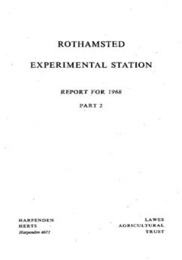
Rothamsted Experimental Station Report for 1968 - Part 2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6. FUNGUS DISEASES OF WHEAT ON BROADBALK, 1843–1967

MARY D. GLYNNE

Introduction

The Broadbalk experiment has provided unique opportunities for studying the incidence of diseases in consecutive wheat crops, how they are affected by manuring and fallowing, and how they vary from year to year. Comparison with wheat grown at the same time in other crop sequences at Rothamsted has shown how the incidence of some diseases, notably eyespot and take-all, differ in different crop rotations and are associated with great differences in yield. This stimulated series of short term (3–8 year) experiments to study in detail effects of previous crops, different amounts of nitrogen and other factors on foot and root diseases and on yields of wheat and barley.

This contribution traces the growth of knowledge about some wheat diseases on Broadbalk from the first records in the farm notebooks, of symptoms in 1852, through the identification of specific causes to surveys. At first incidence and severity of diseases were estimated by eye in the field, then by systematic quantitative sampling. At first all plots were surveyed, but as the need for more intense studies appeared more detailed examinations were needed and fewer plots were examined.

1843–1929. The only records of diseases on Broadbalk before 1930 are those included in the farm notes in the beautifully hand-written vellum-bound 'White Books' (1843–1912 and 1912–57) and in Mr. Keenan's Notebook No. 7 for the year 1867. These notes reflect the excited surprise of the early years when small amounts of chemical salts were seen to increase yields as much as did bulky loads of farmyard manure. Meticulous notes recorded qualities such as brightness, stiffness and colour of straw, plumpness and 'pinkiness' of the harvested grain, and from 1848 notes were made on the standing crop. So it is noteworthy that there is no suggestion of disease until the ninth successive crop. In that year (1852) some early treatments (which included pearl ash, animal charcoal, common salt and even tapioca) were discontinued and 13 plots began to receive their present treatments. The extra nitrogen supplied and the very wet summer (13·3 in. of rain in June–August) doubtless increased lodging which ranged from 'not laid' on some plots to 'very much laid' on those with most nitrogen. Plot 16, which at that time received 172 lb N/acre as ammonium salts was both laid and 'blighted', a term often used to describe effects of rust, mildew, and sometimes, perhaps, take-all. 'Straggling' or 'scrailing', when straws fell haphazardly among upright ones, was recorded from 1856. Both lodging and straggling on Broadbalk were later shown to be partly caused by the eyespot fungus attacking and weakening straw bases.

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Mr. Keenan's notebook for 1867 contains a vivid description of a striped green and yellow wheat plant that may perhaps have been caused by *Cephalosporium gramineum* (Slope, 1961) or by wheat striate mosaic virus, both comparatively recently recognised here.

Year by year more diseases were mentioned in the White Books; ergot from 1882, mildew from 1888, rust from 1892 and smut was noted as present in 1915, but recorded as absent in 1872, suggesting that it occurred in other early years. Weeds had been reported since 1854, and major species recorded for each plot from 1869. There were few references to pests though these included the mysterious 'woolly ear' of 1869; the 'red gum', *Cecidomyia tritici* in 1878, 1881, 1896 and 1904, when ears immediately after blooming were infested by reddish yellow maggots, probably the deposits of a 'small black fly' (presumably the gall midge). The corn aphis (*Sitobion avenae* (F.)) was present in 'enormous quantity' in 1892, identified as *Aphis granaria*, sometimes known as *Aphis Avenae* by Miss Ormerod, the first woman scientist to be associated with Rothamsted. Wireworm damage was suspected in 1889 and many wireworms observed during hand hoeing in 1903. Leaf miner was noted in 1922 and damage by birds occasionally from 1889. During this period lodging and weeds were the most obvious and often recorded troubles, followed by straggling and blighting; there were far fewer references to named diseases, such as mildew and rust caused by airborne pathogens or to pests. Weeds were recognised as serious and led to the fallowing system begun in 1926 (see Table 2·2 p. 23). Diseases were thought to be no worse on Broadbalk than on other fields and the accepted view was that continuous cropping had not led to 'accumulation' of any disease. However, plant pathology was developing fast and the surveys of diseases (and pests by H. F. C. Newton) begun in 1930 were to prove this opinion wrong.

1930–38. Plots of wheat in various experiments at Rothamsted and Woburn were examined several times during the growing season, diagnoses were checked in the laboratory, and visual estimates made in the field of the extent and severity of diseases. In addition to observations of the more noticeable diseases of leaf and ear, these surveys revealed the frequent but variable incidence of foot and root diseases of wheat. Quantitative estimates involving extensive sampling were made in specially interesting experiments such as the continuous wheat at Woburn which was severely attacked by take-all in 1931–33 (Glynne, 1935). On Broadbalk, the recognition of eyespot, caused by *Cercosporella herpotrichoides* Fron. in 1935, and the suspicion in 1937 that the disease increased lodging, showed the need for quantitative surveys. Summaries of the field observations and estimates of disease incidence were recorded annually by Glynne as 'Fungus and other diseases at Rothamsted and Woburn' in Rothamsted Reports for 1930 to 1938.

1938–67. Systematic quantitative surveys of foot and root diseases, begun in 1938, have been continued until the present time. From each plot ten samples were taken (distributed over the plot by taking the first and sixth from randomly selected points within the first fifth, the rest at equal

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distances along and across the plot to fall within each fifth of the plot). Samples taken in spring consisted of the plants in 6 in. of two adjacent rows, and those taken shortly before harvest of 1 ft in two adjacent rows. The results could therefore be presented as number per unit area or as percentages of plants or straws infected. Many people helped with these surveys, but all diagnoses have been made by only two persons (Glynne, 1938–57 and Etheridge, 1958–67). Selected plots were sampled in spring and notes made of diseases. Lodging was measured by pacing lodged areas of all plots shortly before harvest. Most of the results discussed here are from 'harvest' surveys usually taken in July from all sections, in 1938–44 of all 17 plots, in 1945–57 of 8 representative plots (2B, 3, 5, 6, 7, 8, 17 18 and in some years, plot 15); in 1958–64 three plots (2B, 3, 7) were sampled and in 1965–67 only plot 7. Results are referred to in the Plant Pathology section of the Rothamsted Reports each year from 1938, and detailed records are deposited in the Rothamsted Library and the Plant Pathology Department.

Eyespot

Cercosporella herpotrichoides Fron. was first recorded in Britain when eyespot lesions carrying spores were found on wheat on Broadbalk in February 1935 (Glynne, 1936). The fungus had been identified, by spores in pure culture, as the cause of eyespot in N. America (Sprague, 1931) and in France (Foëx & Rosella, 1933). It is prevalent in Britain and other temperate countries and is now recognised as the cause of a serious disease of wheat, sometimes of barley, less often of oats. Eyespot occurred again in 1936, and in 1937 it was very severe on most plots on Broadbalk. The surveys, begun in 1938, have shown how some factors influence eyespot and have suggested how eyespot affects yields, and shown some of its effects on lodging. All the varieties of wheat or barley tested have proved susceptible, but some, notably Cappelle Desprez, are less severely affected than Squarehead's Master, Yeoman or many older varieties.

The chief factors determining eyespot incidence are weather and the amount of fungus surviving from previous crops. Very cold winters may check decay of infected stubble. Spores are produced during damp cool weather from autumn to spring on infected straws on the soil surface. They develop slowly at 5° C, fastest and most profusely at about 10° C, but are not produced above about 20° C. (Glynne, 1953, Salt, 1957). Rain splashes spores on to young plants which become infected and produce more spores which in turn are splashed on to other plants. Warmer weather, usually in April, stops spore production. The fungus grows slowly, penetrating successive leaf sheaths to reach the straws. Early infections penetrate deeply, producing severe lesions that decrease yield and increase the tendency to lodge and straggle. Late infections are more likely to produce superficial lesions, which have little effect on yield but help the fungus to survive. It is therefore important to distinguish between severe (deep) and slight (superficial) lesions, and this has been done in all the surveys.

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TABLE 6·1

The percentage of straws with severe and slight eyespot lesions at harvest, 1938–1957

(Mean of plots 2B, 3, 5, 6, 7, 8, 17, 18)

Harvest year	Years after fallow: 1 Severe	1 Slight	2 Severe	2 Slight	3 Severe	3 Slight	4 Severe	4 Slight	Mean 2, 3, 4 Severe	Mean 2, 3, 4 Slight
1938	**12**	5	**32**	12	**37**	11	**35**	13	**34·6**	11·8
1939	**38**	16	**57**	18	**70**	14	**63**	15	**63·2**	15·4
1940	**31**	20	**45**	26	**44**	25	**42**	24	**43·8**	24·8
1941	**43**	21	**51**	18	**54**	18	**46**	20	**50·4**	18·5
1942	**22**	9	**52**	13	**49**	14	**44**	14	**48·4**	13·9
1943	**30**	18	**57**	22	**57**	23	**55**	21	**56·5**	21·8
1944	**31**	29	**54**	30	**53**	34	**48**	33	**51·6**	32·2
1945	**13**	34	**53**	27	**46**	30	**46**	24	**48·1**	27·1
1946	**17**	43	**49***	41*	**50***	40*	**51**	39	**50·0**	39·9
1947	**2**	9	**18**	38	**11**	22	**10**	19	**13·1**	26·4
1948	**15**	12	**22**	12	**41**	24	**26**	23	**29·6**	19·5
1949	**7**	8	**49**	15	**44**	16	**34**	19	**42·5**	16·9
1950	**38**	21	**57**	17	**51**	20	**50**	17	**52·6**	18·0
1951	**15**	12	**58**	16	**51**	19	**45**	18	**51·4**	18·0
1952	**8**	10	**57**	18	**52**	24	**47**	23	**52·2**	21·6
1953	**17**	29	**35**	23	**48**	27	**39**	23	**40·7**	24·0
1954	**30**	32	**54**	22	**61**	21	**53**	26	**55·9**	22·7
1955	**8**	10	**35**	17	**36**	17	**27**	13	**32·5**	15·4
1956	**9**	23	**24**	25	**26**	20	**31**	26	**26·7**	23·7
1957	**7**	6	**44**	27	**47**	21	**33**	23	**41·2**	23·8
Mean for 20 years	**19·6**	18·4	**45·2**	21·8	**46·3**	21·9	**41·3**	21·6	**44·2**	21·8

* Calculated by missing plot technique, as only two sections were surveyed in 1946.

TABLE 6·2

The percentage of straws with severe and slight eyespot lesions at harvest, 1958–1967

(data supplied by J. Etheridge)

Harvest year	Years after fallow: 1 Severe	1 Slight	2 Severe	2 Slight	3 Severe	3 Slight	4 Severe	4 Slight	Mean 2, 3, 4 Severe	Mean 2, 3, 4 Slight
					Mean of Plots 2B, 3 and 7					
1958	**9**	14	**40**	27	**49**	30	**43**	34	**44·2**	30·3
1959	**2**	5	**10**	10	**11**	21	**12**	10	**11·0**	13·4
1960	**35**	35	**28**	23	**56**	25	**54**	25	**46·0**	24·3
1961	**3**	6	**24**	25	**21**	25	**28**	18	**24·5**	22·7
1962	**13**	25	**17**	22	**17**	33	**20**	32	**17·8**	28·8
1963	**3**	13	**19**	33	**12**	37	**11**	27	**13·9**	32·1
1964	**26†**	42†	**35**	34	**30**	38	**40**	39	**35·0**	37·2
					Plot 7 only					
1965	**15**	25	**27***	28*	**16**	22	**25**	26	**21**	24
1966	**1**	7	**12**	26	**26†**	33*	**17**	29	**15**	27
1967	**20**	15	**48**	21	**42**	20	**57†**	21*	**45**	21

* Section VA, not sprayed with herbicide, is not included in means of 2nd, 3rd and 4th crops. Since May 1964 weedkillers have been applied annually to all other sections (Table 2·2, p. 24).

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Year to year variation. Table 6·1 shows the average proportion of straws with severe and with slight eyespot lesions in eight plots for the years 1938–57 and Table 6·2 the proportion in plots 2B, 3 and 7 for seven years and in one, plot 7 for three years between 1958–67.

Table 6·3 gives the ten-year means and the maximum and minimum incidence during each period.

TABLE 6·3

The percentage of straws infected with eyespot lesions at harvest: ten-year means and maximum and minimum

			Years after fallow								
10-year periods	Number of plots surveyed	Eyespot lesions	1	2	3	4	Means 2, 3, 4	1 Min	1 Max	2, 3, 4 Min	2, 3, 4 Max
1938–47	8	Total	44	71	70	66	69	11	64	40	90
		Severe	24	47	47	44	46	2	43	13	63
		Slight	20	24	23	22	23	5	42	12	40
1948–57	8	Total	32	63	66	59	63	12	62	48	79
		Severe	16	44	45	38	42	7	38	27	56
		Slight	16	19	21	21	20	6	32	15	24
1958–67	3 or 1*	Total	32	51	56	57	54	7	70	24	74
			(29)	(49)	(55)	(56)	(53)				
		Severe	13	26	28	31	28	1	35	11	46
			(11)	(25)	(27)	(30)	(27)				
		Slight	19	25	28	26	26	5	42	13	37
			(18)	(24)	(28)	(26)	(26)				

* 3 plots 1958–64; 1 plot 1965–67.

The mean percentages for 1958–67 adjusted to take account of constant plot-differences in the previous 20 years 1938–57 are shown in brackets.

Weather has a great effect on the severity of eyespot. Lesions usually occur in March, occasionally as early as December. Cool wet weather prolongs sporulation and spring rain helps the fungus to spread and develop. In March and April 1938 there were, respectively, two and three weeks without rain. Square-yard plots on Broadbalk, but outside the main experiment, were watered with the equivalent of ½ in. of rain per week from 14 March to 13 June. Table 6·4 shows that by harvest severe eyespot lesions were more than 3 times as numerous on the watered as on the unwatered plots.

TABLE 6·4

Effect of watering in spring on severity of eyespot at harvest, 1938

(Glynne & Turner, unpublished)

	% straws infected by harvest		
Treatment	Total	Severe	Slight
Control	25	14	11
Watered 14 March–13 June	65	50	15
Standard error	±2·07	±2·25	±1·33

Rainfall, 13 March to 14 June = 2·4 in.
Water applied, 13 March to 14 June = 7 in.

Eyespot was less prevalent on Broadbalk between 1958 and 1967 than previously (Table 6·3), probably because the crops were sown later. Table 6·5 compares the proportion of late-sown crops in three decades with aver-

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age eyespot incidence. The influence of sowing date on eyespot was measured in experiments in 1945 and 1946. In consecutive years plots sown in October had respectively 61 and 92% straws infected, 42 and 55% with severe eyespot lesions, whereas those sown in November had 15 and 69% infected, 7 and 26% with severe lesions by harvest.

TABLE 6·5

Date of sowing and eyespot incidence

Harvest years	No. of crops sown in Oct.	Nov.	Dec.	Jan.	% straws with eyespot, 10 year means of 8 plots: After wheat Severe	After wheat Slight	After fallow Severe	After fallow Slight
1938–1947	8	2	0	0	**46**	23	**24**	20
1948–1957	3	6	1	0	**42**	20	**16**	16
1958–1967	2	5	1	2	**28**	26	**13**	19
					(27)	(26)	**(11)**	(18)

Means for 3 plots 1958–64 and 1 plot 1965–67 adjusted as in Table 6·3 to take account of constant plot differences in the previous years 1938–57 are shown in brackets.

Fallow. The first crop after fallow had an average of less than half as many severe eyespot lesions as the 2nd, 3rd or 4th crops (Table 6·3). The effect was repeated almost every year and with all manurial treatments. Slight lesions were less affected and averaged only about 5% more after wheat than after fallow. The reverse was sometimes true usually in years when more than half the straws after wheat already had severe lesions. The decay of infected stubble during the fallow accounted for the fewer infections. The amount of fungus surviving from the preceding crops was measured by collecting straw bases from equal areas of two plots (3 and 7) in Jan.–March and testing their ability to produce spores (Cox & Cock, 1962). In 1958 an average of 22 potentially infectious straws on 5 sq. yd, left by the 3rd wheat crop, infected 17% plants in spring, 73% straws by harvest. After fallow there was an average of only one infectious straw on the same area and this produced only 1% of infected plants in spring and 26% of straws by harvest in 1958; by contrast, in 1959, one infectious straw infected only 10% of straws by harvest, because the weather was much less favourable to the disease.

From 1938–57 eyespot was most severe in the second or third crops and was usually less in the fourth crop after fallow. This difference was not great but occurred in most years and the 4th crop had an average of 5% less severe eyespot lesions than the 3rd (Table 6·1). It may be relevant that in other field experiments eyespot increased in successive crops and then became less severe as take-all became prevalent. Garner and Dyke showed that the 4th crops yielded slightly more than the 3rd in most plots (p. 39).

After 1957, when wheat tended to be sown later than before, eyespot often only reached its peak in the fourth crop. One half section (IA) carried continuous wheat from 1952, having its fifth crop in 1956. Although there was usually less eyespot in the half section carrying continuous wheat than in the 2nd–4th crops in other plot sections, some of the evidence suggests that this may have been due to herbicides sprayed on to the

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continuous wheat. The possibility that eyespot may decline in successive wheat crops, the effect of herbicides and of the weeds they control now awaits critical study.

Fertilisers. Table 6·6 shows the proportion of straws with severe and slight lesions in all plots for the first seven years surveyed and in eight plots from 1938–57. Much effort has been spent in trying to find a pattern

TABLE 6·6

Effect of the fertiliser treatments on incidence of eyspot at harvest

		% straws with eyespot lesions							
		Mean 7 years 1938–44 Years after fallow				Mean 20 years 1938–57 Years after fallow			
		1		2, 3, 4		1		2, 3, 4	
Plot	Treatment	Severe	Slight	Severe	Slight	Severe	Slight	Severe	Slight
2B	FYM	**34**	17	**54**	16	**23**	18	**48**	21
3	None	**16**	16	**37**	22	**12**	16	**39**	21
5	P K Na Mg	**28**	18	**44**	21	**23**	19	**47**	22
6	N_1 P K Na Mg	**28**	19	**53**	22	**21**	22	**47**	23
7	N_2 P K Na Mg	**38**	18	**57**	20	**26**	20	**47**	23
8	N_3 P K Na Mg	**38**	16	**58**	18	**19**	18	**42**	22
9	N_1*P K Na Mg	**34**	14	**52**	21				
10	N_2	**14**	16	**40**	22				
11	N_2 P	**22**	13	**41**	18				
12	N_2 P Na	**22**	15	**44**	19				
13	N_2 P K	**33**	15	**55**	18				
14	N_2 P Mg	**20**	14	**42**	20				
15	N_2†P K Na Mg	**29**	17	**52**	18				
16	N_2*P K Na Mg	**30**	15	**51**	17				
17‡	N_2	**31**	17	**50**	19	**19**	18	**39**	22
18‡	P K Na Mg	**22**	15	**46**	21	**13**	14	**45**	20
19	R	**26**	15	**52**	18				
	Mean 17 plots	**28**	16	**49**	20				
	8 plots	**30**	17	**50**	20	**20**	18	**44**	22

N_1, N_2, N_3, 43, 86, 129 lb N/acre/year.
N Nitrogen as ammonium salts.
N* Nitrogen as sodium nitrate.
N† All nitrogen as ammonium sulphate in autumn.
‡ Plot 17 and 18 receive PKNaMg or N_2 in alternative years. In subsequent tables 17/18 PKNaMg indicates the plot receiving PKNaMg & 17/18 N_2 the plot with N_2.

of disease response to fertilisers; but their effects proved erratic and much smaller than those of weather or fallow. However, there were some effects which were greatest on severe lesions and in the first crop after fallow. There was least eyespot in plots 3 and 10 which do not get PKNaMg; it was less than the mean in plots 11, 12 and 14, which do not get K. N_2PK (plot 13) and PKNaMg (plot 5) usually had more eyespot. Nitrogen had erratic effects; sometimes the two smaller dressings (plots 6 and 7) increased eyespot more than the largest dressing (plot 8). Alternate dressings of PKNaMg and nitrogen (17/18) were unpredictable, but the 20-year means for these plots, showed most eyespot in crops with nitrogen following fallow, least in those after wheat. Thus on the whole, the better nourished plots had more straws infected at harvest than the poorer plots.

Inconsistent effects of fertilisers were also noted in other countries (Sprague & Fellowes, 1934; Weigert & Weizel, 1935; Oört 1936 & Meijers, 1937), and suggest an interplay of opposing factors. Wheat grown in pots and watered regularly (Glynne, Dion & Weil, 1945) had least severe eyespot in the well nourished and the thinly sown plants, because extra tillers delayed penetration of the central ear-bearing straws by this slow-growing fungus. But in the field, during dry periods, outer infected leaves may die and give eyespot-free plants, especially in thin nutrient-deficient crops. The damper conditions in luxuriant crops favour spread and development of the disease. Thus the percent tillers infected in May is often more in nitrogen-deficient than in well-fed crops, but the percent straws infected by harvest is smaller. (Glynne 1951, Glynne & Salt 1958, Salt 1957). Eyespot is usually most prevalent at harvest in well nourished crops.

Edge effects. Outer rows running east to west consistently had more straws and ears/ft than inner rows; they also had much less severe eyespot and often remained standing when the rest of the plot was lodged. They yielded more than the inner rows, especially in the nutrient-deficient plots 3 and 5. The south edges were better than the north, suggesting a beneficial effect of light and of rapid drying, as well as from extra nutrients and root space provided by the fallow path between plots.

Grain yield. It has not been possible to measure the effect of eyespot on yield on Broadbalk, partly because the largest crops usually have most eyespot and partly because fallow increases yield in other ways than by decreasing eyespot. However, there is a good deal of indirect evidence suggesting the degree of loss.

The Four- and Six-Course Rotation experiments provided comparable

TABLE 6·7

Incidence of eyespot and yield of grain in long-term experiments at Rothamsted

		Means 1938–57						
		% straws with eyespot.				Grain cwt/acre		
		Total	Severe					
Experiment	Previous crops*	Mean	Mean	Min	Max	Mean	Min	Max
Broadbalk	F W W W W F W W W W F W	66	44	13	63	16	10	22
Four-course	W P B Rg (or Be)	45	27	11	54	18	10	24
Broadbalk	W W W F	38	20	2	43	23	17	33
Six-course	P R Sb B C	32	16	1	44	30	19	41
		Means 1952–57						
Broadbalk	W W W F	31	13	8	30	22	19	27
Fosters Ley-arable	Lu Lu Lu	5	2	0	6	37	36	39

*Previous crops

W = Wheat, B = Barley, R = Rye } Susceptible to eyespot

F = fallow
P = potatoes
Rg = ryegrass
Be = beans
Sb = sugar beet
C = clover
Lu = lucerne

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surveys of eyespot incidence and yields for 20 years from 1938. The old varieties grown on them, Squarehead's Master, Red Standard or Yeoman, had similar potential yields, 40–45 cwt/acre. The variety Cappelle now grown can yield over 60 cwt/acre (Glynne & Slope 1959). From 1952 to 1958, Yeoman was also grown on the Ley-Arable experiment, where wheat following three years without cereals had very little eyespot (Salt, 1959). Table 6·7 shows means each including a wide range of fertiliser treatments. Eyespot was the dominant soil-borne disease. Take-all was important only where wheat followed wheat on Broadbalk.

The increase in mean yield of grain from 16 to 37 cwt/acre, associated with a decrease in severe eyespot from 44 to 2% suggested a causal relation and emphasised the need to measure how crop sequence and other factors affect yield and disease. The short-term rotation experiments showed a similar range of yields which were greatest where eyespot was least. (Glynne, Salt & Slope, 1954; Glynne & Slope, 1959; Glynne, 1965).

Yield varied least in the Ley-Arable experiment, where the wheat was almost free from eyespot. The largest yield in the seven years (1952–58) was 42 cwt/acre obtained in 1958, whereas in that year the same variety, Yeoman, with severe eyespot, in the six course rotation experiment yielded only 18 cwt/acre, the least for 30 years (Glynne, 1963).

On Broadbalk the annual means for 8 plots of severe eyespot varied from 13 to 63% after wheat, from 2 to 43% after fallow (Table 6·7), but showed no clear relation to grain yield, which varied respectively from 10–22 and from 17–33 cwt/acre. This is not surprising because weather affects crop and disease independently.

TABLE 6·8

Spring rain, severe eyespot and grain yield (mean of 8 plots)

		% straws with severe eyespot (harvest)		Grain yield cwt/acre	
Harvest year	Rainfall * (in.) Feb.–April	after wheat	after fallow	after wheat	after fallow
1938	1·0	35	12	22	33
1946	5·4	51	17	13	24
1947	9·1	13	2	10	18

* Measured in $\frac{1}{1000}$ acre gauge.

For example much infectious material was left by a severely infected crop in 1937 and eyespot appeared early in 1938, so that 15% and 35% plants were infected in January and February. However, little rain fell from February to the end of April so the fungus did not spread and there was no more disease at harvest (Table 6·8); also the warm summer favoured the crop and yields were large (45 cwt/acre on plot 2B after fallow). In 1946 conditions favoured both the crop and the disease, and yields were moderate (29 cwt/acre on 2B). By contrast in 1947, snow lay till mid-March and conditions were unfavourable to both crop and pathogen, and yields were exceptionally small (21 cwt/acre on 2B).

Number of straws. Yield of grain depends on the number of ear-bearing straws and the weight of grain in the ears. Most straws carried ears. On an

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average (8 plots from 1938–57) there were 15 straws/foot of row but annual averages ranged from 8 in 1947 to 21 in 1956. Table 6·9 shows that the best nourished plots 2B and 8 had most straws.

TABLE 6·9

Mean number of straws per foot of row at harvest 1938–67

Plots	2B	3	5	6	7	8	17/18 PKNaMg	17/18 N_2
After wheat	17	13	14	14	15	16	12	15
After fallow	18	13	15	15	16	17	14	15

After fallow there was an average of one more straw/ft than after wheat but there were years when this difference was reversed or very small; in 1953 there were only 13·9 straws/ft after fallow, 19·6 after wheat, and the extra yield after fallow averaged only 0·8 cwt/acre, the smallest recorded in 20 years (the average increase was 7·7 cwt/acre). The few straws after fallow almost certainly reflected attack by Wheat Bulb fly, *Leptohylemyia coarctata*, which always occurs after fallow, and in 1953 was abnormally prevalent on Broadbalk, and elsewhere was more severe than in any year between 1938 and 1957.

Regression analyses for the Six-Course Rotation experiment showed that annual variation in the number of straws accounted for 18% of the variance in grain yield and together with the number with severe eyespot lesions for 48% of the variance in yield. An extra uninfected straw per foot (at 6 in. spacing) gave an increase of nearly 1 cwt grain/acre whereas a severely diseased straw added only 0·14 cwt/acre (Glynne, 1963). This relation was not found on Broadbalk, perhaps because there were too many other factors affecting yield.

Loss from eyespot. Comparing the yield of grain on straws from Broadbalk with severe, slight and no eyespot lesions showed that slight lesions did not decrease yield, but the average yield of severely infected straws was only half as much as that of healthy ones. On this basis average loss in yield from eyespot would be about 10% after fallow and 22% after wheat (8 plots, 1938–57). Inoculating wheat in pots with the eyespot fungus decreased grain yield by 16% when plants were given much nitrogen and by 44% when given little; it also decreased the number of ears. (Glynne, Dion & Weil, 1945). But all plants in the pots were infected, whereas on Broadbalk many were not, so losses would be less. None of these estimates takes into account the additional loss from lodging caused by eyespot.

Effect of eyespot on lodging. In the wet summer of 1937 all except the poorest plots on Broadbalk were severely lodged. The prevalent idea that lodging was caused by excess nitrogen, rain and wind, could not explain why similar crops were not equally lodged in adjacent fields. For instance, the variety Red Standard with about 90% straws with eyespot lesions was lodged on Broadbalk; so was similarly infected Victor on another field, but nearby an equally heavy crop of Victor with only 5%

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of straws infected remained upright. Such striking differences suggested that eyespot might be one of the causes of lodging. The records of all Broadbalk plots surveyed from 1938 to 1947 (Table 6·10) show that lodging was increased both by weight of straw and by the proportion weakened by severe eyespot lesions.

TABLE 6·10

Effect on percent area lodged of weight of straw and percent with severe eyespot lesions. Broadbalk 1938–47

Straw cwt/acre	0–20	21–50	51–70	71–100	Mean 564 plots
	% straws with severe eyespot lesions				
	% area lodged				
10–30	0	8	13	31	8
30–40	0	9	17	30	11
40–50	3	9	33	44	17
50–60	15	33	55	78	42
60–80	21	78	78	100	58
Mean	2	12	23	45	

When straw yields were less than 40 cwt/acre there was no lodging without eyespot. However, plots with less straw were often recorded as lodged from 1852 onwards. Although varietal differences cannot be ignored, this suggests that eyespot has been prevalent on Broadbalk for a very long time.

Lodging

The importance attached to lodging was shown in the early farm records and in published statements such as that of Lawes and Gilbert (1864) that in 1863 'the heaviest plots (on Broadbalk) would have yielded considerably more had they not been laid so flat, consequently the increase in yield for each increment of ammonia salts beyond 400 lb was less than normal', and Gilbert said that the experimental plots in 1898 were so bad from 'laying and blight' that for the first time since the beginning of the annual reports on the wheat crop, they did not attempt to estimate the wheat yield of the United Kingdom from them. The tentative estimate from selected plots was about 9 bushels less than the eventual estimate of the Board of Agriculture, which suggested a loss of about 30% from 'lodging and blighting'.

The White Books (and Mr. Keenan's Notebook) contain descriptive notes of lodging in some 65 of the 86 years between 1852 and 1937. An attempt has been made to compare these with later records by using an arbitrary system to convert them into percent area lodged. (Table 6·11). Conversions of Mr. B. Weston's descriptive notes in the White Book from 1938–42 agreed well with the independent estimates of percent area lodged made in disease surveys by pacing round lodged areas.

In some years light crops were recorded as 'standing well', in other years there was no record although lodging was recorded on plots with heavier crops. In these circumstances, it has been assumed that no mention signifies no lodging. Table 6·12 shows conversions for 13 plots from 1852–62. Large differences in lodging were associated with manuring. These can only

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TABLE 6·11

Arbitrary system for converting harvest notes into estimated percentage of area lodged at harvest

Notes made just before harvest	% area lodged
No record of lodging when other plots reported lodged	—
Not laid; or good standing crop	0
Little laid; not much laid; stands fairly well	10
Slightly beaten down; a few laid places; a little laid in places; signs of lodging	30
Some laid; more or less, partly, a good deal, half or considerably laid; not quite so much laid as other badly laid plots	50
Much laid; laid	70
Very badly laid; all laid; much beaten down; greatly prostrated; mostly flat	90

partly be explained by differences in straw yield, because some plots of Red Rostock occasionally lodged with as little straw as 30 cwt/acre whereas Squarehead's Master (see Table 6·10) did not lodge with less than 40 cwt/acre. This suggests that Red Rostock had weaker straw or more eyespot, or both. Because lodging by this variety differed more from year to year than could be accounted for by differences in straw yield, or strength, it seems probable that eyespot was present.

TABLE 6·12

Percentage of area estimated as lodged, from farm notes

Plot	Harvest years 1852	1854	1855	1856	1857	1858	1859	1860	1861	1862	Mean of 10 years
2	10	10	0	—	—	10	30	70	0	10	14
3	0	10	—	0	—	0	0	0	0	—	1
5	10	10	—	—	—	0	0	0	0	0	2
6	0	0	—	10	—	0	30	30	0	—	7
7	90	10	10	50	—	10	50	90	10	10	33
8	70	70	70	90	70	90	90	90	90	10	74
10	0	—	10	10	50	10	70	10	0	10	17
11	0	10	70	90	70	90	70	10	90	—	50
12	10	0	30	—	70	10	70	90	10	10	30
13	10	10	30	10	70	10	70	90	—	10	31
14	10	10	30	30	70	—	70	90	—	10	32
17/18 N_2	0	10	10	10	—	0	10	30	0	10	8
17/18 PKNaMg	—	10	—	0	—	0	0	10	0	—	2
Mean of 13 plots	16	12	20	23	31	18	43	47	15	6	23

Notes 1. Plot receiving PKNaMg recorded as 17/18 PKNaMg.
Plot receiving ammonium sulphate as 17/18 N_2.
2. 1853 omitted because wheat was sown in spring instead of autumn.
Variety 1852 Old Red Cluster
1853–1881 Red Rostock
3. Manurial treatments as shown in Table 6·6.

The percent areas lodged in 13 plots are shown in Table 6·13 as 10-year means. They include only the years in which lodging or its absence was recorded and inevitably omit the years when notes were not made on lodging. From 1932, plot-by-plot records were made each year, so the 1st, 2nd, 3rd and 4th crops after fallow can be compared in all plots.

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TABLE 6·13

Mean percentage of area lodged, 1852–1937

Converted from harvest notes (Table 6·11) omitting years in which no notes on lodging were recorded

	1852–62	1867–80	1882–92	1893–1039	1905–20	1921–27	1932–1937	
Number years recorded	10	10	10	10	10	5	6	
Plot							After wheat	After fallow
2B	14	4	17	47	26	10	66	77
3	1	0	0	0	0	0	0	0
5	2	0	0	0	0	0	2	12
6	7	0	1	5	0	2	2	43
7	33	14	37	19	15	0	31	62
8	74	40	58	53	62	10	72	75
10	17	5	0	0	12	0	13	17
11	50	3	11	7	14	0	33	50
12	30	8	4	1	7	0	19	50
13	31	8	3	8	20	0	28	53
14	32	4	6	7	12	6	27	57
17/18 N_2	8	6	3	7	5	0	17	47
17/18 PKNaMg	2	0	0	0	0	0	0	0
Mean 13 plots	23	7	11	12	13	2	24	42

Transition period after fallowing. 1928–31.

Year	Percent area lodged; mean 13 plots. Crop	After fallow for 2 years	After fallow for 4 years
1928	—	0	—
1929	12	—	—
1930	9	62	79
1931	42	—	—

Variety

1852	Old Red Cluster		
1855–81	Red Rostock		
1882–99	Red Club		
1900–1916	Squarehead's Master except	1905	Giant Red
		1910	Browick Red
		1911–1912	Little Joss
1917–37	Red Standard except 1929 Squarehead's Master.		

Manurial treatments as shown in Table 6·6.

The variety grown on Broadbalk was changed several times (see Notes to Table 6·13 & 6·14), and there was no overlap to allow comparison, so there is no evidence to show whether some of the varieties lodged more easily than others. Exhibition material (in cases at Rothamsted) showed in some years relatively small differences between varieties in straw length and response to nitrogen. Thus on plots 5, 7 and 8, respectively, straw lengths ranged from 41–42 in., 53–55 in., and 55–58 in. for Red Rostock in 1869, Red Club in 1899 and for Squarehead's Master in 1943. Such close agreement may well have been coincidental because the same variety differed greatly in different years; in 1878 Red Rostock on these plots measured 39, 62 and 72 in., and in the hot dry summers of 1921 and 1928 the tallest plots of Red Standard (Table 6·14), which closely resembled Squarehead's Master, measured only 44 in. (Plate 1)

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The variety Cappelle-Desprez grown on Broadbalk for the first time in 1968, measured 39 in., 41 in. and 44 in., on the same three plots.

Table 6·14 shows the ten year averages of the proportion of 17 plots lodged from 1938 to 1967 in the 1st and 2nd, 3rd and 4th crops after a one year fallow, measured by pacing beside lodged areas shortly before harvest.

On some plots the extent of lodging in different years ranged from none to almost all. There were also long-term trends; there was much lodging from 1852–62, then considerably less until the fallow was introduced, when there was much more lodging both after crop and after fallow, from 1932–37, and then less from 1938–67. (Tables 6·13 and 6·14).

TABLE 6·14

Percentage of area lodged, 10 year means, 1938–67§

Plot	1938–47 after Crop	1938–47 after Fallow	1948–57 after Crop	1948–57 after Fallow	1958–67† after Crop	1958–67† after Fallow	30 years 1938–67 after Crop	30 years 1938–67 after Fallow
*2B	**32**	39	**27**	40	**33**	41	**31**	40
*3	**0**	1	**0**	0	**0**	0	**0**	0
*5	**2**	3	**22**	9	**16**	28	**13**	13
*6	**4**	5	**12**	17	**20**	33	**12**	18
*7	**19**	24	**25**	24	**17**	33	**20**	27
*8	**51**	45	**36**	39	**48**	42	**45**	43
9	**7**	15	**7**	8	**7**	17	**7**	13
*10	**5**	3	**9**	3	**4**	1	**6**	2
*11	**14**	13	**22**	18	**9**	21	**15**	17
*12	**15**	15	**21**	16	**10**	23	**15**	18
*13	**13**	17	**15**	14	**13**	22	**14**	18
*14	**13**	15	**18**	16	**10**	19	**14**	17
15	**4**	13	**7**	11	**12**	6	**7**	10
16	**35**	32	**27**	30	**33**	28	**32**	30
17/18 N_2	**8**	12	**9**	10	**21**	19	**13**	14
*17/18 PKNaMg	**0**	3	**0**	1	**12**	11	**4**	5
19	**3**	13	**9**	9	**14**	16	**9**	10
Mean 17 plots	**13**	16	**16**	16	**16**	23	**15**	18
*13 plots	**13**	15	**17**	16	**16**	21	**16**	18

* Plots with same treatments since 1852.
† 1958/67 records by J. Etheridge.
§ Variety 1938–67 Squarehead's Master except 1938, 1939, 1944, 1945, Red Standard; 1942, Stand-up.
Manurial treatments as shown in Table 6·6.

There was hardly any lodging on the unmanured plot 3 or on other plots without nitrogen (plot 5 and 17 or 18 alternatively) until vetches (*Vicia sativa*) increased and grew so tall they weighed down the crop. Although this weed was occasionally common earlier (e.g. 1939), it increased greatly in and after 1948 (Warington, 1958) and increased lodging on the plots without nitrogen and to a lesser degree on plots 6 and 9. The vetch seed has a long dormancy so there was often as much after fallow as after crop (see Table 10·11). Each increment of nitrogen increased lodging, sodium nitrate usually more than ammonium sulphate. Ammonium sulphate applied in alternate years (plots 17/18) increased lodging less than when

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applied every year (plot 7). It had less effect when applied in autumn (plot 15) than when some was applied in autumn and some in spring, or when P or K or Na or Mg were omitted (plots 11–14) and least where none of these were applied (plot 10). Plot 2B (FYM), was less lodged than plot 7 until 1889; thereafter it tended to be more lodged than plot 7, less than plot 8.

Variation in straw yield accounted for only part of the effect of weather and nitrogen on lodging, and much more could be explained when the effect of severe eyespot was realised and that it also is influenced by weather and fertilisers. The greater the weight of healthy crops, the more likely they are to lodge. The straws curve down to ground level and lie mostly in one direction. By contrast, when straws are weakened by eyespot they bend sharply in the middle of the lesions close to the ground and fall in many directions (Plate 4). So eyespot lodging often occurs earlier and in lighter crops than non-parasitic lodging, but both types are increased by wind and rain as the crop ripens.

TABLE 6·15

Effect of straw and severe eyespot on lodging

(Means of 8 plots, 2B, 3, 5, 6, 7, 8, 17, 18 for 10 years)

Period	After	Straw (cwt/acre)	% straws with severe eyespot	% area lodged at harvest
1938–47	Wheat*	28	46	15
1948–57		30	42	17
1938–47	Fallow	46	24	16
1948–57		42	15	18

* Mean of 2nd, 3rd and 4th crops after fallow.

The relative importance of weight of straw and the proportion with severe eyespot was clearly shown by comparing the first with subsequent crops after fallow. The first had more straw, but only half as many straws with severe eyespot lesions as subsequent crops; so one factor increased, the other decreased the likelihood of lodging (Table 6·15). During the 20 years from 1938, there was more lodging after fallow in ten, more after wheat in seven, and little or no lodging in three years and there was little difference in the ten-year means.

TABLE 6·16

Effect of lodging on yield of grain

Harvested 14 August 1943 (Glynne & Dion, unpublished)

Date 'lodged'	Grain cwt/acre	No. of grains harvested (in 1000s)	1000 corn weight (g)
30 June	14·2	50·6	26·8
14 July	18·2	65·5	26·2
28 July	21·8	60·6	34·1
Control (standing)	30·9	75·9	38·4
S.E.	±0·76	±1·84	±0·40

As Broadbalk provides no direct way to determine how lodging affects yield, an attempt was made to measure it experimentally. In an upright crop of Juliana wheat, only lightly infected by eyespot, nine randomised yard square plots were artificially lodged by bending each row gently over

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a stick, so that the straws bent but did not break. This was done 6½, 4½ and 2½ weeks before harvest. (Table 6·16).

Plots lodged 17 days before harvest, on 14 August, had 29% less grain than those left standing, a loss approximating closely with that postulated by Gilbert for 1898. But loss increased with earliness of lodging to 54% in plots lodged 45 days before harvest. On Broadbalk, lodging began at different times in different years and usually some parts remained standing, but it seems likely that losses may often have been comparable with the above and were sometimes increased by damage by birds.

Straggling. 'Straggling' and 'scrailing', like 'brackly' and 'shakely', are dialect words used by farmers for centuries to describe cereal crops in which straws fall haphazardly among upright ones. It often precedes lodging, but becomes most obvious in crops too light to lodge even when more than half the straws may have fallen. Straggling was recorded on Broadbalk in 20 years between 1856 and 1903, and in 15 of these years it was noted on the lighter crops when heavier ones lodged. It occurs to some extent every year on Broadbalk and is nearly all caused by weakening of the straws by severe eyespot lesions.

Take-all

The presence of take-all on Broadbalk was suggested by records of symptoms first in 1869 and in ten of the next 20 years. Ears were described as whitened, prematurely ripened, thin chaffy, abortive, empty, undeveloped, black and blighted; grain was described as narrow-gutted, not fully formed, small, poorly developed, of inferior quality, light in weight per bushel, including much offal, and as chicken corn; straw as dark and dwarfish; stubble as very dark and the crop as white and exhausted-looking.

Surveys 1930–38. *Ophiobolus graminis* Sacc. the cause of take-all was first recorded on Broadbalk in June 1930 in the third wheat crop after two years fallow. Eye estimates of its severity on every plot in 1930, 1931 and 1932 showed that it was serious, stunting or killing plants, especially in the poorly nourished plots 3 and 5, and causing scattered dead ears, 'white-heads', in all the better nourished plots. It was less serious in 1933, when the first quantitative estimates on plots 2B, 3, 5, 7 and 14 showed the fungus on roots on 2, 8, 10, 4 and 2% of the straws respectively. The attack was slight in 1934, 1936, 1937 and moderate in 1935.

Take-all was negligible in the first, but common in later crops after fallow. It may have contributed to the large differences in yield in 1930 between the first and third crops after two years fallow, when means of 8 plots (2B, 3, 6, 7, 8, 17, 18) average 18 cwt/acre in the first crop after fallow (sections IV and V) and only 6 cwt/acre in the third (sections I and II). But the contribution of take-all to loss of yield cannot be distinguished from the effects of eyespot, lodging and weeds, or because the yield of the first crop after fallow is increased by nitrogen accumulated in the soil during the fallow year.

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Surveys 1938–1957. Eyespot appears as discrete lesions near ground level and so can easily be recorded numerically. But take-all infection can be slight or extensive on roots and crowns, and roots are easily broken in sampling, so it is more difficult to assess (Cox & Slope, 1963). From 1938 to 1957 take-all was recorded only when it was obvious on roots or crowns, but after 1958 more precise methods were used for sampling and diagnosis, and more take-all was detected.

During the twenty years from 1938 take-all was found in some years in all 17 plots, and in most sections of each. It was scarce in 1938, more prevalent in 1939 especially on the unmanured plot 3, then relatively slight until 1948 when it occurred on most plots, and was more than usually prevalent elsewhere. Improved diagnosis accounts partly, probably not wholly, for the greater incidence of take-all recorded in subsequent years. There was usually little or no take-all in the first crop after fallow, but it was found on most plots where wheat followed wheat. In some years the mean percent straws with roots infected in 8 plots was less than 5%, but more were infected in 1948, 1950, 1954, 1955 and 1957. There was always more take-all in plot 17/18 PKNaMg than in 17/18 N_2 and usually, but not always, most in the nitrogen-deficient plots 3 and 5. Take-all usually infected some plants by March, sometimes by January or February. Usually more take-all was found in June than in July probably because fewer seminal roots were recovered in July and infection often failed to reach the crown roots or crowns.

Although take-all was widespread and produced occasional whiteheads, the most severe symptoms which develop in consecutive wheat crops on other fields were not recorded on the Broadbalk experiment until 1957, when grey patches of dwarfed plants with severe take-all developed between June and August, crossing plot and section boundaries on well defined areas of plots 6, 7, 8, 12, 13, 14, 15 and 19, mostly on sections VB and VA and on some plots extending to section IV. Contrary to usual experience, some of the best nourished plots were the worst affected; thus on plot 8 in sections VA and VB respectively, take-all patches covered about 12 and 85% of the area and grain yields were 19 and only 7 cwt/acre of grain. There seemed to be no explanation until the take-all areas, mapped in the field, were found to coincide, approximately, with the areas shown in R. G. Warren's maps to be the most acid before the corrective liming scheme was begun in 1954. The take-all patches were as extensive on some plots in section VA that had light dressings of lime as on VB that had the heavy dressing of 5 tons/acre; they occurred only in areas that had been acid and where some lime had been supplied. Even the light dressings of lime had lessened acidity so that the most acid areas with pH 4·9 or less in 1954 had almost all changed by 1956 to at least pH 5·3 (Johnston, unpublished records and Table 2·2). This recalled the continuous wheat at Woburn which in 1931–33 (Glynne 1935) had shown that wheat could tolerate a lower pH than take-all, so there was a narrow range just below pH 5 in which wheat grew apparently free from take-all, while at higher pH take-all developed. It seemed possible that these conditions may have prevailed on Broadbalk in the most acid areas before they were limed in 1954 and that when this was corrected take-all developed without inhibition. The addition

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of lime had no apparent effect on the less acid plots and there was as much take-all on plots 3 and 5 on VA that had no lime as on VB with heavy lime. There was more take-all than previously recorded on these plots on both VA and VB and the reason for this is not understood. In 1958 wheat grown in small pots containing soil taken from VA and VB, untreated and with pH altered by adding sulphuric acid, had large root systems with negligible take-all at pH about 4–5 while at higher pH take-all was severe, diminishing root systems, which were also damaged by extreme acidity (Glynne & Cox, 1959). The relation between soil acidity, lime, take-all and growth of wheat need investigation especially near pH 5.

The contrast between the usual mild or moderate effects of take-all on Broadbalk and the much more severe effects on wheat in other fields was first noted in 1931–33 when take-all was very severe in the parallel Continuous Wheat experiment at Woburn. It was severe in the Exhaustion Land experiment at Rothamsted in 1935, when it was only moderate on Broadbalk and then in short-term cereal experiments in 1948 and 1953 (Glynne, 1951, Salt, 1957), and in the first of the short term cereal rotation experiments (Glynne, Salt, & Slope 1954). Thus, in 1953, the 4th consecutive wheat crop without added nitrogen on Great Field had 64% straws with take-all on roots, 36% on crowns in July and about 50% of the area covered by take-all patches, whereas on Broadbalk the comparable plot had only 11% straws with take-all on roots, none on crowns and no take-all patches. Similarly, in the rotation experiment in a field adjacent to Broadbalk, the third wheat crop had 34% straws with take-all on roots or crowns and 7% of the area with take-all patches, whereas the comparable crop on Broadbalk had only 2% on roots. These differences were even more striking in the field. They made it clear that on Broadbalk there must be factors 'inimical' to take-all that prevented it developing in its most severe form (Glynne, Salt & Slope, 1956). By this time increasing knowledge of antibiotics, and the earlier demonstration in other countries that some organisms are antagonistic to *Ophiobolus graminis* in culture (Sanford & Broadfoot, 1931) had suggested that some such agents might be active on Broadbalk. Precise methods for assessing take-all and tracing its development were needed to study this problem (Cox & Slope, 1963).

At Woburn (Continuous Wheat experiment) take-all had increased till 1932 in the 6th consecutive wheat crop after two years fallow, and then declined on all the more severely infected plots. It seemed likely that on Broadbalk take-all might have risen to a peak in early years and then declined because of inhibitory factors. Fragmentary evidence of decline of take-all in continuous wheat began to appear. In 1951 in a short rotation experiment, continuous wheat had less take-all in April, June and July than the 2nd crop after a one-year break. In an experiment with plants in pots outdoors, begun in 1953, in which wheat alternated with various lengths of fallow there was more take-all and less grain in 1958, 1959 and 1960 in the 2nd or 3rd crops than in the 4th, 6th, 7th or 8th (Glynne, 1965). The rise and fall of take-all in consecutive wheat crops and its relation to yield was most convincingly shown and measured in 1960–62 by Slope in a field experiment (Slope, 1963). It was then that the practical importance

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of take-all decline in intensive cereal growing began to be recognised, although yields at Rothamsted are consistently larger on crops free from the disease.

Surveys 1958–67 of take-all are described separately by J. E. Etheridge, (née Cox) pp. 137–139.

Other diseases

Eyespot and take-all seem to be the soil-borne diseases that affect yield most, so are given prominence, but other diseases may also be important.

Brown Footrot, (*Fusarium* sp.), has been recorded almost every year since 1933. Often less than 1%, usually less than 5% of plants in any plot showed the brown discoloured stem bases, but in some years there were more, especially on plots receiving most nitrogen and there were more after fallow than after wheat. In the hot, dry summer of 1938 it was exceptionally severe, produced scattered whiteheads and in wheat after fallow plots 2B, 7 and 8 had respectively 19, 17 and 33% straws infected while plot 3 had only 3%, but yields were unusually large (45, 34, 38 and 22 cwt/acre respectively in these plots).

In 1966, Snyder & Nash (1968) found large populations of *Fusarium roseum* f. *cerealis* 'Culmorum', e.g. 2000–3000 propagules/g of soil in plots continuously sown to wheat and isolated the same fungus from brown lesions on wheat growing in these plots. There were most propagules where complete fertilisers including nitrogen had been supplied. By contrast with Broadbalk, this fungus was rare in Barnfield and in Broadbalk Wilderness, neither of which had grown wheat for at least 80 years. Snyder & Nash also found *Fusarium nivale* on crowns and aerial parts of plants on Broadbalk but not in the soil.

Sharp eyespot (*Rhizoctonia solani*) produces lesions with sharper edges than eyespot and the disease was recognised as distinct before the causal fungus was identified (Glynne & Ritchie, 1943). It has been found on Broadbalk every year since 1940, usually infecting less than 5% of plants. There was slightly more after fallow than after wheat and consistently more in the best nourished plots. The maximum recorded (1938–57) was 26% of straws infected on plot 7 in 1947. The lesions are usually more superficial than severe eyespot lesions and seemed to cause comparatively little damage to the varieties then grown on Broadbalk.

Some pathogens rarely recorded include *Pythium* sp. in 1936 *Melanospora damnosa* associated with *Fusarium culmorum* in 1961 (Glynne & Moore, 1961), two plants with *Gibellina cerealis* in 1967 (Etheridge, Palmer, Slope, unpublished record); *Cephalosporium gramineum* (Slope, 1961) and stubble infected with *Ophiobolus herpotrichus* in 1939 and *Wojnowicia graminis* in 1937.

As in other wheat crops diseases caused by airborne pathogens are sometimes prevalent and damaging. The commonest of these is mildew, (*Erysiphe graminis*). References to 'blight' in farm notes from 1852 may sometimes refer to this disease and mildew was recorded occasionally from 1888. In the 1920s an idea prevailed that this disease was least severe in plots given

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potash, but plot by plot assessments of its severity in the 1930s failed to confirm this, though they showed that the disease was most severe in plots receiving much nitrogen. In 1958 mildew was exceptionally severe and plot differences were accentuated. A method suggested by F. T. Last was used to measure its prevalence. The percent area covered by pustules of the fungus in the top two leaves of 50 plants/plot showed that mildew was much more severe in plots that received nitrogen without potassium (10, 11, 12, 14), than in those with potassium (2B, 7 and 13) and that the disease was more severe after fallow than after wheat (Glynne, 1959). Yellow rust (*Puccinia glumarum* now named *P. striiformis*) and brown rust (*P. triticina* now *P. recondita*) occurred in most years. Leaf spot (*Septoria tritici*) often occurred on lower leaves in spring, *S. nodorum* occasionally on glumes. Loose smut (*Ustilago tritici*) often affected a few ears, and ergot (*Claviceps purpurea*) was only rarely seen in the field but a few sclerotia have occasionally been found in grain samples since 1882.

Conclusion

In the study of soil-borne diseases Broadbalk has been of unique value because it provided a continuing standard for comparing diseases and yields with those of wheat grown in other fields and after different crops. It has shown the extent of annual variation, the effects of a one-year fallow and of widely different fertiliser treatments. Some treatments had opposite effects on different diseases; well nourished crops usually lodged more and had more eyespot, brown footrot, sharp eyespot and mildew but less take-all than poorly nourished crops. After fallow there was less eyespot and take-all but more brown footrot, and mildew than after wheat. Broadbalk also revealed problems that demanded new experiments and modified ideas in each succeeding decade.

Between 1852 and 1929 a few named air-borne pathogens and symptoms of some that were soil-borne had been mentioned occasionally. Lodging alone had been recorded regularly, and recognised as important because it depressed yield and limited its increase with added nitrogen. At this time it was accepted (erroneously) that there was no evidence that diseases 'accumulated' as a result of continuous wheat and that yields on the better plots of Broadbalk were supposed to compare favourably with those obtained elsewhere.

Regular observations of diseases, begun in 1930, showed that take-all was prevalent where wheat followed wheat. Recognition of eyespot in 1935 and its later severity suggested that this disease might help to account for extensive lodging on Broadbalk when equally heavy crops nearby, with much less eyespot, remained standing. This showed the need for the quantitative disease surveys begun in 1938 and still in progress.

In the next decade the surveys showed that severe eyespot and heavy straw were the two main causes of lodging on Broadbalk, and that both were influenced by weather. Wheat on Broadbalk usually had more eyespot, take-all and weeds, and yielded less, than in the long-term rotation experiments or in the first crops after newly ploughed grass. Differences between grain yield of the first wheat crops, and wheat after wheat on

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Broadbalk averaged more than 20 cwt/acre and were inversely related to the severity of eyespot and take-all. But each rotation experiment had been on a different field. So it was obvious that the influence of previous crops on disease and yield must be measured within the same experiments.

Short-term experiments comparing cereals in different rotations began in 1950 and showed similar differences in eyespot, take-all and grain yields depending on the frequency of preceding susceptible crops. Thus in 1955, similarly treated plots where wheat had, or had not, been grown in the previous two years had mean yields of 14 and 44 cwt/acre respectively with Holdfast, and 20 and 56 cwt/acre with Cappelle. The potential yield of Squarehead's Master on this land is about 40–45 cwt/acre, but some of the best plots on Broadbalk, 2B, 7 and 8, yielded an average (1938–57) of only 21 cwt/acre after wheat and 27 cwt/acre after fallow. It has thus become increasingly clear that yields here compared unfavourably with those of wheat grown in rotation with other crops, that some soil-borne diseases had increased because wheat was grown consecutively and that eyespot, lodging and take-all, in addition to weeds, were partly responsible for the small yields on Broadbalk. But the very severe attacks of take-all that developed in successive crops of wheat in the other cereal experiments contrasted with those usual on Broadbalk and suggested the presence there of factors that moderated but did not eliminate the disease. Take-all may have become severe in the early years of the Broadbalk experiment and then declined, as it did in the continuous wheat at Woburn.

This led to a microbiological study, begun in 1958, of the factors that may inhibit take-all. The rise and subsequent decline of take-all in consecutive crops, suggested in other experiments, was shown most clearly and its effects on yield measured in 1960–62. This has been followed by much more detailed and precise studies of this disease on wheat, and on barley.

Faster progress and a richer harvest of ideas are likely to follow the 1968 changes which provide comparisons of continuous wheat, two wheat crops after fallow and wheat after potatoes and beans, using the variety Cappelle.

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TABLE 6·19

Development of take-all on plants and crown roots in spring and summer: Broadbalk wheat (BB) plot 7 ($N_2PKNaMg$) and Great Field I(GF) wheat plots, 1960–65

Year		Crop	April	Early May	Late May or early June	Mid June	July
					% plants with take-all		
1960	BB	4th	—	—	30	—	28*
	GF	4th	59	—	72	—	73*
1961	BB	4th	—	11	37	36	21
	GF	4th	16	47	60	—	93
1962	BB	4th	3	10	24	—	13
	GF	4th	50	41	69	—	67
1963	BB	3rd	0	1	4	5	9
	GF	4th	2	37	57	57	75
1964	BB	3rd	7	11	22	59	50
	GF	4th	1	21	39	67	64
1965	BB	4th	20	43	56	77	94
	GF	4th	36	60	78	93	98
					% crown roots infected on infected plants		
1960	BB	4th	0	0	31	27	40
	GF	4th	2	0	31	58	75
1961	BB	4th	—	18	7	10	18
	GF	4th	—	8	20	33	39
1962	BB	4th	0	0	3	—	2
	GF	4th	0	0	8	—	12
1963	BB	3rd	0	0	6	2	3
	GF	4th	0	1	6	24	38
1964	BB	3rd	0	3	9	21	28
	GF	4th	0	0	3	9	20
1965	BB	4th	0	4	11	13	31
	GF	4th	0	4	9	14	37

* % straws with take-all in 1960.
— = not sampled.

(Cox, 1963) but in 1964 and 1965 its progress did not differ appreciably from that on Great Field, suggesting that in some years *O. graminis* is inhibited on Broadbalk wheat but not in others.

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