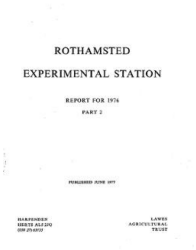
ROTHAMSTED RESEARCH

Rothamsted Experimental Station Report for 1976, Part 2



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A Survey of Fungi in Cereal Roots at Rothamsted, Woburn and Saxmundham, 1970–75

G. A. SALT

Introduction

It may seem surprising that a survey of fungi in cereal roots was undertaken considering the voluminous literature on cereal root- and foot-rot fungi that has accumulated during the last half century. Reviews of this literature have been published from time to time, e.g. by Butler (1961), Nilsson (1969) and Walker (1975). These reviews show that for wheat and barley most of the work has been on two major root-rots of cereals; take-all caused by *Gaeumannomyces graminis*; and common root-rot, a complex disease caused by several fungi the most important being *Helminthosporium sativum* and *Fusarium culmorum*. Whereas take-all is a serious disease in all major wheat growing countries, common root-rot is a serious disease in N. America and parts of Australia but of relatively minor importance in Britain. Many other fungi have been recorded on cereal roots (Sprague, 1950) but, with the exception of *Pythium* species, little is known of their prevalence, distribution, their effects on the host plant and how they are affected by agricultural practices. The majority infect the cortical cells of young roots apparently causing only superficial damage and are regarded as relatively minor pathogens. *Pythium* stands apart in being the only one of this miscellaneous group to cause a disease that has ranked as one of major importance. It was especially damaging on the Canadian prairies between 1920 and the late 1940s (Vanterpool, 1945). Outbreaks were associated with unbalanced nutrition when crops were grown on land low in phosphorus and relatively high in nitrogen content. The disease was favoured by summer fallows and by cold wet springs followed by spells of hot dry weather (Vanterpool & Ledingham, 1930; Vanterpool, 1940, 1952). The disease declined remarkably in importance when nutrient imbalance was corrected and summer fallows avoided. The importance of this disease in Britain is not known but in common with the other lesser known pathogens it is not easy to identify and may be more widespread and damaging than is presently thought.

With increasing intensification of cereal production losses from diseases tend to increase and a greater effort is required to control them. As methods of controlling the major diseases improve, the losses caused by minor diseases become increasingly important. The yield potential of the land and of new improved varieties is often not achieved in practice even where major diseases such as take-all are absent. There is therefore a need for information on the so-called 'minor' pathogens. Macfarlane (1970) has drawn attention to *Lagenocystis* (*Lagena*) *radicicola* which was found in the roots of many species of plants, especially cereals in which it causes a disease of root tips and rootlets. Also common on roots of many species but causing no obvious damage was *Rhizophydium graminis*. Information on the prevalence of other root-infecting fungi and the damage they might be causing seems to be lacking. Not all are harmful; the beneficial effects of the mycorrhizal endophyte *Endogone* is well known and work on this fungus has been reviewed by Mosse (1973). Recently Scott (1970) and Deacon (1973a, b) have shown that take-all infection is delayed or inhibited if roots first become infected by *Phialophora radicicola* var. *graminicola*.

This paper records the prevalence of lesser known fungi, mainly on winter wheat crops grown under a wide variety of cultural treatments and soils at Rothamsted, Woburn and

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Saxmundham. Records are also included from a few other localities where the crop has lacked vigour.

Methods

No single method is entirely satisfactory for a comprehensive survey. Direct microscopic examination of roots is necessary for the several fungi, e.g. *Olpidium*, *Lagenocystis*, *Polymyxa* and *Endogone*, that cannot be grown on agar media. Direct observation is satisfactory for detecting fungi that produce characteristic sporangia, resting spores, microsclerotia, mycelium or other structures by which they can be recognised within the root. It fails to detect or underestimates fungi that do not, or infrequently produce mycelium with characteristic features. Thus *Fusarium* species were not recognised in this survey and *Aureobasidium* was underestimated as only the sclerotial stage could be recognised. Most of the identifiable structures are resting bodies of the fungi and reflect previous fungal activity when conditions may have been different from those at sampling time. The survey would have been more comprehensive if direct observation had been supplemented with isolations of fungi from roots plated on agar media, but this was not possible with the time and resources available. The microscopical examination of thousands of root pieces alone took much time.

Plants were lifted with a hand fork from about six random positions to give a bulk sample of about 50 plants. After washing, a subsample of ten plants or straws was removed, the roots were spread in one direction and cut transversely 4–5 cm below the crown and again 1 cm nearer the crown to give many root segments each 1 cm long. Older roots were cleared in hot 5% NaOH for 15 min (Phillips & Hayman, 1970) before staining by warming in trypan blue and lactophenol, but young roots were stained without prior clearing. From each subsample 30 root segments were mounted in lactophenol on three slides, each with ten segments arranged parallel to each other and to the length of the slide and examined under a binocular microscope using × 10 widefield eyepieces and × 20 and × 40 objectives.

In the first year of the survey infections were recorded separately on main axes and laterals of both seminal and crown roots and on any segment containing a root tip. This detailed analysis added little of value to the survey and was abandoned in subsequent years, when a root segment was recorded as infected if a fungus was seen on any part of it. The number of root segments examined ranged from 1200 in 1970 to 3500 in 1971 and averaged 2500 per year.

Notes on the fungi recorded

Zoosporic fungi with no mycelium (holocarpic). These spread by releasing motile zoospores into the soil water. The zoospores infect root hairs and cortical cells producing within them characteristic sporangia, from which new generations of zoospores may be released, or resting spores which may remain viable in soil for several years after the roots have decayed. These fungi produce no mycelium and cannot be cultured on agar media. The most common genera were *Lagenocystis*, *Polymyxa*, *Ligniera* and *Olpidium*.

Lagenocystis radicicola (Vanterpool and Ledingham) Copeland, first described in 1930 by Vanterpool and Ledingham as *Lagena radicicola* is recognised by its filamentous sporangia and small smooth resting spores (Plate 1a). *Polymyxa graminis*, a member of the Plasmodiophorales, is most easily recognised by clusters of small resting spores (cystosori) which may fill almost every cortical cell in infected parts of roots (Plate 1b). Zoospores of this fungus are known to transmit soil-borne wheat mosaic virus (Rao & Brakke, 1969) and probably oat mosaic virus (Herbert & Panizo, 1975). *Ligniera*, also a member of the Plasmodiophorales, is found mainly in root hairs causing them to swell as

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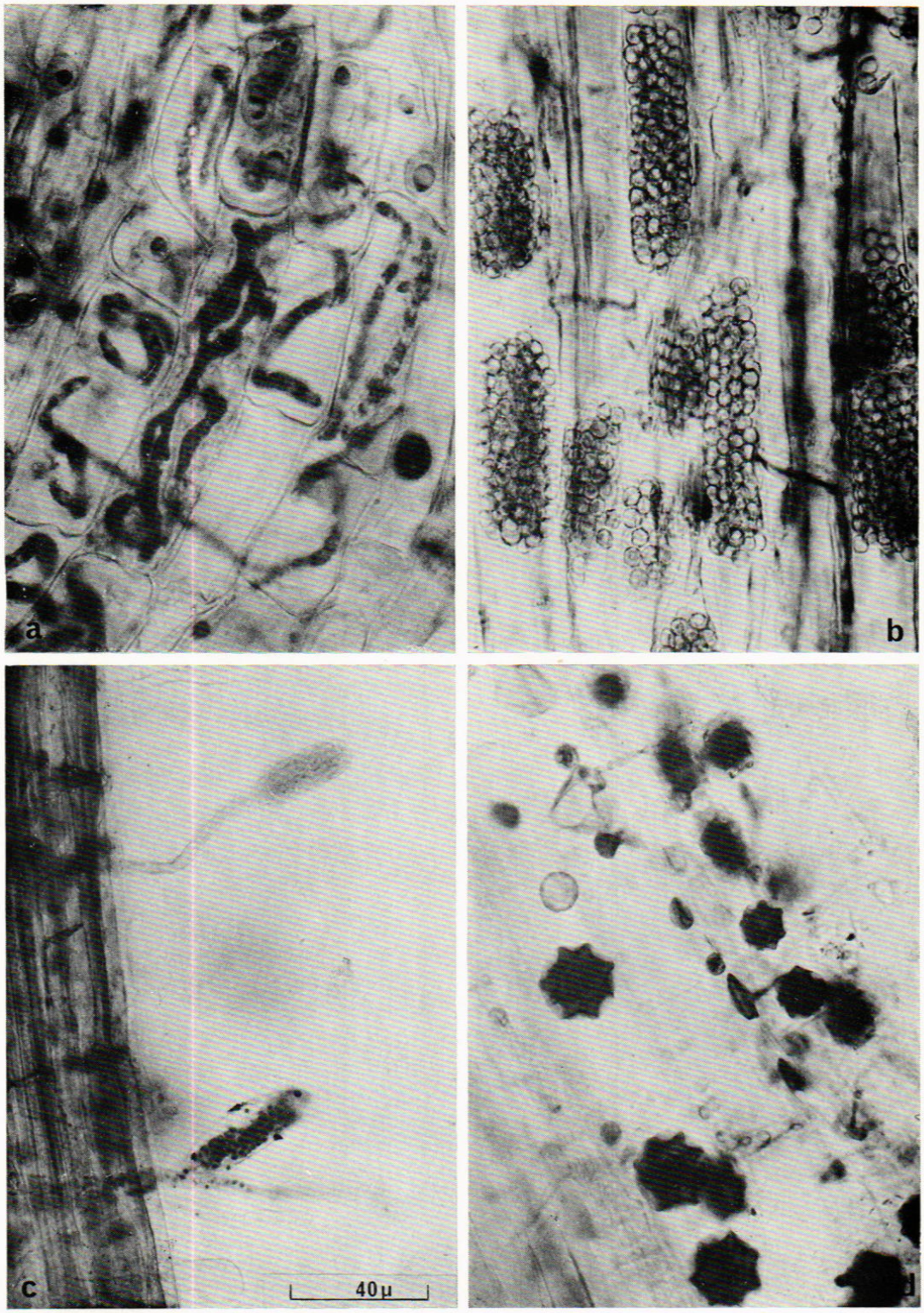

PLATE 1. Zoosporic fungi (holocarpic) (a) *Lagenocystis radicicola*, filamentous sporangia with a few resting spores. (b) *Polymyxa graminis*, cystosori of resting spores. (c) *Ligniera* sp., resting spores in swollen root hairs. (d) *Olpidium* sp., sporangia with exit tubes and stellate resting spores.

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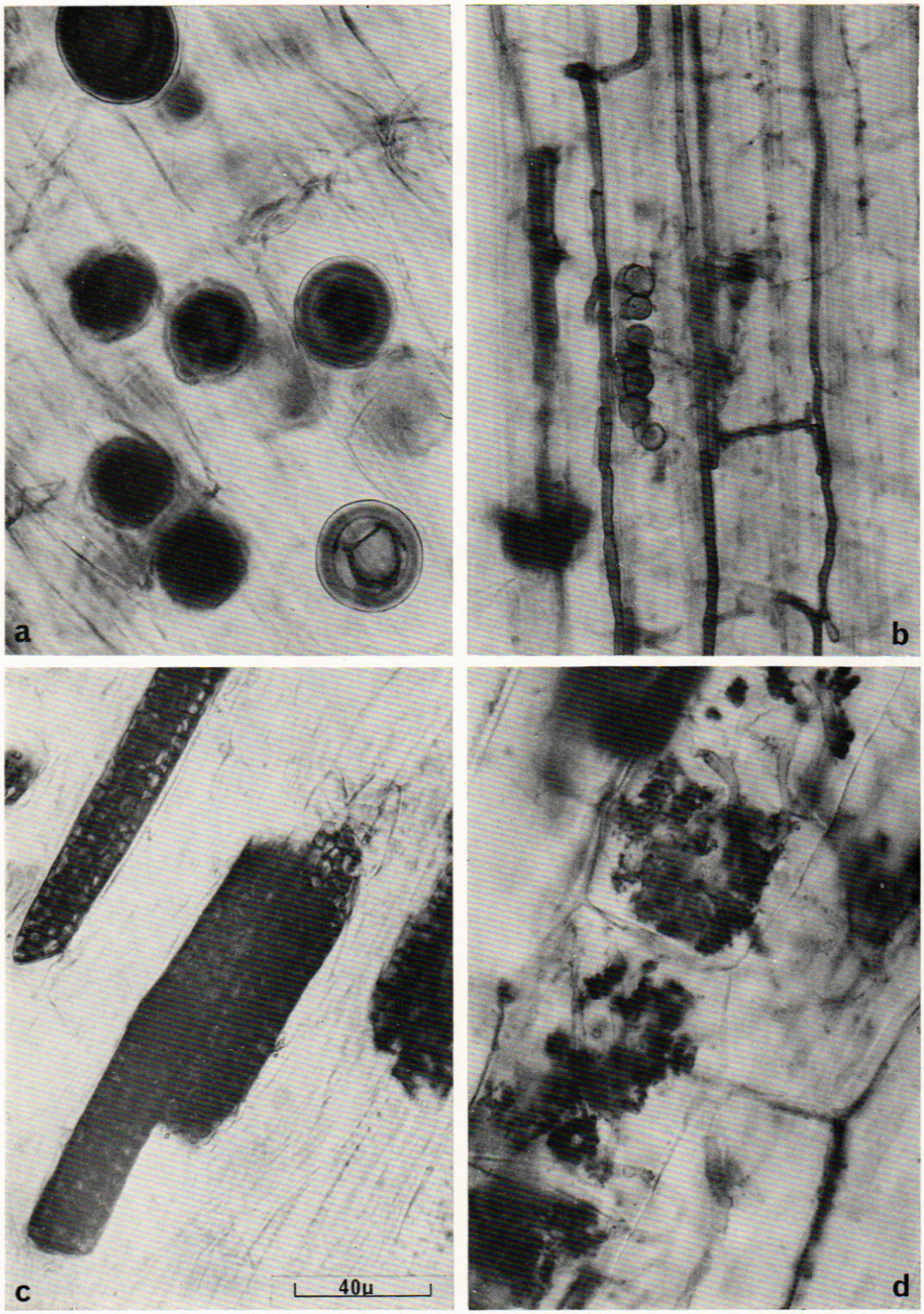

PLATE 2. Mycelial fungi (a) *Pythium arrhenomanes*, oospores. (b) *Phialophora radicicola var. graminicola*, vesicles and brown runner hyphae. (c) *Aureobasidium bolleyi*, dark brown microsclerotia. (d) *Endogone* sp., mycelium and 'arbuscules'.

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they become filled with resting spores (Plate 1c). *Olpidium* is recognised by rows of sac-like sporangia within superficial cells, opening by exit tubes which vary in length according to the distance from the root surface. Resting spores are coarsely wrinkled to give a stellate appearance (Plate 1d).

Mycelial fungi. These have a vegetative mycelium which enables them to penetrate deeply into host tissues, but the mycelium of many cannot be identified until reproductive bodies are formed. Most of this group of fungi can be isolated from the host and identified as pure cultures grown on agar media. *Pythium* species can produce mobile zoospores under moist conditions but are recognised by spherical oospores. Those of *P. arrhenomanes* (Plate 2a) occurred in large numbers accompanied by browning and collapse of cortical tissue, whereas smaller oospores belonging to several other species, e.g. *P. ultimum* and *P. vexans* (Waller, 1971) occurred singly without any root discoloration. The different species of *Pythium* were not identified in this survey, but infections by *P. arrhenomanes* were probably less prevalent on winter wheat than those by other species. Waller (1971) found that only 25% of *Pythium* isolates from wheat, but 60% of those from barley were *P. arrhenomanes*. Several fungi produce brown septate 'runner hyphae' which grow over the surface of roots and send branches into the cortex and sometimes into the vascular tissue causing it to turn brown or black. In this survey fungi with 'runner hyphae' that caused vascular discoloration were ascribed to *Gaeumannomyces graminis*, and those that produced groups of spherical vesicles, each with a pore, and no vascular disease to *Phialophora radicicola* var. *graminicola* (Plate 2b). A closely related fungus *Phialophora radicicola* var. *radicicola* was recorded on only one site in this survey (Stackyard Ley–Arable, Woburn) and is not mentioned again in this paper. Of the other mycelial fungi recorded *Aureobasidium bolleyi* was recognised by dark brown microsclerotia (Plate 2c) within root cortical cells and *Endogone* was easily identified by its large wide hyphae which send branches into cortical cells, filling each with finely divided 'arbuscules' (Plate 2d).

Results

Distribution of fungi on different parts of the root system. Table 1 shows that in March and April *Pythium* was more prevalent on crown than on seminal roots, although the crown roots had only recently emerged, and more root tip segments were infected than segments of older root. This distribution was still evident in May but by July very little *Pythium* was present. By contrast *Olpidium* was more prevalent in seminal than crown roots and showed no preference for root tips. The other holocarpic zoosporic fungi were not prevalent enough to show any marked preferences and appeared to infect all parts equally. Mycelial fungi were found more often on main axes than on lateral roots and on crown roots more often than seminal roots. Unidentified mycelium was prevalent in March and April especially on the young crown roots, but identifiable mycelial fungi increased as plants aged.

These results indicate that specific fungi tend to be more prevalent on certain parts of the root system but for a general survey such detailed records seemed unnecessary and time could be spent more profitably in looking at larger numbers of samples.

Records from Broadbalk winter wheat cv. Cappelle

Seasonal distribution. Fig. 1 shows that roots became infected by *Olpidium* at a very early stage, the incidence of infection was high in the earliest samples taken in January and remained high for the rest of the season. Other holocarpic zoosporic fungi, e.g. *Lagenocystis* and *Polymyxa*, were rare on Broadbalk during the whole five-year period and have not been included in Figs. 1, 2 or 3.

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TABLE 1

Infection of roots of different age and position (March–July, 1970)

Date sampled	March–April					May					July		
Type of root	Seminal roots		Crown roots	Root tip segments	Mean for all roots	Seminal roots		Crown roots		Mean for all roots	Main axes	Laterals	Mean
	Main axes	Laterals				Main axes	Laterals	Main axes	Laterals				
Number examined	330	261	26	68		340	183	269	120		167	94	
	Percentage root segments infected												
Lagenocystis	4	3	6	3	3	1	1	6	2	2	0	0	0
Ligniera	2	0	8	3	1	0	0	0	0	0	0	0	0
Olpidium	16	15	0	12	15	13	9	10	2	10	8	2	6
Polymyxa	1	2	0	2	1	0	0	0	0	0	0	0	0
Pythium	10	12	28	19	12	13	6	16	16	13	2	3	3
Endogone	11	7	4	10	9	23	28	20	12	22	22	21	22
Aureobasidium	0	0	0	0	0	0	0	0	0	0	19	16	18
Gaeumannomyces	0	0	0	0	0	3	2	5	0	3	15	2	10
Phialophora	0	0	0	0	0	0	0	0	0	0	5	0	3
Other mycelium	24	15	64	15	22	8	3	16	1	8	10	12	11

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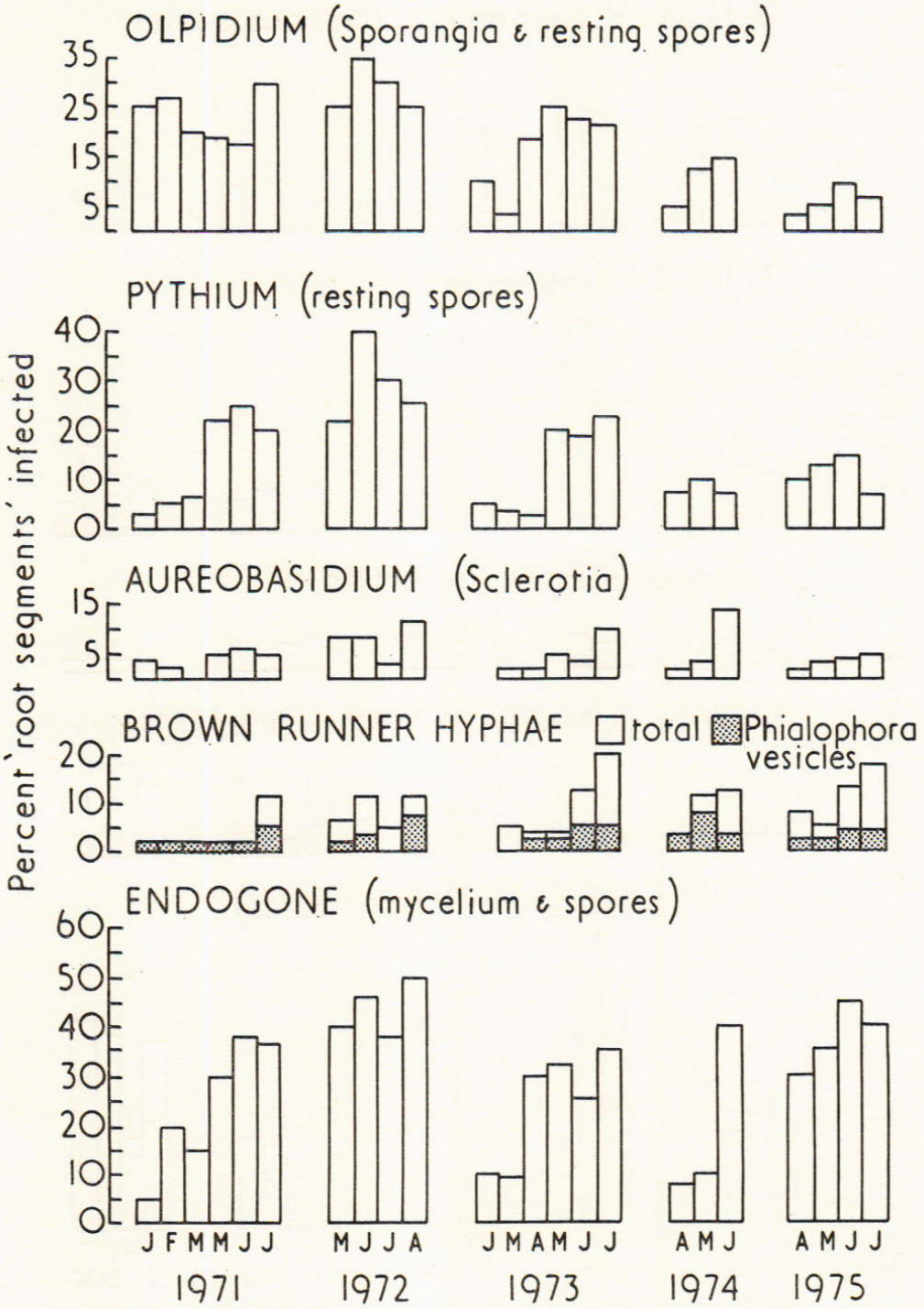

FIG. 1. Seasonal variation in prevalence of fungi in roots of winter wheat on Broadbalk. (Means of cropping sequences and fertiliser treatments.)

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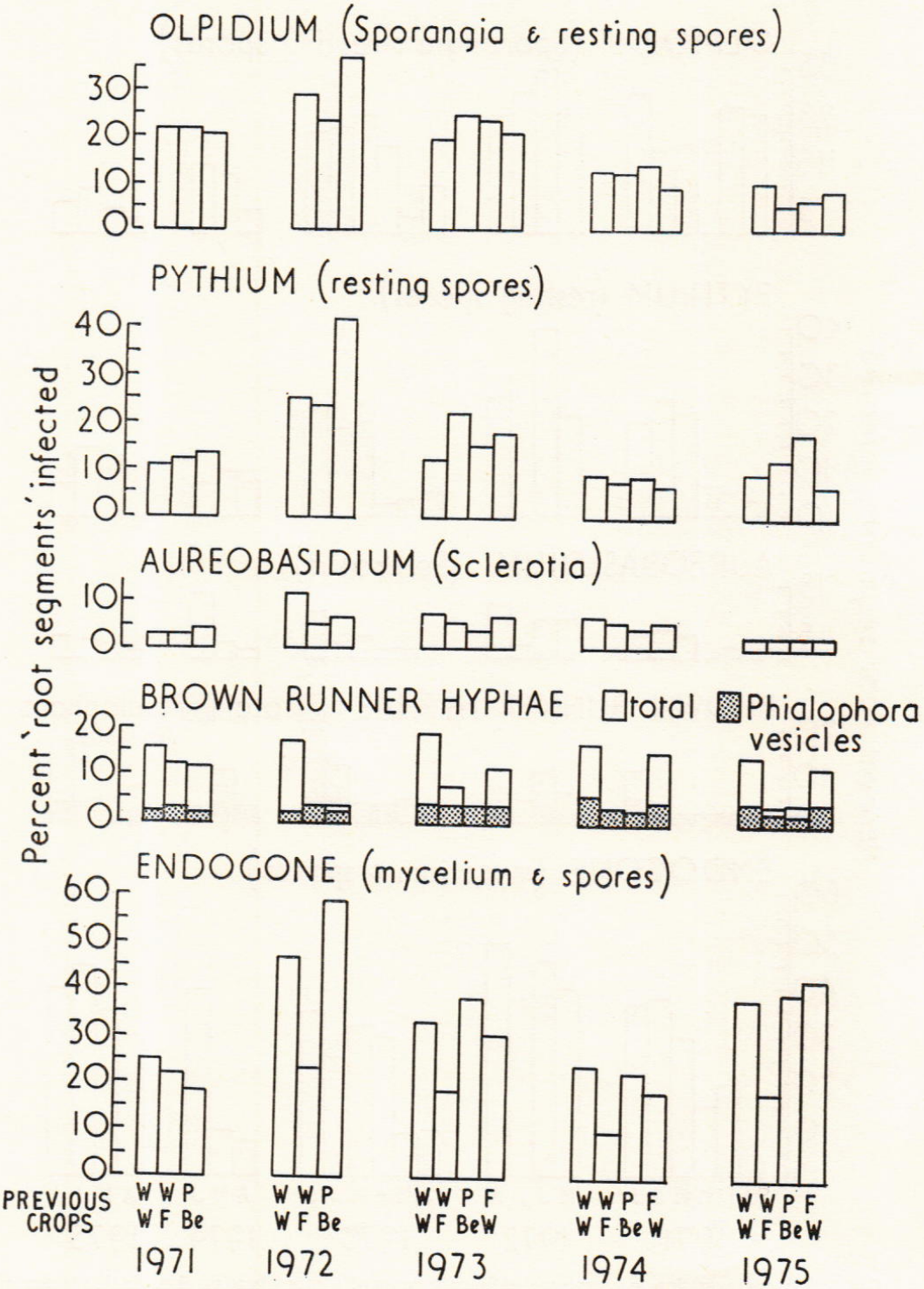

FIG. 2. Effects of previous crops on prevalence of fungi in roots of winter wheat on Broadbalk. (Means of sampling dates and fertiliser treatment.) Winter wheat, W; Fallow, F; Potatoes, P; Field beans, Be.

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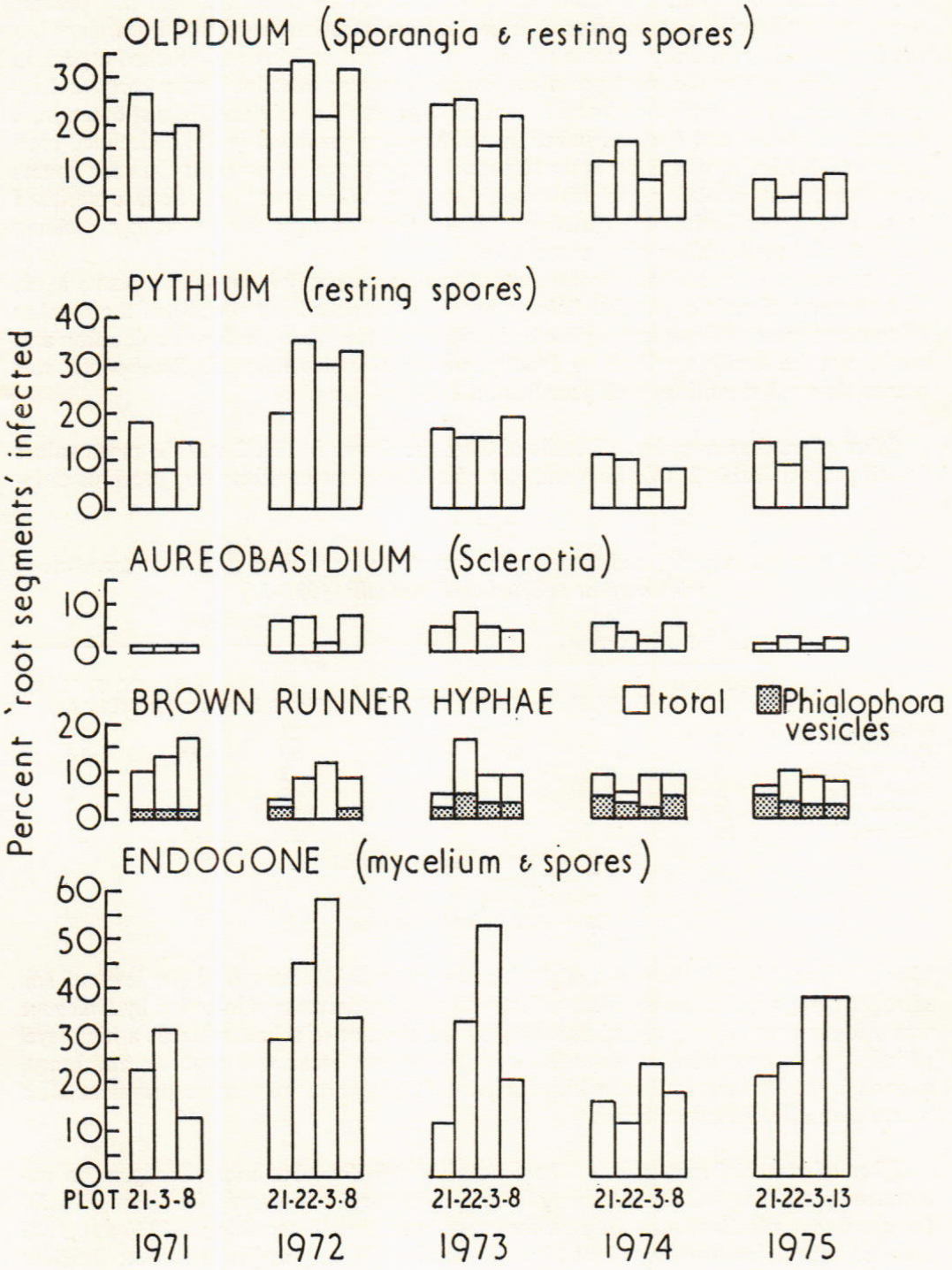

FIG. 3. Effects of fertiliser treatments on prevalence of fungi on roots of winter wheat on Broadbalk. (Means of sampling dates and cropping sequences.)

Plot 21—Farmyard manure + N.
Plot 22—Farmyard manure only.
Plot 3—Nil.
Plot 8 and 13 —N, P, K, Mg.

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In contrast to *Olpidium* mycelial fungi were slower to infect and did not become prevalent until spring and summer. A little *Pythium* infection was found in January but the fungus did not usually become prevalent until April or May and reached a peak in June. *Endogone* was the most prevalent fungus in roots; infection began early and increased steadily through the season to reach a high level by July and August every year, whereas *Olpidium* and *Pythium* infections, which were prevalent in 1972, declined each year until 1975. *Aureobasidium* is usually much more prevalent on roots than the counts of root segments containing sclerotia would suggest. When roots were surface sterilised in sodium hypochlorite and plated on potato dextrose agar the percentage yielding cultures of *Aureobasidium* often exceeded 50%.

The number of roots with brown runner hyphae generally increased as plants aged. The presence of vesicles enabled *Phialophora* to be identified but about half the number of root segments with runner hyphae had neither vesicles nor vascular discoloration and could not be easily ascribed to *Phialophora* or *Gaeumannomyces*. *Phialophora* was present in small quantities each year from the earliest sample.

Effect of previous cropping. Details of these are shown in Fig. 2 and the mean values for all years in Table 2. *Olpidium* and *Aureobasidium* were unaffected by previous crop-

TABLE 2

Effect of previous cropping and fertiliser treatments on mean percentage root segments of winter wheat infected on Broadbalk (1971–75)

	Previous crops			Fertilisers			
				Farmyard manure			
	Continuous wheat	W, W, F	W, P, Be	+N (Plot 2.1)	−N (Plot 2.2)	Nil (Plot 03)	N, P, K, Mg (Plot 08)
Olpidium	18	17	20	20	21	14	19
Pythium	13	15	19	16	17	14	16
Aureobasidium	6	4	4	4	2	1	2
Phialophora	3	2	1	3	2	1	2
Runner hyphae	16	5	4	6	10	10	10
Endogone	33	18	33	20	23	41	25

W = Winter wheat cv. Cappelle
F = Fallow
P = Potatoes
Be = Field beans (*Vicia faba*)

ping whereas *Pythium* showed a slight increase after field beans, a higher level of soil nitrogen being a possible contributory factor. A striking decrease in infection by *Endogone* was evident after fallow, caused probably by the absence of a host whereas a high level of infection was recorded in wheat following a two-year break with potatoes and beans, a good host. Runner hyphae, which included *Phialophora*, were more prevalent after wheat than after fallow or beans.

Effect of manurial treatments. There was less *Olpidium* but more *Endogone* in unmanured plots than in those receiving farmyard manure or inorganic fertilisers (Fig. 3). No consistent effects of manuring on the other fungi were detectable. In 1974 and 1975 samples were taken also from Plot 10 which received N only and is phosphate deficient but *Pythium* was no more prevalent here than in other plots.

Locality and soil type. Between March and April 1970 samples of winter wheat cv. Cappelle were taken from experiments on three different sites with similar cropping histories:

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1. Intensive wheat experiment, Harwood Field, Saxmundham, a sandy clay of the Beccles series (Corbett & Tatler, 1970).
2. Intensive cereal experiment, Stackyard Field, Woburn, a sandy loam of the Cottenham or Stackyard series.
3. Take-all reference plots, Pennells Piece, Rothamsted, Clay-with-flints of the Batcombe series.

TABLE 3

Percentage root segments of winter wheat infected from different localities with similar cropping history (March–April, 1970)

	Olpidium	*Lagenocystis*	*Polymyxa*	*Ligniera*	*Pythium*	*Endogone*	Unidentified mycelium
Harwood's (Saxmundham)	40	15	0	0	1	18	4
Stackyard (Woburn)	8	4	6	6	18	6	38
Pennells Piece (Rothamsted)	10	1	0	0	32	3	19

In each experiment continuous wheat was compared with the first and third wheat crop after beans at Rothamsted and Saxmundham and after ley at Woburn. In Table 3 the cropping sequence data have been averaged to give a direct comparison between sites. The most striking feature was the predominance of different fungi at different sites. For example, the zoosporic fungi *Olpidium* and *Lagenocystis* were both more abundant at Saxmundham than at either Woburn or Rothamsted, whereas *Pythium* was abundant at Rothamsted and rare at Saxmundham. Unidentified fungal mycelium was unusually prevalent in roots from Stackyard, Woburn, but it is not known whether this has anything to do with the poor yields of wheat usually obtained on this field (Johnston, 1974).

Root infections in the Woburn Ley–Arable experiment. There were some interesting contrasts in the prevalence of different fungi in roots of rye in July 1971 (Table 4). *Polymyxa* was more prevalent than *Olpidium*, infecting 68% of root segments in the continuous arable plots, but was absent from roots of rye following a three-year ley. *Pythium* was also more common after arable crops than after ley or sainfoin. *Phialophora*

TABLE 4

Percentage root segments infected in Woburn Ley–Arable rye (July 1971)

	Cropping sequences 1965–71				Residual effect of soil fumigation	
	L	S	Ah	A	Nil	Chloropicrin*
Olpidium	1	1	2	10	5	1
Polymyxa	0	24	23	68	28	29
Pythium	11	15	28	28	20	21
Aureobasidium	4	12	20	11	8	15
Phialophora	22	4	12	2	13	7
Runner hyphae	28	22	36	31	28	29
Endogone	58	28	35	39	37	43

* Chloropicrin applied before previous potato crop planted in 1970

	1965	1966	1967	1968	1969	1970	1971
L =	←———	Grass	———→	Barley	Barley	Potatoes	Rye
S =	←———	Sainfoin	———→	Barley	Barley	Potatoes	Rye
Ah =	Potatoes	Rye	Hay	Barley	Barley	Potatoes	Rye
A =	Potatoes	Rye	Carrots	Barley	Barley	Potatoes	Rye

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was prevalent after ley and rare after arable crops or sainfoin, whereas unidentified runner hyphae probably mostly *Gaeumannomyces*, were more prevalent after arable than after ley cropping and so the total percentage of roots infected with runner hyphae showed little variation with previous cropping.

TABLE 5

Percentage root segments infected in Woburn Ley–Arable wheat (2nd test crop), May 1975

	Cropping sequences 1971–75			
	L	C	Ah	A
Lagenocystis	1	2	2	1
Olpidium	5	4	5	6
Pythium	15	14	9	16
Aureobasidium	1	1	1	0
Phialophora	15	7	8	4
Runner hyphae	28	30	14	9
Endogone	29	48	37	32

	1971	1972	1973	1974	1975
L =	←———	Grass ley	———→	Potatoes	Wheat
C =	←———	Clover	———→	Potatoes	Wheat
Ah =	Potatoes	Barley	Hay	Potatoes	Wheat
A =	Potatoes	Barley	Barley	Potatoes	Wheat

In roots of winter wheat sampled in May 1975 (Table 5) *Polymyxa* was not recorded, *Lagenocystis* and *Olpidium* were not common, and *Pythium* was recorded frequently after both ley and arable cropping sequences. As with rye *Phialophora* was more common in the rotation containing a three-year ley. A low level of infection by unidentified runner hyphae was present in all cropping sequences except the one including sainfoin, which was also the only sequence after which *Phialophora* was not recorded.

Root infections after soil fumigation. In the Woburn Ley–Arable experiment soil fumigation before planting potatoes frequently gave increases in growth and yield of the following cereal crop, which was not affected by take-all or eyespot. To examine the effects of soil fumigation on other root-inhabiting fungi, samples of rye were taken in July 1971 from plots which had been treated and untreated with chloropicrin before planting potatoes the previous season. Table 4 shows that fumigation had no detectable residual effect on infection by any of the fungi recorded. In May 1975, plots of wheat similarly showed no residual effect on fungi of aldicarb applied for the previous potato crop.

In 1971, samples of winter wheat from untreated plots at Rothamsted and Woburn were compared with those from plots that had been drenched with formaldehyde before sowing in the previous autumn. Table 6 shows that this treatment decreased infection by *Olpidium*, *Endogone* and brown runner hyphae of both *Phialophora* and *Gaeumannomyces*. It did not decrease infection by *Lagenocystis*, *Pythium* or *Aureobasidium*. A year later in the second wheat crop after treatment, (f), the numbers of most fungi had recovered to reach the same level as in untreated soil except for *Endogone* which remained low and *Gaeumannomyces* which exceeded the numbers of infections in untreated soil.

Root infection in patches of stunted plants. Several crops were sampled in 1971 and 1972 to see whether patches of poor growth were associated with the prevalence of particular fungi in the roots. In 1971 at Papplewick in Nottinghamshire a crop of spring barley on a very sandy loam with a high population of the nematode *Pratylenchus fallax* was severely stunted in patches. In June the normal crop had more infection by *Pythium* and *Endogone*

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TABLE 6

Percentage root segments of wheat infected after soil fumigation

Field	Sampling date 1971		*Lagenocystis*	*Olpidium*	*Pythium*	*Aureobasidium*	*Phialophora*	*Runner hyphae*	*Endogone*
Butt Close (Woburn)	Feb	—	11	44	0	0	0	0	9
		F	21	21	0	0	0	0	0
	May	—	0	0	3	0	0	8	13
		F	0	0	2	0	0	8	10
	July	—	0	9	10	9	7	37	23
		F	0	15	12	10	1	22	14
		(f)	0	12	10	8	7	50	14
Furzefield (Rothamsted)	May	—	0	1	15	0	0	0	30
		F	0	1	9	0	0	0	9
	July	—	0	9	4	3	0	22	47
		F	0	6	4	5	0	13	31
Summerdells (Rothamsted)	Feb	—	8	27	0	0	0	0	0
		D	15	15	0	0	0	0	0

— Nil; F, formaldehyde drench to soil before sowing; (f), formaldehyde before sowing previous wheat crop; D, dazomet rotovated in before sowing

TABLE 7

Percentage root segments infected from patches of stunted plants

Crop and location	Crop growth	*Olpidium*	*Polymyxa*	*Pythium*	*Aureobasidium*	*Phialophora*	*Runner hyphae*	*Endogone*
Barley								
Papplewick (June 1971)	Poor	0	0	37	7	0	20	37
	Good	3	0	67	7	3	10	60
Winter wheat								
Horseground Woodwalton (July 1971)	Poor	9	4	0	2	0	4	83
	Good	53	0	0	0	0	0	21
Winter wheat								
Middle Hood Woodwalton (April 1972)	Poor	4	0	10	0	0	8	47
	Good	2	0	0	0	0	0	25

TABLE 8

Percentage root segments of winter wheat infected from different sites

		Olpidium	*Polymyxa*	*Lagenocystis*	*Pythium*	*Aureobasidium*	*Phialophora*	*Runner hyphae*	*Endogone*
Little Knott (*Rothamsted*)									
May 1970	1st Wheat	3	0	0	30	0	0	0	7
	3rd Wheat	5	0	3	16	0	0	3	19
	Continuous Wheat	6	0	0	9	0	0	0	30
Pennells Piece (*Rothamsted*)									
June 1971	1st Wheat	3	39	0	10	36	0	3	46
	Continuous Wheat	27	0	0	10	19	0	10	52
May 1972	1st Wheat	33	0	0	35	2	0	7	60
	2nd Wheat	5	25	0	20	0	0	3	35
	Continuous Wheat	18	0	0	12	6	6	3	37
Jan 1973	1st Wheat	2	0	0	13	0	2	5	10
	3rd Wheat	0	0	0	38	0	0	0	10
	Continuous Wheat	3	0	0	5	2	0	5	33
Harwood's (*Saxmundham*)									
June 1971	2nd Wheat	15	0	0	12	6	21	48	79
	4th Wheat	29	0	0	13	0	11	29	78
	6th Wheat	23	0	0	3	10	5	26	67
Lansome (*Woburn*)									
May 1973	1st Wheat*	3	17	0	17	10	0	0	0
	2nd Wheat*	0	37	0	3	3	0	3	7

* Take-all infected plants removed. All roots examined appeared healthy

than the poor crop but runner hyphae, probably of *Gaeumannomyces* was more abundant in the poor crop (Table 7). There was a strong correlation between stunting and the population of *Pratylenchus* and so it would seem that stunting could be attributed mainly to the nematode with some contribution from *Gaeumannomyces* but that other fungi did not appear to be involved.

At Woodwalton in Huntingdonshire wheat crops visited in 1971 and 1972 were uneven in height and plant number and appeared as if they had suffered an earlier wheat bulb fly attack. Differences in growth could not be explained by take-all and the only fungus notably more prevalent on roots from poor plants was *Endogone*. This suggested a possible deficiency of phosphate but the fields had been receiving regular liberal dressings of phosphate.

Root infections in other fields. These are shown in Table 8. A notable feature is the greater abundance of *Pythium* in the first wheat crop than in continuous wheat and this was shown in samples from three different areas—Rothamsted, Saxmundham and Woburn. Also notable was the abundance of *Polymyxa* in the 1st and 2nd wheat crops on some sites. On Pennells Piece, Rothamsted, a heavy infection was found in June 1971 in one rather poorly drained plot. In May 1972 the second wheat crop on the same plot was heavily infected, but in January 1973 and at subsequent dates through the season no trace of infection could be found in the 3rd wheat crop on this plot. Conditions that favoured *Polymyxa* might have been expected to favour *Olpidium* also but unexpectedly *Olpidium* infection was usually slight where *Polymyxa* was prevalent.

Discussion

This was not a comprehensive survey in that direct microscopic examination can reveal only fungi that present recognisable morphological features. It is probably the only method for those fungi that cannot be induced to grow on artificial media. To accomplish the task in a reasonable time only the presence or absence of each fungus in each 1 cm root segment was recorded. A large number of root segments was examined in order to give as reliable an estimate as possible of the prevalence of each fungus. Although it was not done in this survey the same root segments could have been used for estimating the severity of infection by any one of the fungi by counting the number of spores or scoring the amount of mycelium in each root segment. The method as used in this survey has been used for recording fungi in roots of other crops, e.g. field beans (Salt & Hornby, 1973) and potatoes (Salt, 1971).

Zoosporic fungi, being dependent on soil water for spread and having short life-cycles, might have been expected to show large seasonal fluctuations in prevalence. These were not found nor was there any close relationship between prevalence and rainfall distribution. This was probably because a large proportion of infections by these fungi were recorded from resting spores, which persist so long as roots remain intact. The method used was therefore measuring the accumulated total of periods of fungal spread and could not reveal individual 'flushes' of infection that could be related to rainfall or other climatic factors. More frequent sampling and separate records for sporangial numbers would have been necessary to establish any such relationship. There was, however, a general decline in the prevalence of zoosporic fungi including *Pythium* from a peak in 1972 to a low incidence in 1975 (Fig. 1), and this may have reflected the increasing dryness of recent summers. This trend was not shown in the prevalence of mycelial fungi. Holocarpic zoosporic fungi infected roots while plants were still young and became abundant during winter and early spring, whereas *Pythium* and other mycelial fungi spread more slowly and became abundant in late spring or early summer.

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The results indicate widespread occurrence of these fungi in cereal roots and also considerable unexplained variations in their abundance between different localities. Thus *Pythium* spp. were more abundant in roots at Rothamsted than at Woburn or Saxmundham, whereas *Olpidium* was particularly abundant at Saxmundham. *Polymyxa* was more frequently found at Woburn than elsewhere, for example on 68% of root segments of rye on part of the ley arable experiment (Table 4) and on 37% of those of wheat on Lansome (Table 8). At Rothamsted, *Polymyxa* was not found in the many samples from Broadbalk over a five-year priod but infected as many as 39 and 25% of wheat root pieces in 1971 and 1972 respectively from Pennells Piece, situated at the lower end of Broadbalk (Table 8).

There were some large differences in the incidence of *Phialophora* present on root samples from the three contrasting soil types at Rothamsted, Woburn and Saxmundham. Only a small proportion (3–8%) was usually infected but the proportion was greater where a grass ley had been included in the rotation (Tables 4 and 5), as reported by Deacon (1973a, b). Unfortunately, no cereal was sampled immediately following a grass ley.

The prevalence of these fungi was not greatly affected by previous cropping history or fertiliser use except that infection by *Endogone* was more common in unmanured plots and was much diminished after a bare fallow but not after a two-year break of potatoes and field beans. This result could have been expected as Hayman (1970) and Mosse (1973) have also reported that spores of *Endogone* are more numerous in clay soils without fertilisers than in fertilised plots. An increase in soil nitrogen may have contributed to the smaller infection after fallow but as there was no decrease in infection after field beans which would increase soil nitrogen, a decline of viable inoculum in the absence of a host plant offers a more likely explanation of the differences found.

Pythium was usually more prevalent in wheat after field beans than after cereals, possibly an effect of increased soil nitrogen. No relationship was found between *Pythium* infection and phosphate deficiency, contrary to the reported association of *Pythium* infection of wheat with phosphate deficient soils in Canada (Vanterpool, 1945) and reports by Broom (1971) and Slope and Broom (1973) of root-rot of barley involving *Pythium* and other fungi being most prevalent in phosphate-deficient field soils at Rothamsted. In pots of sand at Rothamsted, Macfarlane and Salt (1974) showed that inoculation of barley with *P. arrhenomanes* decreased shoot and root weights most where P was deficient and this difference was more probably a result of greater susceptibility of P-deficient roots to infection than of the inability of a diseased root system to gain sufficient nutrients in a P-deficient medium. Possibly wheat and barley differ in their susceptibility to *Pythium* or in disease expression, or the larger root system and earlier infection by *Endogone* of winter wheat may equip the crop to cope better with phosphate-deficient soils.

Of the various fungi recorded in the survey *Pythium arrhenomanes* is the only one known to cause significant damage and this has been measured in pot experiments only. Waller (1971) reported that *P. arrhenomanes* decreased the height and weight of six-week-old wheat seedlings in pots by about 10%. Macfarlane and Salt (1974) found that barley suffered severely when steam-sterilised soil was inoculated with the fungus, but in natural field soil the effect of inoculation was much more modest and dry weight was decreased by about 20%. Fungi that invade the root cortex are likely to do less damage than those that damage vascular tissue but there is some evidence to suggest that fungi causing only superificial cortical infection may affect plant growth by interfering with nutrient uptake. Thus Salt and Clarkson (1972) showed that wheat grown axenically and inoculated with *P. arrhenomanes* contained less ^{85}Sr and ^{32}P in shoots but more ^{59}Fe in both shoots and roots than did uninoculated plants. Similarly Macfarlane (1972 and 1973) showed that

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cabbage seedlings infected with *Olpidium* showed iron deficiency symptoms sooner than healthy plants. Fitt and Hornby (1975) found that infections by *Gaeumannomyces graminis*, *Aureobasidium bolleyi*, *Cochliobolus sativus* and *Fusarium culmorum* all decreased plant dry weight and increased the proportion of ^{14}C retained in the shoot of 33-day-old plants whose leaves received a 10 min exposure to $^{14}CO_2$. In autoradiographs seminal root axes infected with *C. sativus* and *F. culmorum* were labelled along their whole length whereas those infected with *G. graminis* remained unlabelled because translocation was blocked distally from the point at which vascular tissue was invaded, and ^{14}C accumulated in the crown roots. *A. bolleyi* killed seminal roots early and so they contained no ^{14}C.

These observations raise the problem of how to assess damage and suggest that for lesser-known pathogens a physiological approach may be more rewarding than trying to measure only losses in yield, which are usually exaggerated in pots, especially in sterilised soils, and almost impossible to do at present in natural field soil because of the difficulty in obtaining uninfected controls.

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