard manure plots, however, continued to yield well in the next 2 years. Hall (*The Book of the Rothamsted Experiments*, 1905) considered that the large 1-year residual effects on the N fertiliser plots came from the increases in crop residues in the soils of these plots rather than from any accumulation of unchanged fertiliser ammonium or nitrate. By 1917 the yields of all plots were very low and the farmyard manure residues gave only small increases in the years 1917–22. The yields of the fertiliser plots, including those which had not received N in the wheat and potato experiments, were also a little higher than those of the unmanured plots, but clover residues probably still remained in these plots and provided a little nitrogen for the cereal crops.

The method of measuring residual effects so far adopted, without new additions of any of the three nutrients N, P, K, gave no information on the contribution to yield of any one of the nutrients contained in the residues; nor did it indicate whether one nutrient in the residues was limiting the effects of the others. In the last period, 1949–53, for which yields are given in Table 4, the effects were restricted to the combined effects of the P and K residues by applying a basal N dressing. The increases in yield were large and were similar for the PK fertiliser residues (10 cwt. barley grain/acre)

https://doi.org/10.23637/ERADOC-1-92 *pp 34*

TABLE 4

Exhaustion Land 1902–58

Yields of grain cwt./acre 85% dry matter

Plot	Year: / Crop: / Treatment 1856–1901	1902 Barley	1903 Barley	1904 Oats	1917 Barley	1918 Barley	1919* Barley	1921 Wheat	1922 Barley	1949 Barley	1950 Barley	1951 Barley	1952 Barley	1953 Barley
1	Nil	16·0	4·6	11·1	2·2	3·9	2·2	6·1	5·8	7·6	11·3	13·6	12·9	15·8
2	Nil †	17·1	7·3	10·4	4·3	5·1	3·5	10·1	7·0	10·0	15·1	12·7	10·1	11·8
5	N	28·5	9·2	11·6	2·5	5·6	3·5	10·9	7·8	8·7	12·5	15·2	16·5	17·4
6	N * ‡	30·3	9·0	10·9	3·4	7·6	3·6	12·4	7·9	13·0	14·7	11·2	13·1	14·6
9	P §	16·9	6·4	10·9	3·0	6·9	4·2	15·7	7·5	23·4	24·4	23·4	19·7	20·0
10	PK	12·0	6·2	9·9	3·2	7·1	5·1	15·2	7·0	27·0	26·6	26·4	21·8	21·8
7	NPK	31·0	13·9	14·9	5·6	10·1	5·7	14·1	7·8	23·0	22·2	24·1	21·3	21·4
8	N*PK ‡	32·3	12·6	15·7	5·4	9·2	4·4	14·7	7·8	27·9	26·3	23·8	21·4	20·2
3	F.Y.M.‖	34·2	22·6	26·8	3·5	7·9	5·4	14·1	9·6	26·8	24·2	22·9	23·2	22·4
4	F.Y.M.¶	34·9	21·6	29·6	4·7	7·7	6·0	15·7	9·7	25·9	29·0	25·1	22·8	22·8

* Land fallowed in 1920.
N Ammonium salts.
N* Sodium nitrate.
† Farmyard manure 1876–81, unmanured, 1882–1901.
‡ As ammonium salts, 1856–75; as sodium nitrate, 1876–1901.
§ PK, 1856–75; P, 1876–1901.
‖ Farmyard manure and superphosphate, 1876–1882; farmyard manure only, 1883–1901.
¶ Farmyard manure, sodium nitrate and superphosphate, 1876–81; farmyard manure and superphosphate, 1882; farmyard manure only, 1883–1901.

and the farmyard manure residues (11 cwt./acre). From the large increases on the old farmyard manure plots from 1949 to 1953, compared with the small ones from 1917 to 1922, it was concluded that after a long period of cereal cropping the organic manure residues supplied very little N and that the amounts of available P and K they contained were much more important. Lawes' conclusion that N caused three-quarters of the effect of farmyard manure residues was derived from the results of barley grown on new and relatively new residues. Although the large effects of the farmyard manure and PK fertiliser residues could, when basal N was given, result from the combined effects of P and K, Warren (*Proc. Fertil. Soc.* 1956, No. 37) concluded from the analysis of the crops that the increases with barley resulted almost entirely from P. The analyses of the barley crops also showed that 4–5 lb. more P/acre was removed each year from the PK fertiliser and farmyard manure residue plots than from the unmanured plots. This extra P is a small annual recovery and is equal to only 0·5% of the total P applied either as superphosphate or farmyard manure in the years before 1902. For K the extra amount removed was 15–19 lb./acre, which also represents only a small annual recovery of the K residues.

In 1953 parts of the plots in the west half of the experiment were found to be acid. Differential chalk dressings were applied to the acid area in the winter 1954–55. The whole site continued in barley during the period 1954–56, but in 1957 six crops (barley, spring wheat, potatoes, sugar beet, swedes and kale) were grown in strips across the plots (1, 3, 5, 7 and 9) in the east half of the experiment. The crops were separated by fallow strips which were used for the crops in the next year. Each strip was divided into microplots, and new additions of P and K were superimposed on the old treatments. All plots received a basal dressing of N fertiliser, basal P fertilisers were given when K was being tested and basal K was given where test dressings of P were applied. All fertilisers were applied broadcast except for potatoes where they were put in the bouts. Table 5 shows increases in yields produced by new additions of P and K for the six crops grown in each year.

TABLE 5

The increases in yields given by fresh additions of P and K fertilisers in the Exhaustion Land experiment

Manuring in 1856–1901 period	Increase from new dressing of 1·0 cwt. P_2O_5/acre				Increase from new dressing of potassium fertiliser *			
	No phosphate		Phosphate		No potassium		Potassium	
Year	1957	1958	1957	1958	1957	1958	1957	1958
Barley (cwt. of grain) ...	6	15	0	5	1	0	0	1
Wheat (cwt. of grain) ...	2·5	10	0	2	0	1	0	0·5
Potatoes (tons of tubers) ...	8	8	4	5·5	6·5	5	4	3
Sugar beet (tons of roots) ...	3·5	4·5	0	2	0	3·5	0	0
Swedes (tons)	5	13	0·5	3	0	2	0	0
Kale (tons)	6	6	2·5	2	1	0	2·5	0

* 1·2 cwt. K_2O/acre for potatoes, sugar beet and kale; 0·6 cwt. K_2O/acre for cereals and swedes.

Potatoes, sugar beet and kale responded similarly in both years to new dressings of phosphate where the crops were grown on soil that had received no phosphate from 1856 to 1901 (and none since). The mean yield of sugar beet in 1958 was 50% and of kale 25%

https://doi.org/10.23637/ERADOC-1-92 *pp 36*

greater than in 1957; potatoes gave similar mean yields in the 2 years. On the same soil the response of swedes to new dressings of phosphate was much greater in 1958 (13 tons/acre) than in 1957 (5 tons/acre); the mean yield of swedes in 1958 was double that obtained in 1957. The phosphate residues from the old manuring were sufficient for full crops of barley, wheat, sugar beet and swedes in 1957, but not in 1958. In 1958 the phosphate residues were equivalent to about one-half to four-fifths of the value of the new phosphate fertiliser dressing for these crops. For potatoes and kale the phosphate residues were inadequate in both years: each year the extra yield of potatoes from the residues was only half as great as the increase given by a new dressing of 1 cwt./acre P_2O_5. For kale the corresponding extra yields in the 2 years were about two-thirds as great as the responses to new dressings.

On soil that received no potassium manuring between 1856 and 1901 (and none since) fresh dressings of potassium fertiliser greatly increased yields of potatoes in both years. In 1957 yield of the other crops was little increased by the fresh dressings of potassium; in 1958, however, new dressings of potassium also increased the yields of sugar beet and swedes, but not of cereals or kale. On the plots that had received potassium between 1856 and 1901 barley, wheat, sugar beet and swedes obtained enough potassium in both years from the residues left in the soil. Potatoes, however, responded well to fresh dressings of potassium in both years, kale gave a moderate increase in yield in 1957 only.

The amount of nitrogen mineralised each year from the farmyard manure residues was not measured. It is thought to have been small in recent years, as the average increase in yield from the residues was only 3 cwt. grain/acre in the years 1917–22, when the residues were supplying adequate amounts of P and K for cereals. The experiments have also not assessed the value of the farmyard manure and PK fertiliser residues for crops such as beans, clover, grass and lucerne. Because the annual rates of extraction of P and K from the residues by crops was determined over a short period only, the total amounts of P and K that may still be taken up from the residues cannot be estimated. The experiments indicate, however, that the percentage recoveries in crops of the P and K added as farmyard manure or fertilisers are greater than is commonly supposed.

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