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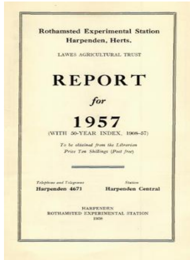

Eyespot of Wheat and Barley

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EYESPOT OF WHEAT AND BARLEY

By

MARY D. GLYNNE AND G. A. SALT

Introduction

A severe disease of wheat, characterized by eye-shaped lesions, was recognized for many years in France (Föex, 1914, 1919; Föex and Rosella, 1930) and in North America (Heald, 1924; McKinney, 1925), but the causative fungus could not be identified because it failed to produce spores in pure culture. Then Sprague (1931) succeeded in obtaining spores of *Cercosporella herpotrichoides* Fron. in pure cultures of the fungus causing eyespot lesions of wheat in Oregon, and Sprague and Fellows (1934) showed that this was also the fungus isolated by Föex in France. Once its identity was established the fungus was recognized in other countries: in Germany (Schaffnit, 1933) and in Denmark (Nielson, 1934); and in 1934 it became severe in Holland, where the wheat acreage had been doubled after the introduction of a wheat subsidy in 1932 (Oört, 1936). These workers, notably Sprague and Fellows (1934) and Oört (1936), found that the disease was influenced by weather and cultural treatments and was worst where cereals were grown frequently. Eyespot is now known to occur in most European countries, in parts of America, Canada, Africa, Australia and New Zealand.

In Britain eyespot was first recognized in the spring of 1935, when wheat on Broadbalk and other fields at Rothamsted were found to have eyespot lesions bearing spores of *C. herpotrichoides* (Glynne, 1936). In the wet summer of 1937 severely lodged wheat on Broadbalk had eyespot lesions on 90 per cent of the straws, whereas equally heavy standing crops on neighbouring fields were almost free from the disease; eyespot was also found associated with lodging in other districts. It then seemed likely that eyespot might increase lodging and reduce yields in this country. A systematic study of the disease was therefore begun to test this possibility, to assess the extent and importance of eyespot in Britain and to obtain quantitative data on the effects of previous cropping and cultural treatments on the disease and on yields of wheat.

Regional surveys were made in many parts of the British Isles, and at Rothamsted the long-term experiments provided a unique opportunity for studying how the disease varies from year to year under similar treatments, and how manurial and other cultural treatments affect its incidence. Problems revealed by field surveys were studied in laboratory, pot and eventually field experiments (these are briefly summarized under the heading "Eyespot" in *Results of Field Experiments* (*R.F.E.*) issued each year by Rothamsted Experimental Station; the Rothamsted Annual Reports also include brief summaries of some of our results, but will not be referred to here). We now summarize our present knowledge of eyespot as it occurs at Rothamsted and in other parts of the British Isles.

Distribution

Eyespot, first reported only in the southern half of England (Glynne, 1942), is now known to occur all over Britain (Glynne, 1944; Storey, 1947; Glynne and Moore, 1949). It is most often severe on the heavier, better wheat land, least on light, well-drained soil. The order of difference is well illustrated by parallel experiments; on the heavy soil at Rothamsted 64 per cent of the wheat straws were infected at harvest, whereas on the light, sandy soil at Woburn the same variety of wheat treated in the same way had only 2 per cent infected. This advantage, however, was offset by the higher incidence at Woburn of take-all, *Ophiobolus graminis* (which is most severe on light sandy soils) (*R.F.E.* 1956).

History

Eyespot had probably been common on Broadbalk for more than 80 years before the disease was recognized there in 1935; lodging had been recorded on the more fertile plots since 1852, straggling on the less fertile since 1854,* and, on this field, both are chiefly caused by eyespot. The disease had evidently been prevalent in this country for an even longer time. Dialect words such as straggling, brackley, scrawly and scrailing, dating back some 200 years, are still used by farmers to describe wheat crops in which straws fall in all directions as the wheat ripens, and we now know that this condition is mostly a consequence of the eyespot disease. It was probably already prevalent in mediaeval times, when winter wheat alternated with fallow or was followed by spring wheat and then fallow, so that when Richard II says, " We'll make foul weather with despised tears; Our sighs and they shall lodge the summer corn, And make a dearth in this revolting land ", Shakespeare (1597) is more likely to have had in mind the untidy sort of lodging caused by eyespot than that associated with over-manuring.

Spore production

The long delay in identifying the fungus is attributable partly to the sterility of its cultures and partly to its slow growth; when attempts were made to isolate it from straw the eyespot fungus was often obscured by more rapidly growing fungi, such as *Fusaria*, which were sometimes mistaken for the causal organism. Sprague (1931) and Sprague and Fellows (1934) obtained spores by growing the fungus in flasks containing cornmeal agar and keeping them outdoors at temperatures fluctuating between —4° and 16° C. The development at Rothamsted of much simpler and more rapid methods for inducing spore formation within a fortnight on small (3-mm.) discs cut from cultures grown in petri dishes, and on infected straws (Glynne, 1953a), have greatly helped both in diagnosis and in studying the disease.

* *Broadbalk White Book* 1843–1912.

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Survival and spread

The fungus survives from one crop to another on pieces of stubble which, lying on the surface of the soil, produce immense numbers of spores in cool, damp weather. On Broadbalk these infected straw bases produce spores abundantly from September to April and in some years later. Spores were produced on infected straws in the laboratory at temperatures below 15° C. They were not detached by blowing dry air at them, but were readily freed and carried in mist droplets. Water falling on infected straws carried the spores in splash droplets up 2 feet or more. They germinate readily in water, and may bud off fresh crops of spores from the mycelium in about a week, but they die if kept dry at room temperature for a few hours. Splashed by rain on to young plants, the spores often infect them at about soil level or in the angle made between the first leaves and shoot or at the edge of the coleoptile enveloping the shoot, where moisture is retained long enough for them to germinate and where they are relatively free from competing micro-organisms. A fresh crop of spores is produced on the infected plants in a few weeks, and these are splashed on to surrounding plants. At Rothamsted spores are seldom found on the growing plants after April. The distance travelled by living spores, depending on that travelled by the splash droplets, must vary widely with rain, wind and temperature. Adjacent plots at Rothamsted retain differences in degree of infection from spring to harvest, suggesting that relatively little spread usually occurs from plot to plot, but in one experiment (*R.F.E.* 1955), in a wet, windy season, the fungus was probably carried some 10 yards from heavily to lightly infected plots, in which the straws developed an unusually high proportion of slight lesions, the result of late infections. The distance eyespot spreads from centres of infection in a healthy crop has been roughly estimated (Oört, 1936), but critical trapping work to determine the distance travelled by spores in the field has not yet been done.

Although very dependent on weather, eyespot incidence also depends on the amount of infective material left by preceding crops. This was measured in an experiment (*R.F.E.* 1957) in which wheat in 1957 followed potatoes preceded by wheat (1955) in one block, and in another block wheat followed wheat preceded by beans. In January and February 1957 the pieces of stubble left on the surface of the soil by the preceding wheat crops were collected from sample areas of land and subjected to sporing tests. The wheat grown in 1955 and 1956 respectively had 60 and 78 per cent straws infected at harvest, and in 1957 the stubble from the first crop provided one and from the second twenty-seven pieces of infected stubble per square yard; from these initial sources, 2 and 47 per cent of the plants growing in the 1957 crop were infected in February and 33 and 79 per cent at harvest. Spread of the disease is favoured by cool, damp weather, which prolongs spore production, gives frequent opportunities for dispersal and infection, especially in luxuriant crops which retain moisture; dry, warm, spring weather not only inhibits spore production, but provides fewer opportunities for dispersal and infection, and infected plants may recover from the disease if the outer leaves die before the fungus has penetrated

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deeply. Brown-bordered lesions, shaped like an eye, appear within a few weeks of infection, usually on the leaf sheaths. The fungus grows slowly, penetrating successive sheaths, and may kill many tillers and sometimes whole plants in early spring. The fungus eventually penetrates and weakens the central ear-bearing straws; whiteheads with small underdeveloped grain may then result, resembling those caused by take-all, or the straws may fall over, causing straggling in light, lodging in heavy crops.

Increase of eyespot in successive cereal crops

The spread and development of the disease depends so much on the weather that its rate of increase varies greatly in different years and in different parts of the country. Measures that effectively control the disease in most years at Rothamsted and in other parts of southern England are therefore often ineffective in the north and west of the British Isles, where it is cooler and damper in spring and summer. The behaviour of the disease at Rothamsted and in South-east England will first be described and then contrasted with that farther north and west.

At Rothamsted the first wheat crop after several years under grass is usually free from eyespot or very lightly infected; the second may be lightly or moderately infected, but the disease usually becomes severe in the third, or in the fourth successive crop of winter wheat; this also happens in other parts of South-east England, but the second wheat crops after grass are occasionally moderately or severely infected in wetter years (Glynne and Moore, 1949); since 1938 this has occurred once at Rothamsted (*R.F.E.* 1944), when a second crop had 63 per cent straws infected at harvest, but the unusually high proportion, 38 per cent, with slight lesions suggested late infection. On old arable land the disease increases in successive wheat crops in the same way as it does after grass, but sometimes seems to do so rather more rapidly; at Rothamsted the second winter-wheat crop (after 2 years under non-susceptible crops) on old arable land has once been very severely infected (*R.F.E.* 1955), and in a long-term experiment, in which the same crop sequences are followed on both types of land, eyespot is usually more severe on the old arable land (Fosters) than on land which was relatively recently under grass (Highfield).

Once a high level of infection has been reached, eyespot incidence fluctuates from year to year and is influenced both by weather and cultural treatments. Thus on Broadbalk, plots on which wheat follows wheat, the mean percentage of straws infected at harvest on eight typical plots has varied from 40 to 90 per cent since 1938.

Early sowing increases the chances of severe infection more in some years than in others; thus wheat sown in October had significantly more straws infected than that sown in November in 2 years and about the same in two other years (*R.F.E.* 1943–46).

Spring-sown crops have not been more than lightly infected at Rothamsted and, though they occasionally suffer moderate to severe infection in other parts of southern England, they are much less severely infected than autumn-sown crops. Barley, though about as susceptible as wheat, is mostly sown in spring, and even when grown continuously at Rothamsted is only lightly infected.

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The infection seems to do little harm to the barley crop, but the infected stubble may produce enough spores to cause severe loss in succeeding wheat crops.

Oats and rye, grown in pot experiments under optimum conditions for infection, developed eyespot lesions more slowly than wheat or barley, and are much less susceptible in the field. One oat crop was moderately infected at Rothamsted, and occasional instances of severe infection of oats have occurred in other south-eastern counties (Glynne and Moore, 1949). However, this happens rather rarely, and at Rothamsted (*R.F.E.* 1953) oats in the rotation were as effective as non-cereal crops in reducing eyespot incidence, but were rather less effective at Sprowston (Batts and Fiddian, 1955). Autumn-sown rye in the six-course rotation at Rothamsted becomes lightly infected, and so, like spring-sown barley, helps the fungus to survive.

In Scotland and Ireland, where cooler, damper weather in late spring and summer favour the spread of infection late in the growing season, eyespot develops more rapidly, so that treatments that rarely lead to severe infection in the south and east often do so in the north and west. Then the second successive crop of winter wheat is often severely infected, spring-sown wheat and barley are often moderately infected in Scotland, severely infected in Ireland; and infected oat crops occur comparatively often (McKay *et al.* 1956).

Although climatic differences account for most of these differences, it is also possible that specialized types of the fungus occur in different regions. In Denmark, wheat and rye grown in a six-course rotation experiment were more severely infected than at Rothamsted. Isolates of the fungus from Danish and English wheat were similar, but that from Danish rye differed from them in cultural characters and infected rye much more severely than did isolates from any other cereal.

Decrease of eyespot under different crops

Land, which had become severely infested by growing successive wheat crops, was used to compare the influence of different crops on eyespot, take-all and weeds appearing in test crops of winter wheat. Crops other than wheat or barley strikingly decreased the infection of subsequent wheat. A single year's break from wheat or barley reduced eyespot; in some years the subsequent wheat crop was lightly, in other years severely, infected. Two-year breaks reduced the disease to a harmless level, and were about as effective as 3-year breaks. Potatoes, beans, fallow and even the slightly susceptible oats and ryegrass all effectively decreased the incidence of eyespot; there were probably differences between them which could be determined in more detailed experiments. These breaks also reduced take-all and weeds and had startling effects on the quantity and quality of grain, which for Squarehead's Master ranged from 15½ cwt./acre in infested plots following wheat to 36 cwt. in plots where eyespot, take-all and weeds had been controlled by previous cropping. Both diseases increased the amount of tailcorn, so that the dressed grain showed even greater differences ranging from 10 in diseased to 33 cwt./acre in healthy crops (*R.F.E.* 1953).

Crop rotation

Regional surveys and field experiments show that, although eyespot incidence varies greatly in the same crop sequence in different years and in different places, the frequency of severe infection is so closely related to previous cropping that this can be used to predict the likelihood of loss from eyespot. Thus at Rothamsted in wheat grown in the four-course rotation experiment (in which wheat and then barley alternate with other crops) the proportion of straws infected at harvest has varied in different years from 3 to 86 per cent; more than half the straws have been infected in 9 out of 20 years. On Broadbalk, where wheat follows wheat, this level has been exceeded in 16 years and in the six-course rotation experiment in only 5 years. Similar effects of previous wheat or barley crops on the frequency of severe infection were evident in regional surveys.

As 2-year breaks (free from self-sown susceptible carriers) have almost always reduced eyespot to a harmless level, it is likely that in some regions the sequence of crops in the four-course rotation experiment might be better if the two non-susceptible crops were grown in successive instead of alternate years, but experiments are needed to discover the conditions under which this would be an improvement. Winter wheat following a 2-year break would normally be free from serious infection; and spring sowing would usually protect the following barley crop from appreciable loss in the south and east, but would fail to do so in the wetter, colder regions. It is, of course, unwise to reverse the order and grow winter wheat after spring barley; the small proportion of plants which become infected in the spring-sown barley after a 2-year break sometimes suffices to affect seriously winter wheat grown the following year, even in the south. This occurred at Rothamsted when, on old arable land, winter wheat following spring barley after a 2-year break was seriously affected by eyespot in 2 out of 4 years (*R.F.E.* 1954, 1955). Three-year breaks, such as occur under grass or lucerne in the Rothamsted ley–arable experiments have consistently given negligible eyespot and correspondingly high yields of wheat.

Lodging

Twenty years ago excess of nitrogen and wet, windy weather were regarded as the chief causes of lodging; but now we know that eyespot is equally important. Very heavy crops may lodge because the straws are not strong enough to withstand the buffeting of wind and rain; then they bend over and lie mostly in one direction. When eyespot has weakened the straw bases, not only do much lighter crops lodge, but the straws, which bend abruptly in the middle of the lesions, fall in all directions and lie flat on the ground; loss from lodging is then added to the direct loss of grain caused by the fungus. Measurements made in many years on hundreds of plots at Rothamsted have shown the highly significant effects on lodging, both of weight of straw and of the proportion with severe eyespot lesions (Glynne, 1951; Salt, 1955). Some idea of their relative effects is shown by mean values obtained on Broadbalk where an increase

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in straw weight from 40 to 60 cwt./acre had about as much effect increasing lodging as an increase from 35 to 85 per cent straws with severe eyespot. Wheat following fallow yielded more straw and a smaller proportion with severe eyespot lesions than wheat following wheat; in some years the heavier straw resulted in more lodging, in other years the lower incidence of eyespot resulted in less lodging than after wheat so that long-term averages of the percentage area lodged after wheat and after fallow were about the same (Glynne, 1954).

Because lodging from eyespot causes more loss than non-parasitic lodging, measures to prevent it are most important where cereals are grown frequently on the same land. These measures depend on reducing the severity of eyespot, reducing weight of straw and increasing straw strength; the last two are important whether eyespot is present or not. The methods likely to affect both eyespot and lodging investigated at Rothamsted include varying fertilizers, rate and date of sowing, the use of short, stiff-strawed varieties and spraying with sulphuric acid.

Fertilizers

Fertilizers influence the incidence of eyespot by their effects on plant growth, and they influence lodging by their effects on the disease and on weight of straw.

Increased tillering produces more layers through which the slow-growing fungus must penetrate before it reaches the central ear-bearing straws, thus reducing the severity of eyespot at harvest; but the greater humidity prevailing within a well-tillered crop favours spread of the fungus and development of the disease; the two effects work in opposite directions.

In pot experiments where all plants are infected as seedlings and kept under humid conditions the effect of tillering predominates and well-nourished plants are less severely infected at harvest than starved ones. Applications of nitrogen (Glynne, Dion and Weil, 1945; Salt, 1953) and of phosphate and potash to soil lacking these nutrients greatly decreased the severity of eyespot. In the field the effect of humidity usually predominates, so that fertilizers tend to increase the severity of eyespot at harvest. Because nitrogen is more often deficient than phosphate or potash, it has received most attention. Annual surveys of wheat on Broadbalk show the mean number of severe eyespot lesions in 16 consecutive years was 50 per cent on plot 7 receiving minerals and nitrogen, and 38 per cent on plot 3 receiving no manure. Application of fertilizers appreciably increased incidence of the disease in 10 years and reduced it in only one year. Nitrogenous fertilizers have increased the proportion of straws infected in most of our field experiments; they also increase weight of straw; both effects increase the tendency to lodge and so reduce response to fertilizers. Restricting the fertilizer, though it reduces lodging, also limits yields, so that other methods of control are preferable.

Soil fertility and disease incidence affect the optimum date for applying nitrogen. Early applications increase the weight of straw and the risk of lodging on the better soils. Thus at Rothamsted, on fertile land heavily infested by eyespot, nitrogen applied to Squarehead's Master in March, April and May had little effect on eyespot; that applied in March increased straw and lodging most, and yielded less grain than that applied in May. Where eyespot was controlled and lodging decreased by spraying with sulphuric acid, grain yields were not significantly affected by the date when nitrogen was applied (Salt, 1955).

By contrast, at Woburn on light, nitrogen-deficient soil, there was much less eyespot and no lodging. Plots of Holdfast which received nitrogen in March had more eyespot and yielded 3 cwt./acre less grain than those which received nitrogen in April. Where nitrogen was withheld until May deficiency symptoms became apparent, and although eyespot incidence was the same as after the April application, yields were 6 cwt./acre less (*R.F.E.* 1955).

Seed rate

Lowering seed rate below normal encourages tillering and promotes drying within the crop, and so helps to reduce the incidence and severity of eyespot at harvest. It also reduces competition between shoots for light and nutrients, and so promotes growth of stronger straws, and this helps healthy (Glynne and Slope, 1957) as well as diseased (Glynne, 1951; Salt, 1955) cereals to resist lodging. In an experiment on eyespot-infested land at Rothamsted (Salt, 1955) reducing seed rate of Squarehead's Master wheat from 3 to 1½ bushels/acre decreased severe eyespot from 74 to 56 per cent straws infected, the area lodged from 72 to 40 per cent and increased grain yield from 20 to 25 cwt./acre. In several experiments plots, sown at the normal seed rate and given nitrogenous fertilizer, suffered so much loss from disease that they yielded less than plots sown at half the seed rate and given no nitrogen; thinly sown plots dressed with nitrogen yielded most grain. Thin sowing has the additional advantage that it reduces the effects of take-all by encouraging plants to produce more roots. Its main disadvantage is that it encourages the growth of weeds, and these must be controlled for thin sowing to be advantageous. Failure to control weeds accounts for inconsistent effects of seed rate on infested land at Rothamsted and Woburn (*R.F.E.* 1955, 1956).

Optimum sowing rates therefore vary, not only with soil, variety, nutrition and weather, but also with disease incidence; they are higher on land free from eyespot and take-all than where either of these diseases is severe.

Varietal susceptibility

Many types of wheat tested in pot experiments all proved susceptible; they included the wild type *Triticum monococcum* and representatives of groups with fourteen, twenty-eight and forty-two chromosomes. Differences in severity of infection of different varieties were evident in field experiments; Deprez 80 had consistently fewer straws infected at harvest than three other varieties (*R.F.E.* 1943–46) and Cappelle (1952) had 31 per cent severely infected straws when Squarehead's Master had 88 per cent. Similar differences were found in a pot experiment (1953) when inoculated Cappelle and Scandia all developed lesions but had only half as many straws severely infected at harvest as four other varieties, and mean loss in grain from infection was 9 per cent in Cappelle, 12 per cent in Scandia, as compared with 20–28 per cent in other varieties. Lower field susceptibility of Cappelle was found in France (Vincent *et al.*, 1952), in Cambridge (Lupton and Macer, 1955) and was evident in experiments at Rothamsted and Woburn (*R.F.E.* 1953–56). Cappelle has the further advantage of a short, strong straw which seldom lodges. Unfortunately it is just as severely attacked by take-all as other varieties, and the serious loss caused by take-all and eyespot are less easily noticed because it yields more than many other varieties; but the serious loss suffered by Cappelle was dramatically apparent in 1955, when, sown in early October on fertile land supplied with ample nutrients, it yielded only 25 cwt./acre on plots severely infested by eyespot and take-all, and 61 cwt./acre where these diseases (and weeds) had been controlled by previous cropping.

Spraying with sulphuric acid

In South-east England cereals were sometimes sprayed with sulphuric acid in spring to control weeds; in France attempts to use it to control foot and root rots gave variable results. At Rothamsted effects of the acid on spore production were studied in the laboratory and its effects on crops studied in field experiments (Dion, 1943). Application of 12½ per cent by volume commercial sulphuric acid at 100 gallons/acre, after sowing and before emergence, stopped spore production on exposed pieces of stubble and prevented early infection of the crop. But the disease spread in spring, possibly from pieces of freshly exposed stubble. The best results followed two sprayings, one applied to the soil in autumn after sowing, the other applied to the crop in early spring. A single spraying was most effective when applied at the five-leaf stage, before the fungus had penetrated beyond the second leaf sheath, which, with outer leaves, was killed by the spray. At Rothamsted this stage is usually reached in the first half of March. By April the fungus had penetrated too deeply to be controlled by spraying, although, like the earlier treatment, it controlled weeds. The acid had little effect on straw yield, but, by reducing eyespot, greatly reduced lodging; it was most successful on well-nourished crops, giving in some years yield increases of 10 cwt./acre (Glynne, 1951; Salt, 1955); but it has sometimes failed to control eyespot or to increase yields (*R.F.E.* 1956; Salt, 1957).

Acid spraying has proved valuable in experiments in which effects of treatments are compared on lightly and heavily infected crops, but its use in farming is likely to be limited. The land is sometimes so wet in early March that the machinery needed for high-volume spraying damages the crop excessively, and reports of low-volume spraying have not been encouraging. But the impressive effects of successful spraying with sulphuric acid suggest that the use of other chemical sprays might usefully be investigated.

Yield of grain

The loss caused by eyespot varies with cultural and manurial treatments; in pot experiments inoculation reduced yields by 19 per cent in well-nourished, by 86 per cent in starved plants; by 22 per cent in thinly and 45 per cent in thickly sown plants. In a series of pot experiments in which all inoculated plants were infected and some straws straggled there was no general lodging, and loss caused by eyespot averaged 33 per cent. Losses of the same magnitude occur in the field, where, although some plants escape infection, loss from lodging must be added to that caused directly by the fungus. Straws with severe lesions, taken from field experiments, yielded only about half as much grain as uninfected straws or those with slight lesions (Glynne, 1944, 1953b).

Take-all and weeds increase with eyespot in field experiments, so that it is often difficult to assess their separate effects. Where eyespot and weeds, but not take-all, were controlled by spraying with sulphuric acid, yields were increased by 46 per cent in 1948, by 39 per cent in 1951. Where take-all was also controlled by previous cropping yield increases have exceeded 80 per cent (*R.F.E.* 1955–56). In experiments which measured effects of previous cropping on a final test crop of winter wheat, take-all and weeds increased and yields decreased in successive wheat crops. Typical figures for plots which carried the first, second and third crops of winter wheat were respectively 37, 28 and 19 cwt./acre for Squarehead's Master in 1953, and in 1956, 37, 24 and 19 cwt./acre for Holdfast, 49, 36 and 24 cwt./acre for Cappelle, and the heaviest crops included least tail corn, so that dressed grain showed even bigger contrasts.

The development of high-yielding varieties which resist lodging, generous application of fertilizers and improved cultural and harvesting methods have greatly increased yields of wheat in recent years. But they fail to give high yields if eyespot and its associated troubles are not controlled. Recognition of the severity and frequency of losses caused by soil-borne diseases have shown that yields of wheat previously regarded as satisfactory are really too low. This has helped to set a higher standard for wheat yields at Rothamsted. Here, yields of 40–45 cwt./acre were regarded as exceptionally high less than a decade ago, but, by deliberately combining favourable treatments on uninfested land, yields of 50–60 cwt./acre have been obtained in each of the last 3 years. Further knowledge and wider application of that already acquired can do much to increase yields of wheat in Britain.

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