Rothamsted Report for 1946

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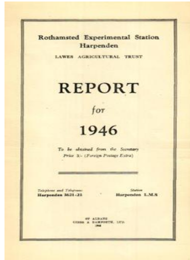
REPORT
for
1946

Special Reviews

Rothamsted Research

Rothamsted Research (1947) *Special Reviews ;* Rothamsted Report For 1946, pp 25 - 64 **- DOI: https://doi.org/10.23637/ERADOC-1-88**

Work of the Physics Department on Natural Evaporation

By H. L. Penman

Introduction: published work up to 1944

Evaporation is a very widespread phenomenon in nature and is largely beyond human control. At one extreme there is large-scale evaporation from the oceans, upon which the supply of rain is dependent; at the other there is small-scale evaporation from plant leaves and other organisms, of importance in micro-climatology. Between the extremes is the broad range of phenomena upon which the return of the rain to the atmosphere depends (1), phenomena of equal interest to the water engineer, the agriculturist and the pedologist. In agriculture, the transpiration of growing crops provides the main evaporation problem, but there is also evaporation from bare soil, regarded favourably when it dries out the land to permit cultivation operations, but too often regarded unfavourably when it is thought to be robbing nearby plants of moisture.

During the past few years the Physics Department has intensified the field studies in evaporation which had their foundation in the work of Dr. Keen over 25 years ago. Experiments were done in cylinders, uncropped, and a study of the retreat of the water table in various soil types, initially saturated, showed that even in the severe drought of 1921 there was little or no water movement from a water table lying at 3 or 4 ft. below the surface of Rothamsted clay soil, and for Woburn sand the limiting depth was about 14 in. (2). These experiments did not show how much water had evaporated from the soil, but, for the local soil, the drain gauges installed by Lawes and Gilbert in 1870 have provided records from which information about amounts and seasonal variation of evaporation from fallow soil could be obtained. The seasonal variation and its dependence on weather factors have become known partly from statistical analyses of the rainfall and drainage records (3, 4, 5), partly from physical reasoning and analysis of the automatic records available since 1925 (6, 7, 8), and partly from laboratory experiments (9). The results have shown that water movement in a soil with only a slight moisture deficit is extremely slow: as the deficit increases, the reluctance to move increases enormously. Drying conditions at the surface of bare soil, initially at field capacity, tend to set up a liquid movement from below to the surface. If the drying rate is small, as it is in winter, the flow of soil water can keep pace with it, so maintaining a steady evaporation rate very nearly equal to that from an open water surface and calculable from weather data. If the drying rate is great, the flow of soil water cannot keep pace with it, and the top layer of soil dries out even though moist soil conditions exist only a few millimetres away. This is characteristic summer behaviour in which the vaporisation takes place some few millimetres below the soil surface: the extra diffusion path thereby imposed reduces evaporation to very small amounts, and the rate ceases to have any dependence on weather factors other than rainfall. Thus, under English summer conditions, bare soil can be regarded as self-mulching, so that surface cultivation other than

https://doi.org/10.23637/ERADOC-1-88

that required for weed killing is a redundant operation as far as moisture conservation is concerned, a conclusion that is in keeping with the Department's findings in cultivation experiments (10).

Recent work: theoretical

The work on bare soil showed the complexity of the problem, but in the later stages there emerged the possibility that an analytical treatment might be successful when the surface was saturated, for a crude aerodynamical estimate of evaporation rates from weather data had been successful in accounting for the observed order of magnitude (6). For a number of reasons it seemed best to apply this analysis to evaporation from an open water surface, and to obtain comparative figures for the ratios of evaporation bare soil/open water and turf/open water under conditions where soil moisture was non-limiting.

Sink strength

Two approaches have been made. In the first, evaporation is regarded as due to a difference in vapour pressure between the evaporating surface and the air above it, the rate of transport depending on the degree of turbulence in the air moving over the surface. Eddies sweeping down onto and across the surface will take up vapour and move away as slightly damper air masses, gradually to mix with their drier surroundings away from the surface. The theory of the process, developed elsewhere (11, 12), leads to the following (simplified) form for the evaporation rate:—

$$E = C\ (e_s - e_d)\ u^{\cdot 76} \qquad (1)$$

where E is the evaporation in unit time, C is a constant involving dimensional and weather factors, e_s and e_d are the water vapour pressures at the evaporating surface and in the air above respectively, and u is the horizontal wind velocity. As the analysis is effectively measuring the ability of the air to take up vapour, i.e. to act as a "sink" for vapour, it is convenient to refer to estimates based on this equation as "sink strength" estimates.

Energy balance

The second approach has been more purely physical. Evaporation is an energy change, and by treating the problem as an example of conservation of energy one might be able to draw up an energy balance sheet leaving evaporation as the only unknown. Little used for land surfaces, as the balance sheet was drawn up it was found to have been extensively used in oceanography (13). During the day, sun and sky light provide a certain measurable amount of energy, of which a small part is reflected and a negligible part used in photosynthesis. Throughout day and night an exchange of long-wave energy takes place between the earth and the water vapour of the atmosphere, partly intercepted by clouds. Precise formulation of this long wave exchange has not yet been achieved (11), but, with this limitation, it is possible to write down an expression for the heat budget (H) of the test surface as a function of incoming sun and sky radiation, mean air temperature, water vapour content of the air and cloudiness. This heat, H, is used up in evaporation, E, in warming the air, K, in warming the evaporating material, S, and in warming the surround of the material, C. Under certain conditions S and C can be ignored: an approximate expression for the ratio of K/E is available (14), and as this ratio is rarely very great it is possible to deduce E from H.

Recent work: experimental

Experiments to test these two approaches were begun in 1944 using the twelve cylinders which Dr. Keen had set up in 1924 round a pit in the meteorological enclosure. Five had been filled with Woburn soil and in 20 years had settled to a near natural state. Each of these five was joined to an empty cylinder at the bottom, so making a set of five U-tubes. Waterproof covers were provided for the empty cylinders, and on two of the soil cylinders turf was laid in the spring of 1944. One of the remaining empty pair was filled to the brim and used as an open water surface. Water was run into the empty arms of the U-tubes until they were brimful and water was standing on the soil surfaces: it was then run out until the water levels had reached pre-determined depths. These were 16 in. below bare and turfed surfaces, 10 in. below bare and turfed surfaces and 5 in. below the remaining bare surface. From the daily measured movements of the water table it was possible to estimate evaporation and transpiration, and contemporary records were taken of surface, air and dew-point temperatures, wind speed, solar radiation, and cloudiness.

Results: open water

The results have not confirmed the expectation based on the sink strength formula. It has been found that the daily evaporation rate from open water is governed by:—

$$E = 0{\cdot}35(1 + 9{\cdot}8 \times 10^{-3} u_2)(e_s - e_d) \text{ mm./day} \qquad (2)$$

where u_2 is the wind velocity in miles/day, and e_s and e_d are in millimetres of mercury. This result, which differs insignificantly from that obtained in a very comprehensive American investigation (15), differs from the formal analysis on the fundamental issue of the value of the evaporation rate at zero wind velocity. The overall mean value of observed evaporation is about two-thirds of the value that would be obtained from eq. 1 for an average wind speed.

The energy balance has been successful for periods of several days in length and has often been successful for single days. A comparison of the two approaches is given in the table below. This gives the run-of-the-wind, the value of H and the observed open water evaporation for a few days in 1945, with two estimates of evaporation alongside. The first of these has been obtained from the energy balance: the second has been obtained from eq. 2, i.e. from a fitted equation.

Observed and Estimated Evaporation: Open Water

Date 1945	u_2 m.p.d.	H (mm./day)	Evaporation (mm./day) Estimated Energy Balance	Estimated Sink Strength	Observed
June					
11	149	3·64	2·6	2·4	2·3
22	92	5·58	5·4	4·2	4·7
July					
1	197	5·01	4·3	4·7	3·2
12	50	5·80	5·0	3·1	3·6
23	128	5·76	4·7	5·7	4·8
Aug.					
3	67	4·11	3·6	4·3	3·6
17	122	3·76	4·0	2·8	2·8
26	63	3·90	3·4	3·4	3·6
Sept.					
8	128	1·53	1·3	1·4	1·8
14	133	1·36	1·4	0·9	1·1
27	146	1·63	2·0	2·3	1·7

Over extended periods the agreements are better, and applications to other data have shown that the residual empirical elements in both approaches are not purely local in their significance.

Results: bare soil

Results for bare soil have been in keeping with those of earlier work. With the water table at 5 in. below the surface the soil remained moist at all times, and the evaporation rate was about 90 per cent. of that from the open water surface in all seasons. At the next depth (10 in.) the behaviour was much the same except in extended periods of hot weather, when slight surface drying occurred, increasing in area during the day and partially recovering during the night. An appreciable decrease in evaporation rate occurred under these conditions. The transition was complete at 16 in. depth. Within two days of rain the surface dried and evaporation fell to negligible amounts: indeed, it was so slight that it was possible to detect movements of the water table due to other physical causes. It is apparent that between 10 and 16 in. under this sandy soil there is a limiting depth from below which upward movement of soil water cannot take place, a result found previously in another way by Dr. Keen.

Results: turf

In 1945 the water table held at 10 in. under turf was lowered to 24 in., so that, over the two years, data are available for water tables at 10, 16 and 24 in. There were no great differences in behaviour, the transpirations and crop yields being very nearly independent of depth of water table. Over a whole year the transpiration from the well watered turf was about three-quarters of the open water evaporation, with a summer maximum of four-fifths and a winter minimum of three-fifths. The crop used only about one half per cent. of incoming short wave energy for building up plant material. During 1946 a third turf surface was used, plentifully fertilized. Summer transpiration from the three surfaces was the same for all, but the newer turf gave a crop yield of more than double that from either of the older surfaces, again about equal. It appears that where there is a plentiful supply of water the crop behaves rather like a piece of wet blotting paper and its consumption of water is forced at one end by sunshine, wind, humidity and temperature: under drier conditions it may be restricted at the other by the inability of the roots to find sufficient water in the soil to keep pace with this external forcing. Although plant growth is also dependent upon weather conditions it is not dependent in the same way, and is more closely linked to nutrient supply and soil conditions.

Application of the results of this work to catchment areas has shown that annual run-off can be estimated from weather data and, in a similar way, specification of times and amounts of necessary irrigation are possible for intensively grown crops.

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DEPARTMENT OF CHEMISTRY

By E. M. Crowther

Several series of investigations involving related work in field, pot and laboratory experiments were continued. Many of these form parts of long-term enquiries under the aegis of committees or conferences of various Government Departments.

The manuring of sugar beet (Ministry of Agriculture Committee on Sugar Beet Research and Education)

This series has continued on comparable lines since 1933. The main set of experiments tests N, P, K, Na and B fertilisers on some twenty commercial farms annually, there being at least one in each of the sugar-beet factory areas. A supplementary series started in 1945 tested nitrate of soda against sulphate of ammonia both in the presence and absence of salt. The results in the first two seasons brought out a definite superiority of nitrate of soda over sulphate of ammonia. This could be ascribed in part to the nutrient value of the sodium, but there was also evidence that nitrate was better than ammonia as a source of available nitrogen, since sodium nitrate gave better results than the mixture of sulphate of ammonia and salt supplying equal amounts of sodium and nitrogen. Where nitrate of soda was used there was little or no further benefit from supplying additional sodium as agricultural salt. So far no clear evidence of improvement in sugar-beet yields by applying borax has been found in over 60 trials on representative soils, but boron effects are known to be markedly seasonal and the work will be continued to provide the opportunity for proper tests when weather conditions aggravate the effects of boron deficiency.

The manuring of peas (Agricultural Improvement Council)

There is a singular lack of experimental evidence about the manurial requirements of peas and beans. Field experiments on beans have been in progress at Rothamsted for several years, and in 1946 a preliminary series of experiments on peas was designed in association with Mr. Shorrock of the Home Grown Threshed Peas Joint Committee and local agricultural officers. The experiments achieved a satisfactory standard of precision. Out of four experiments yields were significantly increased by phosphate in one and by potash in two experiments, but nitrogen, phosphate and potash fertilisers each caused one significant depression in yield. This preliminary series of experiments in which depressions were as frequent as responses suggests that current practice in the manuring of peas rests on an insecure basis. The manurial and cultural problems of any rapidly expanding crop need to be examined systematically by field experiments along lines similar to those employed since 1933 for sugar beet.

Bulky organic manures (Agricultural Research Council)

A series of field experiments at Rothamsted, Woburn and many commercial farms was continued to test a variety of bulky organic manures. The experiments were designed so as to bring out both the nutrient and the physical effects of the manures. The principal materials tested were farmyard manures, sewage sludges, bracken, composts of straw with either sewage sludge or fertilisers, and straw ploughed in directly. Particular attention was given to experiments on horticultural crops and especially to keeping the experiments going over several seasons. In this way evidence has been obtained of physical effects of organic manures in the second or third season of experiments which had shown no such effect in the first year.

The residual manurial values of fertilisers and the manurial value of feeding stuffs

The Director and Dr. Crowther served on a Conference constituted by the Ministry of Agriculture to revise the Voelcker and Hall Tables of residual manurial values. For the first time since this subject was raised by Sir John Lawes in 1870 it was possible to obtain an agreed report acceptable to the interested parties. The Report was published in the Ministry's Journal. The scientific background, including the results of Rothamsted and Woburn residual value experiments, has been summarised (17) in a paper, and the immediate practical problems considered in two lectures (14, 15) to the Central Association of Agricultural Valuers.

Forest nurseries (Forestry Commission Committee on Nutrition Problems in Forest Nurseries)

The new programme of forest planting requires a rapid increase in the production of seedlings and transplants, especially of Sitka Spruce, Scots Pine and other conifers, but many acute problems remain to be solved in nursery practice. Sitka Spruce in particular grows very poorly in many nurseries. A series of manurial experiments was therefore started in 1945 to test fertilisers and composts, alone and in combination, on a range of nurseries, including an established nursery and new ones on old arable land, cleared forest, and cleared heathland. The preliminary results showed that on the sites known by their conditions and by soil analyses to be acutely deficient in nitrogen, phosphate and potash the seedlings and transplants responded strikingly to additions of these plant foods in suitable forms. The effects of various composts could be largely interpreted in terms of their contents of the three major plant foods. On the very poor soil of Wareham Heath there were particularly large responses to each of the elements nitrogen, phosphorus and potassium. Growth was unsatisfactory and visual symptoms of acute nutrient deficiencies were striking where only two of these three elements were added. Some of the past prejudice against the use of fertilisers in forest nurseries on such soils may well have been due to the aggravated symptoms of one nutrient deficiency produced by making good defінciencies in one or two other plant foods. With all three nutrients supplied as fertilisers large vigorous and well-furnished seedlings and transplants were produced in 1946 on what was intrinsically an extremely poor soil.

Some of the experiments were necessarily of complex statistical design because it was necessary to test different amounts and forms of each of the three major elements. Some of the differences between alternative forms of fertiliser have already been demonstrated. In an established nursery at Oxford it was shown that

https://doi.org/10.23637/ERADOC-1-88

the growth of Sitka Spruce could be greatly improved by acidifying the slightly calcareous soil on which this species has consistently failed for a number of years.

Plants from many of the experimental treatments in several nurseries will be planted out in experiments in three forests in 1947 and manurial experiments will also be made in these forests.

This work must be continued over a number of seasons and a variety of soils before a sound manurial policy for forest nurseries can be established. The results of the first two seasons are promising. Apart from their potential value for forestry practice they provide interesting material for studying problems of plant nutrition and soil chemistry at much lower levels of fertility than are obtained with agricultural crops.

FERTILISER PLACEMENT (Agricultural Research Council)

Experiments on potatoes in 1945 showed no differences between alternative methods of applying fertilisers. Through experience gained in the field in 1945 it was possible to suggest a number of improvements in the experimental drill built for this work by the National Institute for Agricultural Engineering (12). An improved drill was used in 1946 in 16 experiments on potatoes in the principal potato-growing areas of south and east England. The methods of fertiliser applications tested were, broadcasting before ridging, broadcasting after ridging, placement in contact with the seed and placement in two sidebands below seed level. There was very little difference in crop yield between broadcasting over ridges and placement in contact with the seed or in sidebands. The normal method of broadcasting over ridged land brings the fertiliser close to the sets and ensures the merits of controlled placement. Nothing is gained by any more elaborate method of applying the fertiliser. This result is at variance with the American experience that banded placement below and to the side of the sets is preferable. The explanation of the discrepancy is no doubt due to the common practice in America of using cut sets which are planted together with fertiliser by machines working on the plot. Broadcasting before ridging was clearly inefficient. Three parts of fertiliser applied before ridging gave about the same yields as two parts of fertiliser applied in any one of the three methods after ridging.

As the result of discussions during 1946 a new experimental drill for fertiliser placement tests on small seeds is being built by the National Institute of Agricultural Engineering. It is hoped to be able to use this in 1947.

PHOSPHATE FERTILISERS (Ministry of Supply)

Field experiments, mainly in collaboration with Advisory Chemists, were laid down to test a variety of forms of phosphate fertilisers, new and old. Yields were obtained from 29 experiments in 1945 and from about 25 in 1946. In the latter year the new fertiliser, silico phosphate, from the Ministry of Supply Experimental Plant at Strood was tested on a variety of soils and crops with promising results (13). Special attention was also given to dicalcium phosphate, both as a more or less pure commercial material and as a major ingredient of mixtures of superphosphate with basic materials. The fuller investigation of dicalcium phosphate is of great theoretical and practical importance. It may be possible in some soils to cut down the wastage of phosphate by rapid fixation. If it can be shown that a phosphate insoluble in water may be almost as active as superphosphate under appropriate conditions there will be good grounds for reviewing the whole position of the water-solubility test in the Regulations of the Fertiliser and Feeding Stuffs Act. At present many promising developments in the production and use of fertilisers are prevented by the commercial and legal customs of treating water-soluble phosphoric acid as having unique merit. This test, originally proposed by Sir John Lawes merely to distinguish between good and bad superphosphate, has outlived its usefulness and is now a serious obstacle to technical progress in many branches of science and technology.

Basic calcium phosphates

All consideration of the reactions and behaviour of phosphates in soils and fertilisers are rendered difficult by the lack of precise data on the equilibria and reactions between lime and phosphoric acid in aqueous systems. Equilibria are difficult to establish and the reactions are complicated by the low solubility, the ease of hydrolysis and the absorptive powers of the solid phases. As an index of the uncertainties it may be stated that there is still considerable doubt as to whether any such material as "tricalcium phosphate" can exist in contact with water, and yet the name and formula of this substance are used in almost all text books and discussions on soils, fertilisers and animal physiology. Until 1926 this hypothetical substance also served in expressing all phosphate analyses under the Fertiliser and Feeding Stuffs Act.

In re-examining the reaction between phosphoric acid and calcium hydroxide solutions evidence was obtained to suggest that some of the anomalies may be explained by the special properties of dicalcium phosphate, which may occur in some of the more alkaline as well as the more acid systems. A Russian method of precipitating basic calcium phosphates by very slow reactions in large volumes of water was found to give promising results.

With the object of finding a more adequate method of characterising available phosphates in fertilisers, studies have been commenced on the calcium citrate system and on the reaction between calcium phosphates and fluorides during extraction processes.

Soil organic matter

In collaboration with the Biochemical Department an investigation is being carried out on certain aspects of soil organic matter. The usual methods of extraction with strongly alkaline solutions may produce artefacts and a search is being made for milder reagents. This led to the consideration of organo-metallic complexes in soil (21), and to a study of autoxidation of soil organic matter in alkaline solution.

Chromatographic analysis gave little success with the "humic acid" complex, but a useful resolution of the so-called "fulvic acid" fraction was achieved by using charcoal.

Some results suggest that mucopolysaccharides or mucoproteins may be present in soil organic matter, but quantitative estimation of these materials and related chemical groups still present great difficulties. Thus no reliable method has yet been found for estimating uronides in soil.

Iron in soils

Several methods of extracting iron from soils and soil colloids were studied with the object of finding better methods for characterising the forms of iron in soils and for studying the movement and deposition of iron compounds in soil formation. The work included a study of stability of iron-humus sols and the properties of complexes of iron and organic acids.

Manganese and other minor elements

In collaboration with the Biochemical Department work was continued on the nature of the so-called "readily reducible" manganese of soils (22). It was found that polycarboxylic and hydroxyacids but not non-substituted acids formed complexes with manganic manganese which are soluble over a wide pH range. Extractants, such as pyrophosphate, polycarboxylic or hydroxy-acids which dissolve polyvalent cations (e.g. manganese, iron and copper) from soil also extract organic matter (27). It was found that organic soils yielded more manganese in alkaline extracts than in neutral ones, and also that this manganese was present in the divalent form (26). Preliminary pot experiments were carried out to test the availability of manganic manganese. A fresh raw sphagnum peat, capable of fixing large amounts of added copper in a form which was soluble in pyrophosphate but not in the salt solutions used to determine "exchangeable" bases, also caused iron and copper chlorosis in oats.

Spectrographic analyses

Sugar beet tops and roots from the standard series of fertiliser trials in 1945 were analysed for many elements, including boron. Many analyses were also made on samples of sugar beet taken in joint work with Mrs. Watson of the Plant Pathology Department and Dr. Hull of the Midland Agricultural College (24). Some of these experiments brought out interesting interactions in plant composition. Thus in one experiment addition of salt greatly reduced the calcium and magnesium contents, and nitrogen greatly increased the manganese contents of the leaves. Manganese sulphate applied ten weeks after sowing was far more effective in raising the manganese contents of the leaves than that applied at sowing.

A paper has been prepared for publication on the mineral composition of oil palms in Nigeria showing various deficiency symptoms and other pathological conditions. Analyses were also made on cotton leaves from South Africa and Sitka Spruce plants from the forest nursery investigations already mentioned.

In a survey of manganese-deficient soils in Hertfordshire in 1945 many samples of cereals and weeds were collected and analysed. Where oats were showing symptoms of manganese deficiency and wheat was free, the wheat nevertheless had lower manganese concentrations in its leaves. Vetches and cleavers both had higher concentrations than the two cereals. It was also found in this survey that chickweed belonged to the "high-sodium" class of plants, with 2·0 per cent. of Na_2O on the dry matter as compared with less than 0·1 per cent. for many other species.

Spectrographic methods for boron and nickel were developed.

Dr. J. B. Hale worked for six months in 1946 with Professor Lundegardh at Uppsala and Professor Goldschmidt of Oslo.

An investigation on the mineral composition of Broadbalk straws over a term of years was completed. The results were examined in relation to manurial treatments and weather conditions. A number of the analytical data were found to be significantly related to the distribution of rain, when examined by Fisher's method of analysis.

Rothamsted classical plots

Steady progress has been made in preparing for analysis the large mass of soil samples taken from Broadbalk in 1945. A similar set was taken from Hoosfield in 1946. Preliminary work has been done in building up apparatus and checking appropriate methods for the critical analyses required in analysing these soil samples.

Analytical and other methods of investigation

Work on rapid and micro-methods of analysis of soil and plants has been continued by several members of the staff. By using a mixture of selenium, copper sulphate and a large amount of potassium sulphate and digesting for one hour the recovery of nitrogen from guanidine was raised to 99 per cent. The micro-Kjeldahl method was developed to deal with from 20 to 30 mg. of dried ground plant material. It was found that the needles of Sitka seedlings have much the same nitrogen, phosphorus and potassium content as the average of the whole plant. It may therefore become possible in future work to judge the nitrogen status of experimental plants by needle samples which are easily collected and analysed.

It was found that moderate amounts of nitrate could be included in the total nitrogen by both micro- and macro-Kjeldahl analyses with salicylic acid even in the presence of appreciable amounts of water.

In extending an earlier method of examining bulky organic manures by measuring the production of carbon dioxide under standard conditions, it was found possible to reduce the labour involved in ensuring good aeration, by designing an apparatus in which hydrogen peroxide automatically supplied additional oxygen as required.

The Ter Meulen-Spithost method for organic carbon in soils has been modified to a compact unit with volumetric determination of the carbon dioxide.

Apparatus

Mr. Nixon and Dr. Lees of the Biochemistry Department have designed and constructed a simple and robust pH meter which incorporates all the normal features of commercially made instruments but has the additional advantages of being driven entirely from dry batteries and of being ready for use a few seconds after switching on. Work has been started on the design of a different type of direct reading pH meter which will be accurate to 0·1 pH and sufficiently stable, light and robust to be used in the field for survey and advisory work or in the laboratory where the more refined instrument is not required.

Technique for grassland experiments

In collaboration with the Statistics Department some 800 samples of pasture grass were taken in 1946 from random points in the High Field Experiment at Rothamsted and in a trial at Biggleswade. Similar samples from High Field in 1945 were bulked and analysed. The purpose of the work is to discover a suitable technique for grassland experiments, especially on the relative production of leys and permanent grass. The High Field experiment provides the opportunity of comparing the starch and protein equivalents of the herbage on a number of plots with the actual live weight increases of the grazing animals.

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DEPARTMENT OF SOIL MICROBIOLOGY

By H. G. Thornton

The following main lines of research were carried out during the year:—

A. Work dealing with the soil micropopulation

1. *Direct examination of organisms in soil*

Estimates of the total numbers of bacteria in soil cannot be obtained from plate counts owing first, to the uncertainty as to whether colonies are developed from single cells or from clumps of bacteria in the soil suspension, and secondly, to the fact that no single nutrient medium will support the growth of all soil bacteria. Total estimates can only be made by the direct counting of bacteria in stained films of soil. A difficulty in preparing such films has been the disturbance of the soil suspension due to surface tension forces during drying, which resulted in an uneven distribution of microorganisms over the dried film. If, however, melted agar be used as a diluent, gelation of the suspension preserves the original distribution of the soil particles and organisms. Moreover such films can be made of known thickness by setting the suspension in a haemocytometer so that the volume of suspension in a measured area of film is readily calculated. The details of the method finally developed by P. T. C. Jones and Janet Mollison are as follows:—

A known quantity of soil is added to 5 c.c. of sterile distilled water and ground in a small sterile crucible. The resulting suspension is poured into a sterile flask. The soil remaining in the crucible is washed in a further 5 c.c. distilled water and the suspended matter added to the flask. The soil suspension is made up to 50 c.c. with melted 1·5 per cent. agar previously filtered and sterilised. The suspension in the flask is well shaken and a drop is placed on a haemocytometer slide of 0·1 mm. depth, immediately covered by a coverslip and allowed to set. The coverslip can be removed under distilled water and the film gently floated on to a microscope slide and allowed to dry. The dried films are then stained for one hour in the following solution:—

Phenol (5 per cent. aqueous)	15 c.c.
Aniline Blue (water-soluble) (1 per cent. aqueous)	1 c.c.
Glacial acetic acid	4 c.c.

(This mixture must be filtered about an hour after preparation.) The films are washed in 95 per cent. alcohol, dehydrated in absolute alcohol and mounted in Euparal. Counts of microorganisms are made in 20 random microscope fields on each of 4 replicate slides. Since the volume of 20 fields is known the number of organisms per gram of soil is readily obtained. For observation with an oil immersion it has been found that a suitable density of soil suspension is obtained by taking an initial quantity of soil such that 0·00000005 gram are contained in the volume represented by 20 microscope fields.

Statistical analysis of bacterial counts from replicate fields shows that the method gives a valid estimate of the soil microflora.

C

Recovery counts of bacterial suspensions added to sterilised soil have given 93 to 98 per cent. recovery. Total numbers of bacterial cells found in natural soils have ranged from 3,000 million to 8,000 million per gram. The method can be adapted to give counts of fragments of fungus mycelium in soil.

2. *Classification of soil bacteria into nutritional groups*

Following the line of work developed by Lochhead in Canada, Mr. A. V. Garcia has studied the bacteria and proactinomycetes that formed colonies on platings from the three plots of Barnfield receiving (Plot 8, O) no manure, (Plot 1, O) farmyard manure, and (Plot 4, A) complete minerals and ammonium sulphate.

Plate counts made from samples taken on eight occasions covering a period from April till November, using several different agar media, invariably gave the highest counts from the farmyard manure plot and the lowest from the unmanured plot. The organisms that grew on platings were classified according to their growth requirements. The soil from the farmyard manure plot was characterised by an especially large percentage of bacteria that require yeast for their growth. The plot with mineral manurng contained a majority of bacteria that could grow on simple media without growth substances.

These studies on the bacteria from the three plots were accompanied by counts of amoebae carried out by Mr. A. V. Garcia and Dr. B. N. Singh.

3. *Microbial decomposition of resinous substances in soil*

Mr. P. C. T. Jones has continued this investigation, carried out at the request of the Road Research Board (D.S.I.R.) and having the practical object of stabilising resins that are added to soil in order to produce a temporary road base resistant to water absorbtion. A number of bacteria and fungi capable of attacking such resins were isolated from soil and classified according to their morphology and biochemical reactions. The breakdown of compacted blocks of soil was found to be correlated with the increase in numbers of such organisms in the blocks. The effects of various antiseptics on the organisms were studied.

4. *Nitrifying bacteria*

Dr. Jane Meiklejohn has commenced work on nitrigying bacteria. The object of the work is to discover what organisms are mainly responsible for nitrification in Rothamsted soils and what effect organic substances have on this process.

5. *Soil actinomycetes*

Mrs. Dagny Oxford's work on this group has been mainly concerned with the investigation of two problems, (1) the factors which affect the development of aerial mycelium and determine the morphology of actinomycetes in soil, in which the type of growth is generally quite uncharacteristic of their species, (2) the lipoid nature of the outer wall of the aerial mycelium and of the spores. The difficulty in wetting the spores, due to this, makes it very difficult to obtain a spore suspension and hence affects the value of actinomycete colony counts obtained from a suspension of soil.

https://doi.org/10.23637/ERADOC-1-88

6. *Mycorrhiza*

Dr. Janet Mollison has surveyed the occurrence of mycorrhizal fungi in clover and in wheat. They were found almost universally in clover and seasonally in wheat. Their importance to the plant has not so far been ascertained since attempts to isolate the fungus in pure culture have not yet succeeded.

7. *Myxobacteria*

Considerable advance in the study of soil myxobacteria has been made during the year by Dr. B. N. Singh whose work is described more fully below and by Dr. R. Y. Stanier who investigated a group of these organisms found to attack chitin.

8. *Conditions influencing the excystation of amoebae*

Miss Lettice Crump has found that the type of bacterial food supplied to soil amoebae influences not only their reproductive rate but also their excystation. This discovery may explain the rapid changes in the proportion of cysts to active forms previously found in soil.

B. Work dealing with the nodule bacteria (*Rhizobium*) of leguminous plants

9. *Dissociation produced in Rhizobium by bacteriophage*

Dr. Janina Kleczkowska studied the influence of bacteriophage on the strain called F12, a "variant", ineffective in fixing nitrogen in the clover plant, which was derived from the effective strain A. Treatment with bacteriophage usually gives rise to the appearance of 'phage resistant variants which also differ from the susceptible parent strain in other characters such as colony appearance and more rarely in behaviour towards the host plant. Fifty variants of F12 obtained by 'phage treatment were tested on the clover plant. Of these one was consistently effective, three were consistently intermediate in nitrogen fication, three others gave inconsistent results on replicate plants and 43 strains remained ineffective. These characters were maintained after several passages through the plant. Similar treatment of the ineffective strain C with bacteriophage produced a variant giving effective and ineffective responses on different replicate plants.

10. *Geographical strains of clover nodule bacteria*

The testing of samples and classification of results continued during this season.

Further tests were also made of the effect of season on nitrogen fixation in continuation of last year's work.

11. *Competition between strains of nodule bacteria*

Mr. S. Bhaduri continued the study of competition between two strains of *Rhizobium*. There is evidence that this is acute between certain strains but not others. No evidence of competition between *Rhizobia* from different "inoculation groups" could be found.

12. *The interaction of the clover plant with Rhizobium*

Dr. P. S. Nutman continued investigations along the following lines:—

(a) *Genetics of the clover plant*

Confirmation was obtained of the work suggesting that resistance to infection in clover was due to the interaction of a recessive gene with a maternally inherited factor. The inheritance of the effectivity response as regards nitrogen fixation appears to be of two kinds (1) a polygenetic inheritance that is apparently not specific to a given bacterial strain and (2) a single gene effect that is highly specific to the bacterial strain concerned. The behaviour of one of these single genes has been exhaustively studied and those of four others have been incompletely investigated. The results suggest that the genes concerned may be allelomorphic.

(b) *Physiological studies*

These have been concerned, first, with the physiologically homologous nature of lateral roots and nodules and, secondly, with the partial inhibition of nodule formation on plants growing in association. A paper on the first of these investigations is being prepared.

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Micro-organisms Capable of the Selective Destruction of Soil Bacteria

By H. G. Thornton

Introduction

The maintenance of satisfactory biochemical activity in a field soil depends on the establishment in it of a population of those types of micro-organisms that produce desirable chemical changes therein. This will be brought about only if the soil environment is suitable. An important factor in this environment is the existence and activity of other micro-organisms that limit the numbers of useful organisms either by competing with them for nutrients, by harmfully changing the chemical environment (as by producing toxic secretions), or by directly eating them. The competition between related strains of nodule bacteria (*Rhizobium*) studied in this department appears to be an example of the first type. The production of antibiotic secretions by fungi and actinomycetes, many of them derived from soil, has been much studied elsewhere and has given rise to a vast literature. Their production by certain of the Myxobacteria, however, has received little previous attention. Some recent investigations in this field are summarised below. There is in soil a considerable and active population of protozoa and related organisms that feed directly on bacteria. This group has been the subject of investigation at Rothamsted for many years.

In the years between 1919 to 1939 the General Microbiology Department carried out many investigations concerning the protozoan fauna of soil whose object was to elucidate the ecological importance of protozoa in soil and particularly their effect on the bacterial population. A systematic survey of the types of protozoa in soils was carried out and a method was developed for the approximate enumeration of protozoa in soil samples (1, 13). With the help of this technique it was shown that the numbers of active amoebae and of flagellates in field soil underwent rapid fluctuations and that the rise and fall in numbers of active amoebae found in daily samplings was on the whole inversely related to that of bacterial numbers found in plate counts (3). Experiments also showed that the presence of amoebae kept down the numbers of bacteria in soil stored in the laboratory (2), so that it seemed reasonable to suppose that they control the size of the fluctuating bacterial population in the field. Laboratory experiments with pure bacterial cultures with and without the addition of protozoa showed, however, that the latter do not always depress the biochemical activity of the bacteria. They may stimulate this activity by keeping the bacteria at a lower numerical level than they would attain in pure cultures. This probably results in the culture remaining in a younger and more active condition (4, 5, 8, 9, 11).

The differential feeding of soil protozoa

It is an interesting question as to how far protozoa are selective in consuming certain species of bacteria and not others. There was some previous work suggesting selective feeding, but the question had been little studied.

To investigate this problem B. N. Singh developed an elegant method in which amoebae could be given a choice of bacterial food supplied as streaks, each of a different bacterial species, disposed in a petri dish in star formation at the centre of which the inoculum of amoebae was applied. Bacteria could be classified into (1) species readily eaten (2) those that were slowly eaten but eventually completely consumed (3) those that were only partly consumed and finally (4) an entirely inedible group (14). No correlation could be found between edibility of bacteria and their gram staining reaction (14, 17), but nearly all pigmented organisms other than yellow and orange were inedible. It is thus possible that certain bacterial pigments afford an advantageous protection against amoebal attack (16, 17). In other cases the edibility or otherwise of a bacterium seems to be determined by a fine difference not readily identified, since strains of Aerobacter similar in morphology and physiology differ in edibility (14). This is also the case with strains of *Rhizobium* (16).

Species of soil amoeba differ somewhat in their preference as regards bacterial food both amongst themselves and from the soil flagellate Cercomonas which also feeds selectively. Amoebae grown on plates or in sterilised soil culture can select edible from inedible bacterial food where both are supplied and, in soil they greatly reduce the numbers of edible bacteria (14). This discovery suggests that they are able in field soil to alter the quality of the bacterial flora as well as limiting its total numbers. It seems likely that this is their more important function.

Bacteria that are inedible to amoebae include certain types whose mere presence whether alone or in mixture with edible forms is definitely toxic to the amoebae. These toxic types include pigmented forms and there is evidence in some cases that the pigment itself is toxic. This is so in the case of the soluble pigment excreted by *Pseudomonas pyocyanea* and in that of *Chromobacterium violaceum* and *Serratia marcescens* whose violet and red pigments are relatively very insoluble in water (17). It seems possible that the further study of bacterial pigments toxic to protozoa may lead to the discovery of substances of importance in the treatment of protozoal diseases.

The estimation of numbers of protozoa in soil samples

This work on the differential feeding of soil protozoa revealed a serious defect in the previous method used for estimating protozoal numbers in soil and made possible the development of an improved method giving valid estimates. The numbers of protozoa in soil are too small to enable them to be counted directly in stained films of soil nor will they form colonies on platings. The methods used are therefore based on observing their presence or absence in a range of soil dilutions. In the methods previously used, a range of dilutions of the soil sample were made and duplicate plates of nutrient agar were inoculated with 1 c.c. portions of each dilution. From the presence or absence of protozoa at each dilution the numbers were estimated, using the Table worked out by Fisher and Yates (6). In this technique the mixed bacteria added with the diluted soil suspension were relied upon to supply food to any protozoa that might be present at that dilution. The selectivity of protozoal feeding habits shows that this method may give invalid results because an individual protozoan may come to lie on the plate amid inedible or even toxic bacteria and thus fail to grow. Apart from this serious defect the previous method was greatly limited in accuracy by the small replication enforced by the use of an entire petri dish for each culture. In his study of bacterial food supply Singh found that a number of bacterial species were readily eaten by all protozoa tested. Thus by applying the diluted soil suspension to a pure culture of such a bacterium placed on the surface of agar without any added nutrients, growth of inedible bacteria from the suspension was checked and a suitable food supply to any protozoa that might be present was assured. Replication of cultures at each dilution was obtained by the use of 8 glass cells per petri dish in each of which a replicate culture was set up (19, 20). Extensive tests have shown the method to give a reliable estimate of the numbers of amoebae and flagellates in soil samples although recovery tests with amoebae show that the estimates are consistently low owing to about 20 per cent. of the amoebae lacking viability. This method has been applied by Singh and Garcia to samples taken from three plots of Barnfield.

The occurrence and distribution of giant Rhizopods in soils

The use of plain (non-nutrient) agar with a pure bacterial culture as food supply has proved an excellent method for the culture and isolation from soil of several groups of soil organisms that derive their food from bacteria but which have until now been considered rare in soil. Amongst these are the giant amoeboid organisms of the genus *Leptomyxa* described by Goodey (7) but not since studied. By using his method of isolation B. N. Singh has found these organisms to be common and widely distributed in soils. They have been found in all of 26 arable and in 12 out of 33 grassland soil samples collected from 10 counties in Great Britain. They occur in variously manured plots from Barnfield and Broadbalk. Approximate estimates give their numbers as of the order of 1,000 per gram. Since they have an individual volume about 1,000 times that of a typical soil amoeba the numbers of bacteria that they must consume to maintain their numbers are likely to be considerable. They resemble amoebae in being specific in their food requirements. Their life cycle and ecology are under investigation.

Acrasieae

A second group of microorganisms, whose presence as regular soil inhabitants has been revealed by the technique of isolations using pure bacterial cultures as food supply, is the Acrasieae. These organisms were formerly believed to be derived from dung, but a number of strains of the genus *Dictyostelium* developed from dilutions of soil added to non-nutrient agar smeared with bacteria edible to protozoa. B. N. Singh has obtained them from 33 out of 38 arable and from 3 out of 29 samples of grassland soils obtained from localities ranging over 10 counties in Great Britain. They occur in all of the variously manured plots of Barnfield and Broadbalk, most of which receive no dung; they are hence true soil inhabitants. The Acrasieae have a life cycle comprising an amoeba-like stage which forms a "pseudoplasmodium" developing into mucor-like fruiting bodies inside which spores are formed. The myxamoebae resemble true amoebae in being differential in their feeding habits although in some cases different species of bacteria are eaten by myxamoebae and true amoebae respectively. The type of bacterial food greatly affects the morphology and occasionally the colour of the fruiting body formed. On some species of bacteria very abnormal fruiting bodies are formed so that the existing classification of the Acrasieae, based on the morphology and colour of the fruiting body, is only applicable where due regard has been taken to the food supply and cultural conditions. When added to sterilised soil supplied with a suitable bacterial culture, Acrasieae can spread through the soil at an approximate rate of 1 in. in 24 hours and will multiply therein, ultimately producing fruiting bodies on the surface. They greatly reduce the bacterial numbers in the soil culture. There is also evidence that they can multiply in fresh unsterilised soil. It thus seems likely that they are a factor affecting the bacterial population in arable soils (18, 22, 23).

Myxobacteria

Methods similar to those used in isolating giant Rhizopods and Acrasieae have revealed the presence in soils of appreciable numbers of the "higher" types of Myxobacteria of the genera *Myxococcus*, *Chondrococcus* and *Archangium* (21). They have been found in all of the 38 samples of arable and in 21 out of 31 samples of grassland soils collected over the counties of Great Britain. Their occurrence in all the classical plots of Barnfield and Broadbalk again shows them to be true soil inhabitants and not dung organisms as was previously supposed. Counts show that the Barnfield farmyard manured plot contains numbers varying from 2,000 to 76,000 per gram. They are also found in large numbers in compost heaps. The higher Myxobacteria feed on true bacteria by the production of secretions that kill and lyse the latter. Dr Singh and Dr. A. E. Oxford, working in collaboration, found that *Myxococcus virescens*, growing on a cell-free medium, produces two substances, an antibiotic agent that acts most powerfully against gram positive bacteria and a bacteriolytic substance which is a proteolytic enzyme and which lyses dead bacteria. It acts most powerfully against gram negative organisms. A further study of the production and activity of these substances may throw much light on the mechanism of antibiotic activity in general.

Number of bacterial species in soil liable to attack

In assuming the ecological importance in soil of holozoic predators and of organisms producing antibiotic secretions, it is important to form some idea of how many of the numerous and widely different species of soil bacteria are susceptible to attack by one or more of these organisms. Dr. Singh has tested the susceptibility of 84 strains of bacteria nearly all from soil, to attack by five holozoic organisms and to three species of Myxobacteria. The same bacterial strains were used in each test and these comprised a wide range of types differing in morphology, growth habit, gram staining and pigment production and included both common species and others relatively rare in soil. He found that any one species of organism could attack about half of the bacterial species tested, the actual percentages being as follows:—

	Percentages of bacterial strains attacked
Large Amoeba	54·8
Small Amoeba	60·7
Leptomyxa	41·7
Dictyostelium giganteum	57·1
D. mucoroides	61·9
Myxococcus virescens	69·0
M. fulvus	53·6
Chondrococcus exiguus	47·4

But the organisms differ markedly in which particular bacterial strains that they attack. On an average the members of any pair of organisms differ in their reaction to 36 per cent. of the bacterial strains tested. As a result of this specificty in attack all but 6 out of the 84 bacterial strains were attacked by at least one of the 8 organisms although only 6 were attacked by all of them.

This test did not cover the fungi or the numerous actinomycetes in soil that produce antibiotic secretions active against gram positive bacteria. It seems likely that very few species of bacteria exist in the soil that are immune to attack by some other micro-organism.

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DEPARTMENT OF BOTANY

By Winifred E. Brenchley

After the cessation of hostilities much of the war-time activity, especially that in association with the Chemical department, was brought to a close, and more time and apparatus was available for the normal work of the Botanical department. The minor element work was extended both in soil and water cultures, and investigations were initiated into certain field problems which had become of increasing importance during the war years.

A. Minor elements—molybdenum

The effect of molybdenum on plants continued to be approached from the two angles of toxicity and nutrition, the former in soil and the latter in nutrient solutions. The work in 1944–45 had strongly supported the hypothesis that the poisonous action of molybdenum is greatly influenced by the nature of the soil, and the factors causing this variation, as well as those bound up with the variability in the beneficial response to traces of the element, continued to be actively sought.

In *soil cultures* the general scheme of the experiments was the same as in 1944–45, though it was now possible to use larger pots for the strong growing tomatoes and Solanum, for which the small size of the pots previously available had introduced a serious limiting factor. Three of the same soils were again tested, Woburn soil and its compost, and the manganese deficient Isleham Fen soil. These were supplemented by two other fen soils, Littleport Fen, which was highly fertile, and Waterbeach Fen, which was definitely acid. In addition the allotment soil was replaced by a good loam, composted as before, and also the effect of manganese added to the Isleham Fen soil was tested in the case of flax.

Tomatoes again proved resistant to the harmful effects of molybdenum in several cases, and where response was obtained it tended to be irregular among the replicates. In Woburn soil the higher dose of molybdenum was fatal at an early date, and the lower dressing caused severe and irregular reduction of crop. The composting of this soil with peat enabled the tomatoes to withstand the harmful action of the lower dressing, and to produce a crop, again extremely variable in weight, with the heavier dose. In the manganese deficient Isleham Fen soil the crop was variable even in the controls, but on the average was quite as good as in some of the other soils. The addition of molybdate approximately halved the average crop for each progressive dose, but the poisonous effect was much less than in Woburn soil. No deleterious effect on the crop was found in any of the other soils tested.

The development of Solanum was adversely affected by both treatments of molybdenum in each of the five soils tested. The composting of both Woburn soil and top spit loam with peat reduced the poisonous action, expecially with the heavier dose, this being specially noticeable in the fruits and roots. In the Isleham Fen soil the controls were much reduced in size owing to the manganese deficiency, but the toxicity of molybdenum was even more marked here than with the other soils. Unfortunately it was not possible to test the effect of added manganese with this species.

With flax in most soils the toxicity of the lower dressing of molybdenum was hardly evident, but it was manifested by the higher dose. In the Isleham Fen soil the crop was much worse than in 1945, as the controls were only one third or one quarter the size, and no seed was produced in either untreated or treated plants. The addition of manganese improved growth all round, raising the dry weights, but leaving the toxic effect of the molybdenum well defined. Very little seed was formed in any of the treated plants, though the controls did better. It was an interesting confirmation that the two adverse factors, deficiency of manganese and excess of molybdenum, were able to function at the same time and that, despite the deficiency or the excess, the action of the other factor was clear and measurable.

In *nutrient solutions* striking beneficial effects had previously been obtained on a number of occasions with lettuce when small quantities of sodium molybdate (supplying 0·1 p.p.m. Mo) were added to the culture solution, and it seemed that this element was probably essential for normal growth for this crop. The results, however, were not always consistent and during the past year an attempt has been made to determine the cause for this lack of uniformity. Various crops, chiefly lettuce, red and wild white clover have been grown in different types of culture solution, and the effect of adding or withholding molybdenum noted in each case. Special attention has been paid to variations in the level of calcium supplied and the pH value of the different nutrient media selected. Lettuce is a quick growing plant and has already given some promising results, but as the varieties chosen were not suitable for summer conditions under glass confirmatory evidence cannot be obtained until next spring. Clovers, on the other hand, have a much longer growing period, and it will be necessary to carry them through the winter before all the available information from even one experiment will have been secured. Up to the present the two crops seem to be responding to the different treatments in a very similar fashion and symptoms of molybdenum deficiency have been well defined in both cases.

B. Vitality of buried weed seeds

Various aspects of the problem of weed seeds buried in the soil are still under consideration. In the experiments on Broadbalk wheat field periodic records of the weed seeds germinating from the soil samples taken in August, 1945, have been made and will be continued for the usual three year period. Until this is completed no comparison is available between the results of this sample and that of 1940, a comparison which will provide evidence as to the effect of the third 5-year fallowing cycle on three of the plots on the field.

Field observations and glasshouse experiments on dormancy and viability of wild oat seeds were continued. Germination of seeds of *A. fatua* vars. buried in soil to depths of 6 in. in pots continued even after the seeds have been at that depth for a year. Eventually it is hoped that information will be obtained about the viability of seeds kept in soil at greater depths, from which no seedlings have yet reached the surface. Preliminary investigations of dormancy in

A. ludoviciana were made using glass germinators. Dr. Mann again sent samples and provided information about Wild Oats at Woburn.

An attempt was made to reduce the amount of viable seed produced by *A. ludoviciana* growing among wheat in the field by dusting the green ears with urethane (isopropylphenylcarbamate) mixed with kaolin, supplied by I.C.I. Although some sterility of Wild Oats was caused by the highest rate of application on the earliest date the method does not seem promising owing to the even greater sterility caused in wheat ears on which the powder fell.

Following an enquiry from the Isle of Man as to the best way of controlling annual nettle (*Urtica urens*), soil samples were sent from the infested area in order that an intensive study might be made regarding its habits of germination, with a view to being able to recommend suitable methods of control. Periodic records of the germination from both top and lower spit samples have been made and will be continued for several years. For comparison, similar records are being kept from soil samples obtained from a field known to be infested with the same species of Urtica at the Woburn Experimental Station. Both these soils are of a light sandy nature, and contain weed species, as well as *Urtica urens*, that do not occur in the heavy clay loam on Broadbalk, and these results will afford useful complementary information to that obtained at Rothamsted, quite apart from the Urtica question.

C.

In addition to the above main lines of enquiry work has been continued on the botanical composition of the herbage on Park Grass and High Field, and also other physiological work is in progress which has not yet reached the stage at which it can be reported.

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SECTION OF CROP PHYSIOLOGY

By D. J. Watson

As in previous years the Section was responsible for the general supervision of the field experiments from the laboratory side. An account of the programme of field experiments is given in a separate report.

The effect of yellows and mosaic virus diseases on the growth of sugar-beet

The Section has cooperated with the Plant Pathology department in designing field experiments, carried out over several years, to measure the loss of yield of sugar beet caused by infection with yellows virus. An account of the results has been published (43).

In 1945 an investigation of the changes in growth induced by infection with yellows virus was begun to determine the physiological causes of the large reduction in the yield of sugar. A field experiment was set up to test the effect of infection at the end of June or in early August of plants sown in mid-April or late in May. In 1946 a comparison was made in another field experiment between the effects of yellows and mosaic infection at two levels of nitrogen supply. On the plots to be infected with yellows infected aphides were placed on each plant, left for about 24 hours and then killed by nicotine fumigation. On the mosaic plots each plant was infected by rubbing one leaf with infected sap. In both years over 2,000 plants were infected in this way. A few plants on the healthy control plots became infected by spread from the infected plots or from outside sources, but the number of accidental infections was too small to affect the results seriously. A sample of about 30 plants was taken from each plot at intervals throughout the period of growth for the determination of fresh and dry weights of lamina, petiole (including the crown) and root, leaf area per plant, leaf number per plant, and the fraction of the total leaf area showing yellowing. The nitrogen content of the different parts of the plant, the sugar content of the root, and, in 1946, the carbohydrate content of the leaf lamina was determined.

In both years yellows infection at the end of June reduced the yield of sugar by nearly 50 per cent., as in the earlier experiments (43). Mosaic infection caused a smaller loss, about 14 per cent. of the yield of healthy plants. The later infection with yellows, in August, 1945, had very little effect. The loss of sugar yield caused by yellows resulted from three distinct effects on growth. The total leaf area of the plant and net assimilation rate were both reduced, and this decreased total dry matter production and hence the yield of roots. The percentage of sugar in the dry matter of the root was also depressed. Mosaic reduced leaf area and net assimilation rate, but did not change the sugar content of the root. Neither disease had any appreciable effect on leaf number; the effects on total leaf area per plant were attributable to a reduction in the size of individual leaves. With both yellows and mosaic the effects on total leaf area were relatively greater than those on net assimilation rate; loss of dry matter yield was mainly the result of the stunting of the leaves. Yellows caused a greater reduction in net assimilation rate in 1946 than in 1945; in 1945 the reduction was less, and in 1946 more, than could be accounted for on the assumption that the yellowed areas of the leaves were incapable of photosynthesis. The difference between the two years may be related to weather conditions; there was more rain and less sunshine in 1946 than in 1945.

The total carbohydrate content (sugars and starch) per cent. of dry matter of the leaf laminae infected with yellows was more than double that of healthy leaves, and the increase was mainly in reducing sugars. It was known previously that starch accumulates in leaves infected with yellows to a greater extent than in healthy leaves, and it was assumed that this was caused by restriction of the translocation of carbohydrate from the leaves. This was shown not to be true, for the loss of carbohydrate between sunset and sunrise was at least as great in infected as in healthy leaves. Infection with mosaic had no effect on the carbohydrate content of the leaf.

The two viruses also differed in their effects on nitrogen content; yellows reduced the nitrogen content of the leaf lamina, while mosaic increased it; yellows increased the nitrogen content of the petiole and root, but mosaic had no effect. Both viruses reduced the total nitrogen uptake.

Physiology of leaf growth

A. G. Morton was appointed in November, 1945, to continue the study of leaf growth, which was interrupted by the departure of R. S. de Ropp. Two papers (44, 45) were published on the results of de Ropp's work on the growth of leaves on excised stem-tips of rye in sterile culture.

Experiments were made to determine whether the effects of varying nutrient supply on leaf size are brought about by changes operating during the stage of cell-division, or later in the stage of cell-extension. A rapid method of estimating the total number of cells in a leaf by microscopic examination was worked out. Material was obtained from sugar beet, grown in pot-culture with varying supply of nitrogen, sodium chloride and water, and from field experiments on several crops, including the Classical experiments where the differences in leaf-size induced by varying nutrition are very large.

The examination of the results has not yet been completed. In the sugar-beet experiment it was found that cell number per leaf depended on nitrogen supply, but not on the supply of sodium chloride or water. All three factors affected cell-size. This result is in agreement with many other demonstrations of the importance of nitrogen supply in controlling meristematic activity.

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DEPARTMENT OF STATISTICS

By F. Yates

During the year 1946 we have suffered from our share of immediate post-war difficulties. In particular, shortage of statisticans trained and experienced in agricultural and biological work has made it very difficult to keep abreast of our commitments. Many more of our Universities are now recognising the need for providing training in research statistics for their students. In the long run this may be expected to bear fruit in an increased supply of able recruits, but for the moment the demands of the Universities for staff have accentuated the scarcity created by increased realization of the importance of statistics in many branches of research.

The position of the Department as a central Statistical Research Centre has been clarified, and work for other stations has continued to expand. Moreover, we have been able to give greater assistance this year than during the war years to the staff of other departments at Rothamsted, and members of the Department have made good progress in writing up completed work.

Field experiments and experimental design

In spite of difficulties the Department has begun to fulfil its new function as consultant in the problems of experimental design arising in other agricultural research stations in this country. During the course of the year the volume of these enquiries has been steadily growing. In addition, the volume of enquiries from our colonial dependencies, particularly in Africa, has been increasing concurrently with the revival of experimental work in these territories. The nature of these enquiries indicates that the Department has a useful function to perform in this respect.

The output of numerical analyses of the results of field experiments at Rothamsted has continued to be high, and we have also carried out a number of analyses for other stations.

Various members of the Department have given assistance to members of other departments at Rothamsted, particularly Entomology, Plant Pathology and Microbiology in the planning and analysis of their experiments.

Dr. Yates continued to serve on the Field Experiments Committee of the Agricultural Improvement Council and on the Supervisory Committee of the Grassland Improvement Station.

Four papers on experimental design have been published in the course of the year. Arising out of work at Rothamsted Mr. Finney completed his description of fractional replication (49). Mr. Kempthorne has given an account of the design and analysis of lattice squares with split plots, a type of design which has proved very useful in investigating the responses to the standard plant nutrients (N, P, K) in conjunction with different organic fertilisers (50). He also developed a simple method of generating complicated designs involving confounding and fractional replication (51). In the course of this work he carried out a further investigation on a point that has often troubled those concerned with modern experimental design, namely that if in a confounded experiment the responses to one of the factors varies from block to block (i.e. interacts with blocks), this will appear in the analysis as a spurious interaction between other factors. Using the results of the fertiliser trials on sugar beet conducted during the war years he confirmed the previous conclusion (based on much less extensive data) that there is no evidence that such interactions are of any importance in practice (52).

Animal experiments

In cooperation with the National Institute for Research in Dairying and the Rowett Research Institute a start has been made on the investigations of problems of design and analysis arising in experiments on animal nutrition and animal husbandry. The development of the technique of experiments on animals has lagged behind that on crops and it is hoped that during the next few years Rothamsted may be in a position actively to continue this work.

Sampling surveys and other sampling problems

Research on statistical problems arising in sampling surveys has been continued during the year. The review of recent developments in sampling and sampling surveys, read before the Royal Statistical Society in January, 1946 (as noted in the 1939–45 report), was well received and has provoked considerable discussion in the course of the year. Some research on systematic sampling has now almost been completed. Progress on the book on sampling surveys has unfortunately been held up by pressure of other work.

A short investigation by Mr. Anscombe and Mr. Quenouille was carried out on the problem of drawing balanced samples. Dr. Yates gave a course of lectures in the Michaelmas term, 1946, at the London School of Economics on "Survey Techniques and Problems". Investigations into the sampling errors of various types of sampling for botanical composition of herbage, etc., have been carried out by Dr. Boyd for Dr. William Davies of the Grassland Improvement Station and for Dr. Iorwerth Jones of the Welsh Plant Breeding Station.

Survey of fertiliser practice

During 1945–6 a survey of Fertiliser Practice was continued in the following provinces: Aberystwyth, Harper Adams, Midlands, Newcastle, Seale Hayne and Wye. Duplicated reports have been issued for the following counties: Cumberland, Gloucestershire, Huntingdonshire, Merioneth, Shropshire, Somerset.

The analysis of the surveys of the following counties was also completed: Durham, Holland division of Lincolnshire, Isle of Ely, Lindsey division of Lincolnshire, Northumberland, South Essex, Warwickshire, Westmorland, West Riding.

Publication of all the reports issued since the inception of the survey is under discussion.

Assessment of yields of grazed pastures by grass cutting techniques and other grassland problems

The work begun in 1945 on the evaluation of the yield of pasture by grazing and by grass-cutting in conjunction with the

Chemistry Department and with the Grassland Improvement Station was continued at Rothamsted in 1946; grass-cutting was also undertaken at one of the R.A.S.E.'s grazing trials at Old Warden, Bedfordshire. The statistical analysis of these experiments and of three others carried out in the Northern, East Midland and Welsh Provinces has been carried out by Dr. Boyd and a duplicated report has been issued.

Mr. A. E. Jones carried out an investigation into the difficulties involved in estimating errors from the live-weight increase of grazing animals. This, however, has still to be reported.

National farm survey

Mr. Kempthorne and Dr. Boyd used the data obtained during the survey to investigate the relationship between the rental value and stock-carrying capacity of land (59). A similar investigation on the labour requirements of farms is in preparation. Maps showing the average rent per acre for every parish in England and Wales have been prepared and form a valuable field for further research. They are of particular interest to the Soil Survey Department.

Mr. Kempthorne has published an account of the methods of analysis by the use of punch-cards which was developed in connection with the analysis of the National Farm Survey (54).

Resazurin research scheme

This work has made excellent progress during 1946 under the supervision of Mr. Kempthorne, assisted by Mr. Quenouille. The original enquiries have been extended to cover investigations on the alcohol precipitation and clot-on-boiling tests which appear for a number of purposes to be better than the Resazurin test; and on the temperature compensation of keeping quality tests in general. Two papers were prepared by Mr. Kempthorne before he left, which it is intended to publish shortly. A further general report on the progress of the scheme has been prepared. It is hoped that a comprehensive report on the whole of the conclusions will be published in the fairly near future when certain further investigations have been completed. The Department will continue to co-operate with the National Agricultural Advisory Service and with the National Institute for Research in Dairying in the supervision of the statistical aspects of the scheme.

Advisory entomologists conference

Mr. Anscombe has acted as statistical advisor to the Advisory Entomologists, and in particular has been concerned with two matters:—

(1) A uniform procedure for estimating potato eelworm cyst populations has been evolved, so that results of sampling carried out in different parts of the country will be comparable and the stage is set for a national survey if that should be required at any time.

(2) A scheme of observation of certain pest insects at stated times of year (the "calendar insects") has been launched, with the object of recording the fluctuation from year to

https://doi.org/10.23637/ERADOC-1-88

year in insect population and in damage done to susceptible crops, and seeing what correlation exists between them. The first year's observations (1946) have provided not only interesting information about the distribution and intensity of infestations but also useful experience of possible methods of sampling. A revised programme of observations for 1947 has been prepared.

Arising from meetings with the Advisory Entomologists there has been some direct advisory work with individuals, in particular regarding the sampling of swede seed crops for insect damage (Wye Agricultural College).

An investigation into methods of fitting negative binomial distributions to insect counts is in progress.

Institute of agricultural parasitology

Extensive trials are to be made of the new insecticide DD against potato eelworm and the Institute of Agricultural Parasitology has been in touch with Mr. Quenouille and Mr. Anscombe on the design and analysis of these trials. A preliminary experiment was conducted at Gamlingay in 1946, in order to gain experience of field and laboratory techniques, in particular of eelworm sampling techniques. The results are being analysed.

Other work

Dr. Yates has continued to serve on the Scientific Advisory Committee of the Ministry of Works. He gave a paper to the Agricultural Educational Association on the place of statistics in agricultural research (61), and prepared a short paper for "Contact" (62).

Mr. Finney published a paper based on work at Rothamsted on the analysis of factorial series of insecticide tests (53).

Mr. Kempthorne spent two months in Greece as part of an international team of observers on the conduct of the elections. A general report on the statistical aspects of this work has subsequently been prepared (60).

Dr. Boyd completed an investigation on the results of experiments on the manuring of beans and peas. The results of all available fertiliser experiments on these crops were summarised and reported (57). The paper also includes an account of the current manurial practice for these crops as shown by the survey of fertiliser practice. A more general duplicated report was prepared by Dr. Boyd and others for the Agricultural Improvement Council.

Mr. Anscombe published two papers concerned with sampling inspection (55, 56). He also delivered a lecture to the Science Masters Association entitled "Statistics in the School Science Course".

Mr. Quenouille assisted members of the physics department in the mathematical theory required for some of their experiments. He has also published a paper on the problem of random flights (48).

Mr. A. E. Jones completed his thesis on random sequences for Ph.D. at London University (47) and was subsequently awarded his degree. He also published a paper on the routine estimation of dispersion from large samples (46).

Dr. Cashen revised her report on the influence of rainfall on the yield and composition of permanent grass at Rothamsted in a form suitable for publication (58).

In addition to supervising numerical analyses of the field experiments Mr. Weil carried out field work in connection with the factory sugar beet and other outside centre experiments.

Staff

Mr. A. E. Jones left in October, 1946, to take up a lectureship at Imperial College. Mr. E. G. Davy joined the staff in April, 1946, from the Royal Air Force, and left in November, 1946, to take up an appointment as Assistant Director at the Observatory, Mauritius. Mr. O. Kempthorne left in December, 1946, to take up an appointment as Research Associate Professor at the Statistical Laboratory, Iowa State College, Ames, Iowa. Mr. M. H. Quenouille was granted leave of absence for a year's research at Cambridge in the academic year 1946–7 and has recently been appointed Lecturer in Statistics at Aberdeen University. Mr. R. T. Eddison, Mr. B. M. Church, Miss Pamela Clarke and Mr. P. Robinson were appointed to the staff at the end of 1946 but did not take up their appointments until 1947. Mr. Robinson is holding a temporary appointment and is returning to Cambridge to read for the Diploma in Mathematical Statistics.

Mr. D. R. Read spent three months from May to August, 1946, in the Department. He was then seconded as Assistant Statistician to the National Institute of Poultry Husbandry, Harper Adams Agricultural College.

Mr. J. Weil has been transferred to the Field Experiments Section where he is primarily concerned with the supervision of field trials.

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DEPARTMENT OF PLANT PATHOLOGY

By F. C. Bawden

Mr. L. Broadbent was given a grant by the A.R.C. for work on potato aphides and replaced Mr. J. P. Doncaster, who returned to the British Museum in January, 1946. Mrs. J. Bradley resigned her post as assistant to Mrs. Watson and was replaced by Miss B. M. Hamlyn in November, 1945. Dr. A. Kleczkowski, who has worked in the Department with a Beit Memorial Fellowship and other awards since 1940, was appointed to the staff in January, 1946. In June, 1946, Mr. J. Blencowe was awarded a research grant by the Sugar Beet Research and Education Committee to work with Mrs. Watson on sugar beet yellows. Mr. I. Macfarlane, Mr. R. P. Chaudhuri and Dr. K. S. Bhargava joined the Department as voluntary workers. During the course of the year the Department has had many visitors, from all parts of the world, who have stayed for periods ranging from one day to six weeks.

In November, 1945, Mr. Bawden visited Spain at the invitation of the Higher Council for Scientific Investigations and gave a course of lectures on virus diseases in Madrid. Mr. Bawden also gave the Cantor Lectures of the Royal Society of Arts. At the invitation of the Directie van de Zuiderzee Polders, Mr. Garrett visited Holland in July, 1946. Miss Glynne also visited Holland in connection with her work on eyespot of wheat and Mrs. Watson visited Holland and Belgium on behalf of the Sugar Beet Research and Education Committee. At the request of the Irish Sugar Corporation Mrs. Watson also visited Eire.

Virus diseases

1. *Laboratory work*

Considerable attention was again given to the various treatments that liberate viruses from infected leaves, and it was found that tobacco plants suffering from mosaic contain much more virus than was previously suspected. This virus sometimes amounts to one-third of the total insoluble nitrogen of the leaf, and accounts for as much as 10 per cent. of the dry matter. Less than a third of the total virus is obtained in the sap (68).

Electron micrographs of preparations of tobacco mosaic virus fractionated by differential ultra-centrifugation revealed particles of different sizes and lengths. The most slowly sedimenting fractions were mainly composed of small, almost spherical particles, but these particles readily aggregated to produce rods of various lengths (74).

The joint work with Mr. L. V. Chilton of Messrs. Ilford, directed to producing more suitable emulsions for the electron microscope, has continued. Attention has this year been directed chiefly towards emulsions desensitized to light, more concentrated and more highly conducting emulsions.

Potato virus X was also obtained from leaf residues by fine grinding and incubation with snail enzymes, but not by trypsin which destroyed the virus in the residues. As with tobacco mosaic virus, potato virus X preparations obtained by grinding leaf residues have different properties from those of preparations made in other ways, probably because they contain a greater proportion of small particles. These particles can be aggregated into long rods by suitable treatments. New strains of virus X have been found which reach higher concentrations in infected sap than those previously used. Yields of 2 g. per litre of sap have been obtained with some of these. The manner in which this virus inactivates and breaks down with various treatments has been studied.

A study was made of substances that reversibly inhibit the infectivity of tobacco mosaic virus. Most of these are substances charged oppositely from the virus and combine with it, often to produce a visible precipitate. The enzyme ribonuclease inhibited infectivity of the virus much more strongly than did other tested proteins which combined with it (78).

2. *Glasshouse work*

Considerable attention has been given to the conditions that affect the susceptibility of plants to infection with viruses. Light intensity was the most important of the variables tested. Reducing illumination in summer to one-third increased susceptibility to tobacco necrosis, tomato bushy stunt, tobacco mosaic and tomato aucuba mosaic viruses by more than five times. Reducing the light intensity also increased the virus content of sap from infected leaves (69).

Fertilisers also influenced susceptibility of plants to infection and the concentration of virus attained in infected plants. Increases of both nitrogen and phosphate reduced the number of local lesions produced by tobacco mosaic virus on *Nicotiana glutinosa* and by aucuba mosaic virus on tobacco. Potash had no significant effect. Phosphate significantly increased the virus content of infected plants, whereas nitrogen gave only a slight increase, and that only in the presence of sufficient phosphate. Virus preparations made from plants given widely different fertilisers did not differ from one another in their infectivities.

Several strains of potato virus Y have been differentiated by their reactions on a range of commercial potato varieties. These vary in the symptoms caused on Majestic from a severe leaf drop streak to a faint mottle. All these forms were transmitted by a number of different aphides, but no vector has been found for the aberrant strain, potato virus C, which causes top-necrosis in Majestic.

Different strains of potato virus X spread at different rates in the field, but even the most rapidly spreading strains infected only 10 per cent. of the healthy potato plants in contact with infected ones. Spread occurs much more rapidly between infected and healthy tomatoes, and in this plant root contact is as effective as foliage contact in spreading virus X (79).

A tobacco necrosis virus was isolated from the leaves and flowers of a naturally-infected *Primula obconica*, which showed no symptoms and in which the virus seemed to occur only in isolated areas. Tobacco necrosis viruses enter and multiply locally in primulas without producing symptoms; movement from the inoculated regions occurs only rarely and fails to give a full systemic infection (67).

The properties of dandelion yellow mosaic virus which causes a severe necrotic disease of lettuce were studied. It is transmitted by the aphides *Myzus ornatus*, *M. ascalonicus* and *Aulacorthum solani*, whereas lettuce mosaic virus is not transmitted by any of these vectors, but by *Myzus persicae* (77).

A yellowing disease has been found associated with a new variety of sugar beet in Ireland. All stocks of the variety were affected, and as the condition appears to be spreading to other varieties it may be a virus disease, possibly related to virus yellows, but this awaits confirmation.

Most of the diseased turnips and swedes examined during the year proved to be infected with cauliflower mosaic virus; the symptoms caused by this vary greatly with fertiliser treatment, and can be completely inhibited by potash deficiency. Both cauliflower mosaic and cabbage black ring-spot viruses (Turnip Virus 1) were shown to be non-persistent viruses.

Common pea mosaic virus was also shown to be a non-persistent virus. Of the three aphides, *Myzus persicae*, *Macrosiphum pisi* and *Aphis fabae*, *M. persicae* proved to be the most effective and *M. pisi* the least effective vector. For enation pea mosaic virus, on the other hand, *M. pisi* proved the best vector.

3. *Field work*

In cooperation with the Crop Physiology Section an experiment was made to determine the effect of infection with sugar beet yellows and mosaic viruses on growth and yield of beet. With the Insecticides Department experiments were made to test the effect of various insecticides, including D.D.T. and Gammexane, on spread of beet yellows virus from infected seed plants. An experiment was also arranged for the British Sugar Corporation to provide material for testing the effect of yellows on sugar content and "Noxious Nitrogen" of the beet.

In cooperation with Advisory Mycologists and others experiments with potato crops on the effect of date of planting and date of lifting, and on the effect of roguing on the spread of rugose mosaic (potato virus Y) and leaf roll, have been continued in Herts., Lincs., and Derby. Results of these experiments will be available in 1947. In 1945 the spread of rugose mosaic was smaller than usual. Leaf roll also increased less than usual in the Southern counties, but more than usual in Northern counties. Most of the transmission of rugose mosaic, and approximately half that of leaf roll, had occurred by the beginning of August. At Rothamsted roguing secondarily diseased plants in mid-July did not substantially reduce the spread of either rugose mosaic or leaf roll. In 1946 the survival of volunteer potatoes from the previous year's crop was of the usual order of from one thousand to four thousand per acre, but only few volunteers survived on the Rothamsted and Woburn Experimental Farms.

A survey of aphides overwintering on field and garden Brassicae, in glass and chitting houses, and on *Prunus* spp. was made during the early months of the year in Beds., Derby., Herts. and Lincs. The relatively mild winter and warm spring enabled the aphides to overwinter and achieve large populations on their winter hosts in many districts. A new site for the overwintering of aphides in this country was discovered, large numbers of the insects being found in mangold and swede clamps. During the autumn counts of aphides were made on mangold and swede crops in Derbys., Herts. and Lincs. Aphis counts were made on potatoes at Rothamsted, in Notts., Lincs., and Derby. Counts were also made by advisory entomologists and other cooperators at nine additional centres. Eighteen adhesive aphis traps were operated in connection with these experiments. Aphis populations of potatoes in the south of England were very small throughout the season; in Derby. and Lincs. they were below those of the previous year, but were still considerably higher than in the south. Trap catches were very small compared with past years.

Mycology

Violet root rot (Helicobasidium purpureum)

A laboratory study of factors affecting the production and growth of the mycelial strands of *H. purpureum* was completed during the year. Progressive infection and rotting of the potato tubers used in this study was obtained only when the tubers were attached to the parent plant and still growing; harvested tubers buried in glass jars of soil could be used, however, for measuring the production and epiphytic growth of mycelial strands in the laboratory. Production and growth of strands increased with concentration of nutrients in meat-malt agar, and especially with that of the malt constituent. Soil acidity depressed strand growth at medium and low but not at high soil moisture content, and not in the soil sand mixture (85).

A technique has been devised for investigating the survival in soil of the sclerotia of *H. purpureum*. Sclerotia are produced on agar plates and buried in glass jars of soil kept in the laboratory, and samples are tested at intervals for viability on carrot seedlings raised in the glasshouse. A new mycological tool, the multiple-point inoculating needle, was devised for this work (86). Preliminary results have indicated that longevity of sclerotia decreased with increase in nutrient concentration of the substrate on which they were formed, and especially with increase of nitrogen.

Clubroot (Plasmodiophora brassicae) of crucifers

A study of resting spore survival in *P. brassicae* by means of the infected root hair count method has indicated that, under suitable soil conditions of light texture, moderate acidity (pH 6·0) and high moisture content (80 per cent. of saturation), some 90 per cent. of the resting spores may germinate spontaneously in the first few weeks, or even days, after their incorporation with fallow soil, in spite of the absence of host plant roots. A proportion of the spores, however, do not germinate spontaneously in fallow soil, and so serve to perpetuate the organism. Experiments with dormancy-breaking stimulants are in progress.

Eyespot (Cercosporella herpotrichoides) of cereals

Regional surveys in E. Anglia and Northants showed increasing trouble from eyespot resulting from intensive cereal cultivation.

The yield of wheat grown in pots and infected by *Cercosporella* *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 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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