

STUDIES OF THE SPREAD, SURVIVAL AND CONTROL OF TAKE-ALL AND
OTHER FOOT AND ROOT DISEASES OF WHEAT AND BARLEY

by

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ABSTRACT

In field experiments the autonomous spread of Gaeumannomyces graminis var. tritici (G.G.T.) from discrete sources of inoculum, consisting of naturally infected stubble and roots, averaged only 10 cm. When cultivations were done in one direction after inoculation the distance of spread was two to three metres. These distances of spread did not seem to account for the development of take-all epidemics or the increase in G.G.T. population observed to occur during first wheat crops.

Another field experiment showed that following different treatment cropping (fallow, lucerne or grass-clover ley), the increase in G.G.T. populations in the first wheat crop soils and the incidence of take-all in the second wheat crop were greater after fallow or lucerne than after grass-clover ley. These differences were not associated with any difference in the survival of G.G.T. during the treatment cropping but were negatively correlated to the populations of Phialophora radicicola var. graminicola (P.R.G.) in the soil. By the third wheat crop the P.R.G. populations after grass-clover had decreased and take-all was prevalent.

The effects of other 'break crops' (clover, beans, oats or maize) and of undersowing barley with trefoil, on the yield and incidence of diseases in two following cereal crops (wheat followed by barley) were tested in three field experiments. The 'break crops' all equally controlled take-all in the wheat test crop, but the incidence of eyespot was unaffected. Undersowing with trefoil had no effect on either disease. In the barley test crop, take-all was uniformly prevalent after all previous crops, although it was decreased by the application of fertiliser nitrogen (Nitrochalk).

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A.

GENERAL INTRODUCTION

Many soil-borne diseases of cereals and particularly take-all, are greatly affected by the frequency of cereal cropping. Therefore an outline of the changes in the pattern of cereal cropping in this country during this century, and especially in the period 1950-1970, is pertinent background in this thesis.

A.1. The pattern of cereal growing in England and Wales

Since the start of this century cereals have been grown on more than half the land area in England and Wales classified as tillage. During this period the proportion of tillage sown to wheat has increased slightly and the proportion of barley has more than doubled, but the proportion of oats has fallen so dramatically that they are only locally an important cereal crop (Table A1).

Table A1

The percentage of total tillage in England and Wales in barley,

wheat and oats.

YEAR	TOTAL TILLAGE 1000, hectares	% OF TILLAGE IN		
		WHEAT	BARLEY	OATS
1900	3,649	20	19	23
1910	3,487	20	18	24
1920	3,856	20	17	24
1930	2,983	18	14	24
1940	3,291	21	15	26
1950	4,235	23	15	18
1960	3,745	22	33	12
1970	4,196	23	45	6

Source Agricultural statistics.

The increase in the total area of cereals has mainly resulted from increased specialisation and simplification of farming systems which increasingly involved the replacement of traditional crop rotations by sequences that include more wheat and barley. Information on the distribution and frequency of this increased cereal growing is suprisingly scanty. However the M.A.F.F. Farm Classification in England and Wales categorises farms according to the number of 'standard man days' devoted to livestock and crop production and since 1964 has separately listed those farms where the cropping was 'mostly cereals'. Table A2 shows the increase in the number of farms classified as 'mostly cereals' and the relative importance of these farms in relation to the total wheat and barley production.

TABLE A2

The number of farms classified as 'mostly cereals' and the proportion their wheat and barley areas are of the total wheat and barley in England and Wales.

	1964	1974
Total holdings (over 274 s.m.d.)	157,391	129,738
Number of holdings classified 'mostly cereals'	6,345	9,053
% of total wheat area on holding " "	17	28
% of total barley area on holdings " "	11	29

Source - M.A.F.F. Farm Classification in England and Wales.

However these national data do not adequately represent the intensity of cereal growing on some land because there are marked regional variations. The increase in specialised cereal growing has mostly occurred in the South and East, thus, in 1970 65% of the 'mostly cereal' holdings were in the Eastern, South Eastern or East Midlands regions of the N.A.A.S. although these regions only

contain 34% of the total holdings of England and Wales. In 1970 farms classified as 'mostly cereals' had, on average, 42% of their total area in barley and 21% in wheat. There are no full national records of the proportion of wheat and barley crops that are grown successively but combined data from the fertiliser surveys 1969-73 (M.G.Hills pers. comm.) showed that 23% of the wheat crops followed one previous cereal crop and a further 17% followed two or more cereals.

These data imply that there has been a great intensification of wheat and barley growing since 1950, particularly in some regions, and that inevitably many more farms grow runs of successive cereals sometimes of long duration.

A.2. Problems of intensive cereal growing

Intensive cereal growing, that is the frequent growing of cereals, often in succession, can lead to increased occurrence and/or severity of weed, pest and disease problems.

The introduction in the late 1940's of selective herbicides for the control of dicotyledenous weeds among cereals was one of the factors that allowed farmers to intensify their cereal growing. However, continued use of these herbicides in intensive cereal sequences resulted in a big increase in grass weeds, particularly of couch, blackgrass and wild oats. Fortunately new selective herbicides have recently been developed that give a considerable degree of control of these grass weeds although the cost is large. Thus weeds in intensive cereals can be overcome even if at present the techniques are not all that widely used.

The only pest that is clearly recognised as increasing when the proportion of successive cereals is increased is cereal cyst nematode (Heterodera avenae) which becomes a potential problem

when the ratio of cereals to other crops in the rotation is 2:1 or more (Collingwood, 1962). Although cereal cyst nematodes occur on all soil types, damage tends to be worst on the lighter soils. The occurrence of serious damage, even on lighter soils, is variable and seems to depend on a complex interaction between the nematode population, soil moisture, soil structure and plant susceptibility. The introduction of resistant varieties of oats and barley, the latter being the cereal most commonly grown on the lighter soils, has helped intensive cereal growers avoid this pest problem.

Foliar pathogens are a serious problem of cereal growing, but because many are so easily dispersed there is little evidence that intensive cereal growing increases their incidence. Lester (1969) suggests that foliar pathogens limit root growth and so become important on crops where root loss from soil-borne pathogens is also prevalent. It is also possible that splash dispersed foliar pathogens, such as Rynchosporium secalis (causing leaf blotch of barley) and Septoria nodorum (causing glume blotch of wheat), which overwinter on infected crop debris may be increased by intensive cereal growing. Although surveys of barley leaf diseases by James (1969) and Melville and Lanham (1972) showed no effect of previous cropping on the incidence of leaf blotch, more recent surveys by King (1977 a & b) report that leaf blotch and glume blotch were sometimes more prevalent on crops that followed susceptible crops.

There is much more evidence to suggest that the incidence of another splash dispersed disease, eyespot caused by Pseudocercospora herpotrichoides,^{italics} which can survive on infected debris for up to three years (Macer, 1961 a) is increased by intensive cereal cropping (Glynne 1950, Ogilvie and Thorpe 1962, Glynne 1965). Loss of yield caused by eyespot results both

through a direct effect on the host and through the indirect effect of lodging (Jorgensen 1964, Scott and Hollins 1974). The introduction of 'resistant' and stiffer strawed varieties such as Cappelle-Desprez greatly decreased the amount of lodging and to a lesser extent the number of straws infected in the presence of the pathogen. Thus Bullen (1964) considered eyespot to be a potential threat rather than a serious problem to intensive cereal growers. Since then the introduction of systemic fungicides that control eyespot (Doodson and Saunders 1969, also see Appendix I, Jenkyn and Prew 1973, Prew and McIntosh 1974) have decreased the importance of eyespot even as a potential threat.

There seems to be general agreement that take-all is the major problem of intensive cereal growing in England and Wales (Bullen 1964, Slope 1968, Lester 1969, Mundy 1969) and a survey of intensively grown wheat in the East Midlands supports this view (Rosser and Chadburn, 1968). There are no varieties resistant to this disease and loss in yield can only be avoided by soil fumigation (Ebbels 1969), which is not commercially practicable, or by including sufficient 'break crops', that is crops which are not susceptible to take-all, in the rotation to prevent the fungal population building up to damaging proportions. Thus intensively grown cereals are always liable to suffer a loss of yield from take-all, although this loss may be decreased either by increasing the amount of N fertiliser applied, especially in barley crops, or by the phenomenon of 'take-all decline' (Slope and Cox 1964, Shipton 1967). Take-all decline, the cause of which is not known, is the decreased prevalence of take-all in consecutive wheat or barley crops that commonly follows the maximum severity of take-all (peak), which is usually between the second and fifth successive crops. Although take-all is less damaging in the 'decline' phase, it is still present and still

causes loss of yield.

A.3. The scope of this thesis

Within this background of the importance of take-all, to much of the more profitable farming enterprises, a major part of this thesis was devoted to field studies of the survival and spread of Gaeumannomyces graminis var. tritici, the causal fungus of take-all. The field epidemiology of the fungus was emphasised partly, because of the limited information on this aspect and partly because the success of future control measures, that may not eliminate the fungus from the soil, could be greatly affected by the ability of the fungus to survive and spread to reinfect new hosts.

The three main experimental sections of the thesis are:-

1. Section C, comprising a field experiment aimed to show the survival of Gaeumannomyces graminis var. tritici under three cropping systems and its subsequent increase in wheat crops following each. In the later years of this experiment measurements were made of changes in populations of another fungus, Phialophora radiculicola var. graminicola Deacon (1974), an avirulent pathogen of wheat and grass roots. There is evidence (see page 29) that interactions between these fungi are important in determining the severity of take-all.

2. Section D describes field experiments done to study the spread of Gaeumannomyces graminis var. tritici from discrete sources of introduced inoculum, and also an experiment where the effect of cultivations on this spread was measured.

3. Section E describes a more general study of the effect of several 'break crops' on the yield and diseases of the subsequent wheat and barley crops, and in which an attempt was made to distinguish, and quantify the benefits of disease control by

'break crops' from the benefits of the nitrogenous residues left by some 'break crops'.

A.4. Take-all disease and its causal fungus

The literature on take-all and its causal fungus is too vast to review in detail in this thesis and would be unnecessary as there are detailed reviews by Butler (1961), Nillsen (1969) and Walker (1975). The literature relevant to the three main sections of this thesis is reviewed in the introductions to each section, and so I give only a brief outline of the fungus and the disease it causes.

Take-all of wheat and barley is a soil-borne root disease caused by the fungus Gaeumannomyces graminis (Sacc) Arx and Olivier (1952) var. tritici Walker (1972). Formerly the fungus was most commonly called Ophiobolus graminis Sacc. a familiar name that had been disputed for a long time. The new nomenclature by Walker (1972) seems now to have been generally accepted. Take-all can also occur on oats but Turner (1940) showed that this was caused by a separate strain of the fungus, Gaeumannomyces graminis var. avenae (E.M.Turner) Dennis (1960).

The fungus is a pathogenic root inhabitant of poor competitive saprophytic ability. In the absence of a live host the fungus survives in the soil as mycelium in dead tissues of plants once infected. The surviving mycelium infects new hosts when they come into contact or close proximity to this mycelium. The fungus grows onto the root surface of the new host where it produces two forms of hyphae. Firstly thin hyaline microhyphae (infection hyphae) which penetrate the epidermal cells and then grow through the cortex to the stele. Lignitubers are often formed in response to this invasion of the host cells by the fungus. Secondly thicker dark walled macrohyphae (runner hyphae) are formed which grow longitudinally

along the surface of the root, microhyphae branch from these runner hyphae to form new infections. As the fungus colonises more of the root macrohyphae also grow longitudinally within the cortex and stele. Once within the stele the fungus disrupts and blocks the cells of the vascular system leading to the appearance of dark brown/black lesions. This blockage of the vascular tissue results in the loss of nutrients and water from that part of the root below the lesion. More detailed descriptions of this infection process are given by Fellows (1928), Russell (1934) and Holden (1975).

Ascospores may in certain circumstances be another means of producing new infections, this spread of the fungus by ascospores is discussed in the introduction to Section D. The ascospores are produced in perithecia which develop in field conditions on infected roots and culm bases. Microconidia are also produced by the fungus and often budded off ascospores, but apart from the initial report of these microconidia by Mangin (1899) there is no record of their germination despite several attempts. So it must at present be assumed that these microconidia do not cause infection.

Symptoms of take-all in the field vary with the severity of the infection, the size of the host root system and with the stress placed on the root system by the plant. Exceptionally severe take-all and very adverse growing conditions can cause seedling death, but usually severe infection causes stunted plants, which prematurely senesce producing bleached ears containing little or no grain. Typically these bleached ears, which are called whiteheads, occur in patches but whiteheads can also result from causes other than take-all and so they do not reliably indicate take-all in a crop. More often take-all causes less obvious damage resulting in short plants bearing small ears which contain much small or shrivelled grain. Yield loss from this less dramatic damage can be of the order

of 5-20%. Crop damage in the presence of the fungus can be lessened by ensuring that the soil has a good structure and is not deficient in moisture and nutrients, especially nitrogen and phosphorus.

B.

GENERAL METHODS

The methods described here are those common to several experiments described in different sections of this thesis. Subsequent reference to these methods will be made by section number and the name of the method.

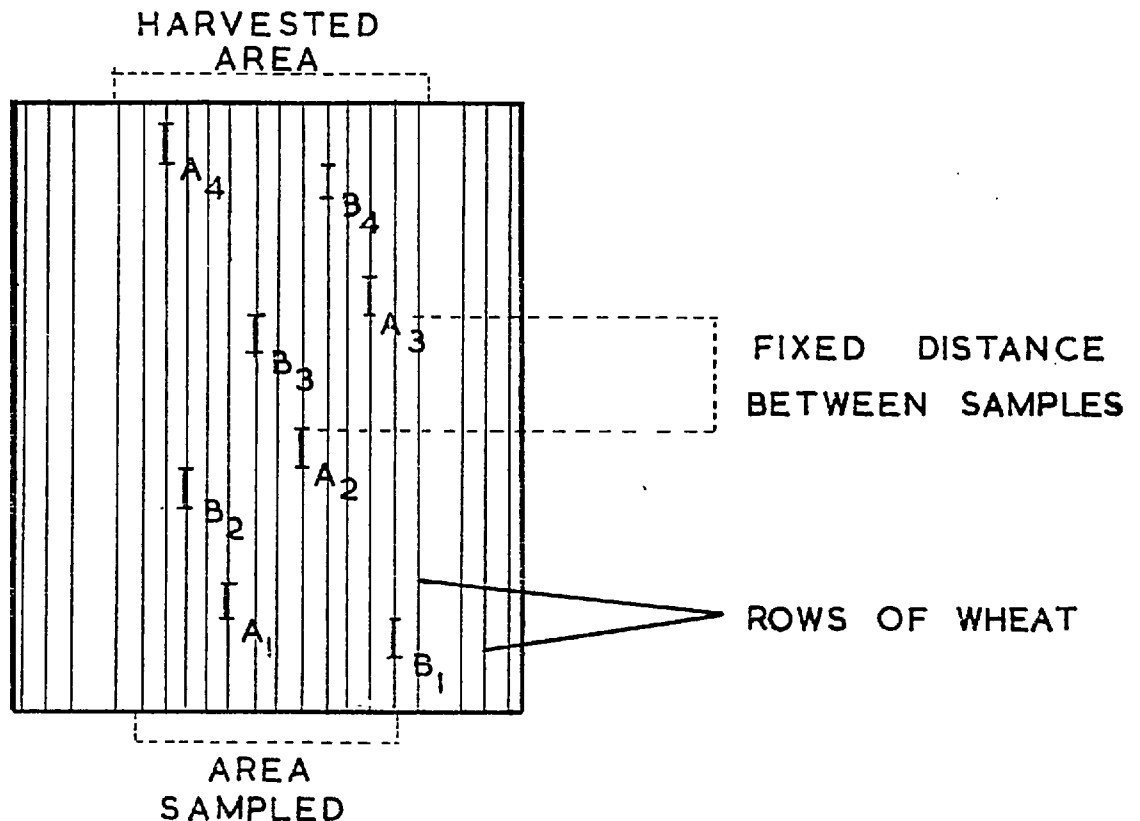
To avoid constant repetition of the cumbersome trinomials Gaumannomyces graminis var. tritici and Phialophora radicicola var. graminicola I have mostly used the abbreviations G.G.T. and P.R.G. respectively.

B.1. CROP SAMPLING AND DISEASE ASSESSMENT

'Fixed Pattern' sampling

Experimental cereal crops were sampled using a 'fixed pattern' distribution of samples (Dyke 1974). On each sampling occasion a pair of random numbers were used to predetermine the position of each set of samples on all plots. The first number of the pair determined the number of rows across the plot, the second the number of paces up the plot of the first sample. When two sets of samples were taken per plot the selection of row numbers was restricted so that one was an odd number, the other even, to ensure that the samples were taken from rows sown by different drill coulter. The maximum number for paces was the length of the plot, in paces, divided by the number of samples to be taken in each set. Similarly the fixed distance, rows across and paces up the plot, between samples in each set was determined by the plot dimensions divided by the number of samples. Fig. B1 illustrates this distribution of samples when two sets of four samples are taken per plot. The edge rows were excluded from the area sampled, though they were included in the area harvested for grain yield.

Fig. B1 Diagram showing 'Fixed Pattern' sampling taking two sets of four samples per plot.



Each sample consisted of the plants from a measured length of row, usually 30 cm, plants were dug to obtain 7-10 cm of root.

Crop samples taken in the spring when the plants were young, Growth Stage (G.S.) 3-6, (Large 1954) were washed and assessed soon after sampling. Crop samples taken in the summer G.S. 10.5 were air dried and stored for later washing and assessment. All samples were pre-soaked in water and then the soil washed from the roots with a controlled jet of water.

Assessment of take-all

To identify the dark brown/black lesions caused by G.G.T. the roots of each plant were examined under water in a white dish. The

extent of infection was assessed either by counting the number of roots with lesions on each plant or by assigning each plant to one of the following four categories:-

Clean - no visible take-all lesions

Slight - less than 25% of roots with take-all lesions

Moderate - between 25% and 75% of roots with take-all lesions

Severe - more than 75% of roots with take-all lesions

These percentages are based on root numbers, but the assessment is by visual impression and not by counting root numbers and therefore the assessment is to a small extent also influenced by the total area of infected root. An arbitrarily weighted disease rating is calculated using the formula

$$\begin{aligned} \text{Take-all rating} = & \% \text{ plants with slight} + 2(\% \text{ plants with moderate}) \\ & + 3(\% \text{ plants with severe}) \end{aligned}$$

Assessment of eyespot and sharp eyespot

These diseases were assessed only on summer samples. Wet straws were stripped of basal leaf sheaths to reveal the lesions on the lower internodes. Each straw was assigned to one of the following categories for each disease, both of which could occur on a single straw:-

Eyespot

Clean - no visible eyespot lesions

Slight - lesion less than half girdles its internode

Moderate - lesion more than half girdles its internode,
with some weakening of the lesioned area

Severe - lesion girdles the whole internode and the straw
is noticeably weakened.

Sharp eyespot

Clean - no visible sharp eyespot lesions

Slight - lesion less than threequarter girdles its internode
Severe - lesion girdles its internode or many small lesions
on the lowest three internodes.

B.2. ASSAY OF SOILS FOR G.G.T. AND P.R.G.

The amount of G.G.T. in the soil had to be assessed by host plant infection (assay) because there is no method of isolating G.G.T. directly from the soil that is suitable for quantitative assessments (Hornby, 1969). Soils were sampled to a depth of 10 or 15 cm with a hollow cylindrical 5 cm diameter soil auger and the cores treated in one of three ways.

Whole core method

The cores, 10 cm long, were inverted into 340 ml white plastic cups (Mono containers 1012) that had four 3 mm diameter drainage holes and contained a 7 mm layer of coarse sand. The surface of the core was pressed to consolidate the soil against the side of the cup. Ten untreated Cappelle-Desprez wheat seeds were sown in each core and covered with a 7 mm layer of cornish grit (3/16th Lee Moor elutriated sand).

Mixed soil method A

The cores, 15 cm long, from each plot were bulked, mixed and crumbled, with alternate air drying and rewetting as necessary for crumbling. Pots, 8 cm square at the top tapering to 6 cm square at the base and 7.5 cm deep, that already contained a 7 mm layer of coarse sand were loosely filled to the brim with soil. The soil was firmed down to 2 cm from the top, 16 untreated Cappelle-Desprez wheat seeds were sown and covered with a 7 mm layer of cornish grit.

Mixed soil method B

Cores, 15 cm long, were bulked and crumbled as in method A. 245 g portions were weighed into pots, 7 cm square at the top

tapering to 5 cm square at the base and 6 cm deep, consolidated and sown with five untreated Cappelle-Cespree wheat seeds and covered with a 5 mm layer of cornish grit.

Pots prepared by any of the above methods were placed in a controlled environment room with the following lighting and temperature regime:-

Temperature °C	10	10	15	15	15	10
Light lumens/m ²	0	40	80	120	80	40
Time h	8	2	2	8	2	2

The lights were 1.52 m warm white fluorescent tubes arranged in banks of 12 giving approximately 120 lumens/m² at plant level. The relative humidity was kept in the range 70-80%. The pots were watered when placed in the controlled environment room and subsequently after periods of six days, five days, and then every fourth day. Assays lasted for five weeks except for those prepared by mixed soil method B which lasted six weeks.

In all assays soils were prepared and sown within a few days of sampling because earlier tests had shown that G.G.T. infectivity varied inconsistently when soils were stored for several weeks at 2°C.

Assessment of G.G.T.

The roots of the seedlings were washed free of soil under a controlled jet of water and examined under water in a white dish using a x2 illuminated magnifier. The number of main seminal axes with take-all lesions were recorded; when none of the plants from a pot had lesions on the main axes but had clearly identifiable lesions on the lateral roots a count of one root infected was recorded to indicate that infection was present.

Assessment of P.R.G.

The root systems of five seedlings were spread out under water in a glass petri dish and two transects approximately 2 cm and 4 cm

from the seed were scanned across all five root systems. This scanning was done using a Wild M5 stereo microscope which gave a field of view for scanning of 8.5 mm using a magnification of x24; where necessary the magnification was increased to x100 to confirm the presence of P.R.G. which was recorded only when runner hyphae and groups of pigmented swollen cells, as described by Deacon (1973 b), were seen in association. Each set of five root systems was given a single score on the scale:-

- 0 = No P.R.G. observed
- 1 = P.R.G. present on less than 25% of roots
- 2 = P.R.G. present on between 25% and 75% of roots
- 3 = P.R.G. present on more than 75% of roots.

The P.R.G. rating for a treatment was the mean of the scores for the replicate pots of that treatment.

C. SURVIVAL OF GAEUMANNOMYCES GRAMINIS VAR. TRITICI : THROUGH DIFFERENT
CROPPING SEQUENCES AND ITS INCREASE ON SUCCESSIVE WINTER WHEAT

C.1. INTRODUCTION

An experiment to study the survival of G.G.T. under different cropping sequences and its subsequent increase on winter wheat was mainly originated because of results obtained from the Rothamsted ley arable experiments.

The Rothamsted ley arable experiments were started on two sites (Highfield and Fosters) in 1948 to study the effect of ley rotations on soil fertility. The different crop sequences that were tested are given below and more detailed information is given in 'Details of the classical and long-term experiments up to 1967 (Rothamsted 1970).

ROTHAMSTED LEY ARABLE EXPERIMENTS CROPPING SEQUENCES

3 YEARS TREATMENT CROPPING FOLLOWED BY 3 YEARS TEST CROPPING

3 YEARS GRASS LEY

3 YEARS GRASS/CLOVER LEY

WHEAT, POTATOES, BARLEY

3 YEARS LUCERNE

HAY, SUGAR BEET, OATS

On each site the experiment consisted of 12 blocks; each year of the six year rotational cycle being present on two blocks every year. In 1967 it was decided to 'phase out' eight of these blocks into continuous winter wheat as they completed their three years test cropping. On the Highfield site the first of these 'phasing out' wheat crops had more take-all after the arable sequence and much more after the lucerne sequence than after the ley sequences. These differences in the amount of take-all were repeated in subsequent years (Slope and Prew, 1972). This joint work was continued to

assess the take-all in the continuous wheat on both sites and to try and establish the cause of these differences (Slope et al. 1975). However as there was only a limited area available for sampling and only one of the sites had shown a consistent effect of cropping sequences on take-all it was decided to start a new experiment.

At the outset of this new experiment it was thought that perhaps the differences in take-all after different crop sequences were associated with the growing of leguminous crops and/or the presence of grass weeds. Leguminous crops had previously been associated with increased amounts of take-all. South African workers had reported more take-all on wheat following lucerne (Putterill, 1924 and Louw, 1957 a and 1957 b) or lupins (Van der Watt, 1965) than after other break crops. Also in France Ponchet and Coppenet (1962) had shown that much more take-all was present on a second wheat crop following red clover than following ryegrass, and suggested that ryegrass was suitable as a break crop. Wehrle and Ogilvie (1955) had previously shown that four grass species Ryegrass (Lolium spp.), Timothy (Phleum pratense), Cocksfoot (Dactylis glomerata) and Meadow fescue (Festuca pratensis) were all equally capable of decreasing take-all to a low level when grown as a break between cereal crops. Thus in spite of the reports that the grasses quoted above and many others are capable of being infected, it seems that they can act as break crops. However in the detailed review by Nillson (1969) of grass species susceptibility to infection there is some indication that the two species used in the Rothamsted ley arable experiment (Festuca pratensis and Phleum pratense) are less susceptible than some of the weed grasses. In view of the ley arable results and these reports on the effects of legumes and grasses on the survival of G.G.T. and also of the reports of Garrett (1944) that survival of G.G.T. was greater under fallow than trefoil, mustard or oats it

was decided that the new experiment should study the survival of G.G.T. under Grass clover ley, Lucerne and Fallow.

A more general review of the work done on the survival of G.G.T. showed that since Davis (1925) first reported that G.G.T. could survive through the winter in the absence of a susceptible host much work has been done studying the length of the survival period and the factors affecting it. A selection of reports of this work showing the range of conditions under which tests were done and the variation in results are given below:-

<u>REFERENCE</u>	<u>TYPE OF INOCULUM</u>	<u>TYPE OF SOIL AND PLACE OF TEST</u>	<u>SURVIVAL PERIOD RECORDED</u>
RUSSELL 1934	INOCULATED OAT HULL	UNCROPPED, STERILISED SOIL IN THE OPEN	STILL PRESENT AFTER 25 MONTHS
GARRETT 1940	INOCULATED WHEAT STRAW	UNCROPPED SOIL IN LABORATORY	NO SURVIVAL AFTER 6 MONTHS
	NATURALLY INFECTED WHEAT STRAW	UNCROPPED SOIL IN THE FIELD	STILL PRESENT AFTER 11 MONTHS
CLARK 1942	NATURALLY INFECTED WHEAT CROWNS	UNCROPPED SOIL IN GLASSHOUSE	NO SURVIVAL AFTER 3 MONTHS IF KEPT MOIST
BUTLER 1959	INOCULATED WHEAT STRAW	UNCROPPED SOIL IN LABORATORY	NO SURVIVAL AFTER 17 MONTHS
PETERSON & CHRISTENSEN 1968	INOCULATED WHEAT STRAW	UNCROPPED SOIL IN THE OPEN	STILL PRESENT AFTER 42 MONTHS
SHIPTON 1972	NATURALLY INFECTED PLANTS	FIELD CROPPED WITH NON-SUSCEPTIBLE CROPS	STILL PRESENT AFTER 66 MONTHS

The range of soil conditions that affected the survival of G.G.T. were first described by Garrett (1938). He showed that the survival of G.G.T. on inoculated wheat straws in soil was decreased in the presence of moisture, warmth, good aeration, other micro-organisms and by a scarcity of nitrogen. Fellows in 1941, using naturally infected plant material confirmed that cool dry conditions increase survival of G.G.T. Garrett (1940) also showed that nitrogen enrichment of the soil increased survival because it allowed the

fungus to utilise more of the carbohydrate reserves of the straw; confirmed by Butler (1953) and Scott (1969 a) though the latter did show that excess nitrogen could shorten the survival period by hastening the exhaustion of the substrate. Much of this work on survival has been done on artificially inoculated material, often in the glasshouse or laboratory and in the few reports where these results have been compared with naturally infected plant material or with experiments done in the field differences in the amounts of G.G.T. surviving have been recorded (Garrett 1940, Chambers and Flentje, 1968). From these differences it seemed that although artificially inoculated material was very convenient there were disadvantages in its use. Other problems relating to the use of an artificially inoculated material in a survival experiment are the choice of isolates and the positioning of a small volume of inoculum. Chambers and Flentje (1967) reported that strongly pathogenic isolates were able to survive better than weakly pathogenic types, and Scott (1969 b) showed that survival was greater above or on the soil surface than when buried. Because of these problems associated with the use of artificially inoculated materials it was decided to use naturally infected material as inoculum in the Survival Experiment reported in this section.

After the planning of this Survival Experiment, Scott (1970) reported that he commonly isolated from grassland P.R.G. and that when wheat seedlings were inoculated with this fungus infection by G.G.T. was limited. Also in 1970 Balis reported that the inoculation of inverted turves with P.R.G. and the subsequent inoculation ten weeks later with G.G.T. limited the infection of the latter. Unfortunately the assessment of P.R.G. was not begun in this Survival Experiment until Deacon (1973 a) made it clear that the naturally occurring populations of P.R.G. in grassland soil limited

the growth of G.G.T. on wheat seedlings.

C.2. MATERIALS AND METHODS

THE SURVIVAL OF TAKE-ALL EXPERIMENT 1970-1974

The experiment was done over four years at Rothamsted Experimental Station on Summerdells I field, which had been previously cropped for two years with field beans. There was some variation of soil type over the experimental site; one block (Plots 01-09) was on an area classified as a flinty clay loam (Batcome series II) and the other two blocks were on a flinty silt loam (Batcome series I). The experiment consisted of one, two, or three years of grass/clover, lucerne or fallow, known as treatment cropping, followed by three, two or one years of winter wheat, known as test cropping.

C.2.1. Treatment Cropping 1971-73.

Treatments:

The treatments, basal operations and layout of the experiment are shown in fig. C1. The seeds mixture for the grass/clover ley contained the same species as those used in the Rothamsted ley arable experiments. The amounts of fertiliser given to the two crops were also those used on the Rothamsted ley arable experiments. These amounts of fertiliser had been adjusted so that the fertiliser applied approximately balanced the nutrients taken off in the harvested crop.

The inoculum consisted of stubble, roots and soil taken on 9 September 1970 from a field (West Barnfield II) in which the wheat crop had been severely infected with take-all. The inoculum was dug from the top 5 cm of the field when the soil was very dry and then stored under cover. Garrett (1938) reported there was no loss of viability of G.G.T. in soil kept air dry during an 18 week

period. Therefore there seemed little risk of the inoculum losing viability during a four week storage period even though it was not quite air dry. On 8 October 1970 the inoculum was thoroughly mixed and weighed into 34.5 Kg lots, one of which was spread on each sub-plot to be inoculated. The inoculum applied to each sub-plot contained all the stubble from an equivalent area of West Barnfield II but obviously did not include all the roots or soil from the area. All the sub-plots were then rotavated twice to a depth of 15 cm in reciprocal directions. This reciprocal rotavation was done to minimise the displacement of the inoculum beyond the plot boundaries. This method of inoculation was designed to give a more uniform distribution than might be expected to occur naturally, while still using naturally infected material.

Assay of G.G.T. and P.R.G. in the soil.

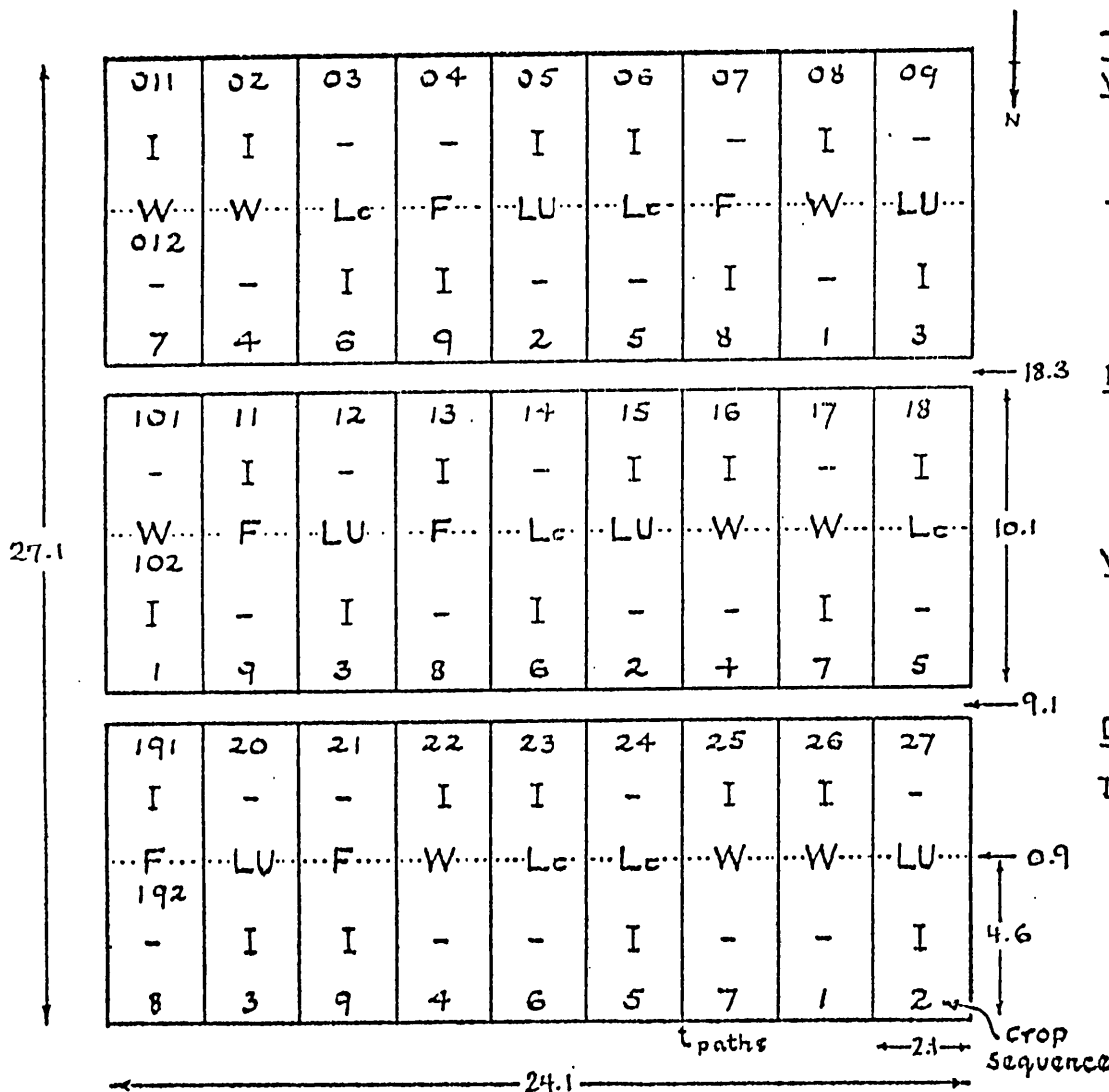
A preliminary sampling was done in January 1971 to determine if the inoculation had been successful. Three soil cores, 5 cm diam. x 10 cm deep, were taken from each inoculated sub-plot inverted into plastic cups and assayed - as described in General Methods, Section B.2. Whole core method.

The inoculated sub-plots while under treatment cropping were sampled on five occasions:-

DATE	CROP SEQUENCES SAMPLED	
JUNE 1971	1, 4, 7.	SERIES I
OCTOBER 1971	2, 5, 8.	
FEBRUARY 1972	2, 5, 8.	SERIES II
JUNE 1972	2, 5, 8.	
JUNE 1973	3, 6, 9.	SERIES III

FIG. C1. Details of the treatments, basal operation and design of Survival of Take-all Experiment.

2nd year SUMMERDELLS I 1972



TREATMENTS, per hectare

Whole Plots

1-9 Crop sequences - See table below

Half Plots Infected in October 1970 only

- No inoculum

I Inoculum, Take-all infected stubble rotavated in.

Basal manuring per hectare

To LU 810 kg } compound fertiliser in winter
 Lc 540 kg } (10:14:28) in winter
 W 270 kg } combine drilled
 W 605 kg } 'Nitro-Chalk' 21 in Spring
 * 125 kg muriate of potash for each cut.

Varieties: W Winter Wheat Cappella - desprez

LU Europe Sown at 22 kg

Lc 11 kg S 48 Timothy } Mixture sown
 22 kg S 215 Meadow fescue } at 37 kg
 3 kg N.Z. White clover } 7 April 1971

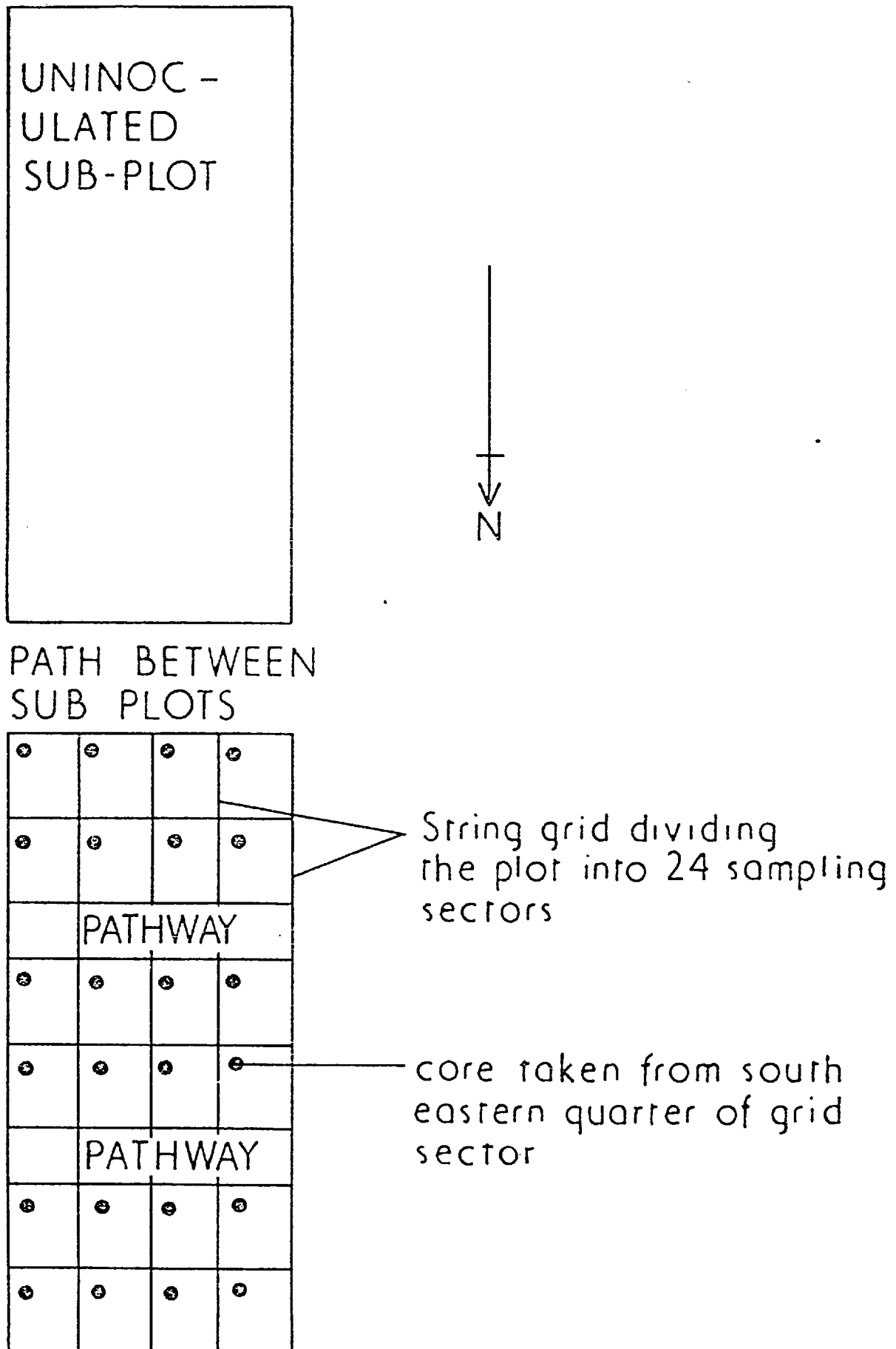
Design: 3 blocks of 9 plots split into 2

Dimensions in metres

Seq	1971	1972	1973	1974
1	LU	W	W	W
2	LU	LU	W	W
3	LU	LU	LU	W
4	Lc	W	W	W
5	Lc	Lc	W	W
6	Lc	Lc	Lc	W
7	F	W	W	W
8	F	F	W	W
9	F	F	F	W

LU Lucerne
 Lc Clover/grass ley
 F Fallow
 W Winter Wheat

FIG. C2. Diagram showing the pattern of soil sampling used in
Survival of Take-all Experiment.



The details of crop sequences are given in fig. C1; the sequences with one years treatment cropping are designated Series I, those with two years treatment cropping Series II and those with three years treatment cropping Series III. On each sampling date 24 cores, 5 cm diam x 10 cm deep, were taken from each sub-plot sampled. The pattern of sampling is shown in fig. C2. The two pathways were cropped but used as walkways, so that the sampling areas could remain untrampled. At each sampling the cores were taken from the same quarter of each grid sector on all plots. The quarter sampled was chosen randomly except that any quarter was not sampled on more than one occasion. The 24 soil cores from each sub-plot were mixed, put into 40 pots and assayed as described in General Methods, Section B.2. Mixed soil method B.

In May 1973 the uninoculated sub-plots of Series III were sampled, 24 cores were taken from each sub-plot on the grid system. The cores were inverted into plastic cups and assayed for G.G.T. as described in General Methods, Section B.2. Whole core method. This assessment of the uninoculated crops for the presence of 'background' inoculum could not be done at the same time as the Series III inoculated plots because of limited space in the controlled environment room.

In June 1973 the seedlings from the assay for G.G.T. were also assessed for the presence of P.R.G.

Production of perithecia on assay seedling roots

An attempt to confirm the diagnosis of G.G.T. was made using a perithecial test similar to the one used by Hornby (1969). After diagnosis for G.G.T. the roots of the assay seedlings from each pot were cut off and put in the bottom of test tubes, 1.5 cm diam x 15 cm deep. The roots were kept moist so that they started rotting and

were kept in the same controlled environment room as used for the assay. After six weeks they were removed and examined under a binocular dissecting microscope for the presence or absence of G.G.T. perithecia.

C.2.2. Wheat Test Cropping 1972-74.

Treatments:

Winter wheat was sown after one, two or three years of treatment cropping. The layout of plots and basal treatments are shown in fig. C1.

As recorded in Section D.2.2. (page 71), the whole of Summerdells I was given 7.5 t of chalk /ha by mistake in September 1972.

Assessment of take-all and P.R.G. on the crop.

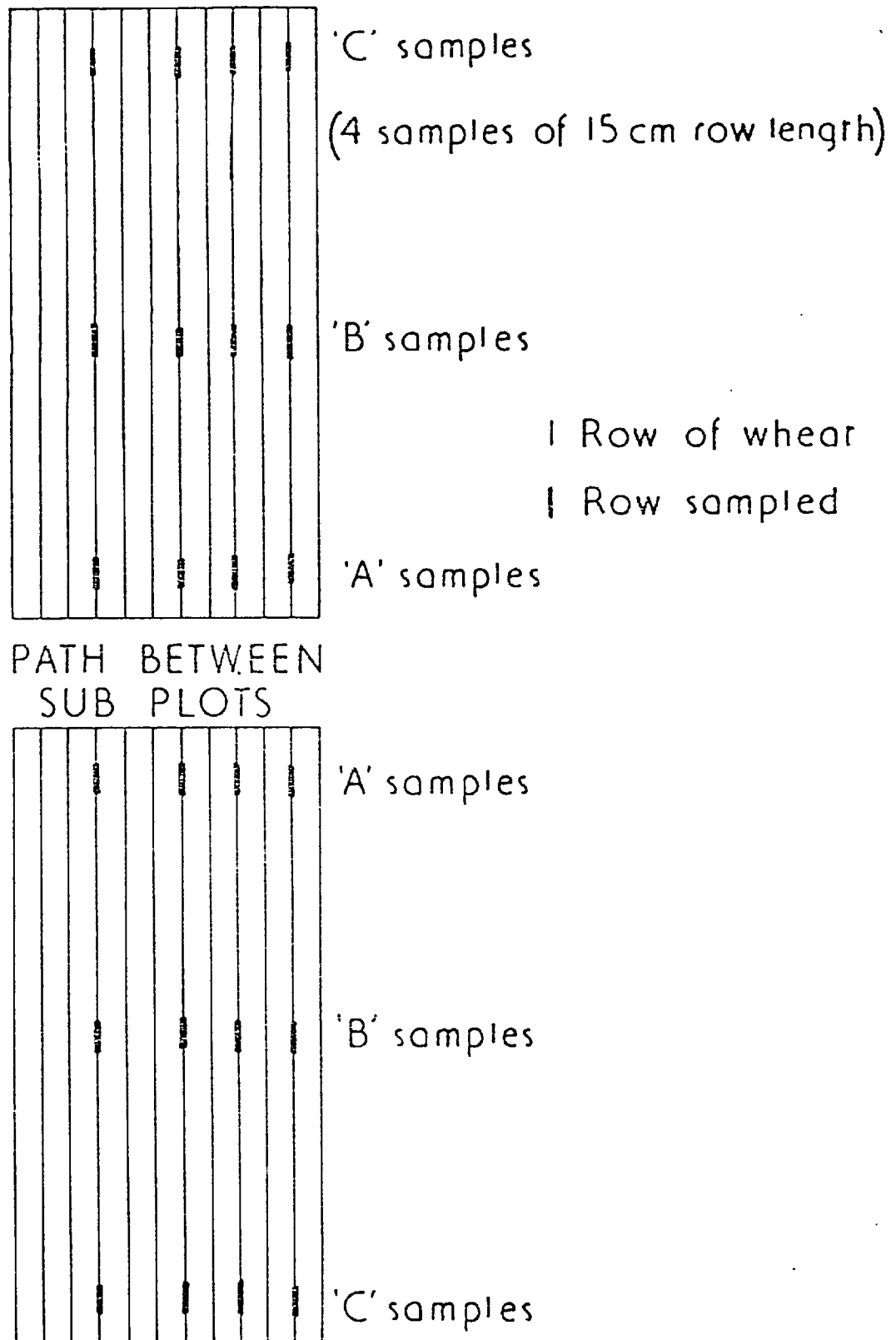
All the winter wheat crops were sampled each spring and summer on the dates given below:-

CROP SEQUENCES	SPRING	SUMMER
1, 4, 7.	27 April 1972	29 June 1972
1, 4, 7, 2, 5, 8.	28 March 1973	4 July 1973
All sequences	26 March 1974	8 July 1974

On each date 12 samples of 15 cm row length were taken per sub-plot, in spring 1972 as two sets of six 'fixed pattern' samples and thereafter as three sets of four samples as shown in fig. C3. This latter method of sampling was chosen so that samples came from three known distances from the centre path of the plot. It was hoped that any significant spread from the inoculated to uninoculated sub-plot that might occur could be detected in differences in take-all on these three samples.

In spring the number of plants and roots infected with G.G.T.

FIG. C3. Diagram showing the pattern of crop sampling used in
Survival of Take-all Experiment.



The rows sampled were randomly chosen for each sampling date but were the same for every sub-plot within each sampling date

was recorded on all occasions and the total number of seminal and crown roots were counted on a sub sample of ten plants/sub-plot on first wheat crops only. Summer samples were examined and take-all recorded as slight, moderate or severe as described in General Methods B.1.

P.R.G. was also assessed in Spring 1974 on a sub sample of 15 plants/sub-plot of the first wheat crops, as described in General Methods except that the whole root system was scanned.

Assay of G.G.T. and P.R.G. in the soil.

The assay for G.G.T. was used to determine whether differences between treatments, particularly in and immediately after the first wheat crops, could be detected when no differences on the crop were observed.

The soils carrying first wheat crops were sampled and assayed each spring and each autumn after ploughing, except those on series I (1972). The dates of sampling, number of cores taken, and assessments done are given below:-

DATE	CROP SEQUENCES SAMPLED	CORES/SUB-PLOT ASSAYED FOR G.G.T.	CORES/SUB-PLOT ALSO ASSESSED FOR P.R.G.
16 Oct. 1972	1, 4, 7	24	-
28 Feb. 1973	2, 5, 8	24	-
2 Oct. 1973	2, 5, 8	24	10
	1, 4, 7	12	10
5 April 1974	3, 6, 9	24	10
10 Sept. 1974*	3, 6, 9	12	-
28 Oct. 1974	ALL SEQUENCES	12	12

* Sampled before ploughing

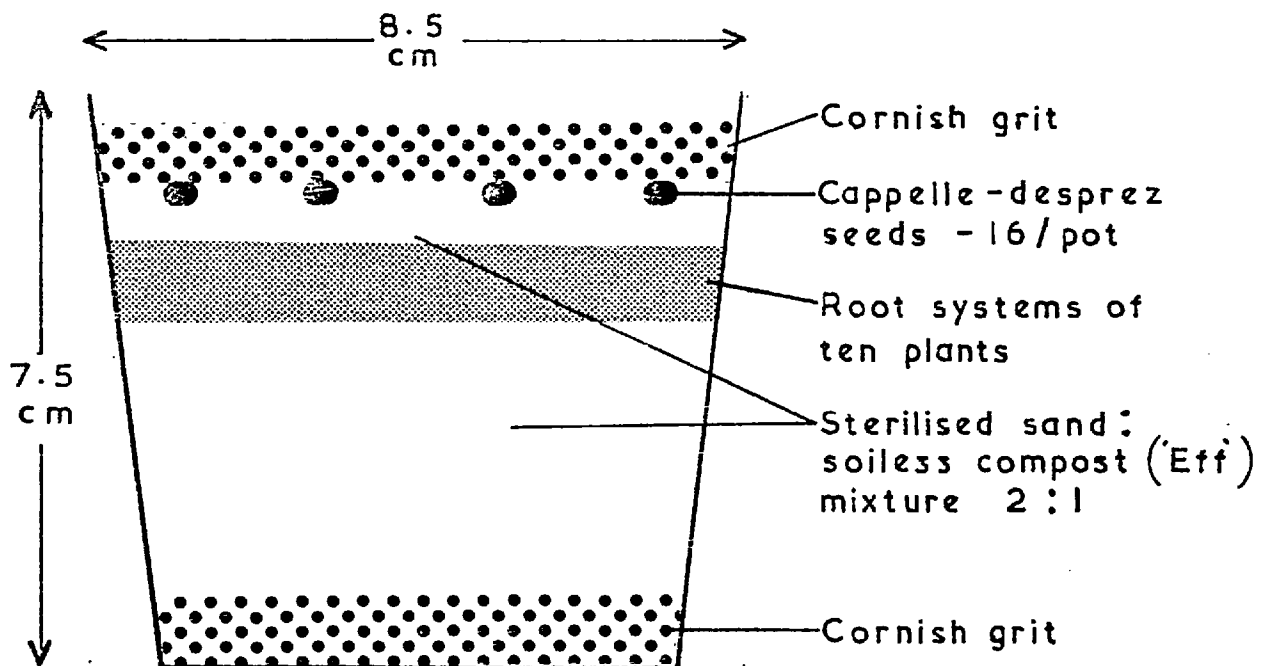
The cores, (5 cm diam x 10 cm deep), were inverted into plastic cups and assayed for G.G.T. as described in General Methods, Section B.2.

Whole core method.

P.R.G. on the seedling roots was also assessed as described in General Methods, Section B.2.

Assay of root systems diagnosed as clean.

The root systems of plants from the 1974 spring and summer first wheat samples (Series III) that had been diagnosed as not having take-all lesions were assayed to see if G.G.T. could be detected. The root systems of ten plants, diagnosed as clean from take-all, were taken from both A and B crop samples. Each lot of ten root systems were cut into approximately 2 cm pieces and placed in a pot as shown below:-



The pots were placed for five weeks in the controlled environment room used for other assays and then the seedlings examined for take-all. P.R.G. was also assessed on the seedlings after the summer sampling.

Soil analysis for phosphorus and potassium.

Soil samples were taken in the autumn of 1973, before sowing the

first, second and third wheat crops to be sure that the amounts of these nutrients did not differ greatly between treatments. This was important because many workers had previously shown that applying phosphate could decrease take-all, Butler 1961 reviewed this work, and more recently work by Slope and Broom (1974) had shown that there was an interaction of phosphorus and potassium on take-all. The soils of all the inoculated sub-plots were sampled on 1 October 1973, from each sub-plot 18 cores (2 cm diam x 20 cm deep) were taken with a semi-cylindrical corer. These cores were air dried and ground. Sub-samples of the ground soils were analysed by Mr. P.R. Poulten of the Rothamsted Chemistry Department, the ammonium acetate-leached K and the sodium bicarbonate-soluble P were measured.

Grain yields.

In August 1973 and 1974 one metre squares of wheat were cut with shears from each sub-plot. The sheaves from these areas were then threshed in a laboratory thresher (Garvie and Welbank, 1967), the moisture contents and weights of the resultant grain samples were measured and in 1974 1000 grain weights were also recorded.

C.3. RESULTS

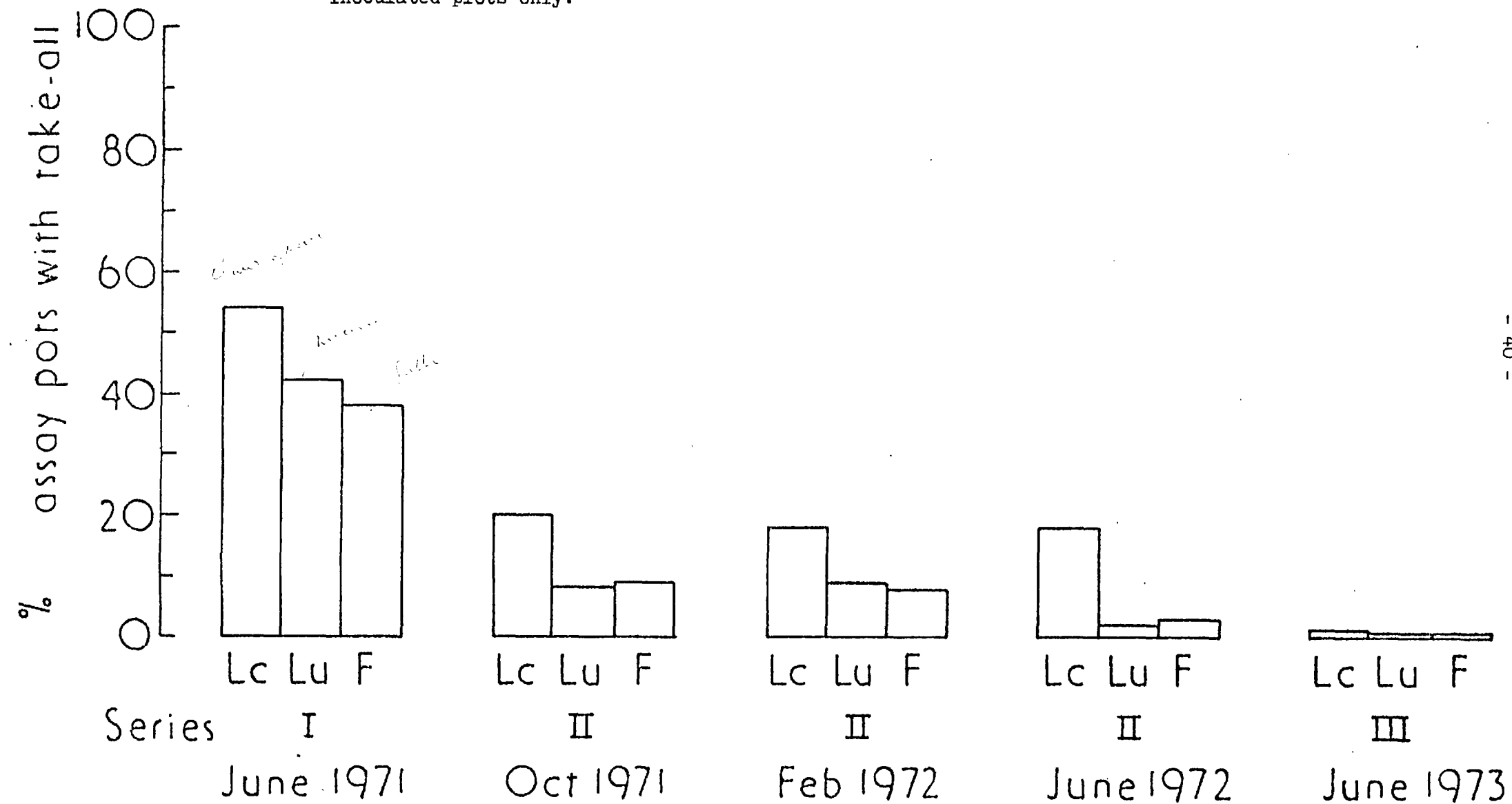
C.3.1. Treatment Cropping 1971-73.

The preliminary sampling in 1971 before the leys were sown showed that G.G.T. was present on all inoculated plots, with an overall average of 66% cores with infected seedlings.

Infectivity of G.G.T. in soils.

Fig. C4 shows that the amount of G.G.T. present decreased rapidly during the first year and continued to diminish until, by the final sampling in June 1973, less than 2% of the pots had

FIG. C4. The infectivity of G.G.T. in soils after different periods of treatment cropping - inoculated plots only.



infected seedlings in the assay. During the three year period the amount of G.G.T. surviving tended to be slightly greater under the grass/clover sequences than under lucerne or fallow. Analysis of the data used in fig. C4 but angularly transformed showed that this tendency of slightly more G.G.T. to be present in the grass/clover sequences was only significant at a probability of 5.0% at the June 1972 sampling.

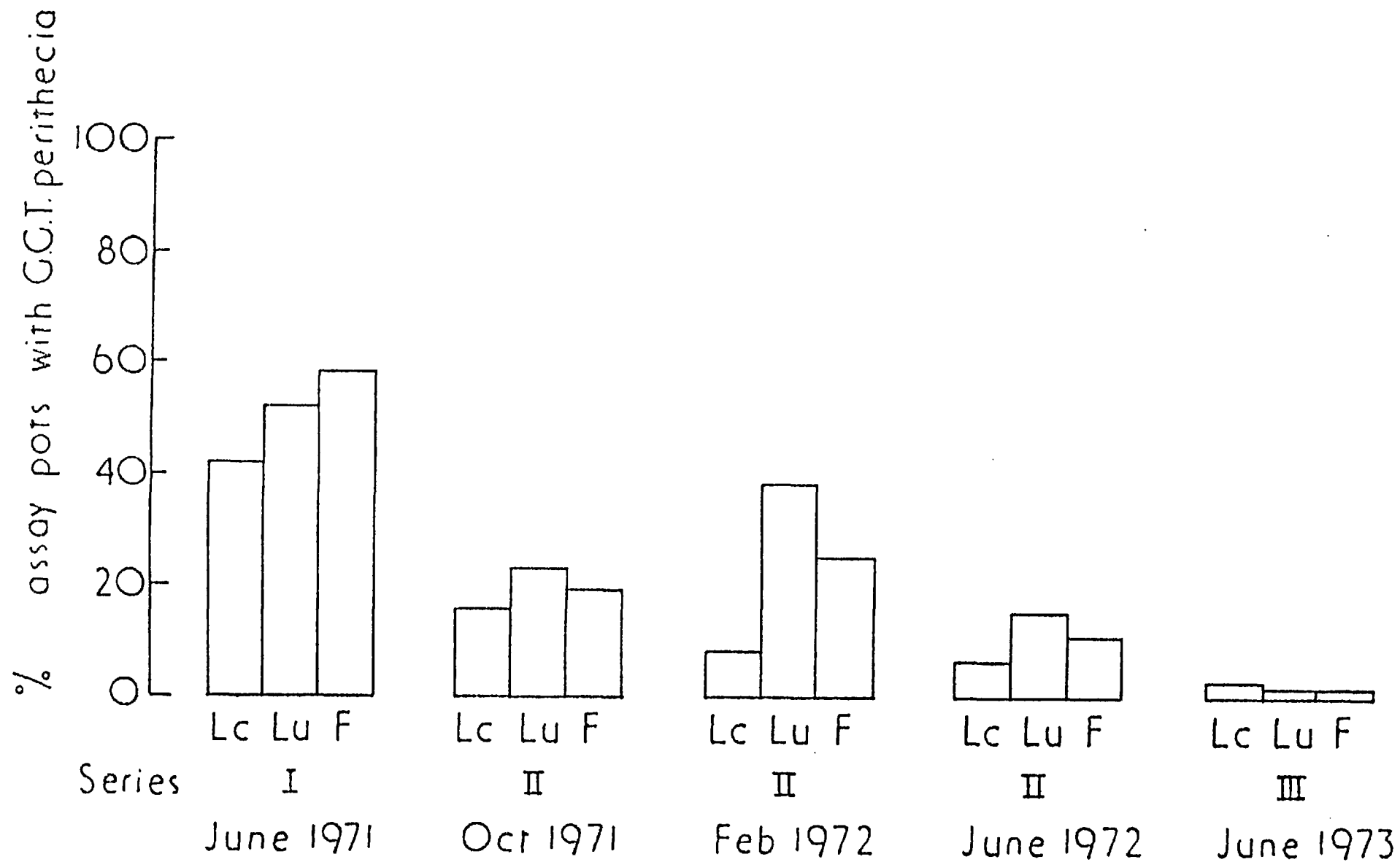
The total number of roots infected on the assay plants and the estimates of infective particles showed the same pattern as the % pots with take-all. The value of the estimated number of infective particles seems doubtful in view of recent reports that mixing of soils can change the number of infections observed on seedlings (MacNish, 1973 a), and that different sizes of infective fragments differ in their infectivity at different temperatures (Hornby, 1975).

After three years of treatment cropping the uninoculated sub-plots did not differ between treatments in the amount of G.G.T. present. All sub-plots had 1.4% cores with take-all compared with 2.0% cores with take-all when the soil was assayed before the experiment was started and with 2.0% pots with take-all in the inoculated sub-plots at the end of three years. Thus it appears that although the vast majority of inoculum disappears from the soil in the first year the small amount remaining can survive a long time.

Production of G.G.T. perithecia.

Fig. C5 shows the production of perithecia on the rotted roots of the assay plants. Perithecial production was very variable but generally decreased over the three year 'treatment cropping' period. By the final sampling in June 1973 very few roots produced perithecia. In contrast to the infectivity results there was a tendency for slightly fewer perithecia to be produced on the grass/clover samples than on lucerne and fallow. When the data used in fig. C5 was

FIG. C5. The production of G.G.T. perithecia on wheat seedling roots grown in soils after different lengths of treatment cropping - inoculated plots only.



angularly transformed the smaller number of perithecia an the grass/ clover was significant at a probability of 5% for the February 1972 sampling and also for the mean of all Series II samplings.

As a method of confirming visual assessments of G.G.T. it posed considerable problems for although perithecia were consistently produced on root systems moderately or severely infected, they were also produced on some root systems on which no lesions had been observed and conversely they were not produced on some root systems on which only a few roots were infected.

Assessment of P.R.G. in soils.

As mentioned in the introduction to this section, assessment of P.R.G. was only done from 1973 onwards, therefore only the population at the end of the three years treatment cropping was assessed. Much P.R.G. was present in the grass/clover sequence, with less present in the lucerne and very little in the fallow sequence. The results are shown below:-

	SEQUENCE	% POTS WITH P.R.G.	P.R.G. RATING
Grass/clover	6	100	2.25
Lucerne	3	55	0.58
Fallow	9	8	0.12
S.E.D. [†]		4.91	0.131

transformed

C.3.2. Wheat Test Cropping 1972-74.

The wheat crops grown after the treatment cropping are referred to as first wheat crops (W1), the wheat crops that followed the first wheat crops are referred to as second wheat crops (W2) and the wheat following these as third wheat crops (W3).

Inoculation did not affect the incidence of take-all on any of

the wheat crops nor did it affect the incidence of either G.G.T. or P.R.G. in the assays.

Assessment of take-all and P.R.G. on the crop.

Tables C1 and C2 show the amount of take-all present on the wheat crops.

On first wheat crops there was little take-all present in spring or summer, and only in Series I (1972) when there was slightly more take-all after grass/clover, was there any difference between cropping treatments. In neither the first wheats nor subsequent wheats was there any consistent difference between the three sets of positional samples. So it would appear that no large amounts of inoculum spread from the inoculated to the uninoculated plots which is perhaps not unexpected as even by October 1971 there was little inoculum surviving. In spring 1974 first wheat crops were also assessed for the presence of P.R.G., this confirmed that the differences in P.R.G. similar to those observed in the assays also occurred on the crop plants. The results are given below:-

	SEQUENCE	% PLANTS WITH P.R.G.
Grass/clover	6	79
Lucerne	3	10
Fallow	9	1
S.E.D. $\pm$ 2.2		

On second wheat crops take-all was fairly severe after lucerne and very severe after fallow but much less so after grass/clover. Comparable treatments on Series I and II usually had very similar amounts of take-all but one plot after lucerne (Plot 27) on Series II had less take-all than the other two lucerne plots in that series,

TABLE C1. The percentage of wheat plants infected with take-all in the spring following different cropping sequences - Means of inoculated and uninoculated plots.

% PLANTS WITH TAKE-ALL						
SERIES	$\overbrace{1972 \quad 1973 \quad 1974}^{W_1}$			$\overbrace{1973 \quad 1974}^{W_2}$		$\overbrace{1974}^{W_3}$
	I	II	III	I	II	I
GRASS/CLOVER	0.2	0.5	0.0	3.6	4.5	21.1
LUCERNE	0.2	0.2	0.0	30.0	23.0	29.3
FALLOW	0.5	0.0	0.8	40.6	44.5	13.4
S.E.D. $\pm$	0.50	2.48	6.16	2.48	6.16	6.16

TABLE C2. The percentage of wheat plants infected with take-all in the summer following different cropping sequences - Means of inoculated and uninoculated plots.

% PLANTS WITH TAKE-ALL						
SERIES	W ₁			W ₂		W ₃
	1972	1973	1974	1973	1974	1974
	I	II	III	I	II	I
GRASS/CLOVER	3.7 (0.6)	3.2 (0.0)	3.8 (0.0)	24.0 (7.1)	25.7 (9.8)	21.0 68.3 (33.3)
LUCERNE	1.1 (0.6)	2.0 (0.0)	2.8 (0.0)	79.0 (46.4)	75.0 (48.1)	20.0 81.8 (37.8)
FALLOW	0.3 (0.0)	2.0 (0.2)	6.4 (2.9)	92.1 (73.5)	98.1 (84.4)	13.0 63.2 (17.6)
S.E.D. $\pm$	1.55 (-)	3.79 (3.58)	10.50 (11.42)	3.79 (3.58)	10.50 (11.42)	6.0 10.50 (11.42)

() Figures in brackets are the % plants moderately or severely infected.

the amounts of take-all are shown below for the three lucerne plots:-

	% Plants with take-all	
	Total	Moderate and severe
Lucerne Plot 27	50	24
Mean of lucerne plots 5, 15	87	46

Plot 27 was accidentally contaminated with some of the grass/clover seeds mixture at the time of sowing the experiment. A similar variation between plots had occurred in the assay of soils in the autumn of 1973, the amounts of G.G.T. and P.R.G. present in Plot 27 and the other two lucerne plots of the same series are given below:-

	% cores with	
	G.G.T.	P.R.G.
Lucerne Plot 27	42	85
Mean of lucerne plots 5, 15	77	48

Thus the accidental contamination of Plot 27 may well have resulted in the increase of P.R.G. and the decrease in G.G.T.

On third wheat crops take-all was prevalent on all crops. In comparison with second wheat crops the same year take-all had increased greatly after grass/clover and decreased in amount and more particularly in severity after fallow.

Assay of G.G.T. and P.R.G. in the wheat soils.

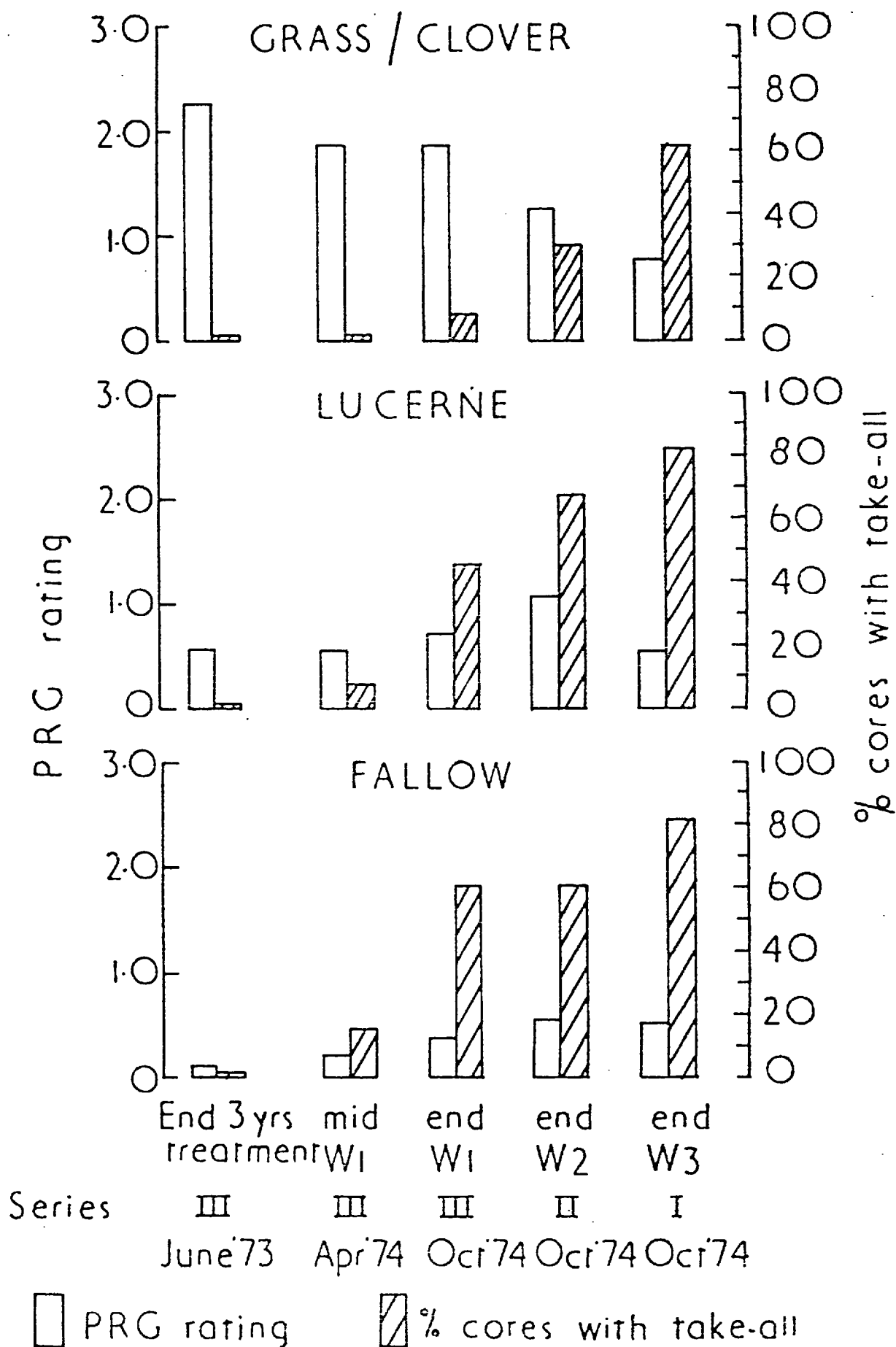
Table C3 shows the incidence of G.G.T. and P.R.G. and fig. C6 compares the amounts of G.G.T. and P.R.G. in the 1974 assays.

Even as early as April (Series III) G.G.T. had increased, particularly on the fallow and lucerne sequences. By October, G.G.T. was abundant after fallow and lucerne but much less so after grass/clover. The three series showed the same pattern between cropping

TABLE C3. The incidence of G.G.T. and P.R.G. in wheat soils following different periods of treatment cropping - Means of inoculated and uninoculated plots.

SERIES	W ₁			W ₂			W ₃		
	SPRING		OCT 1972	AUTUMN			AUTUMN		OCT 1974
	FEB	APRIL		OCT	SEPT	OCT	OCT	OCT	
	1973	1974		1973	1974	1974	1973	1974	
	II	III	I	II	III	III	I	II	I
% CORES WITH TAKE-ALL									
GRASS/CLOVER	3.5	1.4	32.6	15.3	14.5	8.3	77.8	30.6	61.1
LUCERNE	9.7	9.0	72.2	65.3	50.2	45.8	98.6	68.1	81.9
FALLOW	6.3	15.3	81.2	87.5	72.2	61.1	95.8	61.1	81.4
S.E.D. $\pm$	2.84	3.97	6.31	10.22	7.40	8.53	10.22	8.53	8.53
PHIALOPHORA RATING									
GRASS/CLOVER	-	1.87	-	1.95	-	1.88	0.30	1.25	0.78
LUCERNE	-	0.55	-	0.88	-	0.72	0.10	1.08	0.55
FALLOW	-	0.22	-	0.10	-	0.38	0.15	0.55	0.52
S.E.D. $\pm$	-	0.113	-	0.170	-	0.212	0.170	0.212	0.212

FIG. C6. A comparison of G.G.T. and P.R.G. populations in soils at the end of three years treatment cropping and in the soils of the 1974 wheat crops - means of inoculated and uninoculated plots.



sequences, though the amount of G.G.T. tended to decrease with longer periods under treatment crops before the wheat. One reason for the large amounts of G.G.T. found in October might have been that inoculum was broken into many pieces and dispersed during ploughing. However the amount of G.G.T. present in September 1974 before ploughing was slightly greater than after ploughing. The amount of P.R.G. present in both spring and October assays of first wheat crop soils were similar to amounts at the end of three years treatment cropping though there was a slight increase in the amount after fallow.

After the second wheat crop most G.G.T. was present after fallow and lucerne though the amount after grass was much greater than that after the first wheat crop. Conversely the amount of P.R.G. after grass/clover was less than after the first wheat crop but was still more than after fallow or lucerne. However the amounts of both G.G.T. and P.R.G. differed greatly between the two series. Unfortunately with this experimental design there is no way of separating whether this difference between series was a result of the different lengths of treatment cropping or differences in environmental factors between the two years.

After the third wheat crop differences between cropping sequences in amount of G.G.T. were small, there was still slightly less after grass/clover than after lucerne or fallow. There were no significant differences in the amount of P.R.G. between cropping sequences.

Assay of root systems diagnosed as clean.

As the assay of the soils of the first wheat crop had resulted in much greater prevalence of G.G.T. being observed than on the crop roots it seemed possible that an assay of the roots diagnosed as clean might show that much G.G.T. was present on the roots but not

causing visible lesions. However the assay, with ten 'clean' root systems per pot, resulted in little infection either in spring or summer. The results are given below:-

ASSAY OF 'CLEAN' CROP ROOT SYSTEMS 1974 - SERIES III

	% assay Pots with take-all
Spring samples	2.8
Summer samples	5.6

The assay seedlings of the summer samples were also scored for P.R.G. which was found to be present in 70% of the pots, with more after grass/clover (P.R.G. rating 1.5) than after fallow or lucerne (P.R.G. rating 0.6).

Yield and 1000 grain weights.

Where take-all was severe in second and third wheat crops, there was a considerable decrease in yield. (Table C4). 1000 grain weights were also inversely correlated to take-all. (Fig. C7). In Fig. C7 the first wheat crops were omitted from the correlation because they were all lodged which would have limited both the 1000 grain weight and the yield.

Soil analysis for Phosphorus and Potassium.

There was very little difference between sequences in amounts of either phosphorus or potassium in the soils (Table C5). The soil was at the lower end of the agricultural range for both nutrients where small differences might be critical. However as the wheat received 38 Kg P_2O_5 and 75 Kg K_2O per hectare, it seems unlikely that the small differences in nutrients in the soil could have affected the amount of take-all.

TABLE C4. The yields of grain (85% Dry Matter) of wheat crops following different cropping sequences - Means of inoculated and unicoculated plots.

SERIES	GRAIN - g/m ²				
	W ₁		W ₂		W ₃
	1973	1974	1973	1974	1974
	II	III	I	II	I
GRASS/CLOVER	450	480	437	482	346
LUCERNE	430	427	411	312	337
FALLOW	437	366	278	170	421
S.E.D. [†]	46.4	56.4	46.4	56.4	56.4

FIG. C7. Relationship between Take-all rating and 1000 grain weight of wheat - 1974.

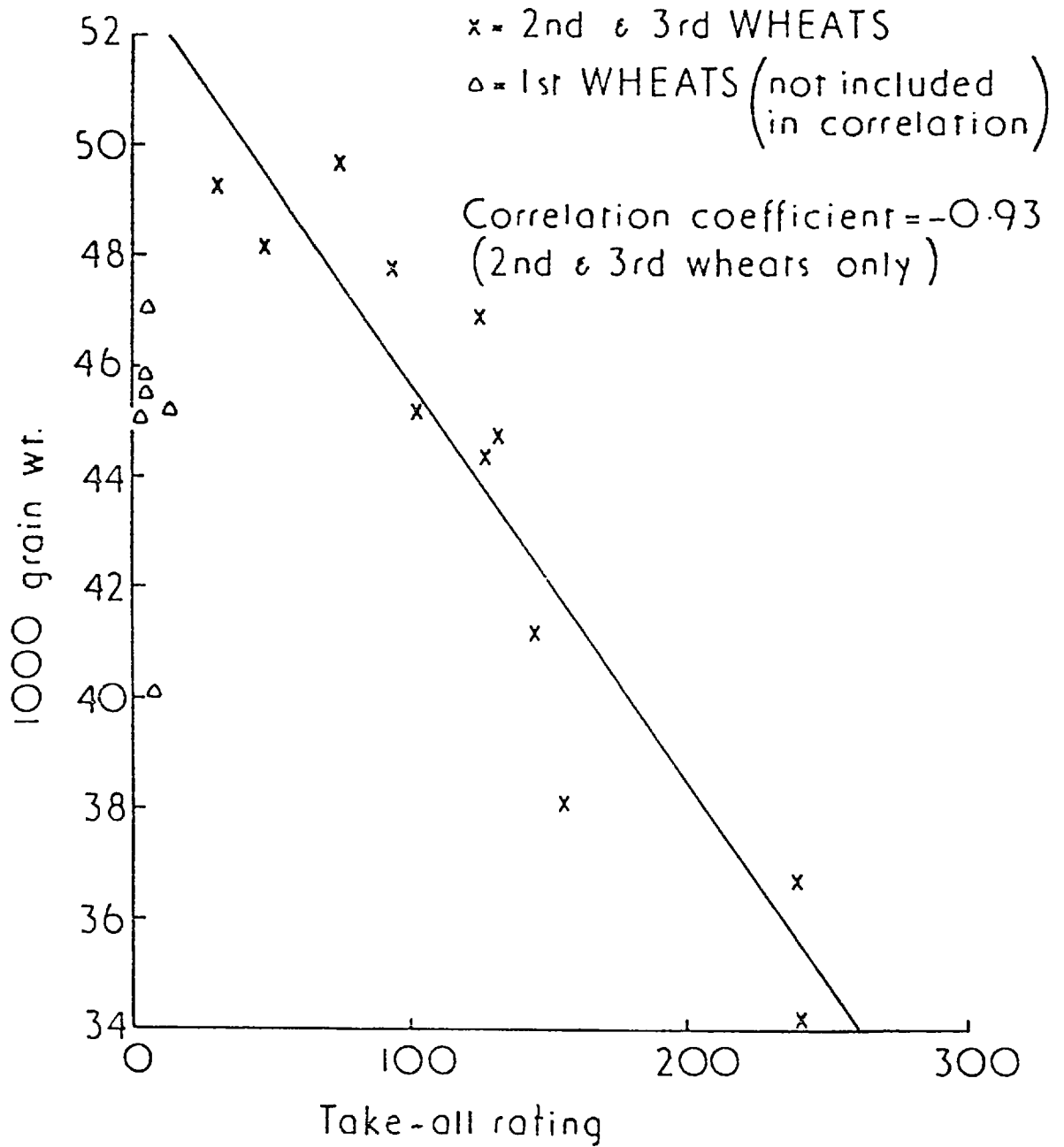


TABLE C5. The amounts of Phosphorus (P) and Potassium (K) in the soils of the different sequences (October 1973) - inoculated plots only.

	BEFORE W ₁		BEFORE W ₂		BEFORE W ₃		MEAN	
	Parts per million in the soil							
	P	K	P	K	P	K	P	K
GRASS/CLOVER	8.3	103.7	11.3	123.3	9.9	91.7	9.8	106.2
LUCERNE	9.5	102.3	11.2	120.3	11.1	114.0	10.6	112.2
FALLOW	11.5	111.0	9.9	127.7	11.4	106.7	10.9	115.1
S.E.D. ±	0.97	14.07	0.97	14.07	0.97	14.07		

C.4. DISCUSSION

The results of this experiment show that the differences in take-all incidence and severity in the successive wheat crops following different treatment cropping were determined less by differences in the survival of inoculum than by the differences in the increase of G.G.T. during the first wheat crop.

The G.G.T. inoculum surviving during the treatment cropping, as measured by the infection of wheat seedlings, quickly decreased to a very small amount, with very little difference between treatments. Indeed the slightly increased survival with grass/clover is the opposite to the effect needed to explain the subsequent amount of take-all in the wheat crops.

The trend for perithecial production to be least after grass/clover is unexplained. Weste and Thrower (1963) and Weste (1970 a) showed that in culture the production of perithecia was much influenced by nutrient supply especially the Carbon : Nitrogen ratio. The six week assay seedlings were grown after different crops without added nutrients and so it is possible that the seedling roots may have differed in their C : N ratio. An alternative explanation is that as the fungus nears the limit of its survival, a change favouring the sexual reproductive state and the production of perithecia is induced and even the subsequent provision of a new substrate (i.e. the seedling root) does not reverse this change. Although other factors have been shown to affect perithecial production, i.e. light intensity and temperature (Weste, 1970 b), immersion in water (Gindrat, 1968), pathogenicity (Chambers and Flentje, 1967) and presence of bacterial contamination (Lemaire et al., 1966), and may have been associated with the variability in these results, there seems no reason why they should affect treatments differently. However by the end of the second and third years of

treatment cropping both the differences between treatments and the total percentages of pots with perithecia were very small and seem unlikely to account for the subsequent differences in take-all. Survival of inoculum could not therefore be associated with the subsequent differences in take-all unless there was inoculum present, but below the detection threshold of the assay. Even so such inoculum could only account for the difference in take-all if it had a very different pattern of survival to the detected inoculum. While it is likely that some inoculum was undetected there seems no reason why the proportion undetected should differ between treatments.

As might be expected from the small amount of G.G.T. surviving there was very little take-all on the first wheat crops as diagnosed by visible lesions. This diagnosis was supported by the very limited infection of seedlings grown on root systems diagnosed as clean. This is in marked contrast to a report by MacNish (1973 b) who found 41% of stubble diagnosed as clean caused infection of seedlings in an assay, however from his report it would appear that his initial diagnosis was mainly based on infection of the sub-crown internode.

Even though the first wheat crops had little take-all the population of G.G.T. in soil cores after these crops were large with big differences between treatments. The slightly greater amount of G.G.T. in September 1974 before ploughing than in October after ploughing would indicate that the widespread presence of G.G.T. was not a result of spread by cultivation and that the G.G.T. population in the post harvest period was not increasing.

Take-all on the second wheat crops reflected the differences in G.G.T. observed in the assay the previous October. Although the second wheat crops had very similar amounts of take-all in Series I

and Series II, there were large differences in the amounts of G.G.T. and P.R.G. between the two series, the cause of which was not determined. However as the take-all on the crop did not differ, it seems likely that these differences in G.G.T. and P.R.G. result either from differences in soil conditions just before or at the time of sampling or from differences within the assay. The September weather of the two years was very different as shown below:-

	MEAN AIR TEMP.	SOIL AT 10cm	RAIN mm
September 1973	14.7°C	13.8°C	64
September 1974	12.0°C	11.5°C	118

Differences in soil moisture at the time of coring affects the consolidation of the soil in the pots and so might affect the watering of the pots during the assay.

In the third wheat crop, the crop after fallow had less take-all than in the second wheat crop and yielded better. This lessening of take-all after it has reached a peak during consecutive cereal crops was named take-all decline by Slope and Cox (1964). In contrast take-all was worse after grass/clover compared to the second wheats though not as severe as on second wheats after either lucerne or fallow.

Some possible reasons for the disparity between the amount of take-all on the first wheat crops and the amount of G.G.T. in the assay following them are discussed in the discussion of Section D.4 (page 97). However these reasons do not explain the differences in amounts of G.G.T. between treatments. Scott (1970), Balis (1970) and Deacon (1973 a) have all reported a decrease in take-all when P.R.G. was present and Deacon (1973) suggests that this cross protection effect is the explanation for the decreased amount of

take-all after leys. This suggestion is entirely compatible with my results (fig. C8) and seems the probable explanation. However it is possible that P.R.G. and G.G.T. respond in opposite ways to some other factor.

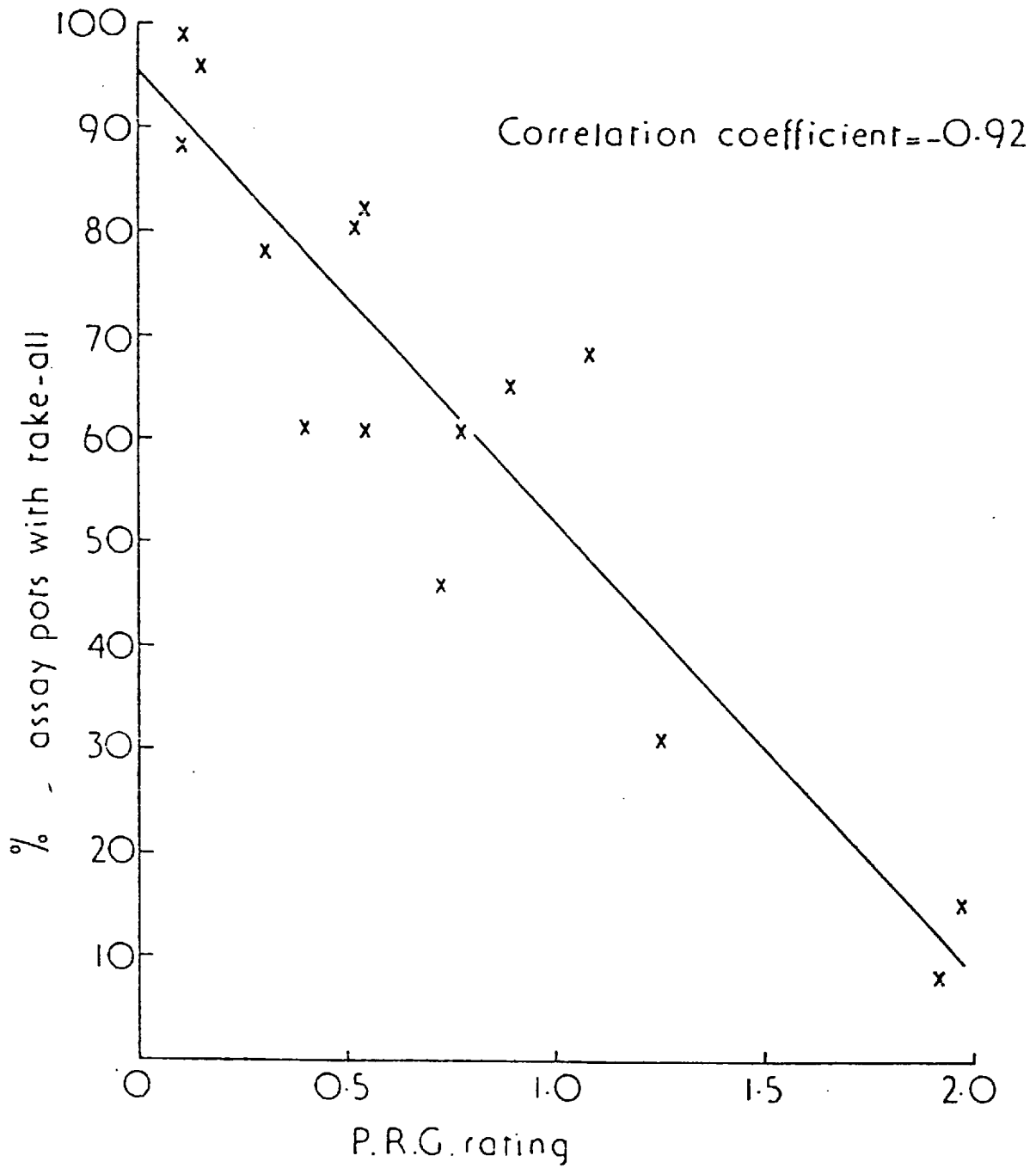
The mechanism by which this cross protection by P.R.G. could be achieved is not clear though some possible ways are as follows:-

- a) Competition for infection sites.
- b) Competition for nutrients in the soil.
- c) Direct antagonism between the fungi.
- d) Infection of host by P.R.G. inducing a change in root exudates.
- e) Infection of host by P.R.G. inducing inhibitory or toxic compounds within the host.

The amount of the root surface covered by P.R.G. on crop and assay plants does not seem sufficient to readily support suggestion a).

The presence of both fungi within small areas of the same root casts doubts on c) as a likely explanation. My results give no indication as to the relative probabilities of b), d) or e) as explanations, but Wong (1974) using Gauemannomyces graminis graminis to provide cross protection against infection by G.G.T. suggests that the explanation could be a specific host response acting within the host.

FIG. C8. Relationship between P.R.G. and G.G.T. in assays of wheat soils in October - means of inoculated and uninoculated plots.



D. STUDIES ON THE SPREAD OF GAEUMANNOMYCES GRAMINIS VAR. TRITICI
WITHIN A WHEAT CROP

D.1. INTRODUCTION

The spread of G.G.T. can be considered in two situations

- a) Distant dispersal into areas where G.G.T. is unrecorded.
- b) Local dispersal within a field from inoculum surviving from a previous infected crop.

The opportunity to study distant dispersal is rare. However the Dutch polders, land newly reclaimed from the sea, did provide such an opportunity and Gerlagh (1968) studied the spread of the fungus into these new soils; he concluded that ascospores were the most likely means of initial infection. Previously it had been shown that ascospores of G.G.T. did not infect wheat roots in non-sterile soil often enough for detection in small experiments (Garrett, 1939) but that in sterile soil or where the roots were above the soil surface infection by ascospores was possible (Brooks, 1965). Gerlagh suggested that the reason that ascospores caused infection in the polders was that these soils had a very limited microflora. In more usual agricultural soils infection by ascospores would seem to be possible only when wheat roots were growing on the soil surface, which would usually occur only when grain shed from a preceeding crop germinates, i.e. volunteer cereals. However, Gregory and Hendon (1967, and pers. comm.) exposed a succession of wheat seedlings with partly exposed roots over a period of a year in a stubble in which they recorded the presence of ascospores for many weeks but none of the exposed seedlings were infected. Thus, although ascospores may be a means of dispersal of G.G.T. in special circumstances, it seems unlikely that they play a significant role in local dispersal under ordinary

field conditions.

Many workers accept that local dispersal of G.G.T. is by its autonomous spread, that is its growth along the roots of a host, and infection of nearby plants where healthy roots are in contact or very close to an infected root. In using this term autonomous spread I have assumed it to also include the added effect of the growth of infected roots.

There is no evidence that within the soil, ^{2/}ascospores or microconidia play a part in local spread though this possibility cannot be ruled out. Padwick (1935) showed the need for live wheat roots to be present for autonomous spread to occur and also that various species of grass roots allowed the fungus to spread at a similar rate to that on wheat roots. Fellows and Ficke (1939) reported that the fungus spread laterally and vertically from infested to uninfested areas in the presence of host roots. They measured the distance of this spread but only in soil in boxes in a glasshouse; their inoculum failed to cause infection in their attempts to repeat the measurements in the field.

Although many workers have studied the factors that affect the growth of G.G.T. in the laboratory or glasshouse over relatively short periods, few have assessed the effect of these factors over the whole season in field conditions. However, three groups of workers have attempted to do so (Adams and Colquhoun 1936, Wehrle and Ogilvie 1956, and Suzuki et al. 1957). These three reports (which will be considered in relation to my results in the discussion) only quote maximum distances of spread with little or no indication of the frequency of occurrence.

The spread of G.G.T. by cultivations has not been demonstrated, but it seems likely that it plays a part in local spread. Cultivations have been shown to spread some other pathogens in the

soil e.g. Keyworth (1942) reported that in hop fields debris from plants infected with Verticillium albo-atrum could be spread by cultivations and cause the infection of healthy plants. The smaller amount of take-all found in direct drilled crops compared to crops drilled after ploughing as reported by Brookes and Dawson (1968) might have been associated with a decrease in the mechanical spread of the fungus in direct drilled crops, but it was certainly not the only cause as even on land where take-all was already widespread direct drilled crops had less take-all.

I report three experiments in which the maximum and average distances of autonomous spread of G.G.T. were measured. In using the term autonomous spread I have assumed that microspores or ascospores were not involved. I also report two experiments in which the maximum and average distances of autonomous spread were compared with those of spread of G.G.T. aided by mechanical dispersal during cultivations.

D.2. MATERIALS AND METHODS

D.2.1 The spread of G.G.T. from infested soil cores (Spread Experiments I (1971), II (1972) and III (1973).)

The three experiments were all done in one field at Rothamsted Experimental Farm, Harpenden, Herts. (Summerdells I). This field was selected because it had been cropped in 1969, 1970 with field beans and had only a small amount of G.G.T. before the experiments began. Inoculum present already in the soil will be called 'background' inoculum. The areas used for spread experiments II and III were fallowed in 1971 and 1971/2 respectively. The soil type on Summerdells I is classified as Batcombe series i.e. a flinty silt loam over clay-with-flints.

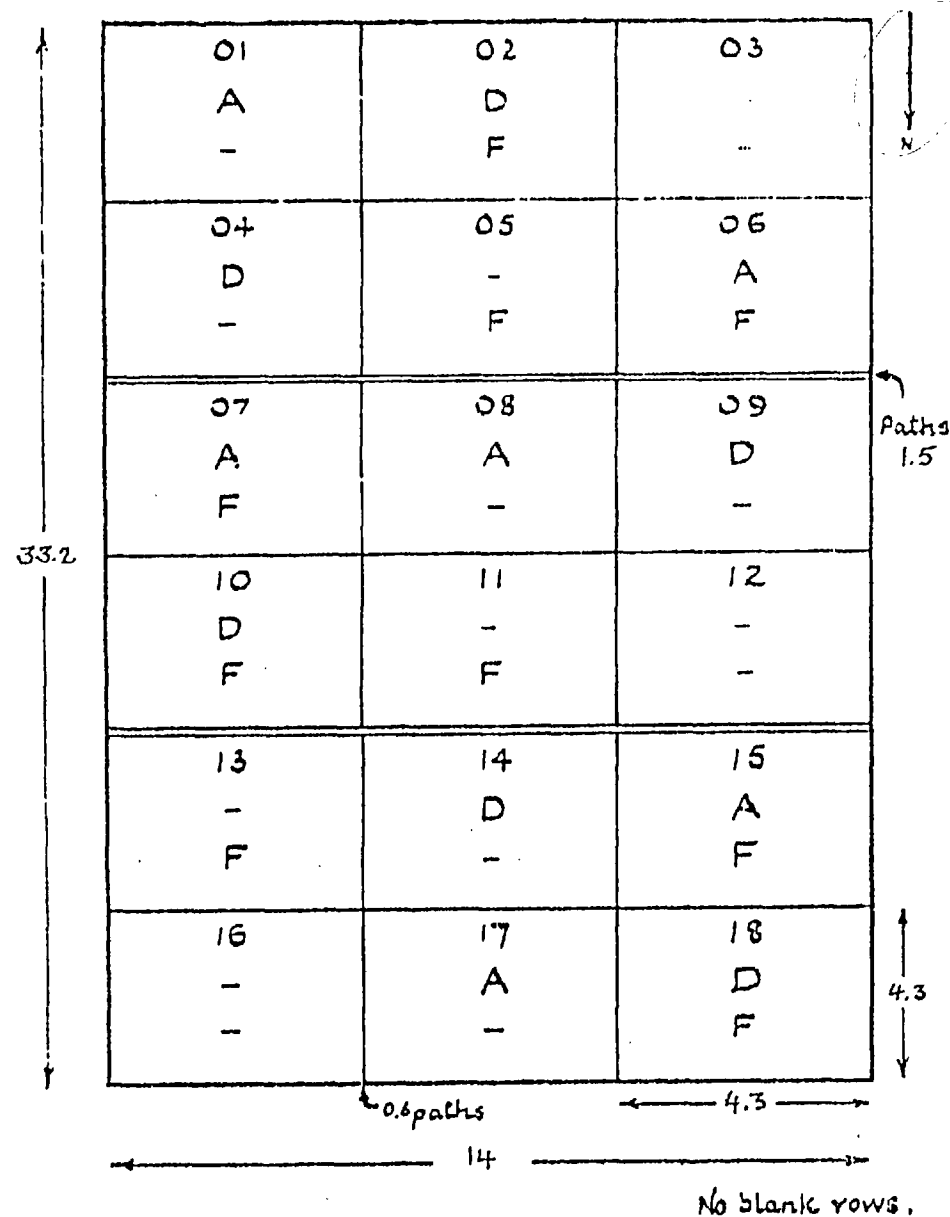
Treatments.

The treatments, basal operations and layout of Spread Experiment I are shown in fig. D1. Dazomet was used to decrease the 'background' inoculum as Ebbels (1969) had shown that it was effective against take-all. As it seemed likely that dazomet could affect the rate of spread of G.G.T. by decreasing antagonistic organisms an equal number of plots not receiving dazomet were included in the hope that the 'background' inoculum would not prevent the spread from the inoculum cores being observed. The dazomet was applied by hand from a 'Kilner' jar with 15 x 4 mm diam. holes in the lid (a 'pepper pot'). The prill was shaken over the surface of the plots in two passes at right angles to each other. The plots were then rotavated twice in reciprocal directions to a depth of 15 cm. This reciprocal rotavation was done to minimise the displacement of the dazomet.

The inoculum consisted of cores 10 cm. deep x 5 cm diameter, sown with six wheat seeds. The soil cores which included stubble, roots and soil, were taken from a field (Pennells Piece) which had grown a third successive wheat crop, and which was known to be infested with G.G.T. This form of inoculum was chosen because it was very similar to naturally occurring inoculum and the cores were convenient small sources of inoculum. A third wheat crop was chosen as the source because G.G.T. was relatively uniformly distributed and causing severe infection. The soil cores were inverted into plastic cups (Mono containers. No. 1012) with 4 x 3 mm diam. drainage holes and sown with the same seed as the plots on the same day. These cores were taken from the cups and 'planted' in the field on 10 December 1970. To avoid compacting the soil or damaging the crop this operation was done from plank bridges, that spanned the plots. The two directions of inoculation treatments, down the row and across the rows (fig. D2) were done because the fungus might be

FIG. D1. The treatments, basal operations and layout of Spread Experiment I.

SUMMERDELLS I 1st year 1971



TREATMENTS

Inoculum*

- None
- A Line of inoculum centrally across all rows
- D Line of inoculum down the centre row only

Fumigant per hectare

- None
- F 450 kg Dazomet in autumn 1970.

Basal manuring per hectare

310 kg compound fertiliser (0:20:20)
N in spring

Variety

Cappelle desprez at 200 kg/ha. Sown 4 Nov 1970.

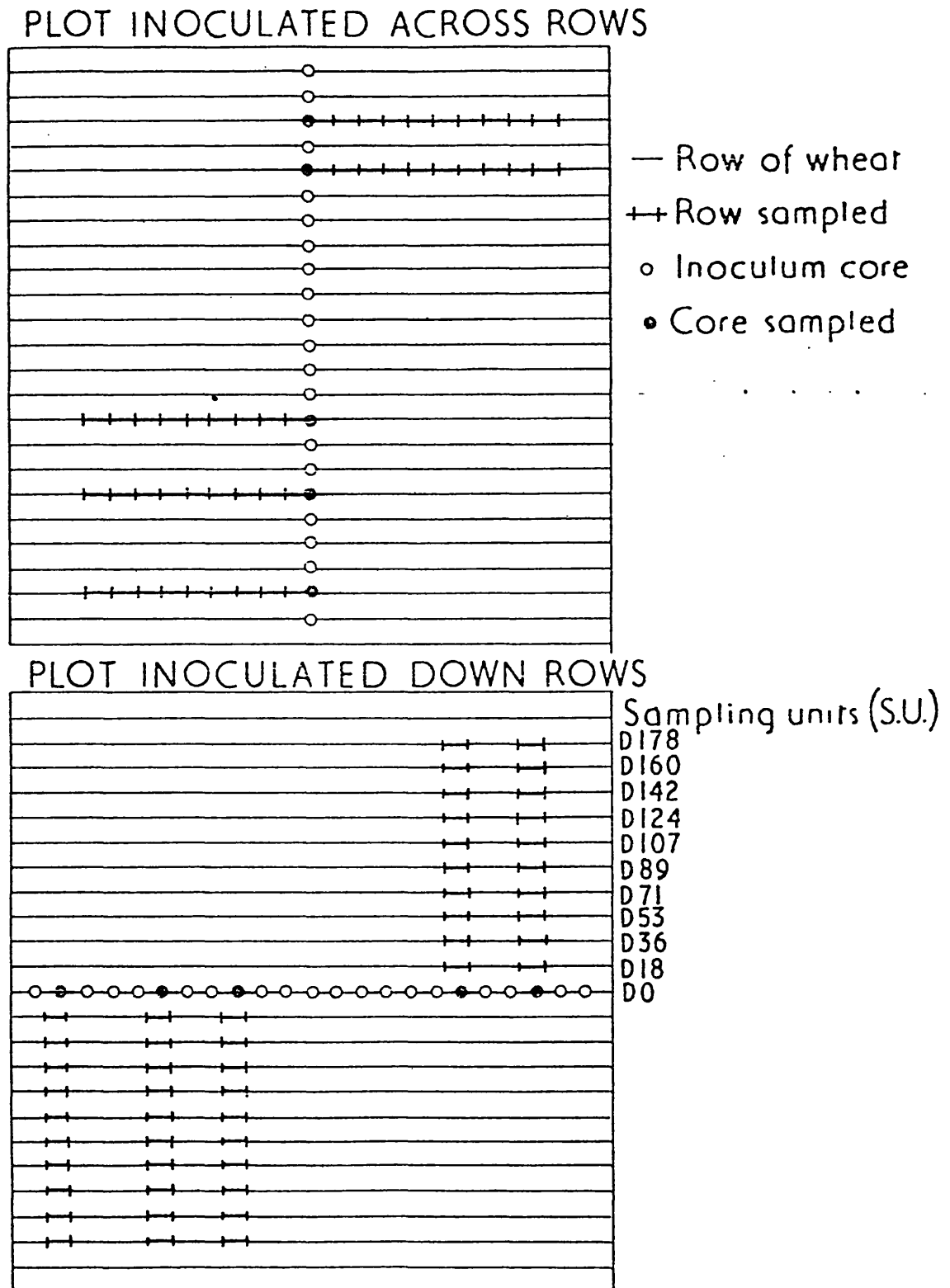
Design: 3 blocks of 6 plots

Dimensions in metres

* Corvetaken from "Cereal Disease Reference Plots", sown with winter wheat in glasshouse on 4 Nov 1970. Corvet planted out in field 10 December 1970
No yields required

FIG. D2. Diagram of the pattern of sampling used in Spread Experiment I.

1971



Sampling units identified by the distance in centimetres of their furthest end from the inoculum core

expected to spread further along rows than between rows as it seems likely that more roots are in contact with each other along rows.

Assay of 'background' inoculum.

The 'background' inoculum was assessed on the sample soil cores which were removed from the field to make a hole for the inoculation cores. The sample cores were placed in plastic cups and assayed by the method described in General Methods - Section B.2 Whole core method.

Crop sampling and diagnosis.

Crops were sampled on 31 March, 1971, 19 May, 1971 and 7 July, 1971; on each occasion five rows of samples were taken perpendicular to the inoculated centre line of each plot to near an edge of the plot in ten contiguous 18 cm lengths, called Sampling Units (S.U.), as shown in fig. D2. The 18 cm length of the S.U. was chosen because it was the distance between rows. Each plant in the D 18 S.U., or small group of plants if they could not be separated in the field, was kept separate and in linear order. The plants from each of the further S.U.s were not separated but each S.U. was kept separate and in order. Because the first sampling showed no infection outside the inoculum cores, in the second and third samplings only S.U.s D0 - D89 were taken. The selection of the rows to be sampled was random with the restriction that no row was sampled that was next to, or on the opposite side of the central inoculum line but in the same row as one from which samples had already been taken. The sample plants were washed, diagnosed and the number of roots with take-all lesions and of plants infected were recorded, as described in General Methods - Section B.1.

Differences in methods used in Spread Experiments II (1972)
and III (1973).

Spread Experiments II and III each consisted of only 3 plots, where the treatment was the same as the plots in Spread Experiment I that were inoculated across the rows and received no dazomet. This change was made because the 'background' inoculum in 1971 did not interfere too much with the measurements and after fallowing the 'background' inoculum should have further decreased. Also an experiment to study the effect of cultivations on the spread of G.G.T. was being undertaken, which also measured autonomous spread. Two sources of inoculum cores were used in each experiment on two halves of the plot in both years. One source was again after a third wheat on Pennells Piece, the other sources were in 1972 after a winter wheat that followed three years spring cereals on Geescroft Field and in 1973 after five years of spring barley on Meadow Field. The Geescroft and Meadow soils were also used as inoculum in the experiments studying the effect of cultivations on the spread of G.G.T. so they provided a common factor between the two types of experiment as well as providing a comparison of inoculum sources within the experiments to study the spread from cores. The method of inoculating and of assay of the sample cores removed were unchanged. Inoculation and sampling dates are given below:-

	Spread Experiment II	Spread Experiment III
	1972	1973
Inoculation	4 November 1971	13 November 1972
First sampling	9 May 1972	16 May 1973
Second sampling	13 July 1972	4 July 1973

Only May and June crop samplings were done in 1972 and 1973 as in the March sampling in 1971 no spread had occurred. The method

of sampling and diagnosis were unchanged from those used on the second and third sampling dates in 1971 except that six instead of five rows per plot were taken on each occasion.

D.2.2 The effect of cultivations on the spread of G.G.T. from a line of inoculum. (Cultivation Experiment I 1972-1973)

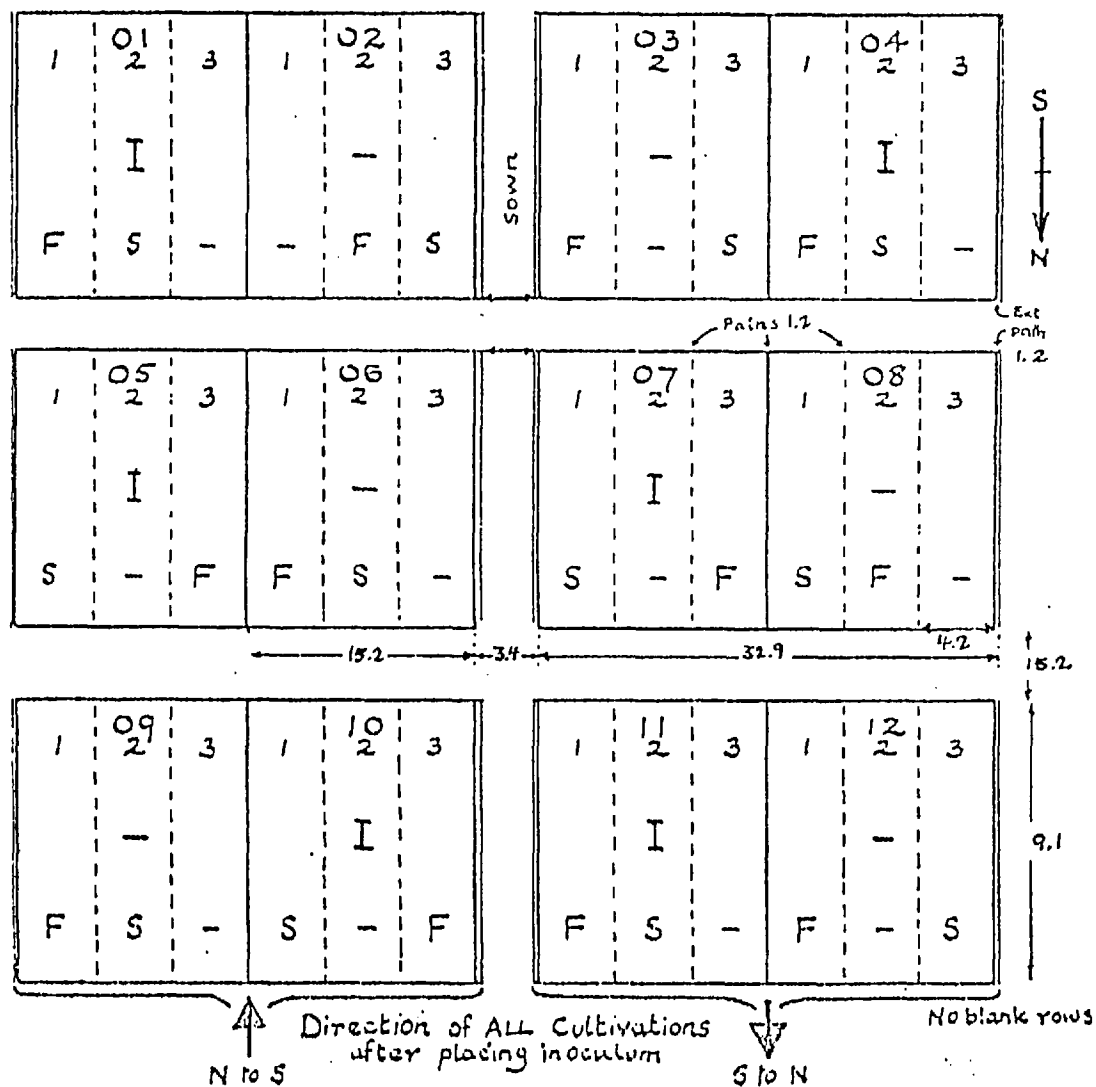
Treatments.

This was a two year experiment done in Summerdells I Field; the treatments, basal operations and design are shown in fig. D3. As the land had been fallowed for a year following two years of beans, it was hoped that the 'background' inoculum would not prevent the assessment of spread by cultivations over the two year period.

Inoculation was only done in the first year. The inoculum consisted of stubble, roots and soil taken from the top 5 cm of Geescroft. This field had been cropped with winter wheat following three years of spring cereals. The inoculum was thoroughly mixed and weighed in 32 kg lots into clean polythene bags and stored for two days. A trench 30 cm wide x 8 cm deep was dug across each plot to be inoculated and partially filled with 64 kg of inoculum. Boards on either side of the trench ensured that all the inoculum went into the trench. The inoculum was forked into the bottom of the trench and then covered with field soil. (Fig. D4).

The cultivations following inoculation were all done in the same direction, southwards on plots 1, 2, 5, 6, 9 and 10 and northwards on plots 3, 4, 7, 8, 11 and 12. Because the site had been fallowed the previous year it was not ploughed in the first year. The cultivations done, in the same direction both years are given below together with typical depths of work of the implements at Rothamsted, although these were not measured on this experiment.

SUMMERDELLS I 1972



TREATMENTS

Inoculum

- , I None, Inoculum placed across the drill rows before sowing w wheat

Nitrogen per

1 None
S Solid 'Nitro-chalk' at 126 kg N
N Foliar Urea/ammonium nitrate at 126 kg N

Cultivations

The effects of cultivations will be assessed on:

- (i) Spread of take-all in direction of cultivation
- (ii) Spread of take-all against direction of cultivation

Variety: Cappelle desprez sown at 200 kg/ha
on 7 Oct 1971

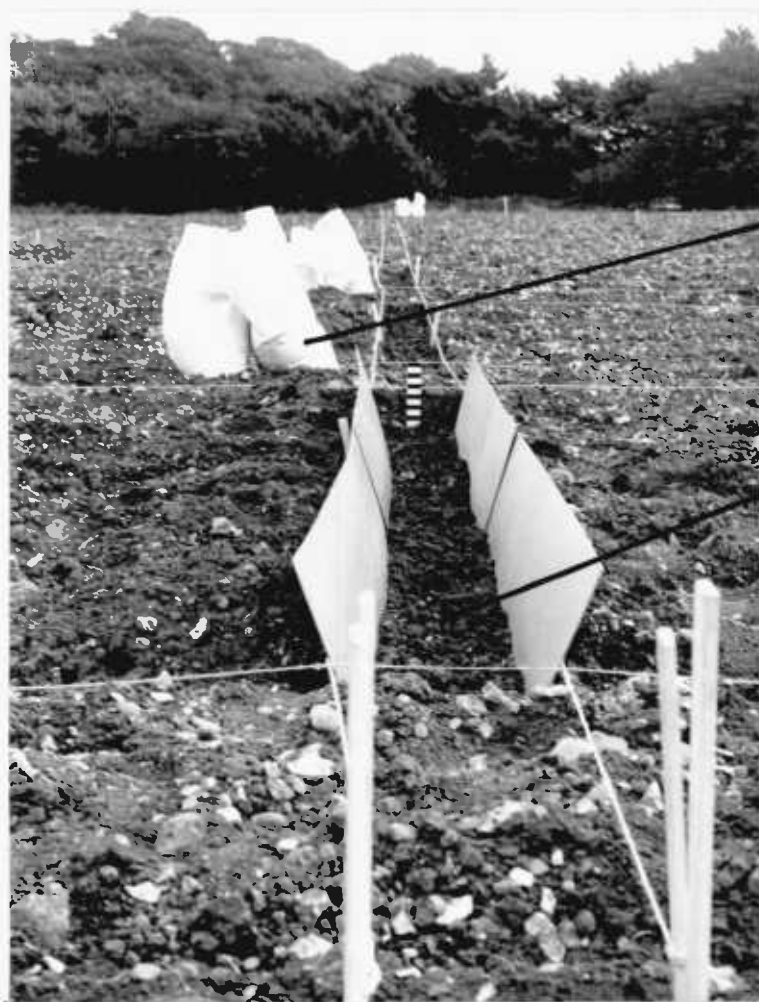
Basal manuring per hectare

251 kg compound fertiliser (0.14:28)
combine drilled

Design: 6 blocks of 2 plots split into 3

Dimensions in metres

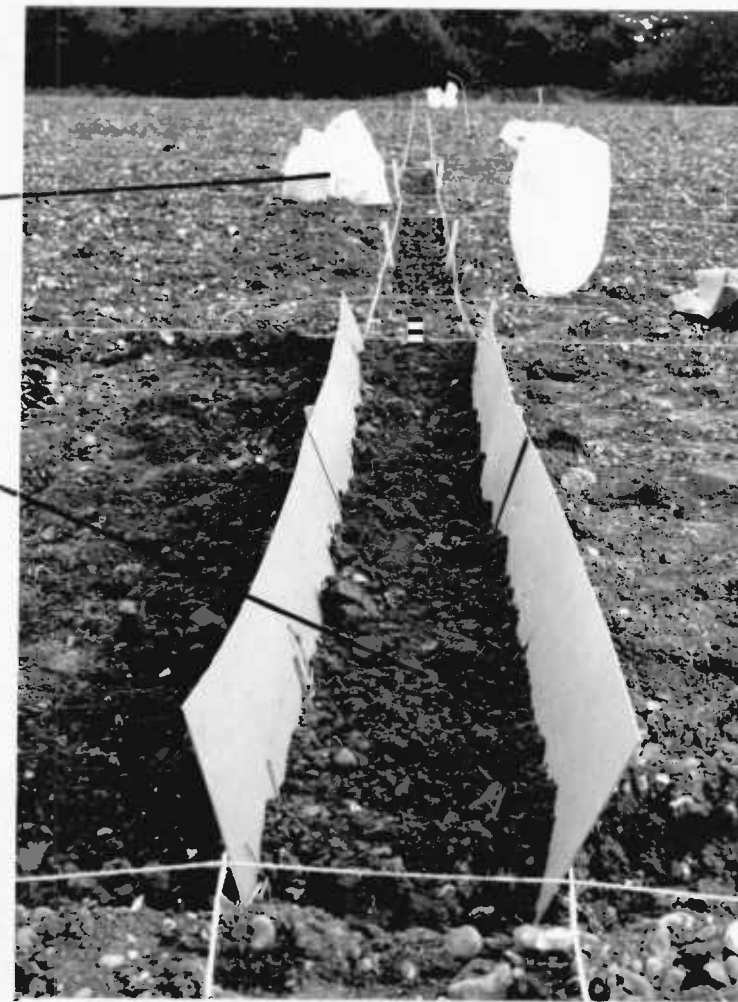
FIG. D4. Photographs showing the method of inoculation used in Cultivation Experiment I.



Strip ready for inoculation

Bags of
inoculum

Inoculum
strip



Strip inoculated and covered
with field soil

	FIRST YEAR	SECOND YEAR	TYPICAL DEPTH OF WORK
Plough	-	✓	23 cm
Power harrow	✓	✓	13 cm
Disc drill	✓	✓	5 cm
Chain harrow	✓	✓	5 cm

The whole field was also limed by mistake before the second year cultivations (7.5 tonnes of chalk applied on 22-9-72), this unfortunately introduced a new factor into the experiment with no untreated area on which to assess its effects.

The solid fertiliser was broadcast on 25 April 1972 as 'Nitro chalk 21' and the liquid fertiliser was applied by knapsack sprayer as 'Agsol 26' (urea/ammonium nitrate compound containing 26% N) at a rate of 1.54 l/sub plot. This application was delayed by bad weather until 8 May 1972. In the second year both fertilisers were given on 27 April 1973. These nitrogen treatments were given because it was thought that applying none or some to the soil or to the foliage might result in different patterns of spread because of changes in the ability of the fungus to infect the roots.

Assessment of mechanical movement of soil during cultivation.

In the first year only, a trench similar to those on inoculated plots was dug in a discard area. Moist soil labelled with a fluorescent powder (Saturn yellow sunbonded pigment series A) was placed in the trench, instead of the inoculum, and covered in the same way. After the cultivations, cores 5 cm diam. x 10 cm deep were taken at intervals along three transects, at right angles to the trench, in the direction of cultivation. The presence or absence of the pigment in the cores was observed under U/V light.

Assessment of % liquid fertiliser falling on the soil.

In order to assess the % of the liquid fertiliser that was retained on the crop a discard area of crop and an area of fallow ground was sprayed with liquid fertiliser to which a known quantity of fluorescein had been added. In both areas plastic petri dish tops with a lip made in one side were placed on the ground before spraying, ten in the open ground and ten pairs in the crop (one in the row and one between the rows). The deposition of fluorescein on each dish was washed off and measured on a fluorimeter. This assessment was repeated in the second year but no results were obtained because the pressure gauge on the sprayer developed a fault after spraying the plots.

Crop sampling and diagnosis.

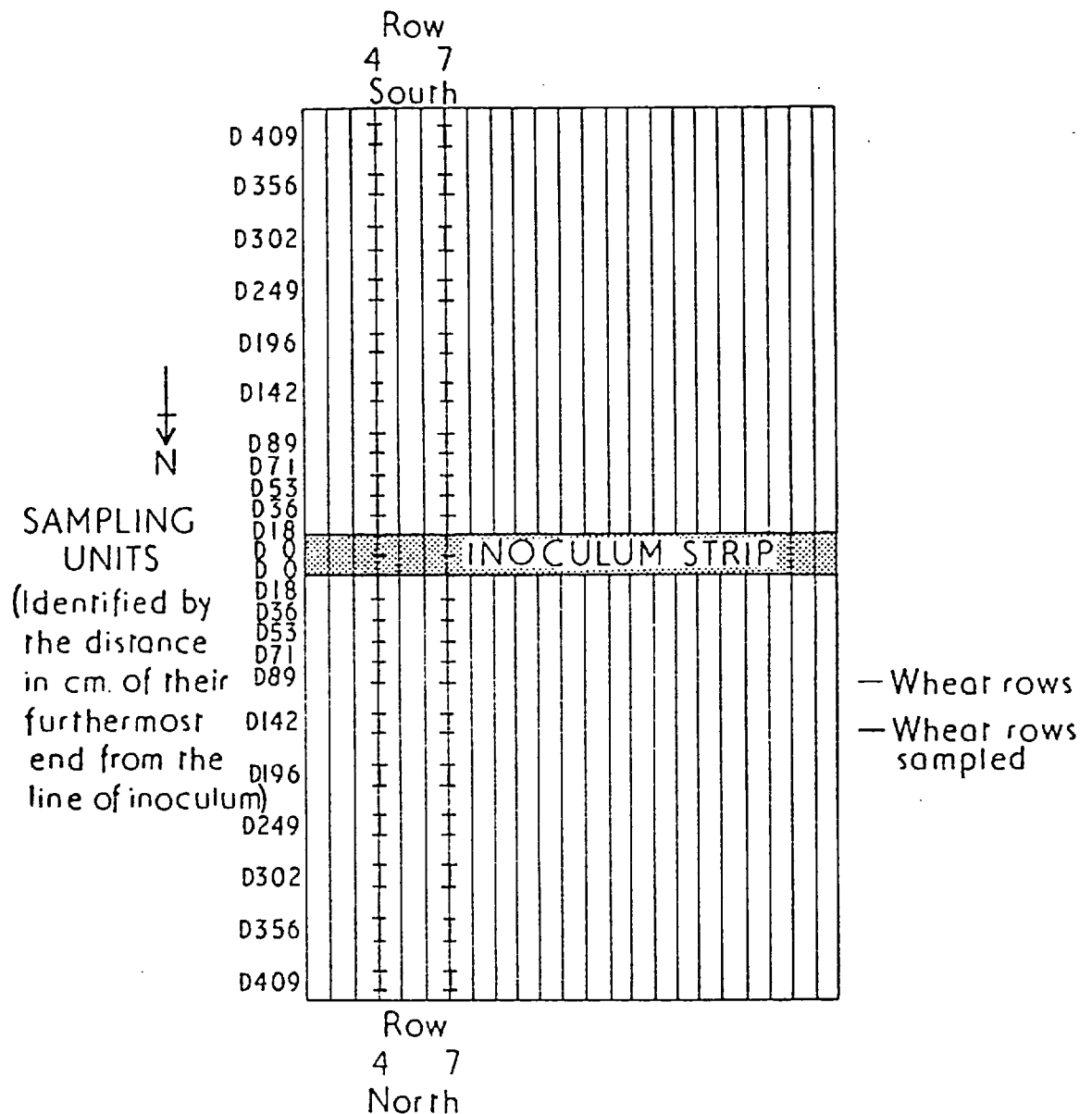
In 1972 the crop was sampled twice (18 May 1972 and 12 July 1972), on each occasion two rows of crop in each inoculated sub plot and two half rows in each uninoculated sub plot were sampled as shown in fig. D5. At the first sampling only plots 1-8 were sampled. The number of infected seminal and crown roots on each plant was recorded and a total root count was made on five plants from S.U.s D 18 and D 196. In 1973 the crop was only sampled once, on 4 July 1973. The diagnosis was the same, except that infected seminal and crown roots were not recorded separately, but only as total infected roots.

D.2.3 The effect of cultivations on the spread of G.G.T. from a line of inoculum. (Cultivation Experiment II 1973-1974).

Treatment.

This was a small experiment intended to confirm the results of the 1972-73 experiment. There were only three plots, which were the same as the solid fertiliser inoculated sub plots of Cultivation

FIG. D5. Diagram of the pattern of sampling used in
Cultivation Experiment I.



In the uninoculated plots the same method of sampling was used but only 2 half rows were sampled one in each direction (eg. row 4 south & row 7 north)

Experiment I (see fig. D3). The source of inoculum was Meadow Field which had been cropped for five years with spring barley. The cultivations done in the first and second years of this experiment were similar to those done in Cultivation Experiment I (see Section D.2.2 page 71) with the exception that in the first year an error was made and spring tines were used instead of a power harrow. The typical working depth of spring tines is 5 cm. Also in the second year observations were made on the two discards on either side of the plots. One of these discard areas was left uncultivated and volunteer wheat allowed to grow and the other discard was cultivated in the same way as the plots, both areas received 126 kg N/ha as nitrochalk.

Crop sampling and diagnosis.

The plots were sampled on 17 May 1973, 4 July 1973 in the first year and 8 July 1974 in the second year by the method shown in fig. D5 except three rows per plot were taken. In the second year 5 x 30 cm row length or equivalent were taken from each of the discard areas, parallel to each of the three plots. Diagnosis in the two years was as for the first and second years of Cultivation Experiment I.

Soil sampling, assay and diagnosis.

Soil core samples were taken on 28 August 1973, before ploughing the stubble of the first year crop, to find whether the more sensitive assessment by assay could detect any spread from the line of inoculum and whether the increase of 'background' inoculum occurred before cultivations. Forty two 5 cm x 10 cm cores were taken from each plot in seven rows of six cores. The central row was taken along the line of the inoculum trench with three parallel rows on either side at distances 27, 62 and 98 cm respectively. Thirty six cores were also

taken from an uninoculated discard beside the plots in rows of six cores taken in line with the 98 cm rows in the plots. The cores were inverted into plastic cups and assayed and diagnosed as described in General Methods, Section B.2 Whole core method.

D.3. RESULTS

D.3.1 Spread of G.G.T. from infested soil cores. (Spread Experiment I. 1971).

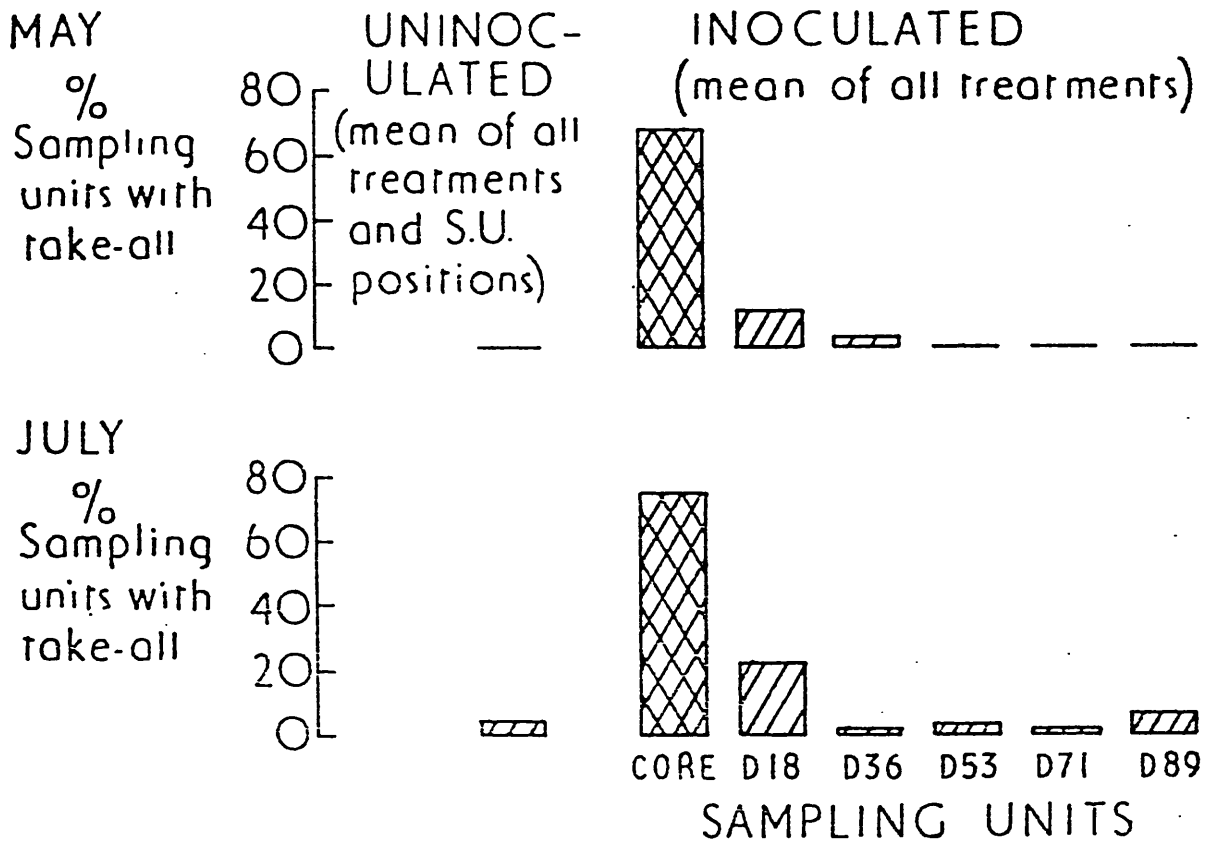
The assay of the sample cores removed during inoculation to measure the 'background' inoculum showed that less than 1% of the cores had any infected plants i.e. only a very small amount of 'background' inoculum was present.

In March almost three quarters of the inoculum cores contained some plants with take-all, most of which were only slightly infected. There had been no spread of infection to plants in surrounding S.U.s.

In May (Fig. D6 and Table D1) there was little change from the March sampling in the number of inoculum cores infected but the number of infected roots they contained had increased. There had been some spread into the D 18 S.U. and a very few infected plants were present in the D 36 S.U. There were no S.U.s with infected plants at greater distances from the core or in any of the uninoculated plots. Neither the dazomet nor the direction of inoculation affected the distance spread or number of roots infected.

In July (Fig. D6 and Table D1) three quarters of the cores contained some plants with take-all and there were more infected roots/core than in May. Nearly a quarter of the D 18 S.U.s contained plants with take-all, mostly these infected plants were next to or only one plant away from the core. A few S.U.s at further distances from the cores and some S.U.s in the uninoculated plots also contained plants with take-all. Dazomet did not affect

FIG. D6. The incidence of take-all at distances from inoculum cores - Spread Experiment I.



% SAMPLING UNITS WITH TAKE-ALL

SAMPLING DATE	INOCULATION	DAZOMET	INOCULUM CORE	D 18	D 36	D 53	D 71	D 89
MAY	ACROSS ROWS	400	87	13	7	0	0	0
		-	47	13	7	0	0	0
	ALONG ROWS	400	73	7	0	0	0	0
		-	67	13	0	0	0	0
	NONE	400	-	0	0	0	0	0
		-	-	0	0	0	0	0
JULY	ACROSS ROWS	400	87	27	0	0	0	0
		-	73	13	7	7	0	13
	DOWN ROWS	400	67	33	0	7	0	7
		-	73	20	0	0	7	7
	NONE	400	-	0	0	33	7	0
		-	-	0	7	7	0	0

TABLE D1. The incidence of take-all at distances from inoculum cores. Spread Experiment I.

	DAZOMET lbs/ acre	Inoculum core	TAKE-ALL				
			D 18	D 36	D 53	D 71	D 89
			IR /core	IR /SU	IR /SU	IR /SU	IR /SU
MAY 1971							
Inoculated	400	3.7	0.1	0.2	0.0	0.0	0.0
across the	-	3.2	0.3	0.1	0.0	0.0	0.0
rows							
Inoculated	400	8.1	0.1	0.0	0.0	0.0	0.0
down the	-	5.2	0.1	0.0	0.0	0.0	0.0
rows							
Uninoculated	400	-	0.0	0.0	0.0	0.0	0.0
	-	-	0.0	0.0	0.0	0.0	0.0
JULY 1971							
Inoculated	400	19.4	2.7	0.0	0.0	0.0	0.0
across the	-	7.2	0.2	0.1	0.3	0.0	0.3
rows							
Inoculated	400	30.5	1.1	0.0	0.1	0.0	0.1
down the	-	7.9	0.3	0.0	0.0	0.1	0.1
rows							
Uninoculated	400	-	0.0	0.0	3.9	0.0	0.0
	-	-	0.0	0.1	0.1	0.0	0.0

IR/SU = G.G.T. infected roots/sampling unit.

the number of these S.U.s with take-all but in the inoculated plots did increase slightly the % of D 18 S.U.s with take-all and also increased the number of roots infected in both the D 18 S.U.s and the cores. The direction of inoculation had no effect.

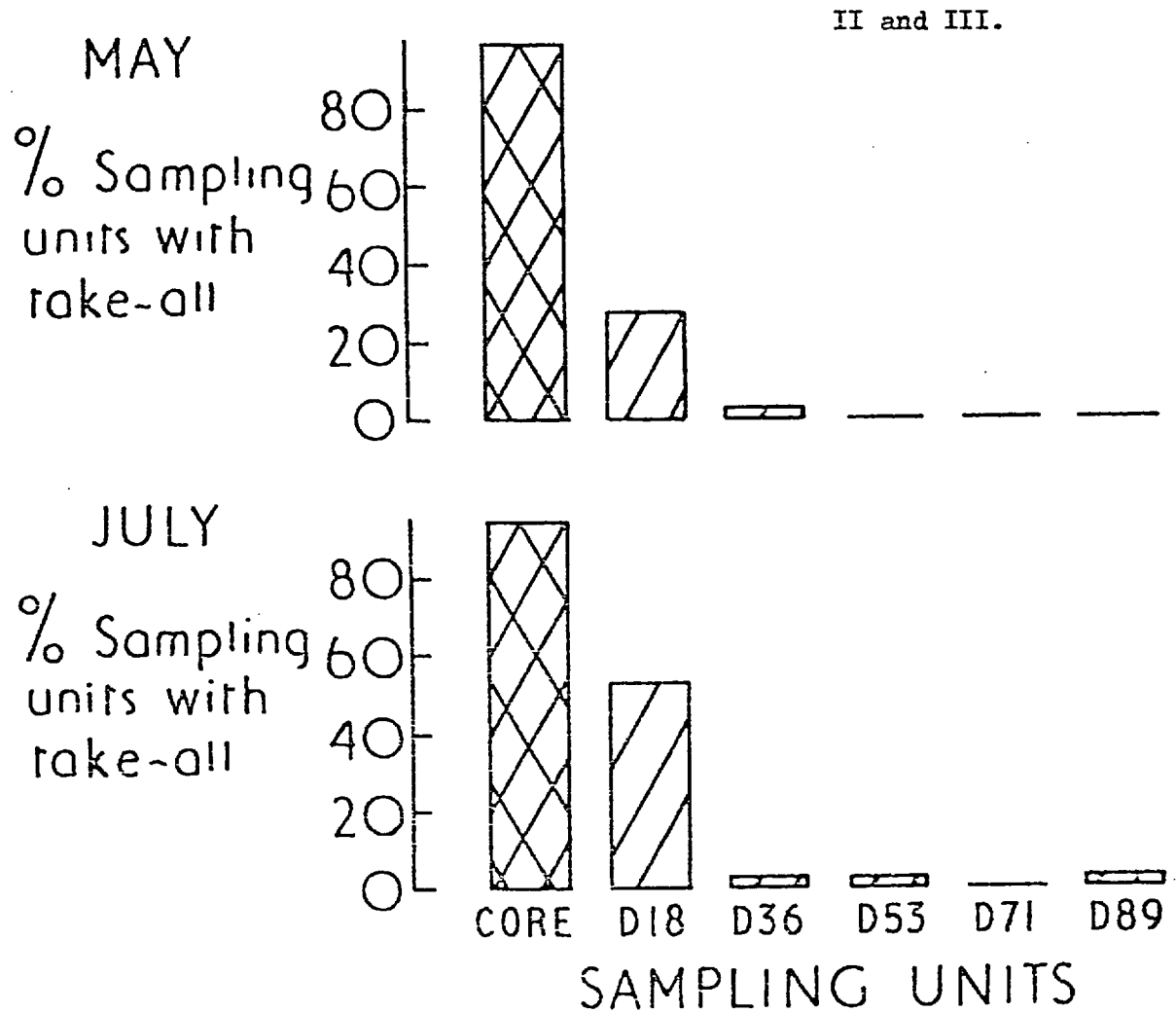
D.3.2 Spread of G.G.T. from infested cores. (Spread Experiments II (1972) and III (1973)).

Of the sample cores 5.6% in 1972 and 0% in 1973 contained plants with take-all when assayed to assess the 'background' inoculum.

In May (Fig. D7 and Table D2) in both years the cores nearly all contained infected plants and infection had spread to some of the D 18 S.U.s but not further, except for a plant with a single root infected in a D 36 S.U. in 1973. The D 18 S.U. between this infected D 36 S.U. and the core was not infected.

In July (Fig. D7 and Table D2) infected plants were present in all inoculum cores and nearly half of the D 18 S.U.s in 1972, and nearly all cores and just over half the D 18 S.U.s in 1973. In 1972 no S.U.s beyond the D 18 S.U. contained infected plants. But in 1973 there were some S.U.s beyond the D 18 S.U. that contained infected plants but only one of these, a D 36 S.U., did not have at least two S.U.s with no infected plants between it and the infected cores. These farther infections would seem to be 'background' infections even though the assay results for 1973 had been negative. The site from which the inoculum came did not affect the distance of spread of G.G.T. though in both years there were differences in the number of roots infected both in the cores and the D 18 S.U.s. In 1973 there were also more of the D 18 S.U.s with take-all when the Meadow inoculum was the source.

FIG. D7. The incidence of take-all at distances from inoculum cores
histograms meaned over inoculum sources and years - Spread Experiments



		% SAMPLING UNITS WITH TAKE-ALL					
DATE OF SAMPLING	SOURCE OF INOCULUM	INOCULUM CORE	D 18	D 36	D 53	D 71	D 89
MAY 1972	PENNELLS	100	33	0	0	0	0
	GEESCROFT	100	11	0	0	0	0
JULY 1972	PENNELLS	100	44	0	0	0	0
	GEESCROFT	100	44	0	0	0	0
MAY 1973	PENNELLS	89	11	11	0	0	0
	MEADOW	100	56	0	0	0	0
JULY 1972	PENNELLS	78	44	11	11*	0	11*
	MEADOW	100	78	0	0	0	0

* at least 2 uninfected sampling units between this infected S.U. and the inoculum core.

TABLE D2. The incidence of take-all at distances from inoculum cores. Spread Experiments II and III.

	CORE	TAKE-ALL ₁				
		D 18	D 36	D 53	D 71	D 89
MAY 1972						
PENNELLS	5.6	0.4	0.0	0.0	0.0	0.0
GEESCROFT	10.0	0.1	0.0	0.0	0.0	0.0
JULY 1972						
PENNELLS	26.8	16.4	0.0	0.0	0.0	0.0
GEESCROFT	14.3	0.7	0.0	0.0	0.0	0.0
MAY 1973						
PENNELLS	12.6	0.1	0.1	0.0	0.0	0.0
GEESCROFT	19.3	0.9	0.0	0.0	0.0	0.0
JULY 1973						
PENNELLS	21.4	3.4	0.1	0.3	0.0	0.1
MEADOW	64.0	25.8	0.0	0.0	0.0	0.0

1 = Infected roots/sampling unit.

D.3.3 The effect of cultivations on the spread of G.G.T. from a line of inoculum. (Cultivation Experiment I 1972-1973).

In the preliminary assessment of soil movement, using soil 'labelled' with fluorescent pigment, strongly fluorescent particles were recorded at distances up to 91 cm from the trench and single specks of fluorescence up to a distance of 244 cm from the trench. (Fig. D8).

The results of the assessment of % liquid fertiliser falling on the soil surface, and the consequent estimation of spray retained on the foliage of the crop is given below:-

	Microlitres of fluorescent solution
Mean from dishes in open	29.60
Mean from dishes in crop	7.45
% spray retained on foliage	= 75%

In May 1972 (Fig. D9 and Table D3) infected plants were present as far as the D356 S.U. in the direction of cultivations. Except for one plant with one infected root only the D 18 S.U. had infected plants present in the direction opposite to that of cultivation, and no infected plants were recorded in the uninoculated plots. The nitrogen fertilisers had no consistent effect on the % S.U.s with take-all but solid nitrogen fertiliser slightly decreased the number of infected roots/S.U. in the inoculated plots (see below).

	Infected roots/S.U.
Solid fertiliser	1.14
Foliar fertiliser	1.74
Nil	2.15
S.E.D. $\pm$	0.56

The nitrogen fertiliser did not affect the total number of seminal and crown roots per plant which were 4.6 and 12.6 respectively.

FIG. D8. Assessment of soil movement with cultivations, by fluorescence of saturn yellow sunbonded pigment 'A' under U/V light.

Cultivation Experiment I First year

	DISTANCE IN CM	TRANSECT		
		A	B	C
	122	—	—	—
	61	—	—	—
	30	—	—	—
	15	—	X	—
	TRENCH WITH SATURN YELLOW			
Direction of cultivations ↓	30	XXX	XXX	XXX
	61	XXX	XXX	XXX
	91	XXX	XX	XX
	122	X	X	XX
	152	X	X	X
	183	X	X	X
	244	X	X	X
	305	—	—	—
	366	—	—	—

XXX = Many soil particles fluorescent

XX = Some " " "

X = Single specks of fluorescence

FIG.D9. The incidence of take-all in May at distances from an inoculum strip after cultivations (meaned over nitrogen rates)

Cultivation Experiment I First year

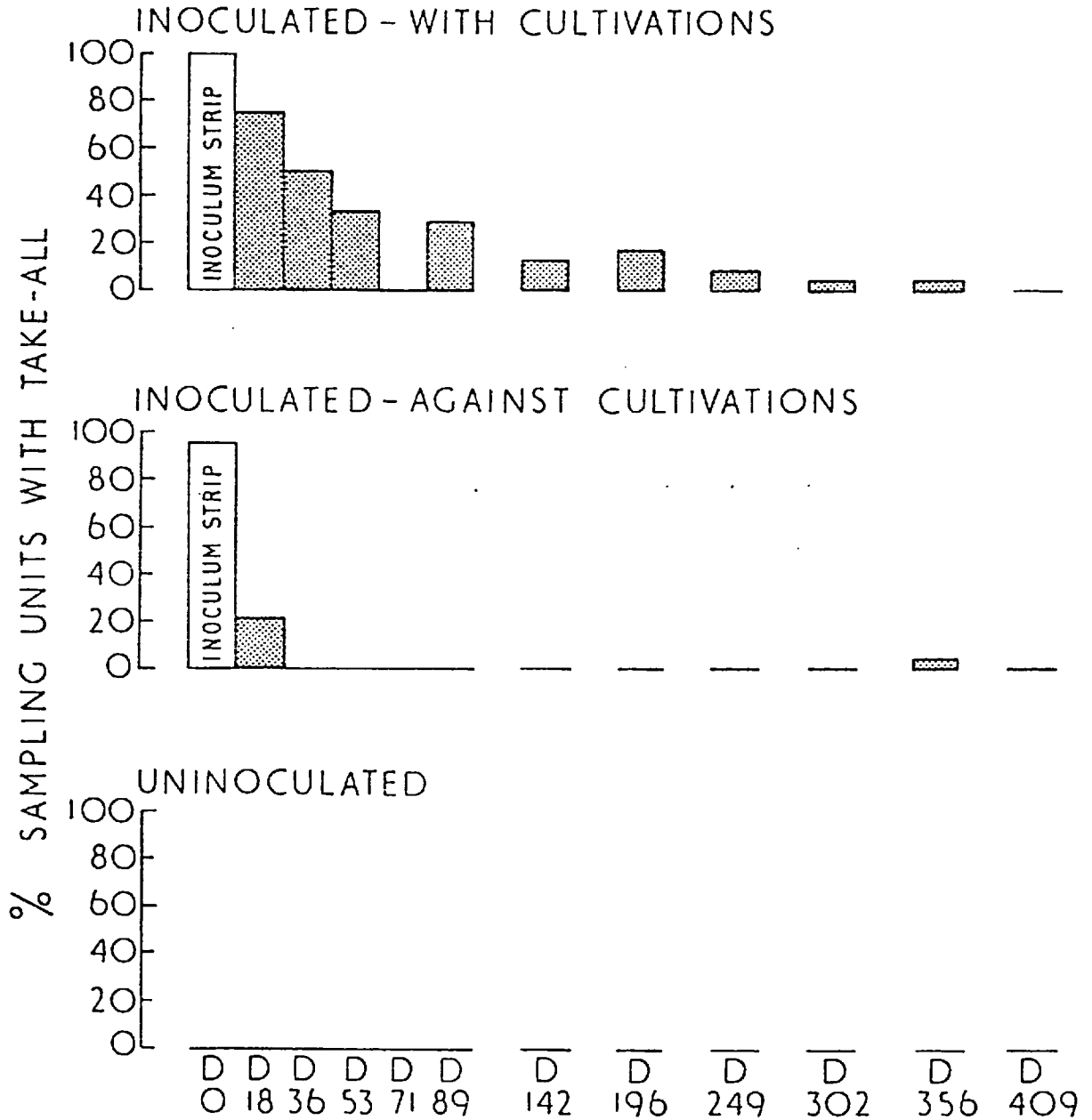


TABLE D3. The incidence of take-all at distances from an inoculum strip after cultivations.

(Meaned over nitrogen rates) Cultivation Experiment I.

NUMBER OF ROOTS WITH TAKE-ALL/SAMPLING UNIT												
	Inoculum strip	D 18	D 36	D 53	D 71	D 89	D 142	D 196	D 249	D 302	D 356	D 409
MAY 1972												
With direction of cultivation	10.5	8.4	2.5	2.8	0.0	0.5	0.3	0.4	0.1	tr	0.1	0.0
Against direction of cultivation	13.3	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	tr	0.0	0.0
Mean of uninoculated S.U.s 0.0												
JULY 1972												
With direction of cultivation	27.4	16.2	9.9	6.5	7.9	2.4	0.5	1.1	0.1	1.7	0.0	0.0
Against direction of cultivation	17.2	2.3	tr	tr	0.0	0.0	0.0	0.0	tr	0.0	0.0	0.0
Mean of uninoculated S.U.s 0.03 (tr)												
JULY 1973												
With direction of cultivation	93.9	72.3	84.6	75.5	70.7	50.6	49.2	68.9	57.8	54.2	57.2	44.0
Against direction of cultivation	78.2	54.9	61.7	54.6	65.8	50.2	62.8	66.4	60.0	65.0	69.0	53.8
Mean of uninoculated S.U.s 46.0												

In July 1972 (Fig. D10) take-all was prevalent as far as the D 89 S.U. in the direction of cultivations, and there was more than 5% of the S.U.s at all distances up to the D 302 S.U. with some infected plants. Against the direction of cultivations only the D 18 S.U. had much take-all; at greater distances there was only a scattering of infected plants, similar to the uninoculated plots which had an average of 1.6% of all the S.U.s with take-all. Nitrogen again had no consistent effect on the distance from the inoculum strip at which take-all was present but solid fertiliser decreased the number of roots infected/S.U. in the inoculated plots (see below).

Infected roots/sampling unit.	
Solid fertiliser	2.7
Liquid fertiliser	4.5
Nil	4.4
S.E.D.	0.69

Nitrogen did not affect the total numbers of seminal and crown roots per plant which were 4.6 and 14.2 respectively.

In July 1973 (Fig. D 11 and Table D3) there was take-all present in at least 80% of S.U.s at all distances from the inoculum strip irrespective of direction of cultivation, and in the uninoculated plots. However the inoculum strip and the S.U.s as far as the D 71 S.U. in the direction of cultivation had slightly more roots infected/S.U. than the uninoculated plots. The infection of plants with take-all was not affected by nitrogen though the total roots/plant was slightly fewer in the unfertilised crops than the crops receiving nitrogen, (16.8 and 22.6 respectively).

FIG. D10. The incidence of take-all in July at distances from an inoculum strip, after cultivations (meaned over nitrogen rates)

Cultivation Experiment I First year

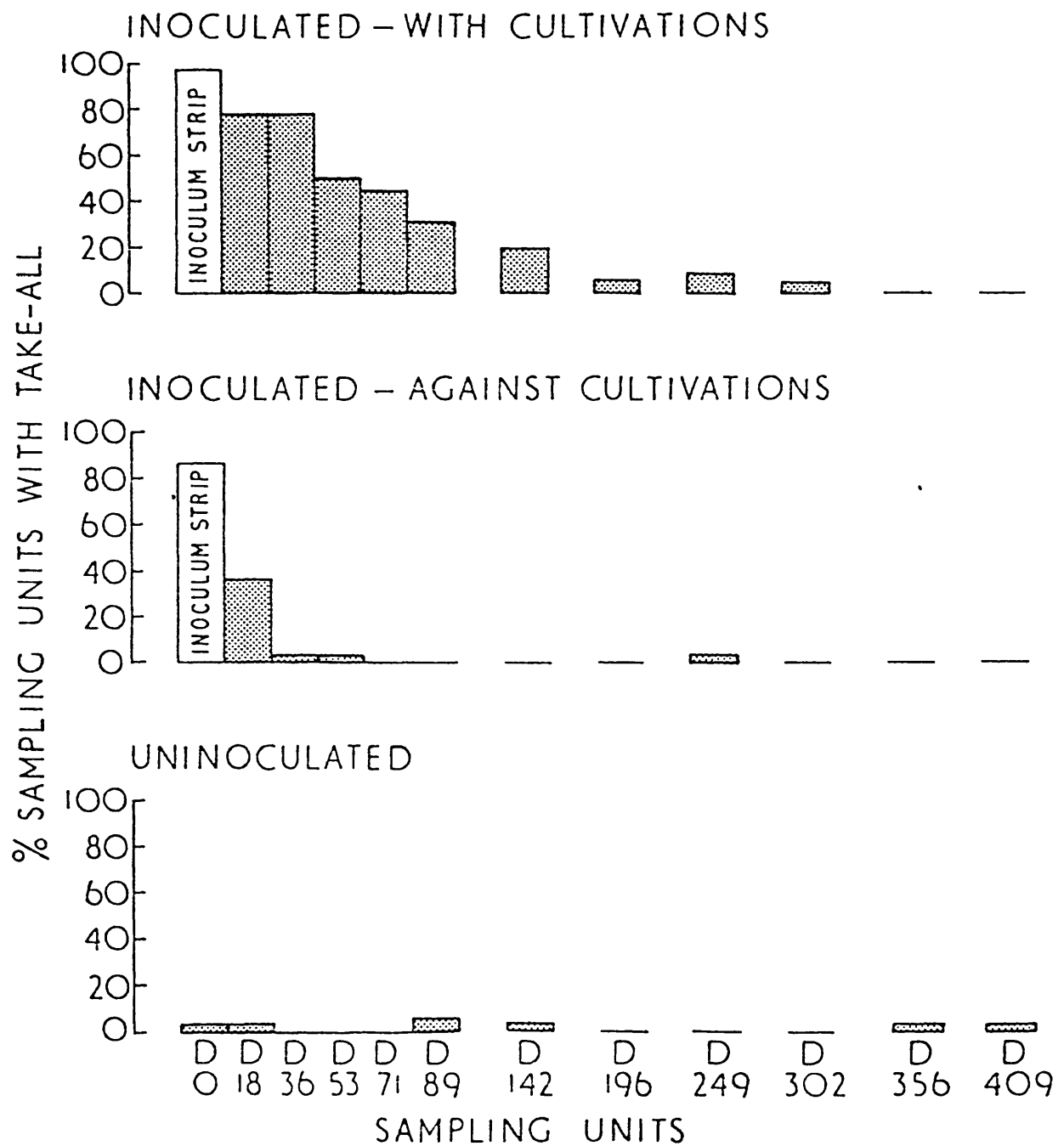
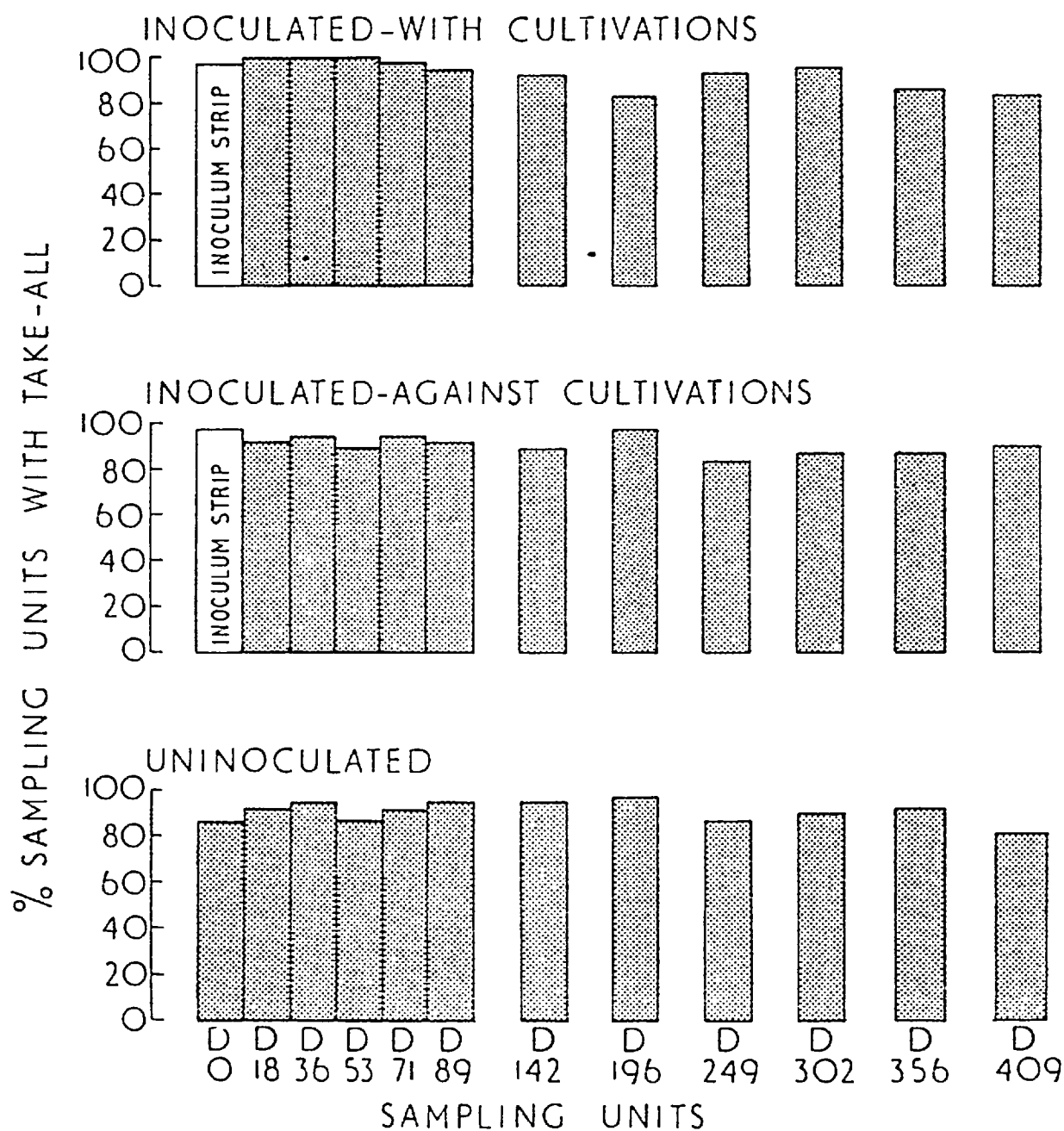


FIG. D11. The incidence of take-all in July at distances from an inoculum strip, after cultivations (meaned over nitrogen rates)

Cultivation Experiment I Second year



D.3.4 The effect of cultivations on the spread of G.G.T. from a line of inoculum. (Cultivation Experiment II 1973-1974).

In May 1973 (Table D4) take-all was present in nearly all the samples from the inoculum strip with an average of 14.6 infected roots/S.U. Take-all was also present on either side of the inoculum strip on scattered plants which had only very slight infections (< 0.1 infected root/S.U.).

In July 1973 (Table D4) plants in the inoculum strip had severe take-all with many more roots infected than were present in the first year of Cultivation Experiment I (76.0 and 22.3 infected roots/S.U. respectively). Take-all was present in half the D 18 S.U.s on either side of the inoculum strip, and a few scattered infected plants were present as far as the D 53 S.U.

The results of the assay done in August 1973 to assess the infestation of the soil on either side of the inoculum strip and also the adjacent uninoculated discard are given below:-

			% cores with Take-all	Infected roots /infected core
		98 cm from inoculum	78	29.8
		62 cm from inoculum	83	26.5
DIRECT		27 cm from inoculum	94	30.2
	OF	Inoculum	100	34.3
CULTIVATIONS		27 cm from inoculum	83	33.6
		62 cm from inoculum	61	27.3
		98 cm from inoculum	89	28.7
		UNINOCULATED discard	84	28.7

From these results it can be seen that the uninoculated discard area had as much G.G.T. present as the areas outside the inoculum strip and this caused as many roots to be infected. This area had not been assayed before the start of the experiment but in autumn

TABLE D4. The incidence of take-all at distances from an inoculum strip after cultivations.

Cultivation Experiment II, First year.

		% Sampling Units with take-all										
	Inoculum strip	D 18	D 36	D 53	D 71	D 89	D 142	D 196	D 249	D 302	D 356	D 409
MAY 1973												
With direction of cultivation	100	11	0	0	11	0	0	0	0	11	0	0
Against direction of cultivation	89	22	22	0	0	33	11	0	0	0	12	12
JULY 1973												
With direction of cultivation	100	44	11	0	0	0	0	0	0	0	0	0
Against direction of cultivation	100	56	11	11	0	0	0	0	0	0	0	0

1972 Spread Experiment III, which was sited only 10 metres away, had no cores with take-all when assayed. A site with a similar previous cropping on the Survival Experiment about 100 m. away had 1.4% cores with take-all when assayed.

In July 1974 there was severe take-all over the whole experiment with no significant difference between the inoculum strip (100% S.U. with take-all, 72 infected roots/S.U.) and all the S.U.s outside the inoculum strip (98% S.U. with take-all and 69 infected roots/S.U.). The cultivated discard had a similar infection. (The equivalent of 100% S.U.s with take-all with 67 infected roots/S.U.). The uncultivated discard also had all the samples infected but only an equivalent of 20 roots infected/S.U. This fewer number of infected roots was a result of the smaller number of volunteer plants in these 30 cm samples.

D.4 DISCUSSION

The major problem encountered in these experiments was the presence of 'background' inoculum which made it very difficult to delimit exact maximum distances of spread of G.G.T. However a general pattern of autonomous spread and of spread aided by cultivation was established.

The maximum distances of autonomous spread of G.G.T. was consistently about 18 cm and spread was only found to have occurred at all in only just over half the rows sampled. There was no major difference in occurrence or distance of spread between the years tested or sources of inoculum used. The method of inoculation using cores might have been thought to limit the spread by smearing the sides of the holes, but as the autonomous spread from the trenches which were not smeared gave the same result this appears unlikely. The average distance of spread when it did occur was

about 10 cm.

The only other work on the spread of G.G.T. done on outside plots in this country (Wehrle and Ogilvie, 1956) recorded a maximum distance of spread of 5 feet (1.52m) which is three times the next largest recorded figure of 20 inches (51 cm) (Adams and Colquhoun, 1935). Two possible explanations for the figure of 1.52 m. are:-

- a) That the site chosen, a light textured soil in a walled garden, was particularly favourable for the growth of G.G.T.
- b) That in spite of the negative result from their three week assay the fungus was present in the soil and infected the plants during the season.

The only other records of measurements of spread in the field come from countries with very different climates to Britain, to which both the host and the fungus might respond differently. Adam and Colquhoun (1935) in Australia reported maximum distances of spread of 20 inches (51 cm), 16 inches (41 cm) and 8 inches (20 cm) for wheat plants spaced in both directions at 2 inches (5 cm), 4 inches (10 cm) and 8 inches (20 cm) respectively. Suzuki et al. (1957) in Japan reported maximum distances of spread of 12, 30 and 45 cm for wheat given chemical fertilisers, wheat straw compost and green alfalfa respectively. Both groups of workers used artificial inoculum and their maximum distances of spread were recorded in soils that Garrett (1936) reports as being very favourable to the spread of G.G.T. i.e. a very sandy soil, and a soil with bulky plant residues incorporated in it. In so far as comparisons can be made, the results of these two groups of workers and my results are similar.

In the first of the experiments studying the effects of cultivation on spread, both in May and June, spread had occurred frequently to a distance of 91 cm and occasionally to 182 cm - 274 cm. The movement of soil 'labelled' with fluorescent dust supported this

result. The different fertiliser applications did not affect the pattern of spread which occurred though the solid fertiliser did slightly decrease the number of infected roots where the disease was present. These nitrogen treatments might have had more effect if the experiment had not followed a fallow, a practice known to leave nitrogen residues in the soil.

There seems to be two possible reasons why the effects of cultivations on spread found in Cultivation Experiment I were not observed in Cultivation Experiment II:-

- a) The inoculum was moved by the cultivations but failed to cause visible lesions on the roots.
- b) The cultivations failed to move the inoculum from the trench.

As the crop in the inoculum strip was more severely infected than in Cultivation Experiment I and spread, presumably autonomous, occurred on both sides of the strip to a distance of 18 cm, there seems no reason to suppose that the inoculum was ineffective. However in Cultivation Experiment II spring tine cultivating was done instead of power harrowing and these tines would probably only penetrate the top 5 cm of soil it is likely that they failed to move any of the inoculum.

The presence of Take-all in nearly all sampling units, of both inoculated and uninoculated crops in the second years of the cultivation experiments prevented any further information on the pattern of spread from the inoculum trenches being obtained. This large amount of take-all in the 2nd wheat crop of the first cultivation experiment might be attributed to the lime applied in the autumn of 1972, however the field had been limed to raise the pH to approx. 8.0 only seven years earlier so the soil should not have been very acid, the same rapid build up was found in the second cultivation experiment

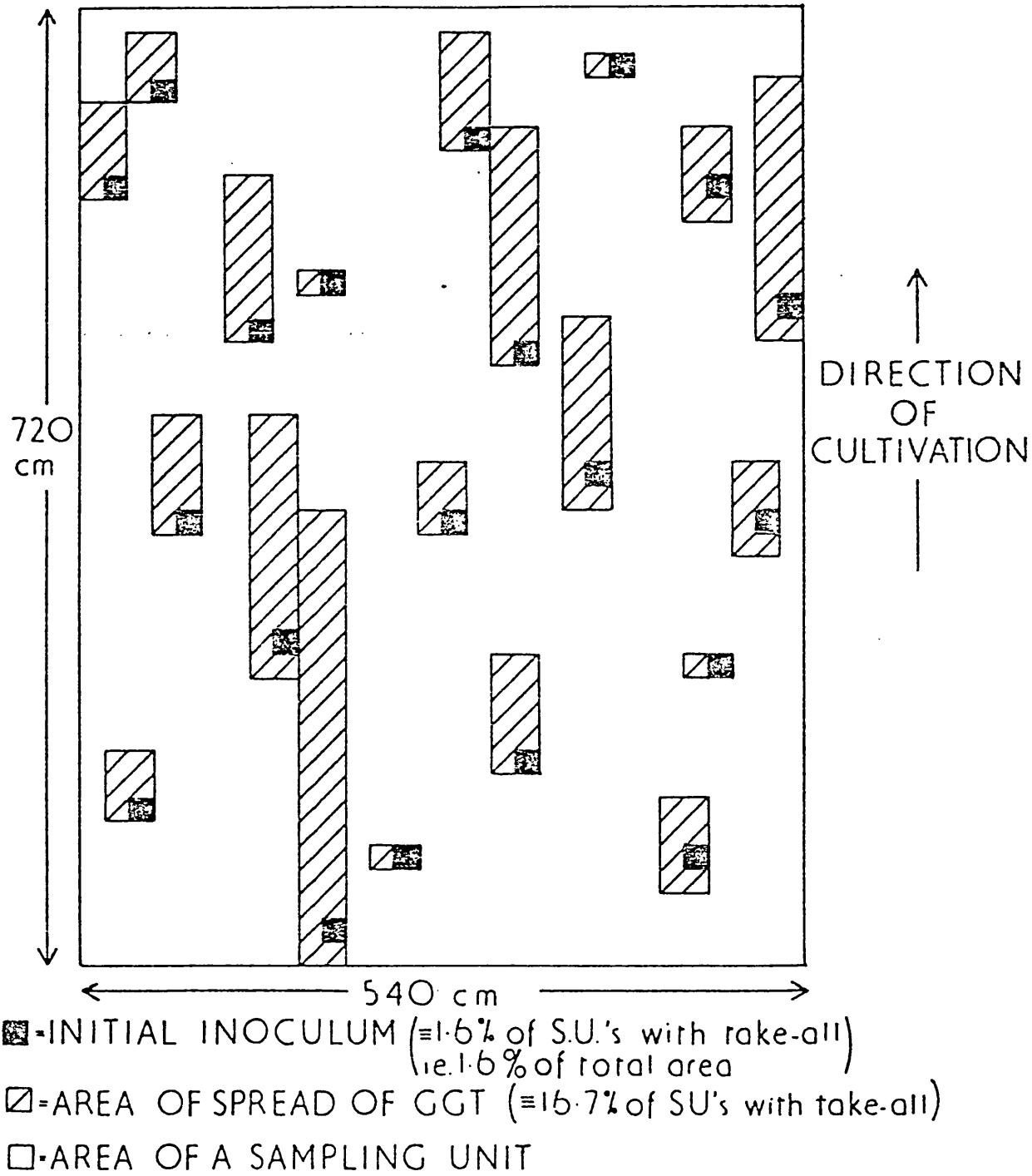
which was limed before the start of its first year. Also Slope and Broom (1973) on a similar soil at Rothamsted found no increase in take-all with liming. It seems most likely that this increase in take-all is not associated with the application of lime.

The possibility that this increase of take-all in the second wheat crop was a result of spread aided by cultivations from the small number of plants (1.6% S.U.s with take-all) in the uninoculated plots is not compatible with the results of spread in the first wheat crop (see fig. D12). Fig. D12 attempts to illustrate the theoretical area of spread which might be expected during a year's wheat crop using the data from my experiments. The diagram is based on the amount of take-all (1.6% of S.U.s infected) in the uninoculated plots at the end of the first wheat crop of Cultivation Experiment I. In ~~fig.~~ ^{Fig.} D12 these 1.6% of S.U.s with take-all have been randomly distributed so that none of the predicted areas of spread overlap. The distances of spread represent the full range of spread found in the inoculated plots of the first wheat in Cultivation Experiment I. (e.g. Take-all was present in 78% of 36 cm S.U.s and in 5% of 196 cm S.U.s). The theoretical pattern of spread thus assumes that mechanical spread from small randomly distributed amounts of inoculum is the same as spread from the inoculum trench. However, as a proportion of the inoculum was not moved from the trench by cultivation it is possible that this assumption overestimates the predicted spread from the 1.6% S.U.s. In ~~fig.~~ ^{Fig.} D12 further to this predicted spread by cultivations an additional area has been added to represent autonomous spread, because in Cultivation Experiment I there was only a limited opportunity for the autonomous spread to be expressed. However, as the additional area represents an autonomous spread of 10 cm from 50% of the inoculum, which was the average of Spread Experiments.

FIG. D12. Diagrammatic representation of the area of spread of G.G.T.

aided by cultivations, from scattered inoculum.

(expressed as % sampling units with take-all)

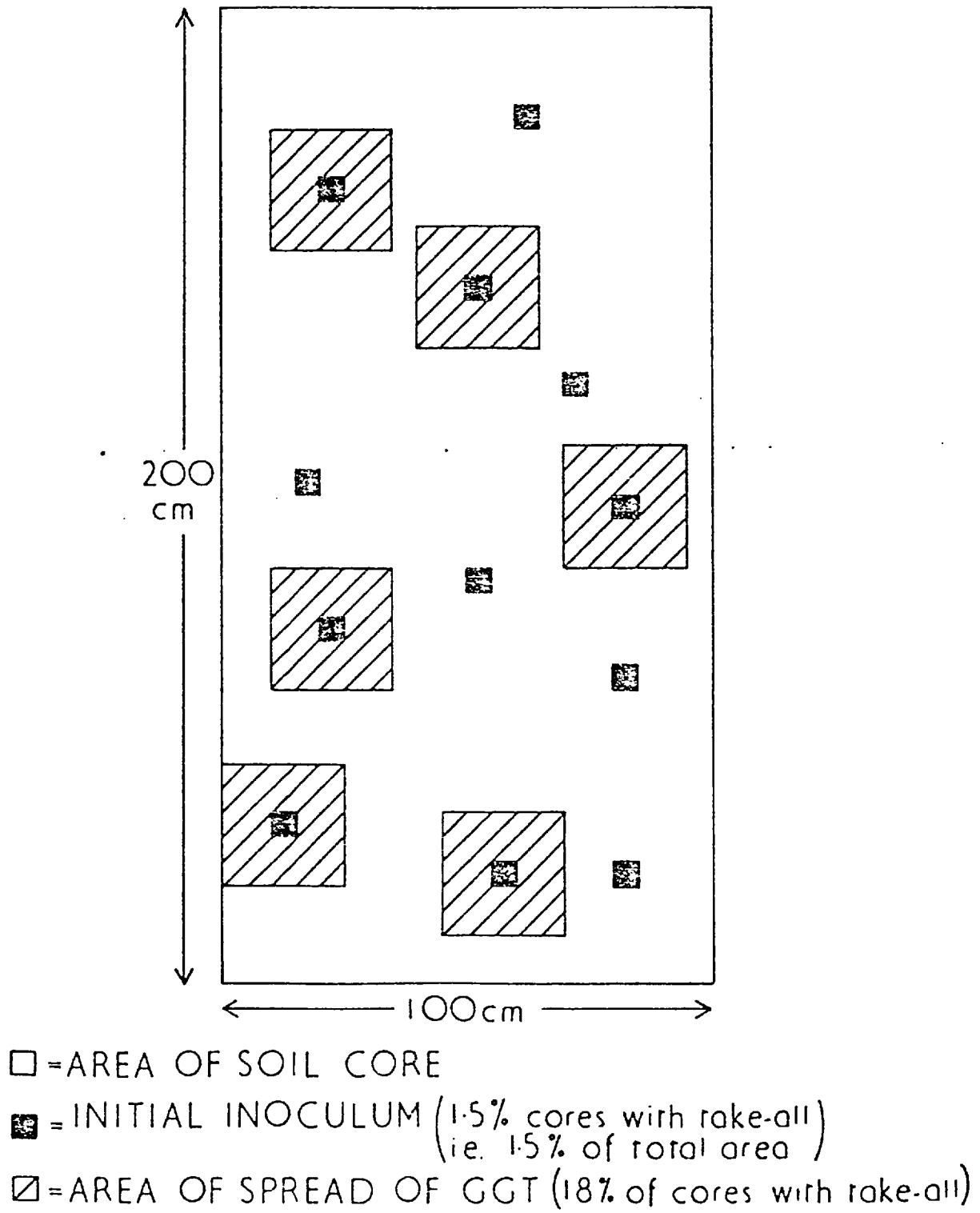


I, II and III, it again probably overestimates the predicted area of spread. Even so the prediction area of spread in fig. D12 would only result in 18.3% S.U.s having take-all at the end of the year in contrast to the actual infection of the uninoculated plots of Cultivation Experiment I at the end of the second year of more than 80% of S.U.s with take-all.

The assay of cores from the second cultivation experiment and its adjacent discards taken after the first wheat but before cultivation of the stubble confirmed that this large increase of take-all in the second wheat crop is not a result of spread by cultivations before the second crop, but takes place during the growth of the first crop. This was also confirmed by the infection of all the samples taken from the 'volunteers' growing in the uncultivated discard. As this increase of take-all occurred on uninoculated as well as inoculated areas the possibility that a very rapid period of spread of G.G.T. from the inoculum strip occurred between the July sampling and harvest can not be the cause.

The rate of autonomous spread as measured in these experiments also precludes as the reason for the increase in take-all, the spread of G.G.T. from the very small amounts of background inoculum present (see ~~fig.~~ fig. D13). Fig. D13 is a theoretical representation of autonomous spread expressed in terms of % cores with take-all in an assay. The initial inoculum is 1.5% cores with take-all, slightly more than the larger of the two figures for the sites adjacent to the second cultivation experiment. In ~~fig.~~ fig. D13 the initially infested cores have been distributed so that there was no overlap in the areas of spread. Spread is assumed to have occurred from 50% of these cores to a distance of 10 cm. With such a pattern of spread the expected % cores with take-all in an assay would be 19% the actual infection in the assay from the field was 80% on the second

FIG. D13. Diagrammatic representation of the area of autonomous spread of G.G.T. (expressed as % assayed soil cores with take-all)



cultivation experiment and 60% on the similar adjacent site of the Survival Experiment.

The increase in take-all occurring in this first wheat crop can not therefore be wholly explained by spread as measured in these experiments. Some further explanation of the increase is needed, three possible explanations are listed below:-

- a) That the fungus spreads much further by autonomous spread along the host roots than 10 cm, but does not cause lesions beyond that distance.
- b) That there is an influx of inoculum during the first wheat crop from outside the area which infects the second wheat crop.
- c) There is background inoculum present in some form in the soil which in the first year is incapable of causing lesions but which builds up, perhaps in response to root exudates, to become infective in the second crop.

Although some spread beyond the visible lesions almost certainly does occur explanation a) does not seem to be a satisfactory answer as uninoculated crops in the second year of the Cultivation Experiment I and cores from uninoculated areas at the end of the first year of Cultivation Experiment II had very similar amounts of take-all as those from inoculated areas. Also it would be expected that unlesioned roots taken from 1st wheat crops if used as inoculum in an assay would result in as much infection as soil taken from the same first wheat crop, this was not found to be so. (See Section C.3.2 page 51).

Explanation b) seems more possible, with wind blown ascospores or very small pieces of debris as the inoculum. However, in the survival experiment differential patterns of infection were observed in the assay in the spring of the 1st wheat crop, and these should

have been reflected in the infection of the crop, in July but this was not so. Therefore unless explanation c) is also accepted explanation b) does not seem possible.

Explanation c) seems the most likely one. Hornby (1975) has shown that the same soil assayed at different temperatures gave different amounts of infection, this demonstrates that the environment affects which pieces of inoculum are capable of causing infection. Brown and Hornby (1971) also reported that small mycelial fragments require a feeding phase, development of saprophytic growth followed by colonisation of root hairs, prior to infection of the seminal axes. Generally hyphae in the root hairs did not grow directly into the root. In their observations infection of the seminal axis occurred within a few weeks of root hair colonisation however it is possible that with even smaller fragments of inoculum this feeding phase may take a whole season. This increase in the ability of the inoculum to cause infection was described by Garrett (1956) as an increase in 'inoculum potential'. The form of this inoculum, that at present is not detected in our assays and how it develops need further study.

E. CONTROL OF SOIL-BORNE PATHOGENS OF CEREALS BY 'BREAK CROPS'

E.1 INTRODUCTION

Although rotations have been in use from the early days of agriculture it was only in the middle of the 19th century that field experiments on crop rotations were started. In one of the first of these rotational experiments, started at Rothamsted in 1852, Lawes and Gilbert (1894) showed that large increases in yield were gained by growing wheat or barley in rotation rather than continuously. They attributed this increase to differences in soil fertility and showed that the application of fertilisers, in particular nitrogen, lessened the differences in yield between rotationally and continuously grown crops.

Early in the 20th century it was recognised that foot and root diseases also contributed to the loss in yield of continuously grown wheat or barley, Waters (1920) and Sprague and Fellows (1934) showed respectively that take-all and eyespot were more common on consecutive wheat crops. Other workers have since shown that a one year 'break', i.e. one year without a susceptible host diminished the G.G.T. population sufficiently to ensure that a following wheat crop suffered little loss from take-all (Russell, 1934) but that a longer break was needed to ensure good control of eyespot (Glynne and Moore, 1949). Macer (1961 b) showed that the long break was needed for eyespot control because Pseudocercospora hepotrichoides could survive on buried straw for at least three years. The effect of a number of different 'break' crops on take-all and/or eyespot have been compared by many workers on the continent, (Bockmann and Knoth 1965; Defosse and Rixhon 1968; Seidel and Fischer 1967; Seidel 1969) and also in this country (Doling and Batts 1960; Hood and Proctor 1961). Generally there was little difference in

the control of take-all or eyespot in the following susceptible cereal but in some experiments oats did not give as good control of either disease as other break crops. However at Rothamsted the strain of the take-all fungus that attacks oats, Gaeumannomyces graminis var. avenae, is not present and spring oats have been effective as break crops (Slope, pers. comm.; Slope and Etheridge, 1971).

The effect of 'break crops' on the succeeding wheat or barley crop may not only be by the decrease in soil-borne pathogens but also by an increase in available soil nutrients, particularly in mineralisable soil nitrogen. Because of the ability of various species of the bacterium Rhizobium to nodulate roots of most leguminous crops and of these nodules to fix nitrogen, leguminous break crops can leave large amounts of available nitrogen. The beneficial effects of available nitrogen left after various one year leys, including a clover ley, on the yield of a following winter wheat crop were reported by Widdowson, Penny and Williams (1963) and Gasser (1968). However in some circumstances break crops may decrease the amount of available nitrogen. Gasser and Mitchel (1968) and Widdowson and Penny (1970) showed that when a grass ley was ploughed in late (November/December) the amount of nitrogen available to the following spring barley was much less than from a preceding spring wheat crop. Cooke (1969) reviews the amounts of nitrogen residues from various crops and relates them to the fertiliser requirements and yields of subsequent crops.

Changes in available nitrogen in soil may also affect the incidence of take-all. For example Garrett and Mann (1948) showed that barley following barley undersown with trefoil had less take-all than when following barley not undersown. They attributed this decrease in take-all to changes in amounts of nitrogen available in

the soil. They suggested that when the trefoil was growing after harvest of the barley, available soil nitrogen was limited and thus the G.G.T. did not survive well; and that when the trefoil was ploughed in it released soil nitrogen thus helping the following barley crop withstand any development of take-all that did occur. Thus it is difficult to distinguish between the effects of decreased fungal population, of changes in mineralisable soil nitrogen and of interactions between them on the yield of wheat or barley following a break crop.

G.V. Dyke and D.B. Slope attempted to resolve this question of the relative benefits of nitrogen residues and decreased soil-borne pathogen populations in an experiment (Dyke, 1968) testing previous cropping systems, including oats and barley, that might be expected to leave different nitrogen residues, on a following spring barley crop. It was hoped that oats and barley would leave almost equal amounts of available nitrogen but that oats would be unaffected by and decrease the pathogen populations as did the other break crops. Because barley is not grown as commonly as winter wheat as the first cereal after a 'break' and also because winter wheat suffers more damage by take-all and eyespot, a series of three experiments were started by G.V. Dyke and myself using the sequence winter wheat then spring barley to test the effects of various previous crops. The previous cropping tested included leguminous crops, which were expected to leave considerable nitrogen residues, clover, beans and trefoil undersown in both oats and barley, and oats and barley by themselves. It was hoped that with this cropping, together with a range of nitrogen applied to the test crops, the effects of diseases and nitrogen residues could be separated and that some measure of their interaction could be obtained particularly from the various undersowing comparisons. Maize was also included

in two of the experiments to test its effectiveness as a break crop to decrease take-all. Robinson and Lucas (1967) had reported that maize was infected by G.G.T. and was not an effective break crop but I had shown (1970) in pot experiments maize did not become infected in naturally infested soil though it did in a soil artificially inoculated with G.G.T. Although the three experiments were done collaboratively by G.V. Dyke and myself, I was solely responsible for the work reported in this section.

E.2 MATERIALS AND METHODS

One experiment was started in each of three successive years on three fields on Rothamsted Experimental Station Farm. The names, soil types and cropping of the three fields are given below:-

	EXPERIMENT I	EXPERIMENT II	EXPERIMENT III
FIELD	LONG HOOS III	GEESCROFT	FOSTERS WEST
SOIL	Sandy clay loam	Flinty silt loam	Flinty silt loam
CROPPING			
1966	spring wheat	-	-
1967	spring beans	oil seed rape	-
1968	winter wheat	spring wheat	spring barley
1969	1st year of expt.	spring barley	oil seed rape
1970		1st year of expt.	winter wheat
1971			1st year of expt.

Each experiment consisted of one years treatment cropping, followed by a winter wheat test crop and then a second test crop of spring barley.

E.2.1 Treatment Cropping

The treatment crops were similar in all three experiments except that maize was not grown in Experiment I:-

1st year treatment crops.

Barley

Barley undersown with trefoil

Oats

Oats undersown with trefoil

Beans

Clover

Maize (Expts II and III only)

Clover and bean crops were given no fertiliser nitrogen. A comparison of two amounts of nitrogen, 50 or 100 kg N/ha, was made on the barley, with and without undersowing in the first two experiments; in the third experiment all barley and oat crops were given 50 kgN/ha. Two amounts of nitrogen, 100 or 200 kg N/ha, were tested on maize in the two experiments it was grown. The varieties, dates of sowing and dates of applying the nitrogen are given in Table E1. The design and amounts of basal fertilisers for Experiment I are given in Fig. E1, the basal fertilising was the same for the other two experiments.

Crop sampling and disease assessment.

The barley crops were sampled in early July each year; two sets of six samples of 30 cm row length were taken using 'Fixed pattern' sampling and assessed for foot and root rots as described in General Methods, Section B.1.

The maize crops were sampled in August 1970 and in September 1971; two sets of six samples, each of two plants, were taken per plot using 'Fixed pattern' sampling and assessed for foot and root

TABLE E1

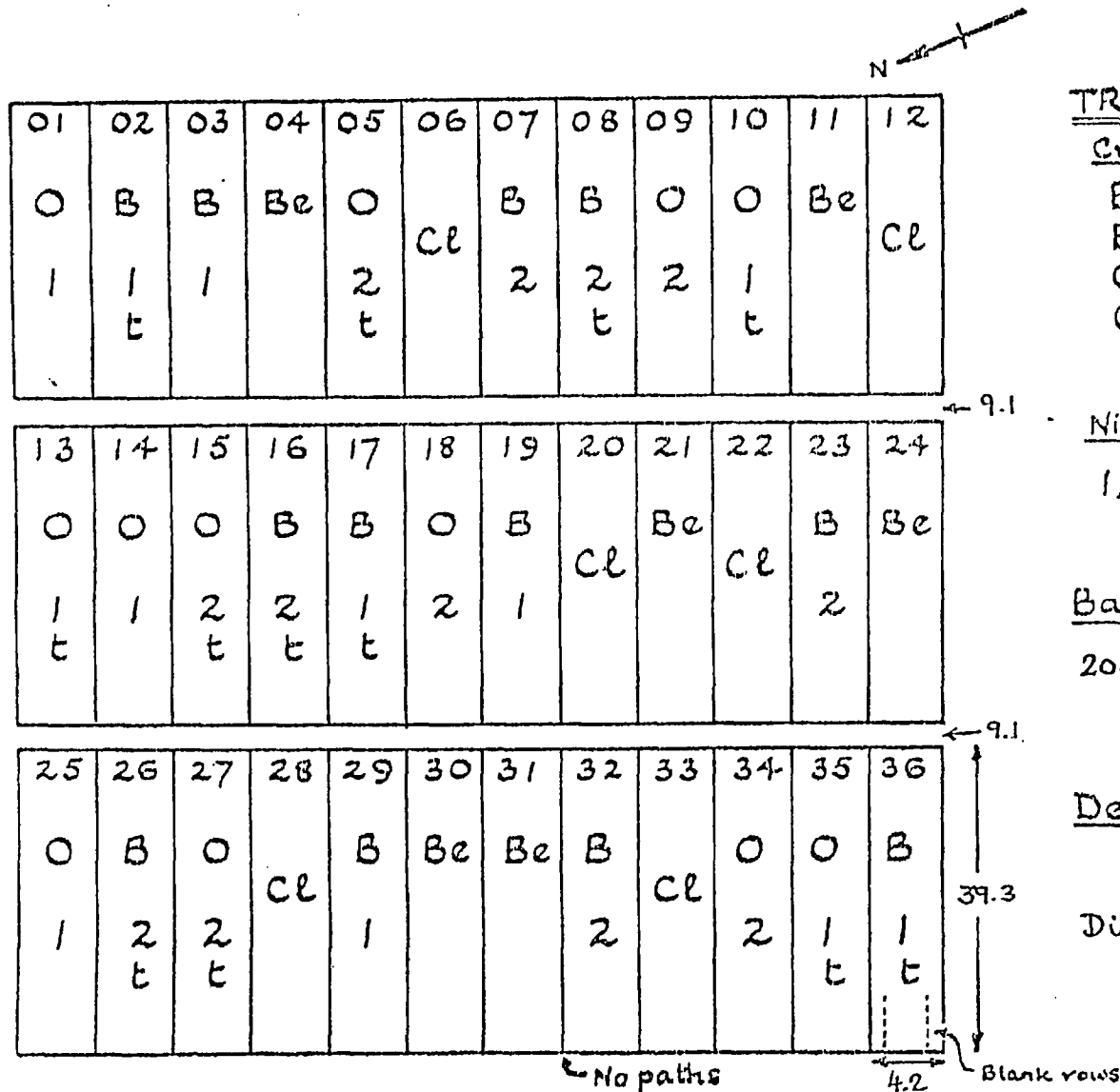
VARIETIES, DATES OF SOWING AND DATES OF NITROGEN APPLICATION FOR THE TREATMENT CROPS

	variety	1969 EXPERIMENT I		variety	1970 EXPERIMENT II		variety	1971 EXPERIMENT III	
		sown	N applied		sown	N applied		sown	N applied
BARLEY	Zephyr	26 March	2 April	Julia	17 April	17 April	Julia	27 Feb.	24 March
OATS	Manod	26 March	2 April	Manod	17 April	17 April	Manod	4 March	24 March
TREFOIL	English*	28 March	-	English*	7 May	-	English*	13 April	-
CLOVER	Broad Red	28 March	-	Broad Red	28 April	-	Essex broad -leaf red	28 April	-
BEANS	Maris Bead	26 March	-	Maris Bead	17 April	-	Maris Bead	25 Feb.	-
MAIZE	-	-	-	Marliking	15 May	17 April	Pioneer 131	10 May	6 May

* All trefoil seed inoculated with Rhizobium

FIG. E1. The design and basal treatments for Experiment I treatment cropping.

LONG Hoos III 1st year 1969



TREATMENTS

Crops

- B Barley
- Be Beans
- Cl Clover
- O Oats
- t Trefoil undersown

Nitrogen per acre

- 1, 2 50, 100 kg N as 'Nitro-Chalk' 21 to barley and oats, in seedbed.

Basal manuring, per

- 200 kg compound fertiliser (0:20:20) across plough furrow

Design: 3 blocks of 12 plots sub-divided in 1970 for N to W. wheat.

Dimensions in metres.

rots as described in General Methods, Section B.1.

Assays for G.G.T.

An assessment of the G.G.T. present in soils after the different treatment cropping was made on four soil cores, 5 cm diameter x 15 cm deep, per plot taken after ploughing in November or early December. The soils were assayed by the mixed soil method 'A' as described in General Methods, Section B.2.

To compare the relative effects of maize and barley on G.G.T. populations it was necessary to know whether the amount of G.G.T. in the maize plots changed during the period between the establishment of the barley and maize crops. Therefore the soils of the maize plots were sampled on two occasions, when the barley and the maize crops respectively had clearly emerged, G.S. 1 (1st leaf stage). The dates of sampling of the two experiments were:-

	EXPERIMENT II	EXPERIMENT III
First core sampling	1 May 1970	16 April 1970
Second core sampling	3 June 1970	1 June 1970

At each sampling eight cores, 5 cm diameter x 15 cm deep, were taken and assayed by the mixed soil method 'A', General Methods, Section B.2.

To see if G.G.T. was carried over on maize roots which had no take-all lesions the root systems of one maize plant assessed as clean from each plot of Experiment III was assayed. The root system was cut into approx. 4 cm long pieces mixed with sand and then assayed as for mixed soil method 'A', Section B.2.

E.2.2 Wheat Test Cropping

All plots were sown in autumn with winter wheat var. Joss Cambier sown at 200 kg/ha combine drilled with 314 kg of 0:20:20 N.P.K. compound fertiliser. An additional dressing of 125 kg K₂O was given

to the clover plots before ploughing. In spring each plot was split to test four amounts of nitrogen fertiliser 0, 50, 100, 150 kg N/ha broadcast as Nitro chalk in April each year. These nitrogen treatments were randomly arranged within each whole plot.

Crop sampling, disease assessments and yields.

One set of four samples of 30 cm row lengths were taken, using fixed pattern sampling, from each sub plot in the first week of July each year and assessed for foot and root rots as described in General Methods, Section B.1.

Crops were combine harvested, grain yields recorded, grain dry matters determined and yields all adjusted to 85% dry matter.

E.2.3 Barley Test Cropping

All sub plots were sown with spring barley var. Julia, which in experiments II and III was dressed with Ethirimol seed dressing, and combine drilled with 314 kg/ha 0:20:20 N.P.K. compound fertiliser. The same amounts of nitrogen were applied to the same sub plots as to the winter wheat test crop.

Crop sampling, disease assessments and yields.

These operations were done as described for the winter wheat test crop except only take-all was assessed.

E.3 RESULTS

E.3.1 Treatment Cropping

Table E2 shows the incidence of take-all and eyespot on barley on all three experiments. Take-all was common in Experiment I but none of the crops were severely attacked. Undersowing had no effect on the incidence of take-all but increasing the nitrogen fertiliser decreased the disease. Eyespot was negligible in Experiment II and only slight in the other two experiments. Neither undersowing nor different amounts of nitrogen affected the incidence of eyespot.

The maize plants had some discoloured roots but the lesions were not typical of take-all and subsequent isolation did not yield G.G.T. In Experiment II 4.9% of the maize stems had sharp eyespot lesions.

Assays for G.G.T.

In the soils after treatment cropping G.G.T. was prevalent after the barley crops in all experiments (Table E3); there was no consistent effect of either undersowing or of different nitrogen applications to the barley crop. There was only little G.G.T. and no differences after any of the break crops.

There was no difference in G.G.T. between the first and second sampling of the maize plots, as shown below:-

	% assay seedling roots with take-all	
	EXPERIMENT II	EXPERIMENT III
1st sampling	27	6
2nd sampling	32	1
S.E.D. $\pm$	4.5	3.4

However in Experiment II, the nitrogen treatments were applied to the maize plots at the time of sowing the barley and so differed in

TABLE E2. The incidence of take-all and eyespot on the spring barley treatment crops for Experiments I, II and III.

		EXPERIMENT I	EXPERIMENT II	EXPERIMENT III
		% PLANTS WITH TAKE-ALL		
BARLEY	kg N/ha 50	40 (8) ¹	27 (0)	26 (6)
BARLEY U/S ³ TREFOIL	50	44 (16)	22 (0)	16 (4)
BARLEY	100	28 (5)	17 (0)	-
BARLEY U/S TREFOIL	100	24 (2)	19 (0)	-
S.E.D. $\pm$		7.49 (5.99)	4.46 (-)	6.22 (3.19)
% STRAWS WITH EYESPOT				
BARLEY	50	23	tr ²	23
BARLEY U/S TREFOIL	50	27	tr	18
BARLEY	100	27	tr	-
BARLEY U/S TREFOIL	100	22	1.0	-
S.E.D. $\pm$		7.12	(-)	3.92

1 figures within brackets are % plants with moderate + severe take-all.

2 tr = <0.5% straws infected

3 U/S = undersown

TABLE E3. The incidence of G.G.T. in soils after different treatment cropping - Experiments I, II and III.

% ROOTS WITH TAKE-ALL

	kg N/ha	EXPERIMENT I	EXPERIMENT II	EXPERIMENT III
BARLEY	50	67	34	15
BARLEY	100	52	41	-
BARLEY U/S ² TREFOIL	50	56	32	25
BARLEY U/S TREFOIL	100	64	30	-
OATS	50	3	5	2
OATS	100	2	3	-
OATS U/S TREFOIL	50	2	5	tr ¹
OATS U/S TREFOIL	100	2	1	-
CLOVER	0	5	2	tr
BEANS	0	3	6	1
MAIZE	100	-	1	1
MAIZE	200	-	1	0
S.E.D. $\pm$		8.99	6.18	4.01

1 tr = less than 0.5% roots infected

2 U/S = undersown

the amount of nitrogen in the soil at both sampling dates, the larger nitrogen dressing decreased the percentage of roots with take-all as shown below:-

Nitrogen applied to the maize plots	% assay seedling roots with take-all
100 kg N/ha	44
200 kg N/ha	23
S.E.D. $\pm$	5.8

In the assay of maize roots from Experiment III, which had been diagnosed as clean, one plant root system of the 12 assayed produced G.G.T. infection on the assay seedlings.

E.3.2 Wheat Test Cropping

Tables E4, E5 and E6 show that take-all was common and severe on wheat following barley in all experiments, but was much less prevalent and mostly slight following all other crops in Experiments I and III. In Experiment II, wheat following crops other than barley had more take-all than on the other two experiments, particularly following some oat plots. Agrostis gigantea was present on this site and developed most abundantly in patches within the oat crop which had been severely damaged by Oscinella frit. The presence of Agrostis gigantea, which is moderately susceptible to G.G.T. may explain the unexpectedly large amounts and irregular occurrence of take-all following the break crops. Increasing the nitrogen applied to the wheat decreased the amount and severity of take-all in Experiment III but its effect on the other two experiments was smaller and inconsistent. There was no consistent effect of either undersowing or the different amounts of nitrogen given to the treatment crops on the incidence of take-all.

Table E7 shows that the wheat yields in Experiment I were

TABLE E4.

The incidence of take-all in July on winter wheat following
different previous cropping - Experiment I 1970.

% PLANTS WITH TAKE-ALL						
TREATMENT CROPPING	kg N/ha	0	50	100	NITROGEN kg/ha. 150	MEAN
BARLEY	50	90 (45) ¹	92 (39)	87 (40)	94 (47)	91 (43)
BARLEY	100	96 (59)	92 (45)	87 (29)	79 (33)	89 (42)
BARLEY U/S ² TREFOIL	50	93 (52)	98 (64)	90 (41)	90 (49)	93 (52)
BARLEY U/S TREFOIL	100	95 (39)	91 (40)	91 (41)	91 (50)	92 (43)
OATS	50	9 (1)	5 (1)	4 (0)	6 (0)	6 (tr)
OATS	100	5 (0)	5 (0)	2 (0)	2 (0)	4 (0)
OATS U/S TREFOIL	50	3 (1)	4 (0)	6 (0)	3 (0)	4 (tr)
OATS U/S TREFOIL	100	9 (1)	3 (0)	6 (0)	7 (0)	6 (tr)
BEANS	0	6 (0)	4 (1)	9 (0)	5 (0)	6 (tr)
CLOVER	0	6 (0)	13 (2)	9 (2)	9 (1)	9 (2)
S.E.D. [±]		6.60 (8.27)			4.40 (5.27)	

1 figures within brackets are % plants moderate + severe take-all

2 U/S = undersown.

TABLE E5.

The incidence of take-all in July on winter wheat following
different previous cropping - Experiment II 1971.

% PLANTS WITH TAKE-ALL						
TREATMENT CROPPING	kg N/ha	NITROGEN kg/ha.				MEAN
		0	50	100	150	
BARLEY	50	84 (53) ¹	88 (56)	81 (48)	79 (49)	83 (51)
BARLEY	100	88 (60)	86 (49)	84 (46)	68 (29)	81 (46)
BARLEY U/S ² TREFOIL	50	93 (65)	98 (74)	86 (56)	81 (40)	89 (58)
BARLEY U/S TREFOIL	100	77 (37)	55 (29)	86 (41)	72 (31)	72 (35)
OATS	50	28 (11)	25 (9)	9 (tr)	5 (0)	17 (5)
OATS	100	19 (3)	4 (0)	5 (0)	9 (2)	9 (1)
OATS U/S TREFOIL	50	47 (20)	30 (6)	10 (3)	10 (4)	24 (9)
OATS U/S TREFOIL	100	33 (12)	11 (0)	13 (2)	13 (4)	17 (5)
MAIZE	100	14 (1)	10 (0)	20 (7)	8 (0)	13 (2)
MAIZE	200	10 (2)	10 (1)	7 (1)	2 (0)	8 (1)
BEANS	0	18 (5)	16 (2)	15 (3)	7 (1)	14 (3)
CLOVER	0	29 (10)	13 (4)	11 (2)	13 (5)	16 (5)
S.E.D. $\pm$		12.05 (8.40)				8.26 (4.52)

1 figures within brackets are % plants with moderate + severe take-all

2 U/S = undersown

TABLE E6.

The incidence of take-all in July on winter wheat following
different previous cropping - Experiment III 1972

% PLANTS WITH TAKE-ALL						
TREATMENT CROPPING	kg N/ha	NITROGEN kg/ha.				MEAN
		0	50	100	150	
BARLEY	50	98 (65) ¹	88 (48)	54 (25)	71 (33)	78 (43)
BARLEY U/S TREFOIL	50	90 (60)	84 (53)	83 (48)	65 (33)	81 (48)
OATS	50	5 (4)	6 (2)	4 (0)	1 (0)	4 (2)
OATS U/S TREFOIL	50	7 (2)	2 (tr)	0 (0)	0 (0)	2 (1)
MAIZE	100	0 (0)	3 (0)	1 (0)	4 (0)	2 (0)
MAIZE	200	18 (9)	4 (0)	2 (tr)	3 (1)	7 (2)
BEANS	0	4 (1)	10 (4)	5 (1)	4 (2)	6 (2)
CLOVER	0	5 (2)	6 (3)	11 (8)	1 (1)	6 (3)
S.E.D. [†]		7.99 (6.66)				3.76 (3.28)

1 figures within brackets are % plants moderate + severe take-all

TABLE E7.

The yield of winter wheat after different previous
cropping in Experiments I, II and III.

TREATMENT CROPPING	kg N/ha	EXPERIMENT I					EXPERIMENT II GRAIN t/ha. nitrogen kg/ha.					EXPERIMENT III				
		0	50	100	150	MEAN	0	50	100	150	MEAN	0	50	100	150	MEAN
BARLEY	50	1.31	1.48	1.90	1.92	1.66	2.73	3.94	4.32	4.26	3.81	2.26	3.93	5.17	4.56	3.98
BARLEY	100	1.18	1.64	2.15	2.35	1.83	2.51	3.90	4.13	4.61	3.79					
BARLEY U/S ¹	50	1.87	1.83	2.23	2.27	2.06	3.38	3.74	4.48	4.20	3.95	3.93	4.73	4.90	4.49	4.51
BARLEY U/S	100	1.72	2.06	2.26	2.11	2.03	3.73	4.47	4.36	4.42	4.25					
OATS	50	2.59	3.35	3.56	3.92	3.35	3.52	4.97	5.50	5.36	4.84	3.19	5.13	5.54	5.09	4.74
OATS	100	2.97	3.70	3.79	4.20	3.66	4.06	5.66	5.71	5.42	5.21					
OATS U/S	50	3.04	3.76	4.15	4.49	3.87	3.65	5.27	5.66	5.18	4.94	4.25	5.29	5.69	5.03	5.07
OATS U/S	100	2.91	3.39	3.98	3.99	3.56	4.40	5.10	5.60	5.36	5.11					
MAIZE	100						4.79	5.59	5.72	5.07	5.29	4.23	5.59	5.40	5.03	5.06
MAIZE	200						5.20	5.70	5.63	5.10	5.41	5.28	5.84	5.37	4.78	5.32
BEANS	0	3.53	4.21	4.29	4.66	4.17	4.53	5.72	5.81	5.54	5.40	4.54	5.48	5.51	4.95	5.41
CLOVER	0	4.60	4.77	4.94	4.95	4.82	4.49	5.56	5.50	5.16	5.18	5.74	6.06	5.21	4.60	5.12
S.E.D. $\pm$			0.301			0.240		0.322			0.194		0.256			0.106

¹ U/S = undersown with trefoil

smaller than in the other two experiments, but in all experiments yields after barley were less with each amount of nitrogen than after other crops. Where given no nitrogen yields of wheat following break crops were smallest after oats and largest after clover or maize, but with increasing amounts of nitrogen these differences decreased. Fig. E2 shows the wheat yields and take-all ratings following some of the treatment crops. Fig. E3 shows the effect of undersowing on the wheat yields and take-all ratings. Where given no nitrogen yields were greater with undersowing though there was no effect on take-all.

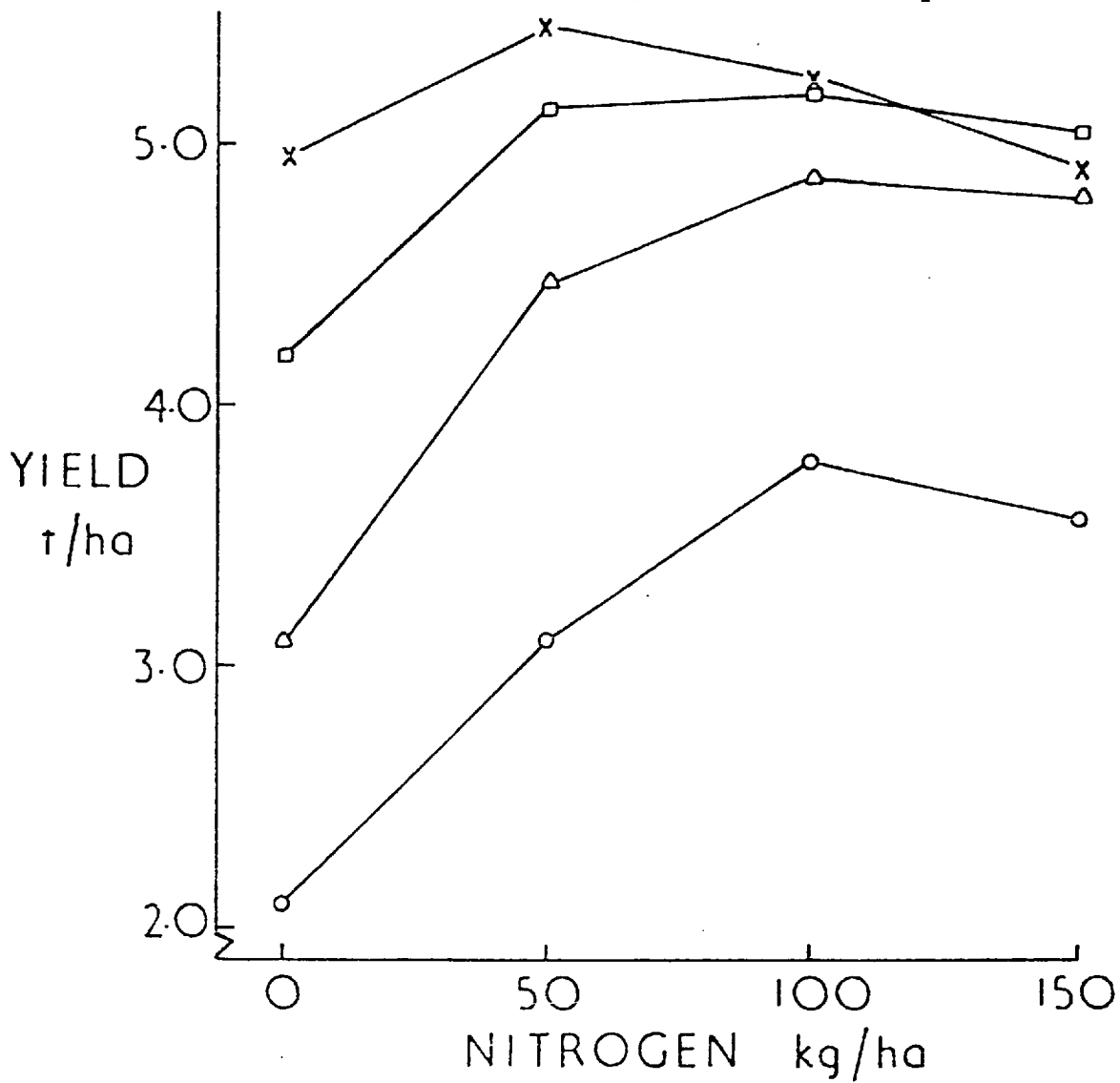
Table E8 shows that the incidence and severity of eyespot differed little between treatments within an experiment but differed much between experiments. In Experiment III the incidence of eyespot was less following oats than following any other crop, this was somewhat unexpected as eyespot can occur on spring oats though it is rarely damaging.

Sharp eyespot was uncommon in all three experiments and was not affected by previous cropping or nitrogen application except in Experiment I where wheat after maize given 100 kg N/ha had 16% straws infected compared with 6-10% straws infected following other crops.

E.3.3 Barley Test Cropping

Tables E9, E10 and E11 show that there was no consistent effect of previous cropping on the incidence of take-all in the barley test crop, though in Experiment II there was slightly less and in Experiment III slightly more take-all following barley treatment crops. In all three experiments the amount and severity of take-all decreased with increasing amounts of nitrogen given to the barley test crop. Although in one experiment (III) this decrease of take-all with increasing nitrogen was less after barley than after the

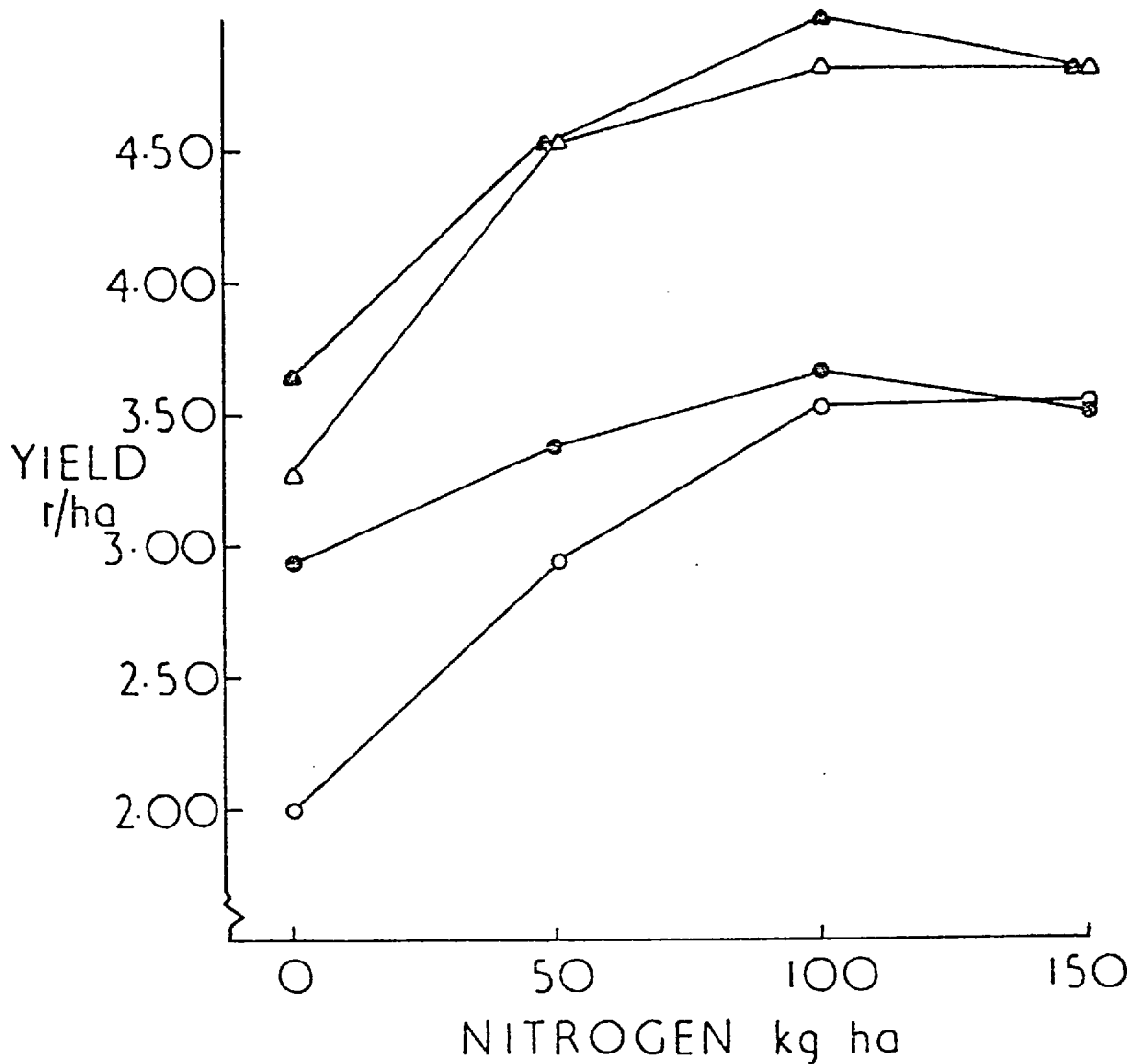
FIG. E2. The effect of different previous cropping on the yield and incidence of take-all of winter wheat
(means of three experiments)



TAKE-ALL RATINGS

	nitrogen kg/ha			
	0	50	100	150
○ BARLEY 1	158	148	119	129
Δ OATS 1	20	17	6	4
□ BEANS	12	12	11	6
X CLOVER	18	14	15	11

FIG. E3. The effect of undersowing barley and oats with trefoil on the yield and incidence of take-all of the subsequent winter wheat (means of three experiments and of nitrogen rates to the barley or oats)



TAKE-ALL RATINGS

	nitrogen kg/ha			
	0	50	100	150
○ BARLEY 1	160	148	122	121
● BARLEY U/S 1	151	147	138	126
△ OATS 1	18	12	5	5
▲ OATS U/S 1	28	11	8	9

TABLE E8.

The incidence of eyespot in July on winter wheat following different previous cropping - Experiments I, II and III. - means of four nitrogen rates.

		% STRAWS WITH EYESPOT		
TREATMENT CROPPING	kg N/ha	1970 EXPERIMENT I	1971 EXPERIMENT II	1972 EXPERIMENT III
BARLEY	50	10 (3) ¹	51 (27)	89 (74)
BARLEY	100	7 (2)	45 (22)	- -
BARLEY U/S ² TREFOIL	50	12 (4)	49 (26)	91 (78)
BARLEY U/S TREFOIL	100	11 (4)	61 (34)	- -
OATS	50	9 (2)	37 (17)	70 (49)
OATS	100	6 (2)	39 (20)	- -
OATS U/S TREFOIL	50	6 (2)	23 (11)	66 (46)
OATS U/S TREFOIL	100	6 (1)	39 (19)	- -
MAIZE	100	- -	25 (13)	81 (59)
MAIZE	200	- -	36 (17)	81 (61)
BEANS	0	8 (2)	38 (20)	85 (68)
CLOVER	0	8 (1)	40 (21)	88 (72)
S.E.D. ¹		2.07 (0.76)	7.69 (5.25)	5.44 (6.72)

¹ Figures within brackets are % straws with moderate + severe eyespot

² U/S = undersown

TABLE E9.

The incidence of take-all in spring barley grown after winter wheat which followed different treatment cropping - Experiment I 1971

% PLANTS WITH TAKE-ALL						
TREATMENT CROPPING	kg N/ha	NITROGEN kg/ha.				MEAN
		0	50	100	150	
BARLEY	50	59 (27) ¹	29 (8)	38 (13)	25 (4)	38 (13)
BARLEY	100	66 (44)	71 (36)	47 (20)	32 (4)	54 (26)
BARLEY U/S ² TREFOIL	50	61 (29)	41 (14)	46 (16)	36 (10)	46 (17)
BARLEY U/S TREFOIL	100	59 (30)	43 (15)	25 (3)	47 (16)	44 (16)
OATS	50	40 (17)	42 (20)	25 (8)	34 (5)	35 (12)
OATS	100	64 (29)	37 (13)	25 (7)	23 (2)	37 (13)
OATS U/S TREFOIL	50	54 (20)	41 (18)	31 (4)	20 (3)	36 (11)
OATS U/S TREFOIL	100	47 (26)	39 (8)	37 (15)	33 (8)	39 (14)
BEANS	0	76 (45)	48 (20)	42 (14)	28 (5)	49 (21)
CLOVER	0	57 (27)	49 (18)	33 (11)	33 (7)	43 (16)
S.E.D. $\pm$		12.36 (9.02)			6.55 (4.18)	

1 figures within brackets are % plants with moderate + severe take-all

2 U/S = undersown

TABLE E10.

The incidence of take-all in spring barley grown after winter wheat which followed different treatment cropping - Experiment II 1972

		% PLANTS WITH TAKE-ALL				
TREATMENT CROPPING	kg N/ha	NITROGEN kg/ha.				MEAN
		0	50	100	150	
BARLEY	50	61 (18)	50 (14) ¹	28 (4)	32 (4)	43 (10)
BARLEY	100	34 (2)	42 (9)	25 (4)	25 (2)	31 (4)
BARLEY U/S ² TREFOIL	50	53 (10)	40 (7)	30 (7)	29 (3)	38 (7)
BARLEY U/S TREFOIL	100	55 (13)	45 (7)	29 (4)	26 (2)	39 (7)
OATS	50	62 (24)	38 (6)	29 (1)	38 (9)	42 (10)
OATS	100	64 (21)	28 (1)	32 (4)	24 (0)	37 (6)
OATS U/S TREFOIL	50	66 (28)	33 (12)	29 (2)	20 (2)	37 (11)
OATS U/S TREFOIL	100	84 (46)	32 (7)	34 (12)	26 (3)	44 (17)
MAIZE	100	82 (42)	58 (23)	36 (5)	38 (7)	53 (19)
MAIZE	200	65 (30)	55 (14)	34 (2)	22 (1)	44 (12)
BEANS	0	58 (21)	54 (22)	46 (16)	32 (7)	48 (16)
CLOVER	0	85 (39)	50 (13)	44 (8)	34 (4)	53 (16)
S.E.D. ±		12.60 (8.25)			6.43 (4.29)	

1 Figures within brackets are % plants with moderate + severe take-all

2 U/S = undersown

TABLE E11.

The incidence of take-all in spring barley grown after winter wheat which followed different treatment cropping - Experiment III 1973

% PLANTS WITH TAKE-ALL						
TREATMENT CROPPING	kg N/ha	NITROGEN kg/ha.				MEAN
		0	50	100	150	
BARLEY	50	70 (16) ¹	69 (14)	56 (2)	51 (3)	61 (9)
BARLEY U/S ² TREFOIL	50	73 (15)	44 (4)	44 (5)	33 (2)	49 (6)
OATS	50	39 (4)	31 (4)	18 (1)	21 (2)	27 (3)
OATS U/S TREFOIL	50	56 (15)	22 (4)	12 (0)	17 (tr)	27 (5)
MAIZE	100	59 (25)	21 (4)	12 (0)	15 (tr)	30 (8)
MAIZE	200	68 (24)	40 (3)	9 (0)	12 (1)	32 (7)
BEANS	0	78 (33)	42 (7)	25 (2)	16 (2)	40 (11)
CLOVER	0	84 (30)	37 (6)	22 (1)	16 (1)	40 (9)
S.E.D. [±]		10.82 (6.69)		6.04 (3.37)		

1 Figures within brackets are % plants with moderate + severe take-all

2 U/S = undersown

break crops.

Table E12 shows that the yields of the barley test crops did not differ consistently with previous cropping. The response to nitrogen also did not differ with treatment cropping (Fig. E4).

E.4 DISCUSSION

In the wheat test crop the incidence of take-all was greatly decreased following all break crops compared with following barley, in contrast the incidence of eyespot was not affected by different previous cropping. As other diseases were infrequent and slight it seems probable that most of the yield increase resulting from disease control by break crops can be attributed to the decrease in take-all, unless take-all and eyespot interact to cause a greater loss in yield together than when present separately. The suggestion of an interaction is not supported by the results of these experiments in which the site with least eyespot (Long Hoos) had the largest yield response to break crops. If it is assumed that barley and oats leave the same amounts of mineralisable soil nitrogen and that in these experiments differences in take-all are the only important disease factor then from fig. E2 the difference in yield between barley and oats is the yield benefit of controlling take-all. The similarity of the shape of the oat and barley nitrogen response curves supports the assumption that they leave the same amount of mineralisable soil nitrogen. Maize was as effective in limiting the take-all in the following wheat crop and was not itself visibly infected but as the assay of 'clean' maize roots did show that G.G.T. could survive on maize roots then it is possible that maize may not always be an effective break crop.

Apart from disease, the only other important effect of the break crops on the yield of the wheat test crops is assumed to be differences

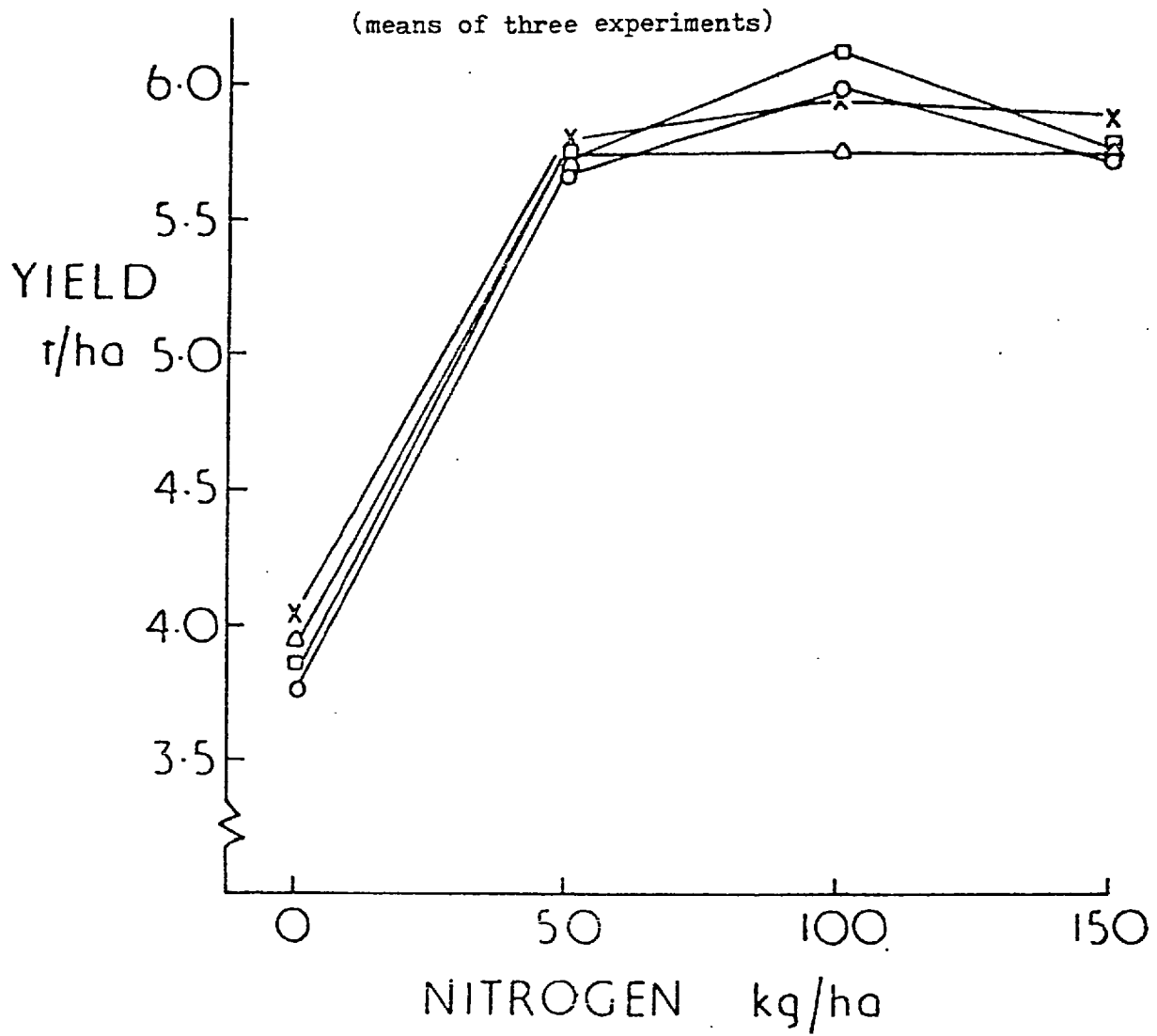
TABLE E12

The yields of spring barley grown after winter wheat which followed
different treatment cropping - Experiments I, II and III.

TREATMENT CROPPING	kg N/ha	EXPERIMENT I					EXPERIMENT II					EXPERIMENT III				
		0	50	100	150	MEAN	0	50	100	150	MEAN	0	50	100	150	MEAN
BARLEY	50	3.06	4.85	6.08	5.50	4.87	4.40	6.29	6.09	5.79	5.64	3.81	5.84	5.83	5.91	5.35
BARLEY	100	3.72	4.46	5.76	5.52	4.86	4.37	5.96	5.52	5.55	5.35					
BARLEY U/S ¹	50	3.95	5.21	5.98	5.42	5.14	4.72	6.44	6.41	5.95	5.88	4.06	6.06	6.19	6.13	5.61
BARLEY U/S	100	3.22	5.20	5.50	5.58	4.88	5.50	6.24	5.95	5.75	5.86					
OATS	50	3.32	5.35	5.20	5.39	4.81	4.69	6.34	5.92	5.67	5.66	3.80	5.60	6.15	6.22	5.44
OATS	100	3.75	4.78	5.90	5.62	5.01	4.43	6.69	6.20	6.35	5.92					
OATS U/S	50	3.83	5.13	5.44	5.12	4.88	4.45	5.68	6.85	5.72	5.68	3.88	5.99	5.94	6.06	5.42
OATS U/S	100	3.46	5.36	5.47	5.31	4.90	4.36	6.24	6.25	6.46	5.83					
MAIZE	100						3.48	6.21	6.69	5.29	5.42	3.46	6.05	5.78	6.26	5.39
MAIZE	200						3.98	6.83	7.08	5.64	5.88	3.97	6.10	5.95	5.86	5.47
BEANS	0	3.11	5.27	5.70	5.40	4.87	4.39	6.13	6.61	6.00	5.78	4.05	5.87	6.06	5.93	5.48
CLOVER	0	3.82	5.41	5.73	5.45	5.10	4.09	5.84	6.40	6.36	5.67	4.18	6.13	5.74	5.87	5.48
S.E.D. ‡			0.413			0.138		0.658			0.260		0.247			0.102

1 U/S = undersown with trefoil

FIG. E4. The yields and incidence of take-all in spring barley grown after winter wheat following different treatment cropping



		TAKE-ALL RATINGS			
		nitrogen kg/ha			
PREVIOUS CROPS		0	50	100	150
O BARLEY 1		88	63	46	40
Δ OATS 1		64	50	28	36
□ BEANS		112	68	50	31
X CLOVER		114	60	40	32

in mineralisable soil nitrogen. Although in general agriculture there are other major effects of break crops on the yield of a following crop, for example soil conditions following the harvesting of root crops in unfavourable conditions, with the crops used in these experiments and with uniform cultivation treatments it seems unlikely that there was any other important effect on yields of the wheat test crops. This conclusion is supported by the results of Ripley (1941), who in rotational experiments in Canada studied the effect of several crops including clover and oats on the yield and nutrition of a range of following crops and showed that, except in soils very deficient in water or phosphorus and potash, differences in yield of crops following clover or oats could mainly be attributed to differences in available nitrogen. Clement and Back (1969) in this country similarly showed that in wheat following different four year leys, where diseases were not an important factor, the variation in yield could mainly be accounted for by differences in mineralisable soil nitrogen. The fact that the maximum yields of the wheat test crop after the different 'break crops' did not differ greatly also suggests that either availability of nitrogen was the major difference between these crops or that increasing nitrogen compensated for any other difference. Assuming differences in soil nitrogen to be the only major difference between the break crops then, as measured by wheat yield, the benefits of nitrogen residues from clover and beans were equivalent to 100 kg and 40 kg fertiliser nitrogen/ha. (Fig. E2).

Undersowing oats or barley with trefoil had no effect on take-all and little effect on yield of the following wheat test crop. Because a winter wheat test crop was used the period that G.G.T. had to survive shortened compared with using a spring cereal and so the effect of undersowing with trefoil might have expected to be

somewhat less. However Hansen (1968) also reported that undersowing a spring cereal with trefoil or clover had no effect on the incidence of take-all in a following spring barley crop. These results conflict with those of Garrett and Mann (1948) who reported that undersowing barley with trefoil decreased the amount of take-all in the following spring barley, however their experimental site was a very sandy soil of low fertility, so changes in nitrogen status of the soil induced by the undersowing treatment might have had a greater effect on G.G.T. populations. In contrast it was on a fertile soil on Mr. F.P. Chamberlain's farm that the observation that undersowing a spring cereal seemed to decrease the incidence of take-all in the following spring cereal was first made (Garrett and Buddin, 1947). Although in this case the crop was undersown with a trefoil ryegrass mixture and so it is possible that the ryegrass may have built up the P.R.G. population. The results from the Survival of Take-all Experiment Section C, suggest that a big P.R.G. population might delay the build up of G.G.T.

The beneficial effect of the break crops did not persist for more than one year so that the barley test crop yields, the incidence of take-all and the nitrogen response curves did not differ with previous cropping. The nitrogen applied to the barley test crop did decrease the incidence of take-all, this decrease in take-all with increasing nitrogen also occurred in the wheat test crops, although less consistently, and it also occurred in one assay.

F.

FINAL DISCUSSION AND CONCLUSIONS

My results have been discussed at the end of each of the three experimental sections (Sections C, D and E), so in this section I present only my conclusions and some speculation on the ways in which the work might be developed or applied.

The experimental programme was based on field studies and the experimental designs and methods were chosen in an attempt to produce crops and disease patterns similar to those encountered in agriculture. The natural variation in environmental conditions and in disease incidence, particularly with infection by G.G.T., that occur in such field studies necessitated undertaking very large sampling programmes eg. the Survival of Take-all Experiment involved assaying 4900 pots of soil and sampling and assessing 2600 measured 15 cm lengths of crop row. The size of these sampling programmes, however, limited the experimentation to a single soil type and so it should be borne in mind that conclusions based on these results may not apply in other conditions particularly on different soil types.

The experiments on the spread of G.G.T. indicated that autonomous spread was limited to a few centimetres. Thus, such spread would seem to be important only within the root system of a plant or its neighbours. Even where inoculum was spread longer distances by cultivations, a consequential increase in crop infection was measured only in the first wheat crop, not in the second where take-all was uniformly prevalent. Thus spread by cultivations is not likely to be an important factor determining the incidence of take-all except, perhaps, in soils where G.G.T. is present in small isolated pockets that would be enlarged by cultivations. Such conditions could occur where no host crop or weed host have grown

for many years, eg. land newly reclaimed from the sea, or in the first wheat crop following a 'break' on land where patches of inoculum remained at the end of break cropping eg. patches of infected weed grasses. My results also give a guide to the separation needed between experimental plots where it may be important to maintain different populations of G.G.T. Provided there was no cross cultivation of plots, unsown paths of a half to one metre should be adequate, but where cultivations are continuous between plots separation should be at least two to three metres and twice this if it is important that no inoculum at all should be transferred.

Thus autonomous spread and spread by cultivations do not seem to be a major factor, except in rare cases, in the development of take-all epidemics and do not explain the increase in G.G.T. shown to occur in first wheat crops. Assays of soil taken from stubble of first wheat crops showed that infestation by G.G.T. was widespread, although few take-all lesions were recorded on the crops. The causes of the build up of inoculum during the first wheat crop and the lack of take-all lesions on the crop are not known. Suggested explanations are (i) inoculum was present prior to the start of the first wheat crop but it was below the detection threshold of the assay, (ii) inoculum eg. ascospores or microconidia, came in from outside the experimental area. However in either case it is necessary to suppose that the inoculum developed during the season; possibly infecting fine roots, perhaps root hairs, that were not recovered by sampling. (iii) Inoculum was present all the time but unable to cause visible lesions because of a suppressing factor e.g. antagonist, which became ineffective by the end of the first wheat crop.

In the Survival Experiment (Section C) assays of soil taken

during crop growth and after harvest of the first wheat crop showed that the increase of G.G.T. during the first wheat crop differed with different previous treatment cropping; the fungus was much more common in the wheat soils after fallow or lucerne than after grass-clover ley. This difference did not seem to be related to survival of inoculum during the treatment cropping. The results showed that, although G.G.T. occurred naturally in the soil up to five years after the previous cereal crop, only little of the introduced inoculum survived more than one year and after three years no difference could be detected between inoculated and uninoculated plots. So, unless inoculum not detected by the assay was differentially present, the survival of inoculum was not a factor determining the differential increase of G.G.T. after different previous cropping. It is possible that wheat is more susceptible to take-all when grown after fallow or lucerne than after grass but a more likely explanation for the differences would seem to be the very large population of P.R.G. present after grass-clover ley.

Estimates of P.R.G. on plants from the first wheat crop and on assay plants grown in soil taken during the crop growth and after harvest showed that populations of P.R.G. and G.G.T. were negatively correlated. Populations of P.R.G. were largest after grass-clover ley and take-all in subsequent wheat crops occurred a year later after grass-clover than after fallow or lucerne. My experiments provided no direct evidence that the large P.R.G. population caused this delay but work by Scott (1970) and Deacon (1973 a) suggests that this is probable. If so, it would be an advantage to maintain populations of P.R.G. during successive wheat crops after grass leys. In my experiment P.R.G. populations fell during the second wheat crop and by the end of it were little larger than after lucerne. Some ways in which large populations might be maintained are:-

1. Annual inoculation of soils with P.R.G. This would be successful if the input of inoculum at least maintained the population established by grass.
2. Undersowing or catch cropping with grass. This depends on the effectiveness of grass to maintain P.R.G. when grown together with wheat and in the short period between crops.
3. Direct drilling of the wheat crops. This is suggested because it seems possible that the difference in the incidence of take-all between ploughed and direct drilled crops following grass reported by Brooks and Dawson (1968) was at least partly related to prolonged persistence of P.R.G. populations with direct drilling.
4. Decreasing available nitrogen in the soil between wheat crops. An idea derived from the report by Garrett (1972) that the saprophytic survival of P.R.G. was favoured by low nitrogen availability in contrast to that of G.G.T. This decreased availability might be achieved by ploughing in straw or green manure eg. undersown grass.

These methods used separately or in combinations might help maintain a large P.R.G. population established by grass ley and in some cases might even build up populations during cereal cropping without the need to grow a ley.

The manipulation of P.R.G. populations offers one possible new method of take-all control. At present, the other main prospect for new control measures lies in the development of effective fungicides but this seems unlikely to be achieved until materials that are translocated downwards, presumably in the phloem, are developed. Until new methods such as these are developed the choice of control measures available to the farmer are the partial control gained

from take-all decline or control by the use of break crops.

The break crops tested (Section D) benefited only the first wheat crop that followed them. The effect of different break crops on the incidence of take-all did not differ; the average yield increase of wheat after oats compared to after barley, i.e. the assumed benefit from the control of take-all, was 1.16 t/ha. The different break crops did leave different amounts of mineralisable soil nitrogen which greatly affected yields of wheat given none or small amounts of fertiliser nitrogen and to a much lesser extent the maximum yield achieved. None of the break crops affected yield, nitrogen response or the incidence of take-all in the second test crop barley. The application of fertiliser nitrogen (Nitrochalk) applied to the test crops decreased the incidence and severity of take-all, particularly in the barley crop, and usually increasing amounts of fertiliser progressively decreased the disease. This conflicts with the recent report by Huber and Watson (1974) that ammonium forms of nitrogen decrease take-all but nitrate forms including Nitrochalk increase it. However an ammonium form of nitrogen was not tested and might have been more effective than Nitrochalk.

Finally from my work it would appear that the critical period in determining the build up of damageing populations of G.G.T. is the first wheat crop. A much more intensive study of G.G.T. populations during this first wheat crop is needed to determine the source of the inoculum and its ability to infect the crop. Further work to try to prolong the effect of P.R.G. in limiting this build up has been suggested but the mechanism of the effect also needs elucidating.

G.

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H.

APPENDIX

H.1. CONJOINT PUBLICATIONS.

Two conjoint publications are submitted as subsidiary matter in support of my candidature.

1. Jenkyn J.F. and Prew R.D. (1973). Activity of six fungicides against cereal foliage and root diseases.

Annals of Applied Biology, 75, 241-252.

(I shared equally in the planning, field execution and writing of this work. The assessment of foliar diseases was done by Dr. Jenkyn and the assessment of foot and root ~~diseases~~ by myself).

2. Prew R.D. and McIntosh A.H. (1975). Effects of Benomyl and other fungicides on take-all, eyespot and sharp eyespot diseases of winter wheat.

Plant Pathology, 24, 67-71.

(Dr. McIntosh advised on the planning of the field experiments and on the choice of fungicides and their application. All other aspects of the work was done solely by myself).

Activity of six fungicides against cereal foliage and root diseases

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(Accepted 2 April 1973)

SUMMARY

During 1970 and 1971 six systemic fungicides were compared as seed dressings and sprays against foliage and root diseases of cereals. The fungicides differed greatly in effectiveness against mildew, loose smut, rusts and eyespot but none controlled take-all. Effects were also noted on germination, seedling growth and leaf-surface microflora.

INTRODUCTION

Until recently the only fungicides commonly used on cereals were the organo-mercurials applied to seed. Fumigation of soil before sowing to control root diseases (Ebbels, 1969; Salt, 1971) and repeated applications of traditional fungicides to control foliar diseases (Last, 1955*a*; Large & Doling, 1963; Jenkins & Jemmett, 1967; James, Jenkins & Jemmett, 1968; Jenkins & Morgan, 1969) proved useful in research but seldom practicable or economic commercially. Now, several groups of very active and partially systemic fungicides (Evans, 1971) have been synthesized which can be effective when applied to foliage as single sprays at low volume or when used as seed dressings, so they have greatly altered the economics of controlling cereal diseases. We report experiments, begun in 1970, which compared six systemic fungicides on spring and winter cereals.

EXPERIMENTAL

Sampling and disease assessments

Seedling emergence was assessed at growth stage (G.S.) 1-2 (Large, 1954) by counting seedlings in 8×1 or 6×0.5 m row lengths/plot. Numbers of straws were estimated from samples taken to assess root disease (except in 1971 (Drapers) where barley straws were counted in 5×1 m row lengths/plot). In experiments with spring barley, seed with loose-smut (*Ustilago nuda*) was used (infection, 2.4%, Zephyr, 1970; and 3.7%, Sultan, 1971) to test also the activity of the fungicides against this disease. Infection in the crops was measured by counting the smutted heads in each whole plot (1970) or half plot (1971).

Foliage disease was assessed by estimating percentage area affected on the top three leaves (leaf 1 = top fully expanded leaf) of ten or twenty-five tillers/plot at several growth stages. Flag leaves from the spring wheat experiment were exposed at G.S. 11.2 over potato dextrose agar (Last, 1955*b*), and colonies of *Sporobolomyces* spp., other yeasts and bacteria, and mycelial fungi that developed were counted.

Foot and root diseases were assessed in spring, before the first sprays were applied or soon after (barley 1971) and again near harvest, usually by sampling 6×15 cm row lengths (spring) and 6×30 cm row lengths (harvest) from all plots, half at each end from areas not harvested for yield. In the winter wheat experiment, 8×30 cm row lengths were sampled at harvest. After washing the spring samples, records were made of the number of plants, seminal and crown roots affected by take-all (*Gaeumannomyces graminis* var. *tritici* formerly called *Ophiobolus graminis*) and the number of plants and shoots affected by eyespot (*Cercospora herpotrichoides*) and sharp eyespot (*Rhizoctonia solani*). In the winter wheat experiment the numbers of plants affected by *Pythium* root rot were also recorded. Harvest samples were stored dry, then later washed and each plant or straw graded as healthy, slight, moderate or severe for take-all and eyespot respectively and each straw healthy, slight or severe for sharp eyespot. Numbers of plants, shoots (spring) and straws (harvest) were also recorded. Seminal and crown roots were counted on five plants from each spring sample from the winter wheat experiment (i.e. 30 plants/plot).

As there is often some delay between seed preparation and drilling, germination of dressed seed kept for 5-7 months after drilling, was measured by sowing in a sand-peat compost.

Table 1. Rates of fungicide applied as seed dressings and sprays to spring barley and spring wheat, Harwoods Piece in 1970

Chemical name	Formulation (% a.i.)	Seed dressing* (kg a.i./ha)	Spray (kg a.i./ha)	Volume of spray application (l/ha)
Benomyl	50	0.28	1.12	393
Ethirimol	80	1.12	1.12	393
Fuberidazole	50	0.035	1.12	393
Triarimol†	4	0.034	0.09	393
Thiophanate methyl	50	1.35	1.68	393
Triforine (powder)	83.4	0.42	—	—
Triforine (liquid)	20	—	0.2	786

* All applied as powders.

† This material has since been withdrawn by the manufacturer.

Spring barley and spring wheat, Harwoods Piece, 1970

Methods. Six fungicides (Table 1) were tested on spring barley (c.v. Zephyr) and spring wheat (cv. Rothwell Sprite) in 1970 on Harwoods Piece which has a shallow flinty, clay loam soil. Previous cropping was barley, spring wheat, spring wheat. The treatments, including plots receiving no fungicide, were arranged in three randomized blocks, in fifteen-row plots of 0.0024 ha of which 0.00085 ha was harvested. The barley was sown at 157 kg/ha and wheat at 191 kg/ha on 22 April, both combine-drilled with 505 kg/ha 20 : 10 : 10 compound fertilizer. Each fungicide was applied as a seed dressing plus two sprays and, where possible, diseases were assessed between applications to separate the effects of seed dressings and sprays. Sprays were applied using a machine designed for small plot work (Wilson, 1972) on 8 June (G.S. 7) and 23 June (G.S. 10.2). The barley was harvested on 13 August and the wheat on 29 August.

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Results. Mildew (*Erysiphe graminis*) was the most prevalent disease in both experiments. Table 2 records its incidence on the third youngest leaf on each of several dates. All chemicals except fuberidazole decreased mildew on barley on 2 June after application as seed dressings. Sprays of all except fuberidazole and triforine continued to suppress it greatly. On spring wheat, control was less but chemicals were similarly ranked, usually ethirimol and triarimol giving most control of mildew followed by benomyl and thiophanate methyl. Triforine was as effective as benomyl and thiophanate-methyl after the first spray, but subsequently gave less control, possibly because too little was used.

Table 2. Area affected by mildew (%) on 3rd youngest leaf of spring barley and spring wheat, Harwoods Piece 1970

Date	Barley				Wheat			
	... 2 June	19 June	2 July	20 July	2 June	19 June	2 July	20 July
Growth stage (G.S.)	... 6-7	10.1	10.5.4- 11.1	11.2	6-7	10	10.5.2	11.1
Untreated	0.3	0.6	3.5	11.3	0.3	3.5	9.6	32.5
Benomyl	0.1	0.0	0.0	0.1	0.1	1.8	2.5	14.1
Ethirimol	0.1	0.0	0.0	0.2	0.1	0.2	0.4	6.5
Fuberidazole	0.3	0.4	2.1	10.2	0.6	3.2	7.8	32.2
Triarimol	0.1	0.0	0.1	0.0	0.1	0.1	1.1	15.0
Thiophanate methyl	0.1	0.0	0.2	0.9	0.3	1.3	2.5	16.0
Triforine	0.1	0.1	0.7	4.1	0.2	1.7	5.2	24.2
Mean	0.2	0.1	0.9	3.8	0.2	1.7	4.1	20.1
S.E. $\pm$	0.04	0.14	0.37	1.87	0.08	0.26	0.91	2.87

Brown rust on barley (*Puccinia hordei*) was the only other prevalent foliage disease, but on average only 1.1 % of the third leaf area of plants from untreated crops was affected at G.S. 11.2. Crops treated with benomyl and triforine had least brown rust (0.5 %) but differences between treatments were not significant.

Flag leaves sampled from benomyl-treated spring wheat and exposed over agar gave fewest colonies of *Sporobolomyces* (Table 3), but the numbers varied greatly. Benomyl and thiophanate methyl decreased the numbers of mycelial fungi which were mostly *Cladosporium* sp. The numbers of colonies of epiphytes, particularly *Sporobolomyces*, were closely related to amounts of mildew on the leaves (Fig. 1) but not to leaf senescence.

Benomyl and triarimol decreased the numbers of smutted ears of barley more than thiophanate methyl (Table 3). We cannot explain why crops treated with triforine had significantly more smutted ears than untreated crops. All seed dressings much decreased numbers of barley seedlings, probably by affecting flow of seed from the drill. Triforine and fuberidazole which were used at the smallest rates of formulated product had least effect. No treatment altered the number of straws/unit area at harvest. Similarly, all chemicals except fuberidazole decreased seedling number in spring wheat (but less than in barley), but only triarimol did so significantly (triarimol plots 47 seedlings, untreated plots 55 seedlings/m of row). Although triarimol decreased also the number of shoots/plant in spring (Table 3) the number of straws/unit area at harvest was not affected.

Table 3. *Effects of fungicides on growth, diseases and yield of spring barley and spring wheat, Harwoods Piece 1970*

Date	...	Barley			Wheat				
		Seedlings/m	Smutted	Yield	Shoots/	<i>Sporobolomyces</i> †	Other yeasts	Mycelial	Yield
		of row	heads/plot*	(t/ha)	plant	3 Aug.	and bacteria†	fungi†	(t/ha)
Growth stage (G.S.)	...	12 May	23 June	13 Aug.	28 May	3 Aug.	3 Aug.	3 Aug.	29 Aug.
		1	10.2	11.4	5	11.2	11.2	11.2	11.4
Untreated		43	94	4.62	1.9	15.1	2.7	7.8	2.76
Benomyl		33	6	5.12	1.9	1.8	0.5	2.4	3.16
Ethirimol		32	95	4.68	1.9	6.2	1.5	6.8	3.27
Fuberidazole		38	95	4.62	1.8	19.5	2.1	4.8	2.95
Triarimol		32	17	4.35	1.5	12.0	1.1	4.8	3.13
Thiophanate methyl		29	45	4.79	1.9	7.8	1.2	3.1	2.90
Triforine		36	125	4.59	2.1	9.9	2.9	6.2	3.45
Mean		35	68	4.68	1.9	10.3	1.7	5.2	3.09
S.E. ±		1.2	8.8	0.22	0.09	5.99	0.64	1.18	0.19

* Plot area 0.0024 ha.

† Colonies/10 cm² leaf exposed.

There was so little eyespot, sharp eyespot, take-all and brown foot rot (*Fusarium culmorum*) that no information on the effects of the fungicides was obtained.

Differences in yield of barley were small (Table 3). All wheat yields were small, although triforine yielded most. After 6 months storage benomyl seed treatment seemed to decrease germination of wheat (from 98 to 90%) but increased that of barley (from 90 to 96%). Germination of grain harvested from plots seemed unaffected by the treatments.

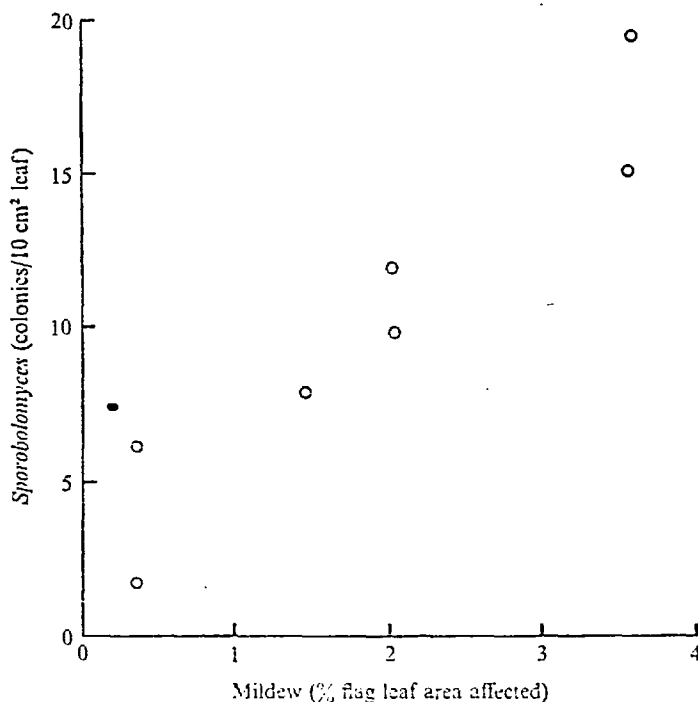


Fig. 1. The relationship between *Sporobolomyces* and amounts of mildew on leaves of spring wheat sampled at G.S. 11.2.

Winter wheat, West Barnfield, 1970-1

Methods. The same fungicides (Table 1) were tested on winter wheat (cv. Cama) in 1970-1 on West Barnfield which has a flinty loam soil. Previous cropping was barley, barley, winter wheat. Plot sizes and experimental design were unchanged, except that an organo mercury seed dressing was included as an extra treatment (0.42 kg formulated product/ha containing 1% organically combined mercury, w/w) and the number of untreated plots was doubled (2/block). Benomyl and thiophanate methyl were applied as before but with a wetter (Spreadite, Murphy Chemical Co.) at 0.75 ml/l. The fuberidazole seed dressing was increased to 0.28 kg a.i./ha and the spray volume was doubled, although the spray rate was unchanged. A new liquid formulation of triarimol (4.5% a.i. E.C.) was used for sprays at 44.5 ml a.i./ha. Triforine spray rates were doubled on manufacturers recommendations, which were not received in time to increase the seed dressing. The wheat was sown on 16 October at 179 kg/ha, combine-drilled with 380 kg 8 : 20 : 16 compound fertilizer and top

Table 4. *Effects of fungicides on foot and root rots, growth and yield of winter wheat, West Barnfield 1971*

Date	...	Seedlings/m of row	Shoots/ plant	Crown roots/ plant	Straws/ plant	Eyespot (% straws)	Sharp eyespot (% straws)	Take-all (% plants)	Yield (t/ha)
Growth stage (G.S.)	...	17 Nov.	11 Mar.	11 Mar.	2 July	2 July	2 July	2 July	27 Aug.
		1	2-3	2-3	10.5.4	10.5.4	10.5.4	10.5.4	11.4
Untreated		54	1.6	1.0	1.4	42	39	64	6.10
Organo-Hg		46	1.6	1.1	1.4	50	43	65	6.08
Benomyl		50	1.9	0.8	1.6	1	58	72	6.31
Ethirimol		54	1.7	1.1	1.6	37	42	76	6.01
Fluberidazole		45	1.4	1.3	1.4	18	57	74	5.82
Triarimol		44	1.0	0.6	1.4	20	42	70	5.51
Thiophanate methyl		47	1.7	1.2	1.5	5	62	66	6.30
Triforine		50	1.6	1.0	1.4	38	45	76	5.61
Mean		49	1.6	1.0	1.5	28	47	70	5.98
S.E. $\pm$		2.6	0.12	0.10	0.08	6.1	4.5	9.1	0.21

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dressed with 600 kg Nitro-chalk (21 % N)/ha. Sprays were applied on 4 May (G.S. 5) and 2 June (G.S. 10). The experiment was harvested on 27 August.

Results. Foliage diseases were not severe for most of the season. In untreated crops in early July (G.S. 10.5.4) only 2% of the area of the second leaf was affected by mildew, compared with less than 1% on crops treated with benomyl, ethirimol, thiophanate methyl and triforine; triarimol had no effect. Brown rust and *Septoria* which, on average, occupied 2 and 6% of the flag leaf area at G.S. 11.2 were not affected by any of the fungicides. Yellow rust (*Puccinia striiformis*) occupied 2% of the flag leaf area of untreated crops at G.S. 11.2, and although it occurred patchily was decreased by triforine and triarimol to less than 1%.

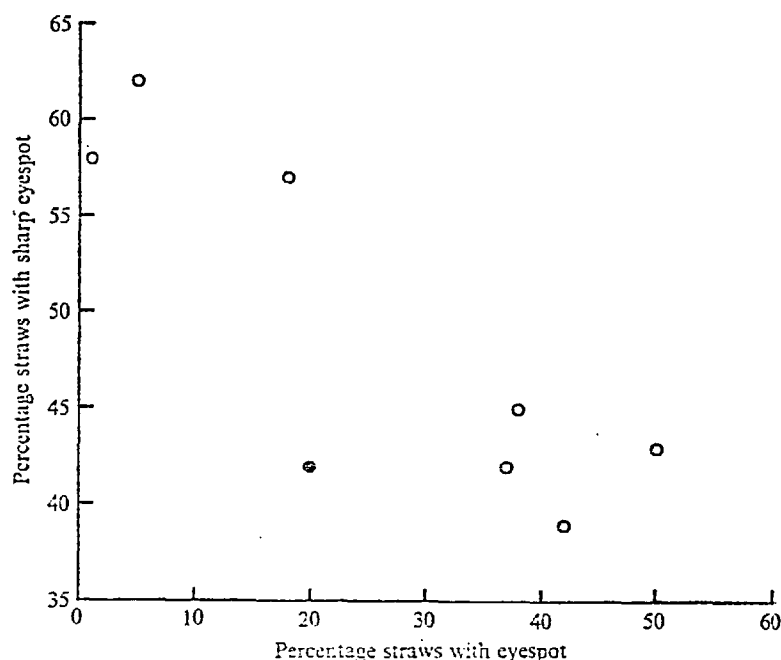


Fig. 2. Amounts of sharp eyespot and eyespot at G.S. 10.5.4 on winter wheat treated with different fungicides (● represents triarimol).

In spring, differences in seedling number (Table 4) were again probably due to differences in flow rates of dressed seeds. At this stage no fungicide affected amounts of sharp eyespot, *Pythium* root rot or take-all. Of seedlings from untreated seed 7% had eyespot, whereas there was no eyespot with triarimol and fewer tillers and crown roots per plant.

By harvest all treatments had equal numbers of straws/plant; take-all was severe (c. 70% plants affected) but none of the fungicides decreased it (Table 4). Eyespot was much decreased by benomyl and thiophanate methyl and a little by fuberidazole and triarimol. Conversely sharp eyespot was increased by benomyl, fuberidazole and thiophanate-methyl, but not by triarimol. Indeed, as Fig. 2 shows, there was generally a negative relationship between eyespot and sharp eyespot.

The grain yields from fungicide-treated crops did not differ significantly from untreated crops. After 6 months storage 99% of untreated seeds retained after drilling germinated but only 84% of those dressed with benomyl and 78% with triarimol.

Spring barley, Drapers, 1971

Methods. Triarimol, thiophanate methyl and triforine were applied as seed dressings (0.034, 1.35 and 0.77 kg a.i./ha respectively) or early or late sprays (44.5 ml, 1.68 kg and 400 ml a.i./ha in 393, 393 and 786 l/ha respectively) to spring barley (cv. Sultan). Untreated plots and plots sown with seed dressed with carboxin plus organo-mercury (0.42 kg formulated product/ha containing 1% combined mercury, w/w) were also included. The experiment was sited in Drapers field which has a flinty silt loam soil. Previous cropping was potatoes, barley, barley. The treatments were arranged in three randomized blocks, in twelve-row plots of 0.0029 ha of which 0.0019 ha was harvested. The barley was sown at 157 kg/ha on 26 March, combine drilled with 505 kg/ha 20 : 10 : 10 compound fertilizer. Sprays were applied on 17 May (G.S. 4) and 15 June (G.S. 10). The experiment was harvested on 19 August.

Table 5. *Effect of seed dressings and sprays on growth, mildew and yield of spring barley, Drapers 1971 (means of 3 fungicides)*

Date	...	Mildew*			Late tillers/ m of row	Yield (t/ha)
		20 May	9 June	14 July		
Growth stage (G.S.)	...	4.5	8	11.1	11.2	11.4
Untreated†		1.6	5.4	64.1	12.6	3.88
Seed dressing		0.2	2.5	60.8	9.7	4.23
Early spray		0.9	0.8	52.7	10.7	4.58
Late spray		1.7	4.5	26.2	20.0	4.12
S.E. ($\pm$) of treatment times (Untreated excluded from analysis)		0.13	0.53	1.41	2.45	0.07

* Percentage area of third youngest leaf affected.

† Mean of seed untreated and dressed with organo-mercury and carboxin.

Results. Average amounts of mildew on 20 May were significantly decreased by the seed dressings and by the first spray (Table 5), which had been applied only 72 h previously. The thiophanate methyl spray had had no effect by this time, but sprays of triarimol and triforine had. Apart from this, triarimol, thiophanate methyl and triforine were equally effective against mildew and in increasing yield. The timing of these fungicides was important and although later treatment extended mildew protection the greatest increase in yield came from the early spray (applied on 17 May at G.S. 4) and amounts of mildew on 9 June were significantly and inversely related to yield (Fig. 3).

Treatments did not significantly affect seedling emergence nor, surprisingly, numbers of mature straws or 1000-grain weights at harvest, but late sprays increased the number of late-formed tillers.

Effects of fungicides on cereal diseases

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Of the seed used in this experiment 3.7 % was infected with loose smut. Untreated plots averaged 583 smutted heads/plot. Triarimol and thiophanate methyl seed dressings decreased this to 352 and 267 smutted heads/plot respectively, but were much less effective than carboxin (four smutted heads). Although triforine again increased the average smutted heads/plot (to 635) the difference was not significant in this experiment.

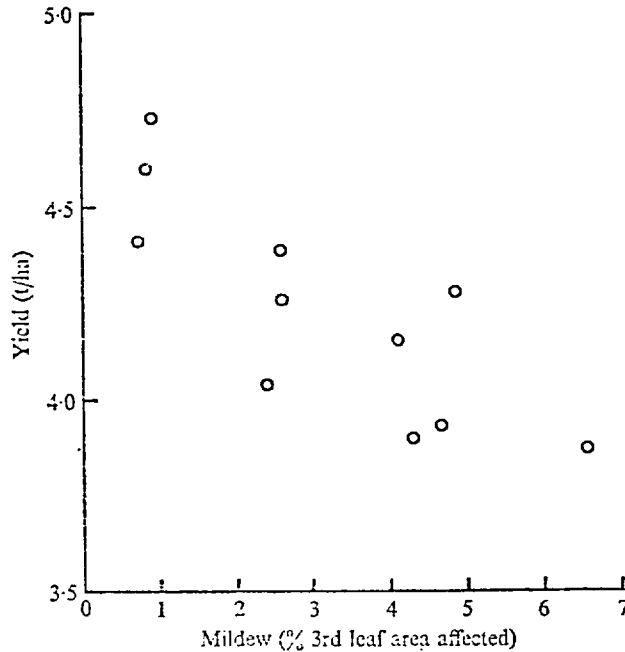


Fig. 3. Relationship between grain yield and amounts of mildew at G.S. 8, 6 days before application of second spray.

At G.S. 11.1 brown rust occupied about 3 % of the area of the second youngest leaf of untreated crops and crops from seed treated with carboxin. Only the late spray of triforine decreased this, to 1.6 %. There was too little foot and root rot for detailed assessments to be worthwhile. Germination of dressed grain after storage for 7 months was not affected by any of the fungicides.

Effects of fungicides on crop growth

None of the fungicides used as sprays directly affected crop growth but seed dressings of triarimol and fuberidazole did, both in the field and in a preliminary pot experiment. In this experiment, done in a cool glasshouse without supplementary lighting in March and April 1970, dressed seed was sown in a peat-sand potting compost.

Triarimol at about 21 g a.i./100 kg seed (0.034 kg a.i./ha affected wheat and barley seedlings in the pot test but only wheat in the field. Affected seedlings had a spiky appearance; the subcrown internode failed to elongate and tillering was delayed.

Fuberidazole was used in the pot experiment at about 90 and 180 g a.i./100 kg seed (0.14 and 0.28 kg a.i./ha). Emergence was unaffected, but seedlings grew slowly and were chlorotic. Most wheat seedlings treated with the larger amount died within 5 wk, whereas other seedlings, although retarded, had almost recovered. Because of these observations we used very little fuberidazole seed dressing on spring wheat and spring barley in 1970 (0.035 kg a.i./ha). Although the amount was increased to 0.28 kg a.i./ha in the winter-wheat experiment none of the previous phytotoxic effects were seen.

In a pot experiment done under similar conditions in June 1970, but testing only fuberidazole, five soils (black fen, loam, clay loam and two sands differing in organic matter content) and the peat-sand compost were used. This confirmed that fuberidazole can be phytotoxic but the symptoms were much less severe and recovery was faster probably because of better growth in June. Symptoms were not influenced by the different soil types.

DISCUSSION

The fungicides used in these experiments differed in spectra of activity and effective concentrations. Yield data were, therefore, difficult to interpret. Fuberidazole decreased only eyespot slightly and, ethirimol only mildew, unless it affected *Sporobolomyces* directly. Benomyl, thiophanate methyl and triarimol were all active against mildew, loose-smut and eyespot. Triforine was the most active against rusts.

Benomyl and thiophanate methyl are both benzimidazoles with the same fungitoxic breakdown product (Selling, Vonk & Sijpesteijn, 1970). Fuberidazole is another benzimidazole which Edgington & Khew (1970) thought to have a similar spectrum of fungitoxicity as benomyl and thiabendazole, although Bartels & MacNeill (1970) found there were differences in mode of action. Triarimol, like ethirimol, is a pyrimidine but has a much wider spectrum of activity.

Where possible each fungicide was tested at a rate based on manufacturer's recommendations, but this may have been too little to control pathogens other than those against which it was recommended.

Fuberidazole was included following a report that it is systemic (Powelson & Cook, 1970). It is used commercially as an alternative to organo-mercury seed dressings at 6 g a.i./100 kg seed but has been used experimentally at rates many times this (Hoffmann, 1970). There have been few reports of phytotoxicity (Powelson & Cook, 1970; Gilpatrick, 1969) even at these large rates and we cannot explain why this occurred in our glasshouse experiments.

Triarimol affected seedling growth adversely but only temporarily. Although it and thiophanate methyl were used at similar rates as seed dressings in 1970 and 1971 their relative activity against loose-smut differed. In 1970 triarimol was more effective than thiophanate methyl (81.9 and 52.4 % control respectively) but in 1971 the reverse was true (39.6 and 54.2 % control).

Maximum benefit from controlling mildew requires careful timing of sprays. In 1971, seed dressings and early sprays were better than late sprays because mildew developed early, but in other situations later sprays can be best (Evans, Rickard &

Whitehead, 1969). However, it may be misleading to extrapolate from small plot experiments, especially on spray timing, to field situations as interactions may occur between plots (Jenkyn & Bainbridge, 1973).

Take-all was not affected by any of the fungicides but eyespot and sharp eyespot were, the latter being increased by some. Eyespot was greatly decreased by triarimol in spring and by benomyl, thiophanate methyl, and to a lesser extent, fuberidazole and triarimol by summer. Usually effects on eyespot and sharp eyespot were inverse, but triarimol decreased eyespot only; possibly a result of the effect of triarimol in delaying tillering, and preventing elongation of the subcrown internode. The results do not suggest whether fungicides that increased sharp eyespot did so directly or by decreasing an antagonist of *Rhizoctonia*. Our experiments tested seed dressings and sprays together but benomyl sprays alone are known to be effective against eyespot (Doodson & Saunders, 1969; Prew & McIntosh, 1970), although benefit from seed dressings seems temporary (Prew & McIntosh, 1971). Benomyl has been reported to increase sharp eyespot on wheat (Prew & McIntosh, 1971) and rye (Hoeven & Bollen, 1972).

Last (1955*b*, 1970) showed that incidence of *Sporobolomyces* can be affected by senescence, diseases and leaf damage and we found it closely related to amounts of mildew. We cannot therefore attribute differences in colonies to any of the fungicides although those, such as benomyl, with a broad spectrum of activity might be responsible. Although the technique used to assess *Sporobolomyces* is intended for species with actively discharged spores, it showed differences in mycelial fungi, predominantly *Cladosporium*, that probably reflect differences in colonization or contamination of the leaves. Crops treated with benomyl and thiophanate methyl gave fewest *Cladosporium* colonies and had much brighter straw (Evans *et al.* 1969). Possibly the effect of broad spectrum fungicides against leaf surface micro-organisms may explain why fungicides give yield increases or prolong the life of green leaves even when disease caused by recognized pathogens is very slight (Jenkins, Melville & Jemmett, 1972).

There was evidence that fungicides, particularly benomyl, decreased germination of wheat after storage for 6 months. Ethirimol is the only one now used commercially as a seed dressing against mildew, but this factor should be considered before other fungicides are recommended as dressings of seed that may need to be stored.

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Effects of Benomyl and Other Fungicides on Take-all, Eyespot and Sharp Eyespot Diseases of Winter Wheat

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SUMMARY

In field trials at Rothamsted, benomyl, thiabendazole, oxycarboxin and 'Plondrel' were tested as sprays or seed dressings on winter wheat. None of the treatments affected take-all (*Gaeumannomyces graminis*) but benomyl and thiabendazole sprays decreased eyespot (*Cercospora herpotrichoides*) and increased sharp eyespot (*Rhizoctonia solani*). Further field and glasshouse experiments confirmed that sharp eyespot was increased by the application of benomyl and showed that it was also increased by the absence of *C. herpotrichoides*.

INTRODUCTION

As long ago as 1951 it was shown that eyespot could be decreased by sulphuric acid sprays (Glynne, 1951) and, more recently, take-all was temporarily controlled with soil fumigants (Ebbels, 1969); however, neither treatment was economic. The development of new systemic fungicides renewed hope for a chemical control of foot and root diseases of cereals. We report field experiments in 1969 and 1970 which tested the effect of several fungicides on foot and root diseases of winter wheat and a further field and a glasshouse experiment which studied the interactions between benomyl, *C. herpotrichoides* and *R. solani*.

FIELD EXPERIMENT 1—1969

Benomyl, oxycarboxin or 'Plondrel' (diethyl phthalimidophosphonothioate, previously known as 'Dow M2452' and 'Dowco 199') were sprayed on Cappelle-Desprez winter wheat grown as the tenth successive cereal susceptible to take-all. The wheat was sown in October and the fungicides applied by knapsack sprayer on 10 April at growth stage (G.S.) 3 (Large, 1954). Each fungicide formulated as a wettable powder was used at 1.1 and 5.6 kg a.i./ha in 337 l. water/ha. Seven plots of 0.002 ha were arranged in each of four randomized blocks. Six samples, each of the plants from 15 cm of row, were taken randomly from each plot on 27 May and six 30 cm samples were taken on 30 June; the plants were washed and examined for symptoms of take-all, eyespot and sharp eyespot.

TABLE 1

*Effect of fungicide sprays (1.1 kg a.i./ha) on the incidence of
foot and root diseases of winter wheat—Experiment 1, 1969*

	Eyespot (% shoots)	Sharp eyespot (% shoots)	Eyespot (% straws)	Sharp eyespot (% straws)	Take-all (% plants)	Yield (t/ha)
	27 May	27 May	30 June	30 June	30 June	30 Aug.
Untreated	6	44	10	36	58	5.85
Benomyl	0	62	1	54	55	6.31
'Plondrel'	5	35	9	51	52	5.73
Oxycarboxin	4	46	7	48	53	5.89
S.E.D. $\pm$	2.99	7.97	3.30	8.07	7.25	0.539

Results

Table 1 gives only the results of applying 1.1 kg a.i./ha because, with one exception, the larger amount had no greater effect. The exception was benomyl, which in spring samples gave 62 per cent of shoots with sharp eyespot at 1.1 kg a.i./ha and 38 per cent shoots infected at 5.6 kg a.i./ha.

FIELD EXPERIMENT 2—1970

Benomyl 50 per cent W.P., oxycarboxin 75 per cent W.P. and thiabendazole 60 per cent W.P. were applied to Cappelle-Desprez seed at 1 or 4 g formulated product/kg of seed; to ensure that the larger amount was applied evenly, the seed was pre-treated with 'Celacol M.M 10' methyl cellulose solution at 60 ml of 3 per cent aqueous solution/kg of seed and treated with fungicide while still wet. The wheat was sown in October, on a site previously cropped with 11 wheat or barley crops, at 180 kg of seed/ha. With the addition of a second untreated plot per block, the experimental design and methods of sampling and diagnosis were as for Experiment 1.

Results

The larger amount of thiabendazole and possibly of benomyl, decreased eyespot in April but no effect persisted to June (Table 2). In contrast, sharp eyespot was unaffected in April but was increased in June by both amounts of benomyl and thiabendazole; this increase in sharp eyespot did not decrease yields.

TABLE 2

Effect of fungicide seed dressings (4 g formulated product/kg of seed) on the incidence of foot and root diseases of winter wheat—Experiment 2, 1970

	Eyespot (% shoots)	Sharp eyespot (% shoots)	Eyespot (% straws)	Sharp eyespot (% straws)	Take-all (% plants)	Yield (t/ha)
	20 April	20 April	26 June	26 June	26 June	27 Aug.
Untreated	20	6	8	15	27	4.52
Benomyl	12	9	8	36	24	4.69
Oxycarboxin	13	8	14	19	22	4.76
Thiabendazole	9	5	11	30	24	4.73
S.E.D. $\pm$	5.84	3.05	2.64	7.40	6.75	0.219

FIELD EXPERIMENT 3—1971

Benomyl seed dressing (0.28 kg a.i./ha) and spray (1.1 kg a.i./ha) were applied alone or together to Cappelle-Desprez and Gaines winter wheats. Two 'nil' treatments were included, viz: untreated seed (two plots/cultivar in each block) and seed treated with 0.42 kg/ha of Shellstar 1 per cent organo-mercury seed dressing. The wheat was sown in October at 180 kg/ha and the spray was applied by knapsack sprayer at 1,120 l./ha on 23 March (G.S. 2-3). The previous cropping was winter wheat, barley, barley, winter wheat. Twelve plots of 0.0024 ha were replicated in three randomized blocks. Samples (6 x 30 cm of row) were taken in April (G.S. 3-4) and in June from each plot. Diagnosis was as before except in spring when infection on main shoots and 1st, 2nd and 3rd tillers was recorded separately.

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Results

Disease incidence varied considerably between plots but, on average, Cappelle-Desprez wheat had more sharp eyespot and less eyespot than Gaines. As both cultivars behaved similarly Table 3 shows average effects of benomyl. In April most lesions of each disease were on the main shoot with fewer lesions on each subsequent tiller, except where benomyl spray was applied, virtually eliminating eyespot on all shoots. Take-all was present and damaging but detailed assessments were not made.

TABLE 3

Effect of benomyl as a seed dressing (S.D.) and as a spray (S) on the incidence of foot diseases of winter wheat—Experiment 3, 1971

(Means of Cappelle-Desprez and Gaines wheats)

	Eyespot (% shoots)	Sharp eyespot (% shoots)	Eyespot (% straws)	Sharp eyespot (% straws)	Yield (t/ha)
	19 April	19 April	28 June	28 June	27 Aug.
Untreated	4	20	31	25	5.62
Organo-mercury	4	21	36	23	5.77
S.D.					
Benomyl S.D.	5	18	35	32	5.42
Benomyl S.	1	25	1	31	5.82
Benomyl S.D.+S.	1	15	2	32	6.04
S.E.D.±	1.39	3.59	6.32	4.67	0.267
between untreated and treatment means					

GLASSHOUSE EXPERIMENT 2—1972

The experiment compared all combinations of *C. herpotrichoides* inoculation and a benomyl spray, in a 2 × 2 factorial design with eight replicate blocks, on the incidence of *R. solani*. In an unheated glasshouse without supplementary lighting, Cappelle-Desprez wheat was sown (10 seeds/127 mm diameter pot) on 14 December; all pots were inoculated 40 days later with a 3 mm layer of a sand maize meal culture of *R. solani* and covered with a 5 mm surface layer of cornish grit. Inoculation with *C. herpotrichoides* was done by placing a 4 mm disc of potato dextrose agar, bearing sporulating *C. herpotrichoides* adjacent to each seedling on 23 January; unfortunately, these discs did not continue to sporulate satisfactorily so a second rather late inoculation was done on 6 March. On 27 March, benomyl was sprayed at 3 mg a.i. in 4 ml of water/pot. On 7 June the number of plants with eyespot was recorded and sharp eyespot was assessed in the following ways: (a) a rating on a 1 to 5 scale (1 = 1–20 per cent, 5 = 80–100 per cent) of the areas of straw affected on the lowest internodes that exceeded 1 cm in length; (b) the number of lesions on higher internodes; (c) the height of the top-most lesion.

Results

Only 11 per cent of plants had eyespot but despite this, inoculation with *C. herpotrichoides* decreased the incidence of sharp eyespot above the first internode. On the first internode benomyl greatly increased the incidence of sharp eyespot. (Table 4).

2-B

TABLE 4

*Effects on sharp eyespot infection of benomyl and
Cercospora herpotrichoides—1973*

	No Benomyl*	Benomyl*	No <i>Cercospora</i> †	<i>Cercospora</i> †	S.E.D. of means within treatments
Infection rating on 1st internode	1.5	2.6	2.0	2.0	0.116
Number of lesions above 1st internode	3.4	3.6	4.0	3.0	0.49
Height of topmost lesion (cm)	5.6	5.6	6.1	5.1	0.39

*Means of with and without *Cercospora*

†Means of with and without benomyl

DISCUSSION

In the field, take-all was not affected by any of the fungicides. This conflicts with the decreased take-all infection of seedlings with benomyl reported by Scott and Hollins (1972). However the closeness of the layer of artificial inoculum to the benomyl dressed seed in their pots may account for the difference.

One benomyl spray, given at a time when it could have been mixed with herbicide, almost completely controlled eyespot. Sprays applied at a later growth stage (G.S. 7-8) and smaller amounts of benomyl can also be effective (Witchalls and Close, 1971; Fehrmann and Schrödter, 1972). In glasshouse tests, Defosse (1970) showed that benomyl seed dressing protected seedlings against *C. herpotrichoides*, but in our field experiments neither benomyl nor thiabendazole seed dressings prevented or decreased the severity of infections on the straws.

Most of the fungicides, and especially benomyl, increased sharp eyespot as seed dressings and as sprays. Hoeven and Bollen (1972) showed a similar increase in sharp eyespot and decrease of eyespot on rye sprayed with benomyl; they also showed that in culture *R. solani* is less sensitive to benomyl than *C. herpotrichoides*. This may explain why the larger rate of benomyl in Experiment 1 did not increase sharp eyespot in the spring. There was often most sharp eyespot when there was least eyespot, an effect noted in earlier experiments at Rothamsted (Glynne, 1951; D. B. Slope, pers. comm.). In the glasshouse experiment the incidence of sharp eyespot was increased by benomyl but decreased by the presence of *C. herpotrichoides* inoculum even on plants which had no eyespot lesions.

In the field, decreasing eyespot had little effect on yield probably because there was not enough on 'nil' plots to cause lodging and because take-all limited all the yields. Sharp eyespot appeared to have no effect on yield.

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