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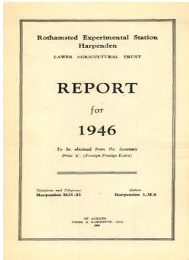

Take-all of Wheat and Barley

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herpotrichoides was depressed while that in healthy control plants was little affected by too high a seed rate. Spraying with sulphuric acid in March increased the yield of infected plants, but not of healthy control plants. Spraying too late, i.e. mid-April, had little effect on yield of infected but reduced that of control plants. In a factorial field experiment on infected wheat, spraying with sulphuric acid in March reduced the area lodged from 90 to 30 per cent. Increase in seed rate and increase in top dressing with ammonium sulphate increased the area of crop lodged. Late-sown crops generally yielded less than early sown except with long strawed varieties which were badly lodged through disease in the earlier sowings.

The susceptibility to *C. herpotrichoides* of different hosts decreased in the following order: wheat, barley, oats, wild oats, rye.

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Take-all of Wheat and Barley

The take-all disease of wheat and barley, caused by *Ophiobolus graminis* Sacc., has been one of the main problems studied in the Department for the past 10 years. Mr. S. D. Garrett started his investigations of soil conditions that influence the occurrence of take-all at the Waite Agricultural Research Institute of Adelaide, South Australia, in 1932, and continued them when he came to Rothamsted in 1936. With the successful completion of a field experiment on the control of take-all, this comprehensive investigation has now been concluded. In the succeeding pages Mr. Garrett summarizes the results and conclusions to be drawn from his work.

Preliminary investigations in the glasshouse using earthenware pots containing 4 kg. of soil gave disappointing results, so a more precise method was sought. This was achieved by working in the laboratory and using glass tumblers holding 2–300 gm. soil as containers. The glass-tumbler method was first used to study the effect of soil conditions upon the rate of growth of the runner hyphae of *O. graminis* along the roots of wheat seedlings; growth was more rapid in light-textured than in heavy-textured soils, which agreed with the greater prevalence of take-all on light-textured soils in South Australia. Growth of the runner hyphae was found to be most rapid around 24° C., and wheat seedlings were most severely affected by the disease at this temperature (1).

Growth of the hyphae of *O. graminis* along wheat seedling roots was found to increase both with improvement in soil aeration and with rise in pH value of the soil, being most rapid in light-textured alkaline soils. Evidence was put forward for the hypothesis that the factor limiting rate of growth of the runner hyphae in heavy-textured and in acid soils was the accumulation of respiratory carbon dioxide in the micro-climate of the root surface zone. Good correlation was obtained between soil conditions optimum for growth of runner hyphae along the roots in these laboratory experiments, and those known to favour the field incidence of take-all in South Australia and elsewhere. This coincidence was epitomised as follows: "Rate of growth of the fungus along the root system must be one of the chief factors determining whether

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the attack be fatal to the plant or not. The speed with which the fungus reaches the crown region from one or more foci of infection on outlying parts of the root system may be the decisive factor in the recovery or otherwise of the plant. Once the fungus has established itself around the crown, new secondary roots may be destroyed almost at their inception" (2, 3).

Attention was next concentrated on the effect of soil conditions upon the survival of *O. graminis* in infected crop residues. It was thought that soil conditions unfavourable for vegetative activity, but not for dormancy of the fungus, would tend to promote longevity, and this was found to be so. The fungus survived for longer in air-dry soil, in moist soil at 2°–3° C., or in water-logged soil, than in soil at medium moisture content (50 per cent. saturation) and a temperature of 17°–20° C. But under soil conditions favourable for general microbiological activity, the factor limiting survival of *O. graminis* was found to be the supply of nitrogen, whether contained in the original infected plant material or supplied during its decomposition by the surrounding soil. All forms of nitrogen added to the soil, whether organic, ammonium, or nitrate nitrogen, increased the survival of *O. graminis*. Conversely, nitrogen-poor organic materials, which undergo rapid decomposition in the soil, such as glucose, starch and grass-meal, shortened the life of *O. graminis* by taking up available nitrogen from the soil. It was also shown that the life of the fungus could be greatly shortened simply by crowding the infected straws closely together with the minimum of surrounding interstitial soil. Finally, *O. graminis* was found to survive for longer in fallow than in soil under growing plants of trefoil, oats or mustard, an effect which was attributed to absorption of available soil nitrogen by the green plants.

In soils well supplied with nitrogen, and therefore favourable to longevity of *O. graminis*, the fungus was found to continue a slow mycelial development within the cells of the infected host tissues. In tissues deprived of nitrogen, however, the fungus did not continue to develop, presumably because of lack of the nitrogen required to form new hyphal branches. It appears likely that the old hyphae eventually die of carbohydrate starvation, because the surrounding substrate is exhausted; survival of the fungus is somewhat prolonged by a twice-weekly shaking of infected straws in 3 per cent. dextrose solution (4, 5, 6).

In the field *O. graminis* persists in the soil not only in infected residues of wheat and barley crops, but also in the living and dead infected roots and haulms of susceptible grass species. The relative importance of different species of grasses in the propagation of *O. graminis* was investigated as directly as possible, by infecting grasses with a minimal dose of non-persistent inoculum. The grasses were then grown in boxes for 2 months in the glasshouse, after which time the turves were inverted in the boxes, and the survival of *O. graminis* was assessed by planting test wheat seedlings at approximately monthly intervals up to 5 months. Of 16 grass species tested, *Agrostis* spp. were the most effective as propagators of *O. graminis* and *Phleum pratense* the least; *P. pratense* was virtually a non-propagator. The two rye-grasses, *Lolium italicum* and *L. perenne*, were 7th and 8th on the list of effectiveness as propagators, but it must be emphasised that the grasses were only grown for 2 months before the sods were inverted. Subsequent field surveys have shown that temporary leys containing rye-grasses do not usually lead to outbreaks of take-all in the first wheat crop immediately following them; it therefore seems possible that susceptibility of the rye-grasses to infection by *O. graminis* decreases with age (7).

Oats has been reported from most countries as highly resistant or immune to take-all. In view of persistent reports of oats affected by take-all in Wales, infected material was secured from there, and the pathogen isolated. This proved to be a biologically distinct strain of *Ophiobolus graminis*, which was a vigorous parasite of oats as well as of wheat and barley, whereas the high resistance of oats to infection by *Ophiobolus graminis sensu stricto* was confirmed in these experiments. The biological strain from Wales was also found to differ morphologically from *O. graminis* proper, inasmuch as the ascospores were significantly longer, a difference which has since afforded a reliable method for identifying the oat-attacking strain. This biological strain has been elevated to varietal rank, under the name of *Ophiobolus graminis* var. *Avenae* E. M. Turner (8). *O. graminis* var. *Avenae* has since been identified on oat crops grown in the West and North of England, and in Scotland (9), but it has not so far been found in the South or East of England.

The investigations so far described have been concerned with *O. graminis* as a soil-borne fungus, and it is therefore necessary to point out that the fungus can be air-borne, by means of its ascospores, which are forcibly ejected from the perithecia formed on infected stems of cereals and grasses (10). All early attempts to obtain infection of the roots of wheat seedlings with ascospores failed. Success was later obtained, however, when seedlings raised in sterile soil were inoculated. Infection was also obtained in sterile sand, though not in non-sterile sand. It seems that, in the absence of accessory nutrients, the food reserves of the ascospores are insufficient for the initiation of root infection. In sterile sand, accessory nutrients adequate for establishment of infection are thought to be provided by root excretions, which must remain wholly available to the germinating ascospores, but in unsterile sand the root excretions are possibly assimilated by the micro-organisms of the rhizosphere before the germinating ascospores can benefit therefrom (11).

The account of the epidemiology of take-all thus far presented is incomplete inasmuch as nothing has been said of the reaction of the host plant to infection. The most important factors affecting host resistance seem to be (1) supply of plant nutrients (2) temperature. It seems probable that the resistance of the wheat plant to infection decreases with rise in temperature, and that this, as well as increased activity of *Ophiobolus*, contributes to make 24° C. the optimum temperature for development of take-all. The effect of plant nutrients upon the development of the disease was studied in sand culture, under full rates and one-third rates of nitrogen, phosphate and potash manuring. In plants grown under two-thirds deficiencies of N, P and K, infection reduced yield by 24, 49 and 21 per cent. respectively, of that of the non-inoculated control plants. But in plants grown with full nutrients, infection failed significantly to reduce yield. This effect of liberal manuring with NPK in reducing loss of yield caused by infection can be explained by the increased production of new crown roots by the host plant. Many of the extra new crown roots produced as a result of manuring may remain free from infection for a considerable period; the chances of disease escape increase with the distance of *O. graminis* from the site of root initiation, the crown. The apparent tolerance to infection of the fully manured plants is not brought about by any increase in resistance of roots to infection, but by this disease escape mechanism; indeed, in this experiment, the roots of plants grown in full nutrient solution were actually more severely infected than were those of plants grown in the nitrogen-deficient solution. Abundance of nitrogen therefore seems to decrease the resistance of individual roots to infection, but, by increasing the total number of new roots produced, to increase the chances of disease escape for the plant as a whole (12).

Concurrently with these investigations in the laboratory and glasshouse the behaviour of the take-all disease was observed in the field by means of crop surveys, which were made chiefly in the Southern Advisory Province, in collaboration with Mr. W. Buddin. In the long perspective of traditional English agriculture, take-all has not been a disease of much importance, as it has been kept within bounds by the practice of crop rotation. Two exceptional circumstances, however, have favoured the disease and made possible these field investigations: firstly, the temporary popularity of intensive "mechanised" cereal growing under the economic difficulties of the early nineteen-thirties, and, secondly, the intensive cereal growing rendered necessary by the 1939–45 War. In particular, the growing of several consecutive crops of wheat upon the site of ploughed-up grassland favoured the development of take-all. The surveys also showed the importance of certain perennial rhizomatous grass weeds, notably species of *Agrostis* and *Holcus*, and *Agropyron repens*, as propagators of *O. graminis*; the prevalence of such weeds often completely nullifies the value of a rotation otherwise adequate for the control of take-all (13).

From the experience gained in the laboratory and glasshouse investigations and the field surveys described above a field experiment on control of take-all was designed and carried out at the Woburn Experimental Station, from 1943 to 1946, in collaboration with Drs. D. J. Watson and H. H. Mann. In view of the fact that take-all can be controlled by a 3 or 4-course rotation, or often indeed by a 2-course rotation, such as that of sugar beet and barley, the only practical problem to be solved was that of controlling the disease under continuous cultivation of a susceptible cereal crop. Field experience has repeatedly shown that it is difficult to control take-all in consecutive crops of autumn-sown wheat, as the interval between harvest and drilling of the next crop is too short for hyphae of *O. graminis* in the infected crop residues to die. More latitude is allowed by a succession of spring-sown wheat or barley crops; in particular, the system practised by Mr. F. P. Chamberlain, of Benson, Oxfordshire, for the last 15 years, seemed worthy of trial. The Chamberlain system consists essentially of the sowing of trefoil (*Medicago Lupulina*) along with the barley in spring; the trefoil makes a good growth in autumn after barley harvest, and is ploughed-under in late winter or early spring as preparation for the next barley crop. In theory, this system appears ideal for the control of take-all; the active growth of the trefoil in autumn should deprive *O. graminis* in the infected barley residues of the nitrogen essential for its prolonged survival, whereas liberation of nitrogen from the ploughed-under trefoil in late spring should help the following barley crop to tolerate infection from the over-wintering inoculum.

In this field experiment at Woburn, 6 autumn treatments were compared, *viz.* growth of trefoil with and without sulphate of ammonia, ploughing-in of additional straw with and without sulphate of ammonia, early ploughing without other treatment, and late ploughing with stubble cleaning but no other treatment. Half the barley plots received sulphate of ammonia in spring, and half received a combined spring dressing of phosphate and potash; the number of treatments in the factorial design was 24 ($6 \times 2 \times 2$). Wheat was drilled in autumn, 1943, and was followed by spring-sown barley in 1945 and again in 1946, so that in 1946 the cumulative effect of 2 years' treatments was obtained. Both in 1945 and in 1946 sulphate of ammonia in spring substantially reduced disease rating and increased yield; combined phosphate and potash produced a similar effect, which was greater in the second year. For that half of the experiment receiving sulphate of ammonia in spring, the best autumn treatments both for disease control and for grain yield were those in which trefoil was grown. Application of sulphate of ammonia to the trefoil in autumn increased grain yield but also slightly increased the incidence of take-all; the effect of autumn nitrogen in assisting overwintering survival of *O. graminis* evidently counterbalanced its effect in promoting disease escape of the growing barley crop in the following spring. It seems likely, therefore, that if the sulphate of ammonia had been applied not to the trefoil in autumn but to the barley in spring, so as to have doubled the spring dressing, it would have reduced incidence of take-all and given a greater increase in grain yield.

In the foregoing account of investigations at Rothamsted no mention has been made of previous or contemporaneous work by other investigators; references to this work can be found in the original papers cited here, and also in a review published in 1942 (14).

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