PROJECT REPORT No. 268

TAKE-ALL IN WINTER WHEAT: EFFECTS OF SILTHIOFAM (LATITUDE) AND OTHER MANAGEMENT FACTORS

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By

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CONTENTS

ABSTRACT

Factors known to affect the progress of take-all, such as sowing date, soil moisture, rotation, cereal species and variety, were assessed with and without silthiofam seed treatment (Latitude). Four field experiments were undertaken in each of 3 harvest years 1998, 1999 and 2000, at ADAS Rosemaund in Herefordshire, a site characterised by moderate to severe take-all infections. In all experiments, autumn plant populations, grain yield, specific weight, and thousand grain weight were measured. Detailed take-all progression analysis was also made for each experiment on a minimum of six occasions, with timings and intensity of monitoring being dependent on the specific experimental objectives. Measurements of root length density were also taken in one experiment.

The use of silthiofam consistently reduced disease levels, although the effects of silthiofam on disease progress in 1st wheats was reduced due to lower levels of initial infection compared with wheats following cereals. Analysis of disease progress curves suggested that the reduced disease levels were due to a reduction in the primary infection of the crop in the autumn. In both 1999 and 2000, silthiofam increased effective root length density. In 2000, when rooting density was close to the critical level of 1cm cm^{-3}, this increase in effective root length density had a marked effect on water use and N uptake. Yield response to treatment ranged from 0 to 1.53 t ha^{-1}, with a mean yield response seen in 2nd wheats of 0.59 t ha^{-1}. Specific and thousand grain weights were also improved by the use of silthiofam, as a result of the improved assimilate supply during grain fill. Barley generally showed little or no yield response, despite reductions in disease levels. This may be attributed to better disease tolerance due to barley having more crown roots, and an earlier harvest compared to wheat, reducing vulnerability to disease induced drought. Silthiofam increased yield across all drilling dates, however, optimum drilling date was not altered. Yield loss due to early drilling was reduced by the use of silthiofam. Despite take-all levels declining with delayed sowing, yield improvements following the use of silthiofam were maintained. This may be due to reduced root growth from later sowings producing crops more sensitive to root loss due to take-all.

Analysis across years indicated that the magnitude of the response to silthiofam is likely to be variety dependent. The use of silthiofam therefore, decreased the yield loss due to inappropriate choice of drilling date or variety for take-all risk wheats, and thereby increased the flexibility of husbandry decisions. However, in order to obtain the maximum output the use of silthiofam should be integrated with the best current practice for the production of crops at risk from take-all.

At a current seed treatment cost of £162 t^{-1}, growers using a standard seed rate of 320 seeds m-2 would require a yield response of approximately 0.35 t ha^{-1} in order to break even. By optimising seed rate growers may see more benefit from take-all control, for example sowing at 120 seeds m^{-2} reduces the break even yield response to 0.13t ha^{-1}.

The water retentive soil at Rosemaund and its location in the West Midlands mean that crops can suffer from moderate to severe take-all infections, but may not suffer the same yield penalty as crops on free draining soils or land in drier areas of the country. Nevertheless the break even yield response was on average exceeded in second wheats in this project. In areas at greater risk of take-all induced yield losses the likelihood of a positive economic response to the use of silthiofam is high.

SUMMARY

Introduction

The importance of take-all is greater for UK growers than for many continental competitors. Survey data for the UK, Germany and France shows that the percentage of non-first wheats at risk from take-all, ranged between 36-59%, 15-23% and 10-13% respectively for the years 1990 to 1995 (P. O'Reilley, Monsanto, pers. comm.). Set-aside in the form of natural regeneration, has also been found to be an incomplete break from take-all (Jones *et al*., 1996) thus first wheats following set-aside are also at risk.

By reducing root function, take-all reduces the efficiency with which crop inputs are captured and/or utilised, constrains rotations and affects choice of variety by requiring specific genotypic traits to minimise the deleterious effects of root loss.

A novel fungicide molecule (silthiofam), which provides effective control of take-all when applied as a seed treatment was commercially released in Ireland (as Latitude) in 2000 and in the UK in 2001. Take-all control is likely to have a significant impact on the cereals industry, improving the profitability of a significant proportion of the UK wheat crop and reducing a major constraint on rotational planning.

Silthiofam shows a high level of specificity against the causal agent of take-all *(Gaeumannomyces graminis* var. *tritici*). Average yield responses to silthiofam seed treatment in field experiments carried out by Monsanto, on winter wheat in the UK, where visual symptoms of take-all where present, ranged from 1.0 to 3.2 t/ha. Across all experiments, the response to treatment averaged 0.8 t/ha on second wheats to 1.0 t/ha on third wheats. These average results agree with earlier calculations of yield loss attributable to take-all (Vaiydanathan *et al*., 1987), but hide a wide range of variation, which arises from a number of interrelated processes, namely:

I. The progress of the epidemic
II. The effect of the epidemic on crop growth
III. The impact of variety, rotation and sowing date on take-all control.

These processes interact with genotype, environment and crop management decisions.

Historically, the complexity of the interactions between pathogen, host and environment, and the difficulty of controlling the disease experimentally to measure its effects without affecting other variables has limited the progress of take-all research. However, silthiofam provides a tool to manipulate take-all and quantify its effects, with the minimum of affects on other variables.

The effects of sowing date, rotation, and variety on the severity of take-all and likely yield loss have been extensively studied (eg Hornby, 1998). From this body of work has arisen best practice management of take-all risk wheat crops. Second or subsequent crops therefore, tend to be sown later than first wheats and where possible a take-all tolerant variety chosen. What is not known, however, is how this 'best practice' should be altered when using a specific take-all control seed treatment (silthiofam). Depending on the mode of action and level of control achieved, best practice when using the product could vary from using agronomic practices to minimise the severity and impact of the disease as presently practised for second and subsequent wheats, to growing all wheat crops employing best practice for first wheats.

Aims and objectives

1. To provide information and knowledge to improve the prediction of circumstances under which economic responses to take-all control could be expected
2. To identify the implications of take-all control for variety choice
3. Determine how crop management decisions should be adjusted to maximise the benefits of treatment
4. To test the long term effects of treatment on rotation planning

Materials and methods

Experimental design and treatments

Four field experiments were undertaken at ADAS Rosemaund in Herefordshire, a site characterised by moderate to severe take-all infections.

Experiment 1: The Effect of rotational position on take-all control

Three separate rotations were set up using winter wheat, winter barley and oilseed rape. Rotations ranged from continuous winter wheat to a 4-course oilseed cereal rotation, with all cereals being grow either with or without silthiofam (Table 1). In any one year four of the five points in each rotation was represented. This provided a suitable range of rotational positions in each season.

Table 1. Rotational experiment design.

Rotation 1		Rotation 2		Rotation 3	
W.W	W.W +	W.W	W.W +	W.W	W.W +
W.W	W.W +	W.W	W.W +	W.W	W.W +
W.B	W.B +	OSR	OSR	W.W	W.W +
OSR	OSR	W.W	W.W +	W.W	W.W +
W.W	W.W +	W.W	W.W +	W.W	W.W +

WW = winter wheat
WB = winter barley including some winter malting varieties
OSR = Oilseed rape
+ = treated with silthiofam

Each treatment was replicated four times. Treatments were also fully randomised within blocks, with a plot size of 3.5m by 24m.

Experiment 2: Effect of variety on take-all control

A minimum of 10 varieties were selected in each of the three seasons (1997/8,1998/9, and 1999/2000) to represent a range of tolerance to take-all (Table 2). These were sown on third wheat sites, and were grown with either a standard seed treatment fludioxonil (5g ai 100kg^{-1} as Beret Gold) or with the standard seed treatment plus silthiofam (25g ai 100kg^{-1}).
The experimental design was a two way factorial with four replicates. Treatments were fully randomised within blocks and plot size was 2m by 24m.

Table 2. Varieties assessed at Rosemaund for the effects of take-all

1997-98	1998-99	1999-2000
Abbot	Abbot	Abbot
Buster	Buster	-
-	Cockpit	Cockpit
Consort	Consort	Consort
Equinox	Equinox	Equinox
Hereward	-	-
Hunter	-	-
-	Hybrid 2	-
-	Madrigal	Madrigal
Maverick	Maverick	-
Rialto	Rialto	Rialto
Riband	Riband	Riband
-	Savannah	Savannah
Spark	Spark	Spark
-	-	Claire
-	-	Napier
-	-	Charger

Experiment 3: Effect of sowing date on take-all control

One variety (cv. Equinox) which has good standing power and is considered to be relatively intolerant of take-all infection was chosen to test the implications of take-all control over a range of sowing dates. In all years, 5 or 6 sowing dates were chosen, with the first sowing were invariably in early October, and subsequent sowings ranged into February (1997-98), early December (1998-99) and mid-November (1999-00). In 1997-98 the previous crop was winter wheat, in the 1998-99 winter barley. In 1999-00 the experiment was done on both first and third wheats to assess any shift in the optimum drilling date. Previous crops were winter oats and winter wheat.

In 1997-98 and 1998-99 seed was treated with either the standard treatment as in experiment 2, the standard seed treatment plus silthiofam at 25g ai $100kg^{-1}$, or silthiofam at 50g ai $100kg^{-1}$. A split plot design was used with sowing date on main plots and seed treatments on sub-plots in four replicates. Sub plots were 2m by 24 m in size. In 1999-00 seed was treated with either a standard treatment, standard seed treatment + silthiofam at 25g ai $100kg^{-1}$ or fluquinconazole 75g ai $100kg^{-1}$ + proclhoraz 14g ai $100kg^{-1}$ seed. The design was a split-split plot with sowing date on main plots, rotational position on sub-plots and seed treatment on sub-sub-plots.

Experiment 4: Effect of soil water availability on take-all control

In each of three seasons (1997/8,1998/9, and 1999/2000), a single variety Equinox was chosen, on which a series of irrigation treatments was imposed (Table 3) to manipulate the take all epidemic, with and without silthiofam seed treatment. In 1997, these were planted in third wheat position; in 1998 winter wheat was sown after winter barley and in 1999 the crop was a second wheat.

A split plot design with main plots of irrigation and sub-plots of seed treatment in four replicates was used. In 1997-98 sub plots were 3.5m by 24m, with discard plots between each main plot. In 1998-99 and 1999-00 sub plots were 6m by 24m and were further sub-divided into sub-sub-plots of 2m by 10m for improved precision of sampling and combining.

Table 3. Irrigation/seed treatments.

Treatment	Irrigation	Silthiofam
1	None	+
2	None	-
3	Autumn + spring	+
4	Autumn + spring	-
5	June/July	+
6	June/July	-
7	Full	+
8	Full	-

Measurements

In all experiments, autumn plant populations grain yield, specific weight, and thousand grain weight were measured. Detailed take-all assessments was also conducted for each experiment on a minimum of six occasions with timings and intensity of monitoring being dependent the specific objectives of each experiment. Each take-all assessment was done on a sample of 20-25 plants/plot. A take-all index (TAI) score was given to each plant, depending on the % of the root system colonised by the fungus using a modified form of that described by Clarkson and Polley (1981):

Scale	Category
0% = healthy roots	0
1-10%	1
11-30%	2
31-60%	3
61-100%	4

$$\frac{(0a+10b+30c+60d+100e)}{t} = \text{TAI}$$

where *a,b,c,d,e* represent the numbers of plants in each of the five categories and *t* is the total number of plants examined.
The proportion of diseased roots was calculated from the same data, thus;

PDR = Total number of infected primary root axes / Total number of primary root axes.

The irrigation experiment also included assessment of root growth by the number of crown roots, and measurements of crop biomass, nitrogen uptake, canopy size and shoot counts at GS 31 and GS65. The varietal response trial also included measurements of crop biomass, nitrogen uptake, maximum canopy size, soluble carbohydrates and shoot counts at GS 65. Measurements of crop biomass, ear number, grains/ear and harvest index at pre-harvest, were taken for all experiments with the exception of the rotational trial.

Results and Discussion

Disease Progress

Figure 1 illustrates the effects of seed treatment and irrigation on disease progress. In both the irrigation treatments, the use of silthiofam significantly reduced the subsequent disease levels observed. This effect was also seen across cereal species (Figure 2), and rotational positions, although the effects of silthiofam on disease progress in 1st wheats was reduced due to lower levels of initial infection. The effectiveness of silthiofam at reducing take-all levels in crops at risk from the disease is in agreement with the work of Spink *et al*. (1998) and Beale *et al*. (1998). The series of experiments presented here has shown that reduction in take-all levels is consistent, but not always statistically significant throughout the season. This also supports the work of Schoeny and Lucas (1999). The effect of silthiofam on the disease progress curves was to delay take-all progress delaying the point of inflection of the disease progress curve (Figure 1). This supports the work of Schoeny and Lucas (1999) who attributed this to a delay in the primary infection cycle.

Irrigation was also shown to also increase the rate of disease progress. This was thought to be because soil moisture conditions were more optimal for take-all development.

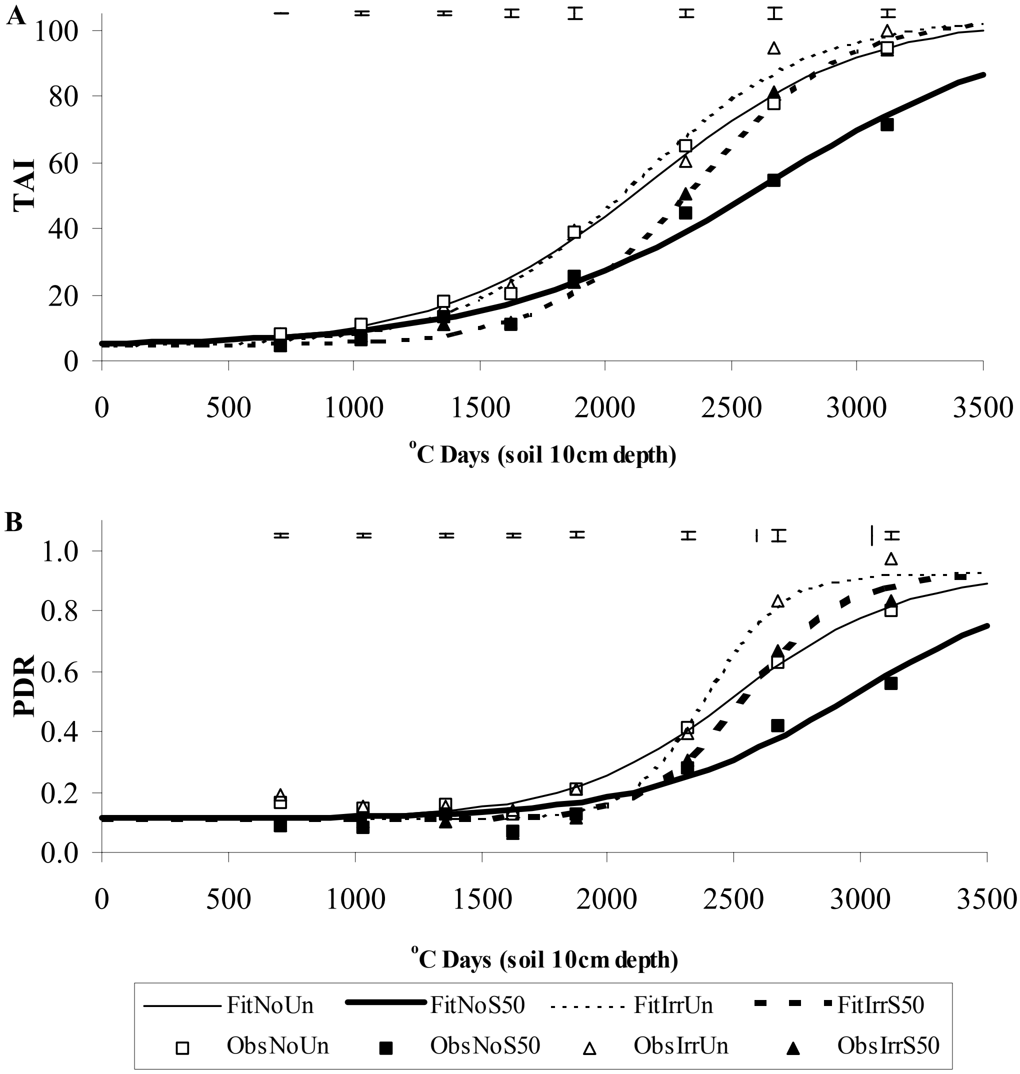

Figure.1 Fitted and observed take-all index (A) or proportion of diseased roots (B) with °C days at 10cm soil depth in unirrigated (No) or irrigated (Irr) treatments without (Un) or with (S50) 50g silthiofam 100kg^{-1} seed – Irrigation experiment 2000. Error bars are SEDs for comparing silthiofam (capped) or irrigation (uncapped) means.

There was a poor correlation between the reduction in disease achieved through the use of silthiofam and the yield improvement (Figure 2). This highlights the necessity of examining the impact of take-all on below ground resource capture in order to understand, and ultimately be better able to predict, the implications for yield. Inherent variability of yield data and the patchy nature of take-all infection may also add to the variability seen.

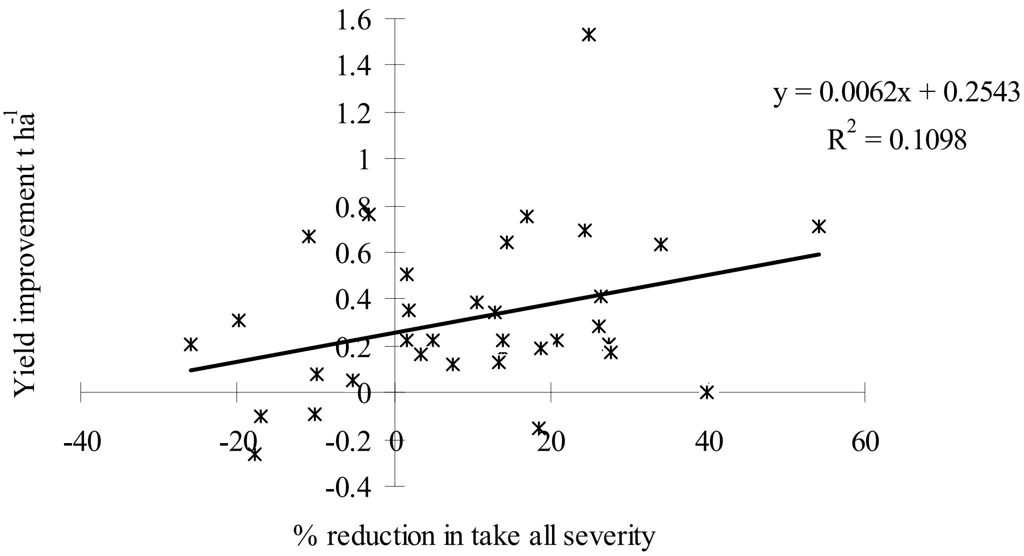

Figure 2. Regression analysis to indicate the relationship between reductions in take-all severity (as measured by take all indices) and yield increase for all varieties in all seasons.

Resource capture

It is known that take-all infects and disrupts the xylem and phloem, and that this leads to a reduction in water and nutrient uptake through infected roots. There are also indications that take-all may reduce the total size of the root system which may, depending on soil moisture availability, reduce the capacity of the crop to take up water. Nitrogen uptake may also be reduced in high take-all situations. However, while laboratory work has suggested the mechanism by which take-all may be responsible for yield losses in wheat, its relevance in the field has not been explored in such a way that quantifiable reductions in root growth and below-ground resource capture can be attributed solely to take-all. In addition, the relative importance of soil moisture on root growth, root losses to take-all infection and depth of water extraction have not been investigated.

When take-all infects a root system a reduction in root function and therefore a decrease in water uptake per unit root length density (RLD) might be expected. Take-all affects the vascular system at the point it infects the root. Therefore, even though only a small portion of the root near the soil surface has been infected, its entire length may be rendered non-functional. To account for this a figure for 'effective root length density' (ERLD) was calculated from RLD using data for the proportion of diseased crown roots. The relationship between ERLD and season-long water uptake was then examined and compared with that in previous work in the absence of take-all (Barraclough, Kuhlmann and Weir, 1989; van Noordwijk, 1983).

The work at ADAS Rosemaund indicated that the effective root length density (ERLD) at mid-grainfill declined with depth in both years in an exponential manner (Figure 3). Where the chemical was present ERLD was significantly increased in the 0-40 cm horizon in 1999 (P=0.026), and in the 20-60 cm horizon in 2000 (P=0.002). Irrigation in 2000 also consistently reduced ERLD at all depths. The magnitude of the irrigation effect was slightly larger than the chemical, irrigation decreasing ERLD by 0.437 cm cm^{-3} and the chemical increasing ERLD by 0.291 cm cm^{-3}.

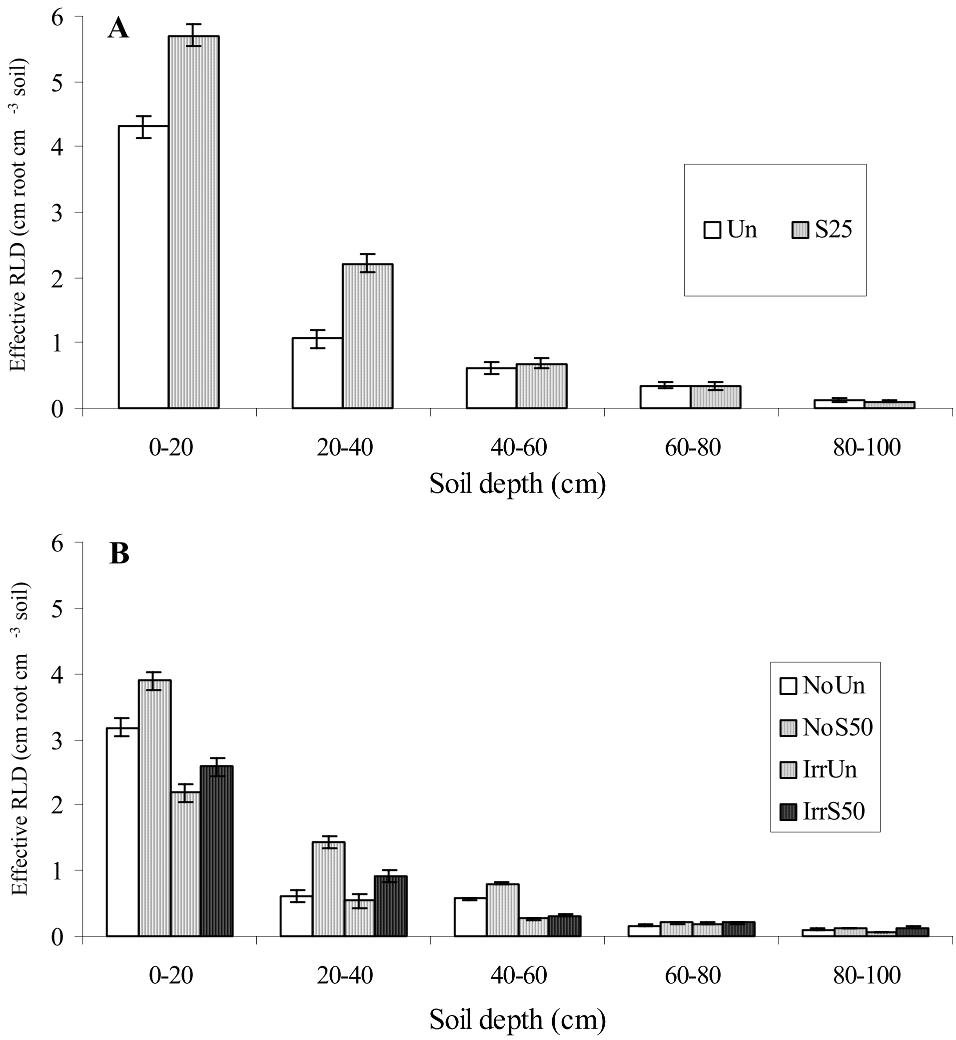

Figure 3. Effective root length density (cm cm^{-3}) at mid-grainfill at different soil depths in 1999 (A) and 2000 (B). 1999 data is for unirrigated sub-plots only. Error bars are SEDs for comparing chemical and irrigation means at individual depths. (S25) = 25g silthiofam 100kg^{-1} seed (for other abbreviations see figure 1).

Increased levels of take-all in the absence of silthiofam did not affect seasonal water use to 1.2 m soil depth or nitrogen uptake by the crop in 1999, but these were significantly decreased in 2000 (Figure 4). The difference in treatment effects between the years could have been due to seasonal differences in RLD, effects of silthiofam on take-all, or resource availability. It appears in this case that water and nitrogen uptake may not have been significantly affected in 1999 mainly because ERLD was generally higher in 1999, even though there was a larger difference in disease levels with and without silthiofam in 1999 than in 2000.

ERLD measurements estimate resource-capture capability. The results in 1999 support the idea that greater RLD allowed water uptake to be maintained despite infection with take-all, as the ERLD remaining was still sufficient to acquire the necessary below ground resources. Given that the difference in ERLD levels with and without silthiofam were much greater in 1999 than 2000, especially in the 0-20 cm layer, it might have been expected that water uptake would be affected more in 1999. However water uptake does not begin to be significantly affected until RLD falls close to 1 cm root cm^{-3} soil (van Noordwijk, 1983; Barraclough, Kuhlman and Weir, 1989). Averaging across treatments, ERLD was around 33% higher in 1999 than in 2000, and, therefore, despite the greater difference in ERLD due to take-all in this year, an effect on water and nitrogen uptake would be less likely. In 2000

ERLD values were much closer to critical values of RLD, and this could explain why treatment effects on water and nitrogen use were greater (Figure 4).

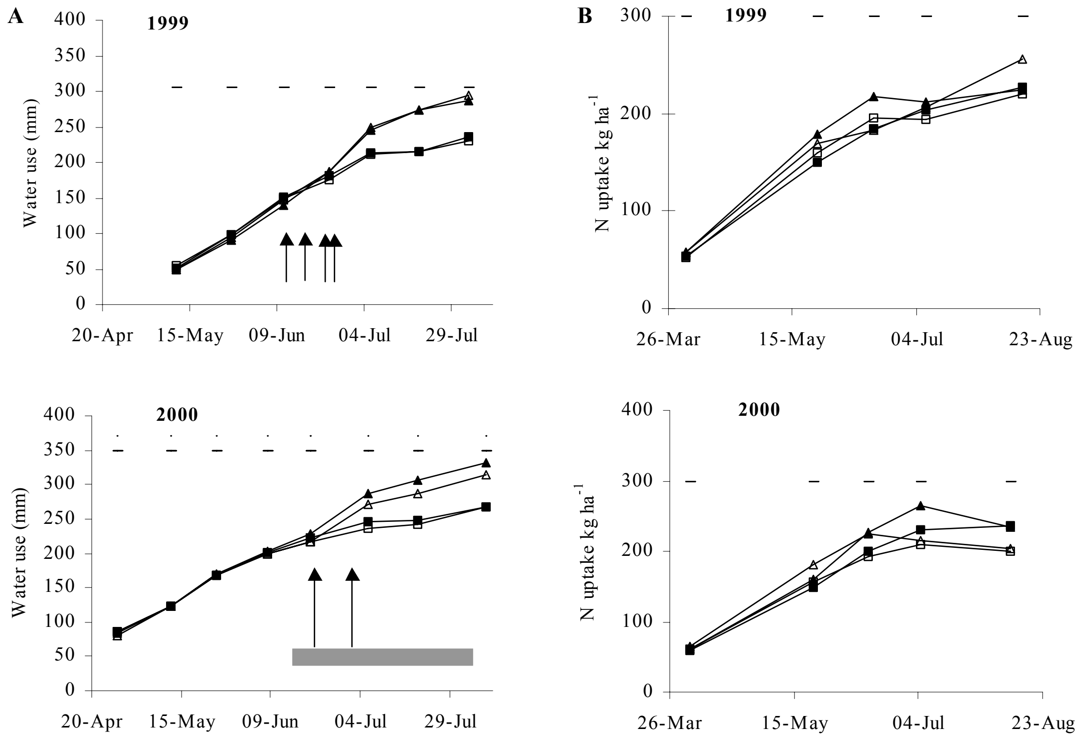

Figure 4. A Cumulative water use - end of field capacity to harvest in 1999 and 2000 in unirrigated (squares), irrigated (triangles),sub-plots without silthiofam (open symbols) or with silthiofam (closed symbols). Arrows indicate application of 20 mm of irrigation, shaded areas indicate periods when shelters were present on unirrigated treatments. SEDs are capped error bars for comparing irrigation means and uncapped error bars for comparing chemical means. B Total nitrogen uptake over the season for winter wheat (for symbols see A) in the 1999 and 2000 irrigation experiment. Error bars are SEDs for comparing chemical means at individual sampling dates.

Rotational position

The severity of take-all across a rotation depends on a dynamic balance between the pathogen and antagonistic / competitive soil micro-organisms. During a first wheat crop the level of the take-all organism in the soil is low, as it competes poorly in the absence of a susceptible host during the preceding break. Substantial disease development during subsequent crops in the rotation seems to be required before an antagonistic microflora can establish and initiate take-all decline. A more detailed review of the effects of rotational position on take-all can be found in Appendix 1.

This experiment has not been concluded, but results from the first 3 years are shown in Figure 5.

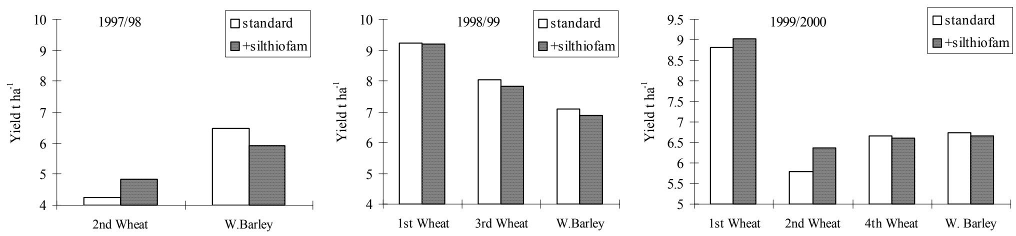

Figure 5. The effect of silthiofam on crops at different rotational positions in each of the seasons.

The responsiveness to take-all control varied with rotational position. Barley yield appeared to be unaffected by the application of silthiofam. However, in both 1997-98 and 1999-2000, the 2nd wheats showed a positive response to silthiofam with a 0.58 t ha^{-1} and 0.59 t ha^{-1} mean yield increase respectively. First, third and fourth wheats and winter barley showed few positive effects in any of the three years.

These results are consistent with take-all under normal circumstances being most damaging during the 2nd or 3rd seasons, before the phenomenon of take-all decline restricts disease progress. It is worth noting that despite no yield advantage being seen on this site in 3rd wheats the varieties trial sown in a third wheat site did show positive effects of silthiofam indicating that positive yield responses to silthiofam are possible in third wheat situations.

Despite the positive effects of silthiofam at reducing take-all indices in barley, no positive yield benefit was seen. In the 2nd wheat plots however, a yield improvement was associated with reduced take-all indices where silthiofam was used. This difference in yield response between cereal species which was seen in all years, may be due to a combination of better tolerance and avoidance of yield effects in winter barley. Barley has been shown to have lower overall infection levels, which has been attributed to the production of more crown roots in barley (Asher, 1972b; Cunningham *et al*., 1968), effectively diluting the presence of the disease. This was indicative of disease tolerance rather than resistance to the pathogen. The faster development and earlier harvest of winter barley also makes it less vulnerable to late season disease induced drought, hence avoiding yield effects.

The trend for increased severity of take-all with subsequent plantings of wheat was seen in the 1998-99 and 1999-2000 growing seasons. However within all crop types there were only small differences in take-all severity between those treated with and without silthiofam.

Varietal Response

In both 1998 and 1999, the application of silthiofam gave a significant yield advantage across the varieties with increases in yield of 0.57 t ha^{-1} and 0.23 t ha^{-1} respectively. In the 2000 season the mean yield increase of 0.18 t ha^{-1} seen across the varieties was not statistically significant due to the inherent variability of the data. Table 3 shows the yield response of each variety in each year. Some caution should be taken in interpreting the results of Charger, Napier and Claire as these were only sown in one season (1999-2000), when the lowest responses were seen.

Table 3. The yield response (t ha^{-1}) to silthiofam application, for all varieties in all years.

	1997-98	1998-99	1999-2000
Abbot	0	0.18	0.13
Buster	0.76	0.22	-
Cockpit	-	-0.15	0.64
Consort	0.71	0.67	0.34
Equinox	1.53	0.22	0.08
Hereward	0.28	-	-
Hunter	0.21	-	-
Hybrid 2	-	0.19	-
Madrigal	-	0.39	0.12
Maverick	0.69	0.05	-
Rialto	0.63	0.17	-0.1
Riband	0.51	0.41	0.75
Savannah	-	0.31	-0.26
Spark	0.35	0.22	0.22
Claire	-	-	-0.09
Napier	-	-	0.21
Charger	-	-	0.16
Mean	0.57	0.24	0.18

A cross year analysis for the 6 varieties that were grown in all three seasons (Figure 6) showed a trend (*P*= 0.076) for varieties such as Equinox, Consort and Riband to show the greatest response to silthiofam. Abbot, Spark and Rialto appeared to respond less, possibly due to higher levels of disease tolerance.

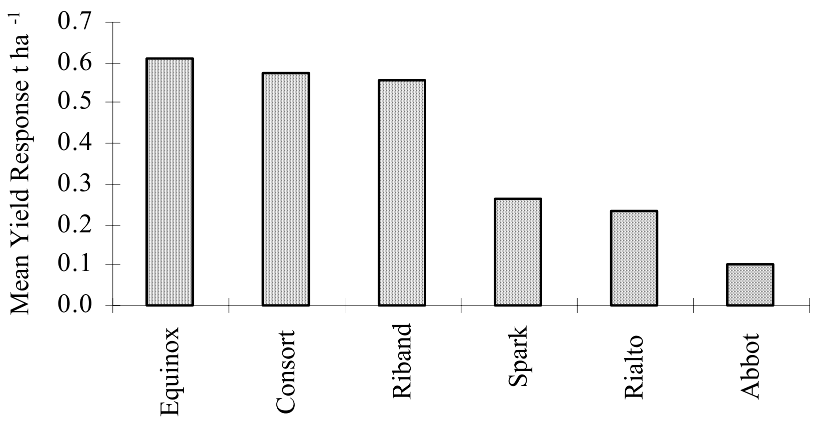

Figure 6. The mean yield increase in t ha^{-1} as a result of silthiofam application across years averaged across years for varieties grown in all three seasons. SED for seed treatment x variety interaction means is 0.204 ($P = 0.076$).

Take-all assessments also indicated that silthiofam led to a significant reduction in take-all severity (as measured by final take-all indices) in the 1998 and 1999 season, across all varieties. Mean reductions were of the order of 24% in 1998 and 10% in 1999. There was not however any significant reduction in take-all due to silthiofam in 2000. This could explain why yield responses to silthiofam were at there lowest in the 2000 season.

Sowing Date Response

Silthiofam gave a consistent yield response irrespective of sowing date in all years (Figure 7). Mean yield responses across sowing dates of 0.66, 0.14, and 0.57 t ha^{-1} were recorded for 1997/98, 1998/99 and 1999/00. In both 1997/98 and 1999/00 seasons, yield was reduced across all treatments from sowing in the first week of October, compared to later drillings. In the 1998/99 season, when the previous crop was winter barley, yields of crops not treated with silthiofam also followed this trend, but the yield penalty was lower and treated crops showed the highest yield at this first sowing (Figure 8).

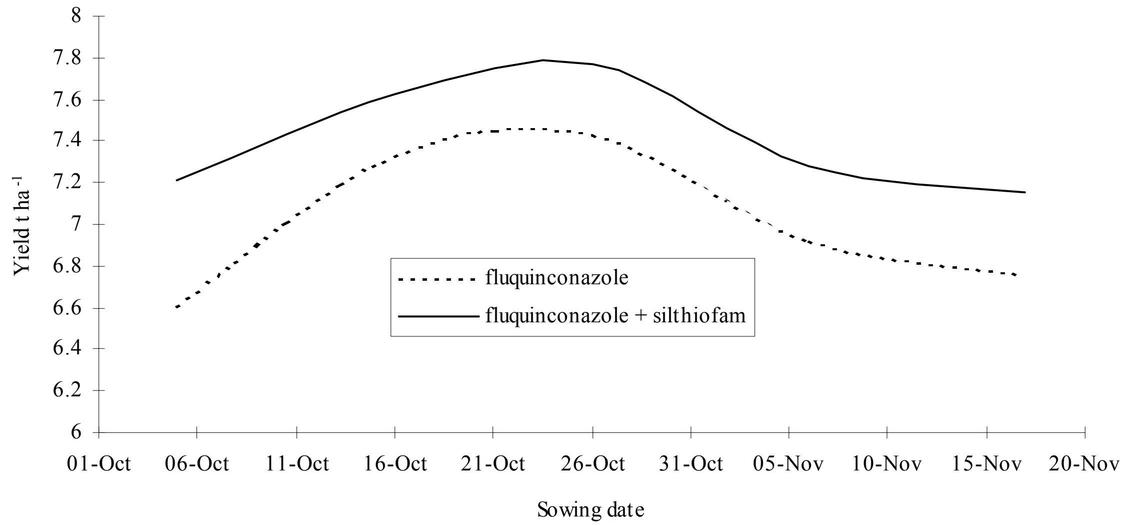

Figure 7. The effect of sowing date and seed treatment on yield of non-first wheats, ADAS Rosemaund, 1998-2000.

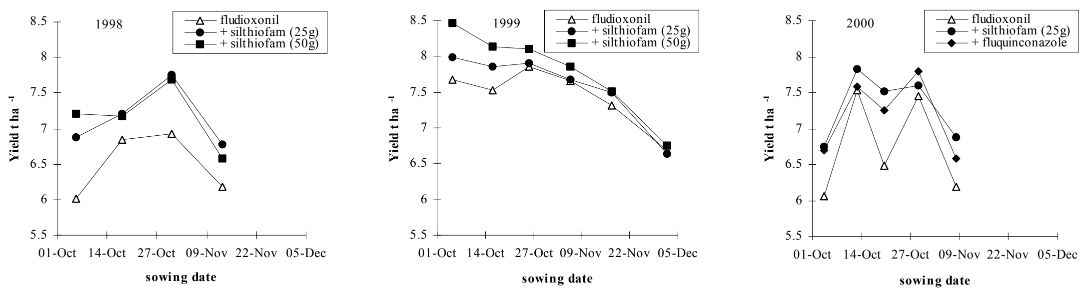

Figure 8. The effect of sowing date on the yield and yield response to take-all control seed treatments, ADAS Rosemaund, 1997-98, 1998-99 and 1999-2000.

Grain quality

Grain quality was improved by silthiofam treatment. In both 1997/98 and 1999/00 growing seasons silthiofam increased the specific weight by 1.1 kg hl^{-1} (P=0.004), and 0.73 kg hl^{-1} respectively. This appeared to be consistent across sowing dates. Thousand grain weight was also improved in 1997/98 by 2.04 g across all sowing dates. This could be expected as take-all generally affects grainfill, so improvements in assimilate supply as a result of a lower level of infection would lead to increased grain weight.

Take-all development

Take-all indices (Figure 9) in 1997/98 were significantly lower in wheat crops treated with silthiofam (*P*=0.047). Indices were also reduced by later sowing (*P*=0.001), and there was a significant interaction between sowing date and seed treatment, whereby the difference in take-all indices between treated and untreated seed was reduced with later sowing (*P*=0.047). In the 1998/99 season, final take-all indices were reduced by later sowing (*P*=0.003), however indices did not significantly vary with seed treatment and no interaction was present.
In 1999/00 both silthiofam and fluquinconazole significantly reduced take-all indices levels. Although the graph suggests that this reduction was larger at the earlier drilling dates there was no significant effect of drilling date and there was no interaction between drilling date and seed treatment.

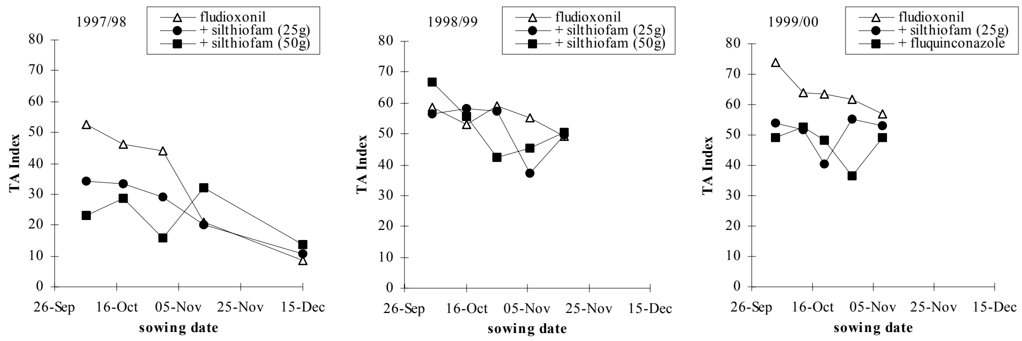

Fig 9. Final take-all indices of winter wheat grown across a range of sowing dates with and without take all control, in the 1997/98, 1998/99, and 1999/00 season. SEDs for comparing seed treatment differences = 3.28 (24 df), 3.580 (36 df) and 2.029 (60 df) in 1997/98, 1998/99 and 1999/00 respectively.

The lack of a yield penalty in early drilled plots in 1998/99 (Figure 8) is reflected by the lack of any clear effect of seed treatment on take-all indices in this year. This could be a result of reduced carry over and earlier harvesting of the previous winter barley crop. In both the 1997/98 and 1999/00 seasons, the yield improvement can be explained by the reduction in take-all achieved. The convergence of TA indices from the different seed treatments with later sowing implies that silthiofam has the largest effect on take-all control at the earlier drilling dates. However, despite lower observed differences in take-all control, yield improvements following the use of silthiofam were maintained with later sowings. This disparity may be due to less root growth from later sowings making these more likely to be affected by the smaller differences in take-all levels between treated and untreated plots.

Cost effectiveness of take-all control

Cost effectiveness of fungicide treatments is of primary importance to the grower. Treatment of seed with silthiofam in the autumn of 2001 was at the cost of £162 t^{-1}. If seeds are sown at a standard seed rate of 320 seeds m^{-2} this equates to a cost of approximately £25.9 ha^{-1} (assuming a thousand seed weight of 50 g). This gives a break even yield response of approximately 0.35 t ha^{-1} (assuming a wheat price of £75 t^{-1}).
The greatest economic benefits to growers may be seen at reduced seed rates. With the cost of treatment greatly increasing the price of seed, seed rates need to be optimal. Assuming 120 seeds m^{-2} would be necessary to reach an early October target plant population of 80 plants m^{-2} (Spink et al., 2000), seed treatment costs per unit area could be as low as £9.7 ha^{-1} reducing the break even yield response to 0.13 t ha^{-1} (Figure 10).

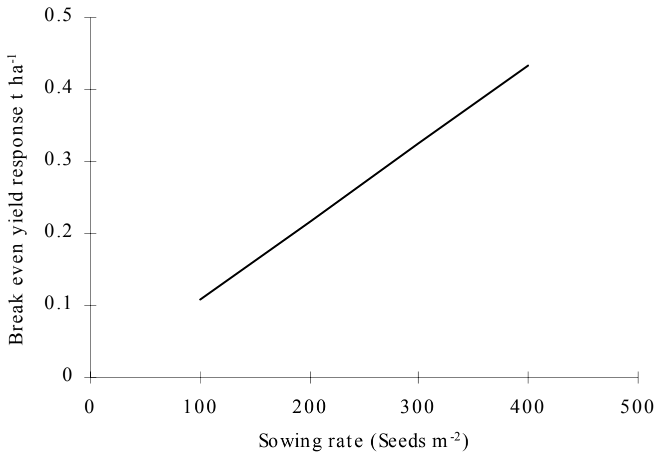

Figure 10. The effect of seed rate on the yield required to cover the cost of silthiofam seed treatment (assuming a thousand grain weight of 50 g and a wheat price of £75 t^{-1}).

In the three years of field experiments at Rosemaund, a site characterised by moderate to severe take-all levels, yield responses ranged from 0 to 1.53 t ha^{-1} with a mean yield response seen in 2nd wheats of 0.59 t ha^{-1}. Thus it appears that, in high take-all risk situations, the yield benefits achieved would outweigh the cost of treatment.

APPENDIX 1

DISEASE PROGRESS

Introduction

In order to study the effects of take-all on below-ground resource capture, differing levels of take-all must be obtained without altering the crop in any other way. This Appendix will briefly review the factors affecting take-all levels, before examining the effects of Latitude (from here on referred to as silthiofam), irrigation and rotation on disease progress. As a crop progresses through its life cycle the principal destination for resources alter and different crop structures are produced. In order to understand the impact of take-all on crop growth and yield, one must first understand the progress of the disease epidemic and how this fits with the development of the crop. Furthermore to understand the likely impact of any take-all control measure on crop growth, one must first understand how it affects disease progress.

Host-and-pathogen-growth factors that alter the shape of the disease progress curve.

Take-all disease epidemics are known to progress in two phases. When a crop is established, innoculum of take-all in the soil or on the residues of a previous crop or other susceptible plant species infects the root system, this is frequently described as the primary infection. This is followed by a period through the winter, when there is no further apparent increase in the disease as temperatures are too low for further disease growth. Once soil temperatures rise in the spring there begins a secondary phase of infection as the disease spreads from root to root of the existing crop. A number of factors related to host and pathogen growth have been implicated in the resulting shape of the Disease Progress Curve (DPC) and therefore the timing and severity of take-all epidemics:

1) Carrying capacity of the crop i.e. root growth. (Werker, Gilligan and Hornby 1991)
2) Planting density – this affects the carrying capacity. (Colbach, Lucas and Meynard 1997)
3) 1^o inoculum density. (Gilligan and Kleczkowski, 1997)
4) Inoculum decay rates. (Bailey and Gilligan, 1999)
5) Rate of fungal growth arising from 1^o inoculum.
6) Maximum distance for 1^o infection. (Gilligan, 1994).
7) Rate of 1^o infection – a function of 1, 2, 3, 4, 5 and 6 above.
8) 2^o inoculum density. (Bailey and Gilligan, 1999)
9) Maximum distance of 2^o infection.
10) Rate of 2^o infection – a function of 1, 2, 8, and 9 above.

These factors affect the parameters of logistic-type functions used to model the DPC by either reducing final levels of disease (upper asymptote), rate of infection or timing of infection, which can be measured as the point of inflection. The factors 1-10 relate to host and pathogen growth, but other factors can also influence the DPC. These can include biotic and abiotic factors, both of which can be affected by crop husbandry. These will be considered below.

Other factors that can alter the shape of the DPC

Soil water

Take-all *(Gaeumannomyces graminis* var. *tritici* or Ggt) needs adequate water to survive and proliferate on wheat roots (Hornby, 1998; Cook, 1981). In the initial infection phase the soil moisture content is probably the most important factor. As the fungus infects and grows within the plant however then host water potential will determine disease progress. Infection initiation and growth of ectotrophic hyphae therefore is more likely to be affected by soil than plant water, and vice versa for endophytic hyphae.

In soils, Ggt has been shown to consistently grow better at 60% water holding capacity (whc; 0.8 kPa and –0.2 kPa in a sandy loam and a yellow sand respectively) than at 30% whc (Grose, Parker and Sivasithamparam 1984). There is some evidence Ggt is inhibited by supra-optimal levels of soil water (Heritage *et al*. 1989). In laboratory experiments it was shown that in soil with 80% water filled pores (WFP) the maximum distance for 1^{o} infection through soil at 15^{o}C was reduced.

Associations between seasonal rainfall and take-all in the field have been made in several studies. Hall and Sutton (1998) found no significant or consistent correlation between rainfall levels and take-all incidence and severity in two years of field experiments on wheat in south-western Ontario, Canada. However, they did find that take-all severity increased in the year where there was more spring rainfall. Smiley, Collins and Rasmussen (1996) found that take-all was associated with rainfall, and take-all was most severe in the year with the wettest autumn and spring in 3 years of field trials in Oregon, USA.

The literature generally associates more severe take-all epidemics in the field with increased seasonal rainfall. This association however may be confounded by other environmental factors in different years. Most of the field studies in this area have measured take-all levels at a single point in the season, therefore the effects of soil moisture on the shape of the progress curve remain to be defined.

Measurements of dependence of Ggt growth on soil moisture in the field under UK conditions are not available. One would expect however that water would not be a limiting factor to growth of Ggt during the winter and early spring unless supra-optimal quantities were available. Thus initial infection processes should not be impeded in fields with adequate drainage. As the season progresses however, water may become limiting especially in certain soils. Therefore it is possible that progress of the take-all epidemic may be retarded because of inadequate soil moisture for additional growth and lesion formation, and inadequate plant moisture for enlargement of existing lesions.

Soil temperature

Ggt is capable of growing over a wide range of temperatures (Huber, 1981), and has a world-wide distribution in wheat-growing areas (Garrett, 1981). Laboratory experiments have shown that Ggt has an optimum temperature for growth both *in vitro* and *in vivo* of between 20-29^{o}C (Grose, Parker and Sivasithamparam 1984, Smiley, Fowler and Reynolds 1986, Demitrijeviæ 1968). These optima depend on water potential (Cook and Christen 1976), presumably in the soil and in the plant. Above this optimum, growth of Ggt slows down, until at 35^{o}C it is unable to grow regardless of osmotic conditions (Demitrijeviæ 1968).

The main effect of temperature in the UK are exerted in the winter and early spring when they are too low to support growth of Ggt or host material. From late spring through the summer months temperatures rise towards the optimum for Ggt growth, but rarely if ever reach the maximum. The only way therefore that temperature could have an effect on take-all progress is if there is a delay in the increase seen in late spring, which could delay the disease's progress. However, the above is conjecture in the absence of hard data.

Rotation

Werker, Gilligan and Hornby (1991) found progress in first wheats (FW) was best described using a rectilinear function, this was also the case in second or subsequent wheats (SSW) where there was low disease pressure. In conditions of high disease pressure in SSW and continuous wheats (CW) progress was best described using a quadratic function. The authors inferred that these results were due to differing levels of 1^o and 2^o infection. In FW the 1^o infection levels were very low, leading to reduced 2^o infection. In SSW under high disease pressure 1^o infection was low (because of low inoculum levels from the previous FW crop), but 2^o infection was high. In CW 1^o infection levels were high because of high levels of inocula from the previous wheat crops, but 2^o infection events were rare due to the presence of some inhibitory agent in the soil. Colbach and Huet (1995) found that take-all incidence started to drop after 3.6 wheat sequences. This confirms the presence of take-all decline in their situation, but individual DPCs within years were not analysed. It does show however that crop succession has to be borne in mind when planning take-all progression experiments. Any sequence over 4 years is likely to show reduced rather than increased take-all levels, with possible effects on the DPC as described by Werker *et al*. (1991) above.
Thus in different rotations 1^o inoculum levels are thought to be the main factor affecting subsequent progress of the DPC. In continuous wheats TAD may be due to a inhibition of 2^o infection processes by as yet unidentified agents.

Cereal species

Ggt is found primarily on wheat and barley but is also associated with a wide range of gramineae (Deacon, 1981). Some isolates have been shown to infect oats (Yeates, 1986), Ggt and has even been reported to infect some dicotyledons (Nilsson, 1969, quoted in Walker, 1981). The majority of studies comparing the levels of take-all between wheat and barley have shown that wheat tends to have higher levels of disease (Asher 1972b, Shipton 1972, Bailey *et al*. 1998), or that there was no significant difference between the two crops (Cunningham *et al*. 1968). Take-all is also known to affect to a lesser degree both triticale and rye (Hollins, Scott and Gregory 1986).
Thus it appears that while Ggt can infect a range of cereals, infection occurs to the greatest extent on wheat crops. However, as yet there is no modelling work available that has compared DPCs for wheat with those of other crop species.

Fungicides

Although some chemicals have been found to stop Ggt growth *in vitro*, effects in the field were disappointing (Bateman, 1989). Bateman *et al*. (1994) found sterol biosynthesis-inhibiting fungicides to only partially control take-all and Gardner *et al*. (1998) found that fungicides were ineffective compared to other methods of control and not economical.
Recently a novel chemical of the hindered sylyl amide class has been formulated by Monsanto (Beale *et al*., 1998). This has been developed into the seed-treatment fungicide Latitude (active ingredient is Silthiofam), and has shown significant and consistent control of take-all under both laboratory and field conditions (Beale *et al*., 1998; Spink *et al*., 1998; Schoeny, Jeuffroy and Lucas, 2001). Its mode of action is thought to be inhibition of ATP transport from the mitochondria (Joseph-Horne *et al*., 2000).
Schoeny and Lucas (1999) fitted a Weibull function to disease severity data and compared the resulting curves from plants treated with 2 rates of silthiofam to those without. Silthiofam increased the point of inflection, indicating a delay in epidemic progress. No other DPC parameters were affected by the chemical. The authors attributed the effect on the point of inflection to a delay in root to root spread and extension of root lesions.

Summary

The effects of soil moisture, rotation, crop species and a novel chemical control on the progress of the take-all epidemic have been studied in field situations.

While it appears to be generally accepted that take-all epidemics are positively correlated with increasing soil moisture previous studies have relied on rainfalls across years for different soil moisture levels. This limits their usefulness because of the confounding effects of other factors. In addition, none of the previous field studies has have quantified effects of soil moisture on the shape of the take-all DPC progress, most studies only describe take-all at one point in the season.

Rotation has received much attention since it has been the most effective method of controlling take-all. However, its effects on the shape of the DPC have only been characterised by one group (Werker, Gilligan and Hornby, 1991).

Barley suffers less from take-all than wheat but comparisons of DPCs of wheat and barley are few. Thus although final levels of take-all may be lower, at what point in the crop's growth cycle this difference becomes apparent is unknown.

Silthiofam, a novel chemical control of take-all, significantly delays the onset of a take-all epidemic by 300-800 degree days depending on dose and site under field conditions in western France (Schoeny and Lucas, 1999) and in other parts of Europe (Beale *et al*., 1998). However, these effects remain to be confirmed in UK conditions. It seems that silthiofam may be a useful tool for manipulating take-all levels for research purposes.

This study aims to:

1) Assess the efficacy of silthiofam in manipulating take-all for research purposes.
2) Determine effects of silthiofam on the parameters of the take-all DPC progress under UK conditions.
3) Determine effects of differences in soil moisture in the spring and summer on the parameters of the take-all DPC progress.
4) Elucidate how rotation is affecting the DPC, and from this what disease and plant growth factors may be responsible.
5) Examine differences in parameters of the DPC of wheat and barley to establish what factors may be responsible for lower levels of disease seen in barley crops.

Materials and methods

Two experiments, an irrigation x seed-dressing experiment and a rotation x seed-dressing experiment, were designed to investigate the effects of soil moisture, rotation, crop species and a novel chemical control on the progress of the take-all epidemic.

Site details

Both experiments were conducted on a silty-clay loam of the Bromyard series, at ADAS Rosemaund, Preston Wynne, Hereford, a site characterised by moderate to severe take-all infections. In each experiment the land was ploughed and suitably cultivated prior to drilling at a seed rate of 350 seeds/m^2 in early October. Fertilisers, pesticides and growth regulators were applied as required. Crops were harvested in August.

Irrigation x seed dressing experiment

This experiment was carried out in two seasons, 1998/9 and 1999/2000.

Irrigation treatments

Four irrigation treatments were originally intended to be applied throughout the season:
1) Unirrigated.
2) Spring irrigated only - this was intended to increase the levels of Ggt infection, exposing - the crop to a late-season stress.
3) June/July irrigation only - this was intended to allow below-ground resource capture and hence crop growth to be maintained despite infection by take-all.
4) Full irrigation - to give a combination of effects listed under irrigation regimes 2 and 3 above.

Spring irrigation, to maintain soil moisture close to field capacity, was expected to have two effects: firstly, increased levels of Ggt infection in the crop (e.g. Trolldenier, 1981) and, secondly, stimulation of growth of roots in the upper layers of soil (e.g. Barraclough, Kuhlman and Weir, 1989; Chaudhary and Bhatnagar, 1980; Zhang *et al.*, 1998). It was thought that take-all root loss would outweigh the effects of any extra root growth, leading to a net reduction in the size of the root system. However, high rainfall in the springs of 1999 and 2000 meant that spring irrigation was inappropriate, therefore there was no spring irrigation treatment, and hence also no full irrigation. In the late irrigation treatment water was applied as necessary from the beginning of June through to harvest. The irrigation was applied to maintain soil moisture deficit (SMD) in irrigated plots to < 50 mm as determined by the ADAS Irriguide program (Bailey & Spackman, 1996). Irrigation was applied 20 mm at a time on the following dates:

Irrigation applied (mm)	Date of application
20	16/6/99
20	25/6/99
20	2/7/99
20	7/7/99
20	21/6/00
20	29/6/00

In 2000 rainfall was excluded from the non-late irrigated treatments by use of a rain shelter (Haygrove tunnels, Herefordshire, UK). By this method 40 mm of rainfall was excluded from the unirrigated sub-plots.

Silthiofam seed treatment

Silthiofam seed treatment was applied at two rates, nil with standard seed treatment only (Beret gold), and standard seed treatment + silthiofam @ 25g a.i./100 kg seed in 1999 and @ 50g a.i./100 kg seed in 2000. It was hoped that this should give two contrasting levels of Ggt in the experiment for which effects on resource capture could be investigated.

Experimental design

In both years the design was a randomised block split-plot layout, with irrigation treatments randomised on main plots and chemical seed treatments randomised on sub-plots. Four replicates for each treatment combination were present giving a total of 32 experimental sub-plots of dimensions 6x24 m. Each sub-plot was further sub-divided into six sub-sub-plots (dimensions 2x10 m), two of which were used for combine yields, and the remaining four for biomass, root growth, and take-all assessments. The sub-sub-plot system for sampling was in place to take account of the patchy nature of Ggt infection.

Rotational-position x seed dressing experiment

To assess the effect of rotation and cereal species on take-all progress a similar set of measurements was conducted on wheat and barley in both 1997/8 and 1999/2000 on plots subjected to different previous cereal cropping.

22 separate rotations were set up at the start of the experiment (in the autumn of 1997) using winter wheat, winter barley and oilseed rape. These were grown on a site pre-planted in the previous season with winter field beans to create the appropriate low take all risk conditions at the start of the experiment. Rotations ranged from continuous winter wheat to a 3 course oilseed cereal rotation, with all cereals being grow either with or without silthiofam.

Table 1. Rotational experiment design

Rotation	1997	1998	1999	2000	2001	2002	2003
1	ww1	ww2+	ww3+	ww4+	ww5+	Ww6+	ww7
1	ww1	ww2-	ww3-	ww4-	ww5-	Ww6-	ww7
1	ww1	ww2+	ww3+	ww4+	osr	Ww1+	ww2
1	ww1	ww2-	ww3-	ww4-	osr	Ww1-	ww2
1	ww1	ww2+	ww3+	osr	ww1+	Ww2+	ww3
1	ww1	ww2-	ww3-	osr	ww1-	Ww2-	ww3
1	ww1	ww2+	osr	ww1+	ww2+	Ww3+	ww4
1	ww1	ww2-	osr	ww1-	ww2-	Ww3-	ww4
1	ww1	osr	ww1+	ww2+	ww3+	Ww4+	ww5
1	ww1	osr	ww1-	ww2-	ww3-	Ww4-	ww5
2	ww1	ww2+	osr	ww1+	ww2+	Osr	ww1
2	ww1	ww2-	osr	ww1-	ww2-	Osr	ww1
2	ww1	ww2+	ww3+	osr	ww1+	Ww2+	ww3
2	ww1	ww2-	ww3-	osr	ww1-	Ww2-	ww3
2	ww1	osr	ww1+	ww2+	osr	Ww1+	ww2
2	ww1	osr	ww1-	ww2-	osr	Ww1-	ww2
3	ww1	wb+	osr	ww1+	ww2+	Wb+	ww4
3	ww1	wb-	osr	ww1-	ww2-	Wb-	ww4
3	ww1	ww2+	wb+	osr	ww1+	Ww2+	ww3
3	ww1	ww2-	wb-	osr	ww1-	Ww2-	ww3
3	ww1	ww2+	ww3+	wb+	osr	Ww1+	ww2
3	ww1	ww2-	ww3-	wb-	osr	Ww1-	ww2
3	ww1	osr	ww1+	ww2+	wb+	Osr	ww1
3	ww1	osr	ww1-	ww2-	wb-	Osr	ww1

WW = winter wheat
WB = winter barley including some winter malting varieties
OSR = Oilseed rape
+ = treated with silthiofam

Each treatment was replicated four times. Treatments were also fully randomised within blocks, with a plot size of 3m by 24m.

Measurements of disease progress

Within the irrigation x seed dressing experiment, twenty five plants were taken from each sub-plot s approximately every 14 days in 1999 and once a month in 2000. Six or seven plants were taken from each sub-sub-plot. Records were made for each plant of tiller number, seminal root number, number of primary crown root axes, number of infected seminal roots and number of infected crown roots. The following equation was used to calculate the proportion of diseased roots from this data.

$$PDR = \frac{\text{Total number of infected primary root axes}}{\text{Total number of primary root axes}}$$

In addition a take-all index score was given to the plant, depending on the % of the root system colonised by the fungus. This method used was a modified form of that described by Clarkson and Polley (1981):

Scale	Category
0% = healthy roots	0
1-10%	1
11-30%	2
31-60%	3
61-100%	4

A take-all index for the split plot as a whole was calculated using the following equation:

$$\frac{(0a+10b+30c+60d+100e)}{t} = TAI$$

where *a,b,c,d,e* represented the numbers of plants in each of the five categories and *t* was the total number of plants examined.
Incidence was expressed for the sub-plot using the following equation:

$$\frac{\text{Number of plants with take-all}}{\text{Number of plants assessed}} \times 100$$

Results were also expressed as numbers of uninfected roots per tiller; this gave an estimate of the ability of the crop to tolerate take-all infection. All meteorological data was recorded using an agromet station within 1 km of the field sites.

Results

Irrigation x seed dressing experiment

In both seasons a slow increase in TAI and PDR values throughout the winter and early spring was followed by a rapid increase after the end of March in 1999 and after the end of April in 2000 (due to a colder spring). This was linked with the increase in soil temperatures to above 10^{o}C.

1998/9

Fitted and observed take-all index values are shown in Figure 1.1A. Silthiofam significantly decreased TAI from 15/12/98 with the exception of the last two sampling dates. Irrigation had no significant effect on TAI on any dates, and there were no significant interactions between silthiofam and irrigation treatments.
Figure 1.1B shows fitted and observed data for proportions of diseased roots (PDR) with thermal time. Effects of silthiofam did not become meaningful until the onset of rapid increase in PDR and there were no obvious consistent effects of irrigation except at the last sampling date. ANOVA calculations suggested that silthiofam significantly decreased PDR on all but the last two sampling dates. Irrigation had no significant effect on any of the sampling dates. There were no significant interactions between silthiofam and the irrigation treatment.

For both TAI and PDR a logistic equation of the form:

Y=A+C(1+exp(-B*(X-M))), where

A is the lower asymptote
C is the upper asymptote
B is the rate of increase
M is the point of inflection
X is ^{o}C days above 0^{o}C at 10cm soil depth .
Y is the calculated TAI or PDR

was fitted to the observed data and parallel regression analysis performed. For the TAI and PDR data the percentage variance accounted for by a single logistic curve fitted to all data was 84.8, and 82.4 respectively . The percentage variance accounted for was significantly improved (to 86.1 for TAI and 84.1 for PDR) by fitting separate logistic curves for the four treatment combinations allowing the point of inflection (M) to vary. Allowing other parameters to vary did not improve the fits.
In both TAI and PDR scores M was increased where silthiofam was used by over 200^{o}C days. Confidence limits for M (Table 1.1) showed that the unirrigated/treated sub-plots had a significantly higher value than either of the untreated treatments. The unirrigated/treated sub-plots were intermediate. However, lack of irrigation by itself did not increase M significantly.

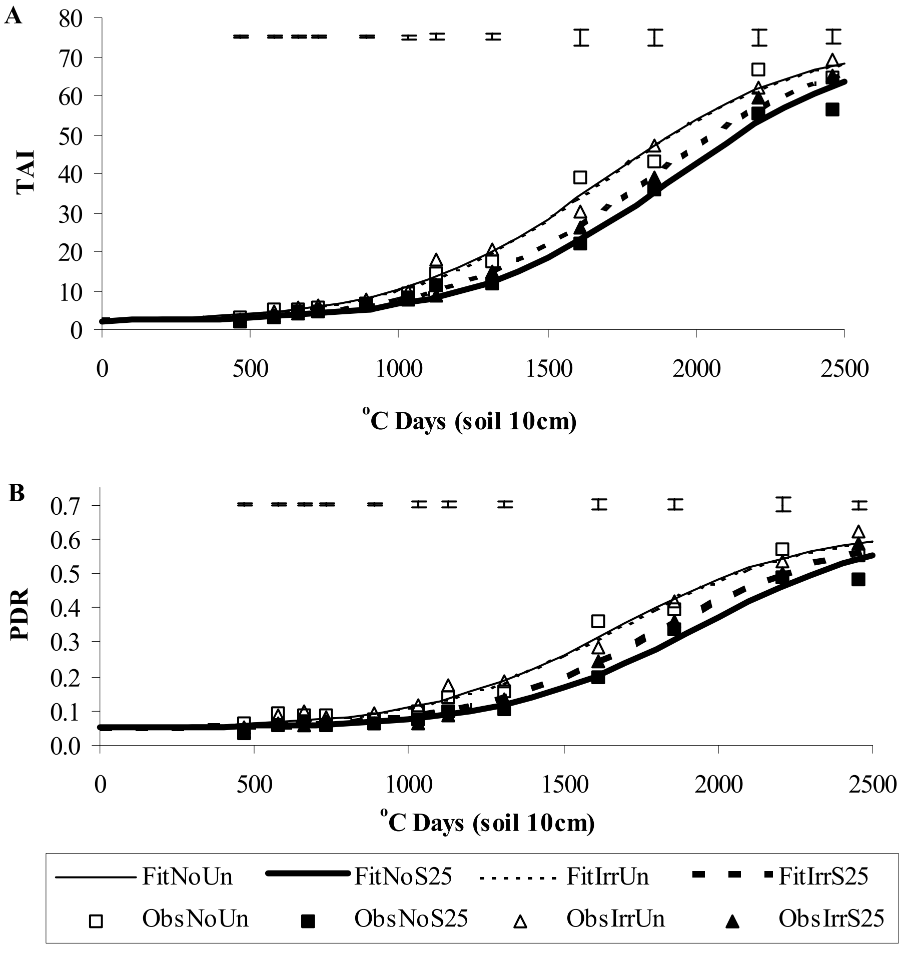

Figure 1.1 Irrigation/seed dressing experiment 1998/9. Take-all index (TAI) (A) and proportion of diseased roots (PDR) (B) with ^{o}C days at soil depth of 10cm in unirrigated (No) and irrigated (Irr) treatments without (Un) or with (S25) silthiofam at 25g a.i. 100 kg^{-1} seed. Error bars indicate SEDs for the chemical treatment. Both figures show the fitted (Fit) and observed (Obs) values.

Table 1.2 Irrigation/seed dressing experiment 1998/9. Point of inflection (M), and confidence intervals (p=0.05, CI) for fitted take-all index (TAI) and proportion of diseased roots (PDR) values

Trt	**M mean TAI**	**M mean PDR**	**Units**
No/Un	1684±104a[z]	1671±102a	M = ^{o}C days at 10cm soil depth
No/S25	1914±101b	1928± 101b	[z]Means the same letters are not
Irr/Un	1691±104a	1678±102a	Different at p=0.05 when
Irr/S25	1827±103ab	1831±102ab	Comparing confidence intervals

<u>1999-2000</u>

Fitted and observed values of TAI and PDR for the irrigation/seed dressing experiment 2000 are shown in figure 1.2. ANOVA at individual sampling dates indicated that silthiofam significantly ($p \leq 0.05$) reduced TAI and PDR at all sampling dates.
Irrigation seemed to increase TAI and PDR from 19/6/00, but only significantly on 17/7/00 (p=0.016) for TAI and the last two sampling dates for PDR (p=0.013 and 0.042 respectively). There was a slight reduction in TAI on 26/4/00 in unirrigated treatments. There were no interactions between chemical and irrigation treatments.

When the logistic equation, referred to at the start of the results section, was fitted to all TAI data percentage variance accounted for was 89.1. Separate curves were fitted for different treatments allowing M and then M and B to vary. Both significantly improved the fit of the data(% variance accounted for = 93.4 and 94.4 respectively).

Figure 1.2 shows treatment curves separated out by allowing both M and B to vary. Confidence intervals (Table 1.3) show that unirrigated/treated sub-plots had significantly higher M values than all other treatments. Irrigated/treated sub-plots had a significantly higher M value compared to irrigated/untreated sub-plots. Thus silthiofam increased M with and without irrigation, but its effects were significantly greater with no irrigation. Irrigation by itself had no significant effect on M. B however was significantly increased with irrigation (Table 1.3). There was no significant effect of silthiofam within individual irrigation treatments, suggesting that irrigation significantly increased the rate of increase of the disease, but that silthiofam had no effect.

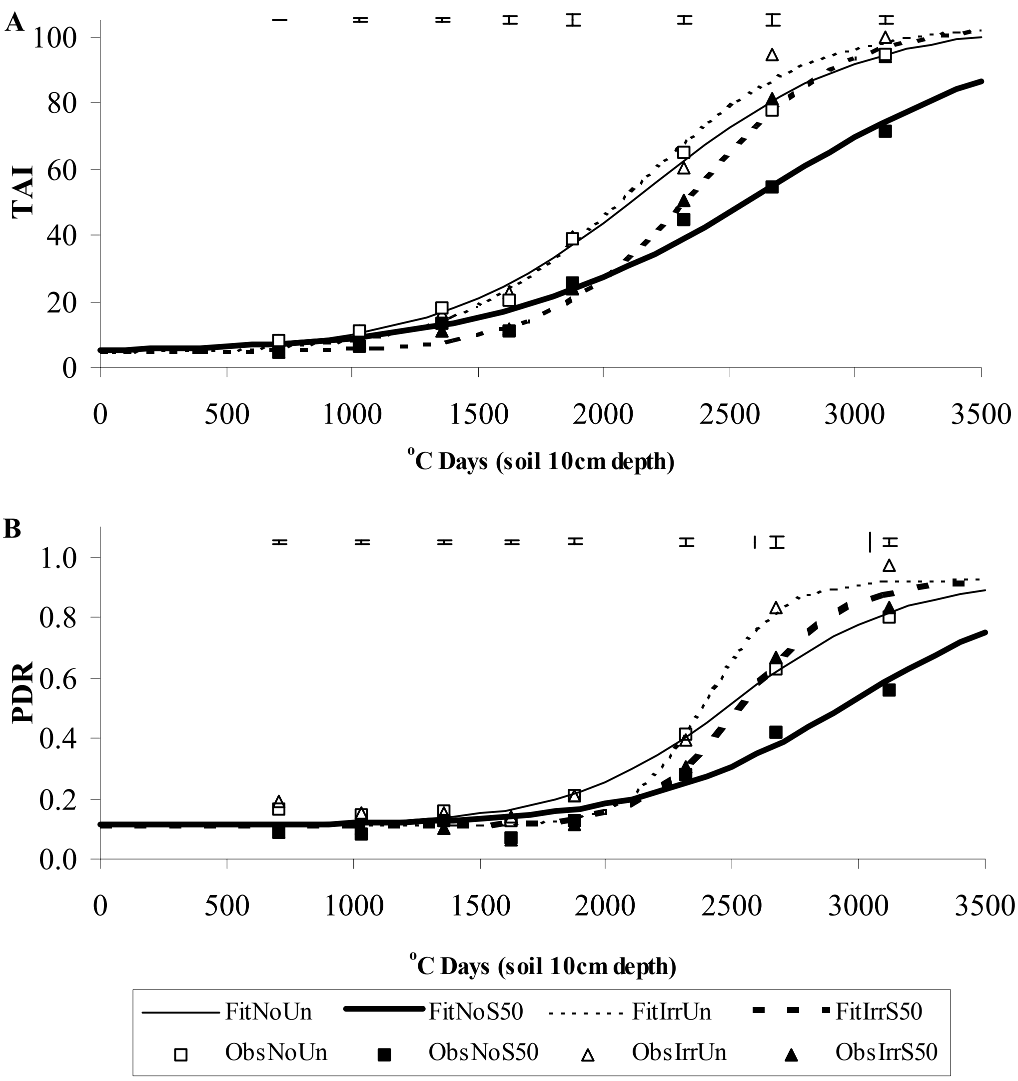

Figure 1.2. Fitted (Fit) and observed (Obs) take-all index (A) or proportion of diseased roots (B) with °C days at 10cm soil depth in unirrigated (No) or irrigated (Irr) treatments without (Un) or with (S50) silthiofam at 25g a.i. 100 kg^{-1} seed. – Irrigation/seed dressing experiment 1999/2000. Error bars - SEDs for comparing silthiofam (capped) or irrigation (uncapped) means.

Table 1.3. Irrigation/seed dressing experiment 1999/2000. Point of inflection (M), rate (B) and confidence intervals (p=0.05, CI) for fitted take-all index (TAI) and proportion of diseased roots (PDR) values.

Trt	TAI M	TAI B	PDR M	PDR B
NoUn	2181±90a	0.0024± 0.00038ac	2507± 89ab[z]	0.003±0.00055a
NoS50	2658± 88c	0.0019± 0.0003bc	2970±88c	0.0025±0.0005a
IrrUn	2126± 91a	0.0029± 0.0005a	2395± 90b	0.0067±0.0009b
IrrS50	2369±89b	0.0034±0.00064a	2550± 88a	0.0051±0.0012b

Units:
M = °C days at 10cm soil depth
B = rate of increase in TAI/PDR per °C day at 10cm soil depth
[z]Means within a column with the same letters are not significantly different at p=0.05 after comparing confidence intervals.Treatments refer to unirrigated without silthiofam (NoUn), unirrigated with silthiofam at 50g a.i. 100kg^{-1} seed (NoS50), irrigated without silthiofam (IrrUn) and irrigated with silthiofam at 50g a.i. 100kg^{-1} seed (IrrS50).

Cereal rotation experiment 1997/98

Fitted and observed TAI levels taken for winter barley and winter wheat (both after wheat) are shown in Figure 1.3. Similar to the previous DPC for 1999 (see section Irrigation and seed dressing experiment above) there were slow increases in TAI throughout the cold winter months followed by a rapid progression after April, when temperatures began to rise. ANOVA showed that there was significantly higher TAI in wheat compared to barley on all dates except 8/1/98, and 9/2/98. Silthiofam consistently reduced TAI throughout the season, significantly so on 10/3/98 and 27/7/98. At no point was there any significant interaction between crop and silthiofam effects.
A logistic equation (as described earlier) was fitted to the data against ^{o}C days of temperature from sowing at a soil depth of 10cm (Figure 1.3). Percentage variance accounted for when fitting the equation to all the data was 76.5. Curve fitting was significantly improved only when treatments were separated out by different M values (percentage variance accounted for = 87.6). Therefore curves in Figure 1.3 relate only to separate M values. Confidence limits (p=0.05) suggested that barley at both levels of silthiofam had significantly higher M than untreated wheat (Table 1.4) indicating that the crop effects were greater than silthiofam effects.

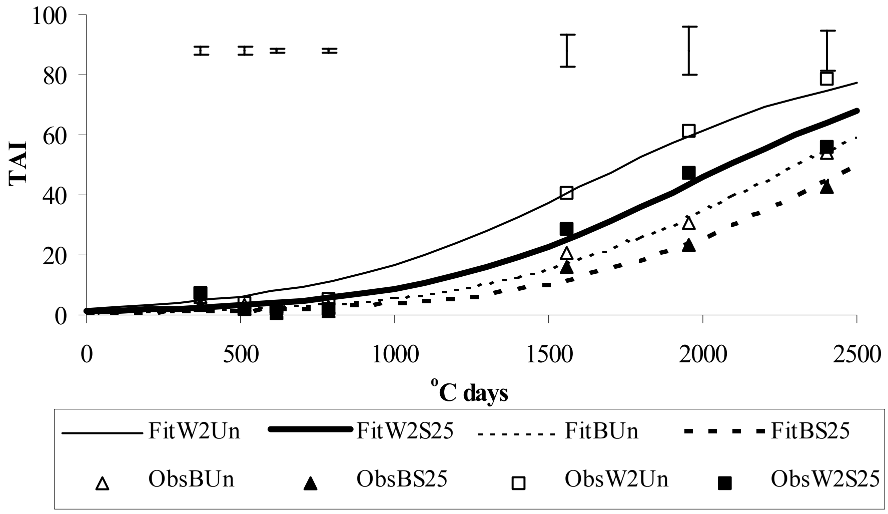

Figure 1.3. Fitted (Fit) and observed (Obs) values of take-all index (TAI) with ^{o}C days at soil depth of 10cm in a second wheat (W2) and winter barley (B) without (Un) or with (S25) silthiofam at 25g a.i. 100 kg^{-1} seed. Rotation x seed dressing experiment 1997/8. Error bars indicate SEDs for the chemical treatment means and crop treatment means.

Table 1.4. Rotation x seed dressing experiment 1997/8. Point of inflection (M) means for logistic equation y=a+c(1+exp(-b*(x-m))) fitted to take-all index (TAI) data.

Trt	M mean
BUn	2184± 254a[z]
BS25	2389± 260ac
W2Un	1632± 285b
W2S25	1964±258abc

Units:
M = ^{o}C days at 10cm soil depth
[z]Means within a column with the same letters are not significantly different at p=0.05 after comparing confidence intervals.
For treatments see figure 1.3.

Rotational position x seed dressing experiment 1999/2000

Take-all index (TAI) data for the experiment are shown in Figure 1.4. ANOVA revealed that silthiofam significantly reduced TAI on the following dates: 21/2/00; 17/4/00 and 1/6/00. First wheats had significantly lower TAI than 3rd wheats on 21/2/00, 17/4/00, 17/7/00 and 21/8/00. There were significant interactions between silthiofam and rotation on 21/2/00, 17/4/00 and 1/6/00, with silthiofam (at both rates) reducing TAI in 3rd wheats but not 1st wheats. The effect of rotation on TAI was much larger than the effect of silthiofam.
Figure 1.4B shows the progression of take-all measured as PDR. silthiofam significantly reduced PDR compared with the untreated plants on 21/2/00 and 17/4/00. This was significant at both dates for the S25 application, but only on 17/4/00 for the S50 treatment. 1st wheats had significantly lower PDR on: 30/11/99; 21/2/00; 17/7/00 and 21/8/00. Significant interactions between the rotation and silthiofam treatments were observed on: 21/2/00; 17/4/00 and 1/6/00. In 1st wheats silthiofam did not consistently significantly affect PDR. In 3rd wheats silthiofam significantly reduced PDR compared to untreated plants at both levels of silthiofam on 21/2/00 and 17/4/00, and with S25 on 1/6/00.
Fitting a logistic curve or exponential curves to these datasets was not possible.

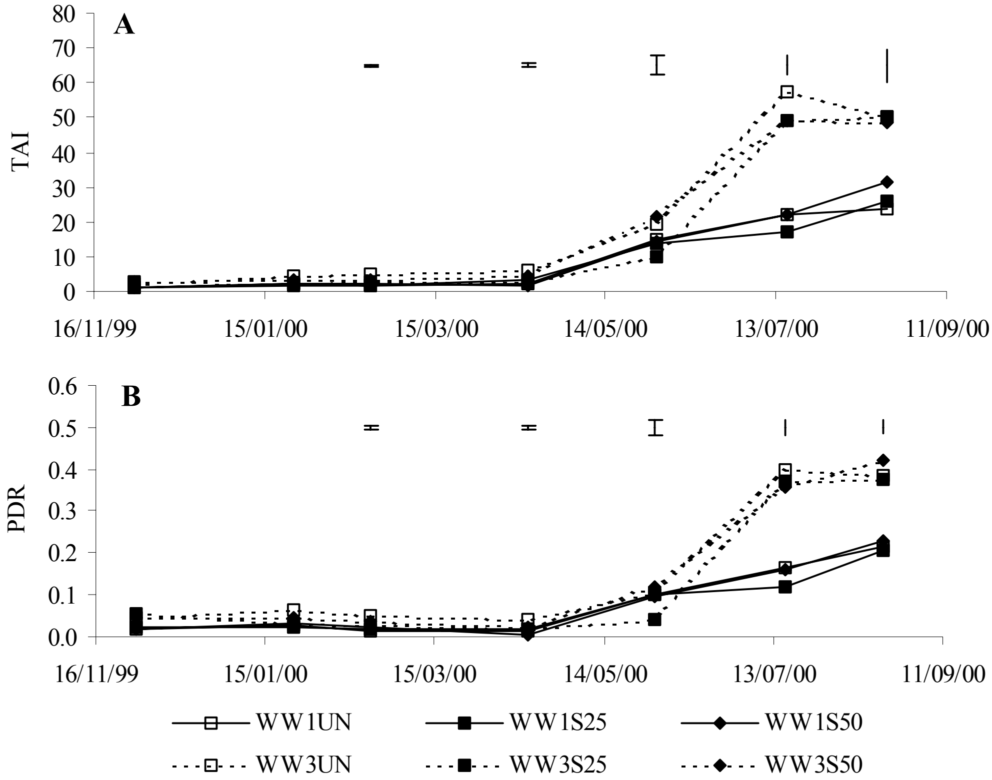

Figure 1.4. Take all progression curves for rotational position/seed dressing experiment 2000. Take-all measured as either take-all index (A - TAI) or proportion of diseased roots (B - PDR) in 1st wheats (WW1) or 3rd wheats (WW3) with 50g a.i. 100 kg seed^{-1} (S50), 25g a.i. 100 kg seed^{-1} (S25), or without (UN) silthiofam seed treatment. Error bars indicate SED for chemical/rotation interaction and rotation treatment averages (capped and uncapped).

Discussion

Chemical effects

The results in the previous section on first, second and third wheats showed that silthiofam significantly reduces take-all levels in crops at risk from the disease confirming the work of Spink *et al*. (1998) and Beale *et al*. (1998). The series of experiments presented here have shown that reduction in take-all levels is consistent, but not always significant throughout the season, supporting the work of Schoeny and Lucas (1999).
The use of silthiofam at 50g a.i. 100 kg^{-1} seed, did not consistently offer improved control over the lower rate of fungicide. This inconsistency of improvement was seen by Schoeny and Lucas (1999). This result also supports the conclusion of Beale *et al*. (1998) that the optimum rate of silthiofam for take-all control was 25g a.i. 100 kg^{-1} seed.
This study showed that silthiofam increased the point of inflection (M), delaying the epidemic in both irrigation experiments using both take-all assessment methods. This supports the work of Schoeny and Lucas (1999) who concluded that this was due to a delay in the 1^o infection cycle. Our results suggest that silthiofam did not affect the rate of increase of take-all (B) which describes the rapid take-all increase seen in all experiments from April/May. These results are consistent with the reported mode of action of the chemical which provides a zone of protection around the seed and young plant in the vapour phase of the soil. It is unlikely that silthiofam could have persisted long enough in the soil to affect any 2^o infection parameters. In accordance with the model of Gilligan (1994) it seems likely that silthiofam delays the epidemic by either decreasing the maximum distance between pathogen and host at which the fungus can successfully execute a 1^o infection or effectively reducing the 1^o inoculum density.
In two out of three field experiments silthiofam delayed the take-all epidemic, although these effects are most likely to be through effects early in the season, this leads to delays in epidemic progress later in the year. If a crop could continue to grow without reaching maturity the shape of curve would probably be the same as without silthiofam, but displaced in time. This supports work by Schoeny and Lucas (1999) who found that silthiofam affected early infection processes only.
The extent to which silthiofam delayed the epidemic was similar where chemical application rates were the same. Between 200-260^{o}C days at 25g a.i. 100 kg^{-1} seed and 460-480^{o}C days at 50g a.i. 100 kg^{-1} seed where no irrigation was applied. Irrigation reduced the delaying effect to around 150^{o}C days at all levels of silthiofam. Thus the early benefits silthiofam provides may be offset by increased soil moisture. Schoeny and Lucas (1999) found that the epidemic was delayed by 416 and 533^{o}C days for the two different rates of chemical, which are rather higher than the values found in this study, possibly due to the different field locations and different years where the experiments were run. The effects of irrigation on the DPC will be discussed further in later sections.

Other factor's effects on take-all and interaction with silthiofam

<u>Cereal species effects</u>

The point of inflection in barley on TAI curves was significantly greater than wheat. This implies that the disease's progress under conditions at Rosemaund is delayed in barley, reducing disease levels later in the season. This is analogous to effects of silthiofam in untreated/treated wheat comparisons. However, it is not possible to infer at what stage crop species might be exerting an effect on the DPC. Reduced disease levels observed in barley in some studies have been attributed to the production of more crown roots in barley (Asher, 1972b; Cunningham *et al*., 1968) which effectively diluted the presence of the disease when assessed as percentage infected area since there was more healthy tissue. This was indicative of disease tolerance rather than resistance to the pathogen. In Asher (1972b) barley plants initially had a significantly higher percentage of roots infected with take-all than wheat. Later, however, barley had a significantly lower percentage of roots infected than wheat, and a significantly higher number of healthy roots. Increased host availability through increased root numbers could allow more infection processes, by decreasing the distance for 2^{o} infection described in Gilligan (1994). That this did not occur indicates that the distance for 2^{o} infection was not limiting disease increase, and that increased root production in barley more than outstripped disease increase. Root counts were not made in the rotation 1998 experiment so it is not possible to confirm whether this dilution of disease severity by increased root production occurred in barley. Overall the results tend to confirm the idea that barley suffers less from take-all than wheat.

Irrigation effects

In the original irrigation experiment design spring irrigation was intended to remove any inhibition to growth of Ggt due to dry conditions. The aim was to obtain differing levels of take-all and this expectation was supported by previous findings that spring rainfall could influence take-all epidemics (Roget and Rovira, 1991; Hall and Sutton, 1998). In the event spring irrigation was reduced to a single application in late May 2000, and was omitted altogether in 1999 due to high spring rainfall. Summer irrigation was intended to affect plant growth, and to have only limited effects on the take-all epidemic.
However, summer irrigation did have an affect on take-all progress. No previous work has looked at interactions between irrigation and silthiofam but in this study the effect of the chemical's on M were more pronounced without irrigation. It is possible that silthiofam's effects of delaying disease progress were partially offset by the application of summer irrigation allowing increased infection as was intended by the spring irrigation. However, in both years during the period of irrigation percentage water contents were approximately 30% for the unirrigated and 40% for the irrigated treatments in the top 20 cm of soil. Previous work suggests that take-all epidemics can be halted in conditions of inadequate moisture (e.g. Murray, Heenan and Taylor, 1991), or stimulated where more moisture is available (Trolldenier, 1981). In this study irrigation increased the rate of PDR increase (B) in the summer months in 2000. This increase could be due to the increased soil moisture availability. Alternatively, it could indicate that reduced soil moisture inhibits root to root spread more than extension of existing lesions.

Although the 2000 Irrigation experiment showed that summer irrigation had an effect on B, the 1999 experiment did not. Rainfall and its distribution during these years was similar (247 mm and 243.5 mm rainfall between 1^{st} April and harvest for 1999 and 2000 respectively). Average ambient air temperatures were also similar in this period, 13.94°C and 13.4°C for 1999 and 2000 respectively. In addition the disparity in water availability in each year was similar. 80 mm of irrigation was applied in 1999 to the irrigated treatment, 40 mm was applied in 2000 to the irrigated treatments but another 40 mm was excluded by the rainshelters from the unirrigated treatment.
It is possible that conditions under the rain shelters in 2000 were deleterious to take-all progression. The maximum and average air temperatures inside the rain shelters were about 3°C greater than outside (average maximum air temperature between 4/7/00 and 24/7/00 28.2°C inside compared to 24.7°C outside, average daily means 17.35°C and 19.65°C respectively). Soil temperatures were not recorded under the rain shelters, but mean daily soil temperature at 10cm and mean daily air temperature data from 3 years at Rosemaund correlate very well. Grose *et al.* (1984) showed that take-all's growth in soil in the absence of a host can be inhibited in non-sterile soils at 26°C compared to growth at 18°C. Smiley, Fowler and Reynolds (1986) showed that take-all levels on roots were reduced at 29°C compared to 24°C. Therefore it is possible that the irrigation effect on B seen in the 2000 experiment is in fact a temperature inhibition effect.
The application of irrigation in the summer seems to have had less effect on take-all than silthiofam. The only point at which the epidemic may have been affected by irrigation occurred in the 2000 experiment, and as described this effect may have been confounded by the increased temperatures observed in the rain shelter. In contrast silthiofam consistently reduced take-all levels independently of other factors.

Rotation effects

The rotation experiment confirms that second and subsequent wheats suffer more from take-all than first wheats. Because a logistic equation could not be fitted to the data due to insufficient sampling times, that DPCs for the different rotations could not be described in terms of point of inflection or rate of increase.
Beale *et al.* (1998) found that silthiofam gave less absolute control of take-all measured as TAI at lower disease pressures although it was not stated whether the control at different disease pressures was significant or not. Current results show that applying silthiofam on first wheats, does not result in significant control of take-all. With the same field and environmental conditions but with high disease pressure, significant reduction of take-all levels was seen with silthiofam.
This indicates that application of Silthiofam where disease pressure is low is analogous to delayed sowing of wheat crops after a non-cereal break in that there is no additional benefit in controlling the disease.

Comparison of factors affecting the DPC

Four factors were tested for their ability to alter the DPC, silthiofam, irrigation, wheat sequence and cereal species.
In absolute values rotational position of the wheat crop was found to have the greatest effect on disease progress. Later in the season take-all levels in first wheats were around half that of take-all levels in third wheats, reducing TAI by 47 units and PDR by 0.2. Next was cereal species, the barley crop ~~,~~ reducing TAI by 24 units. Effects of silthiofam varied considerably between the different experiments. If the sampling periods are divided into pre-June 'early' and post-June 'late' periods silthiofam reduced take-all by between 0.6 and 8 TAI units in the early period and between 2 and 15 TAI units later. Corresponding figures for PDR are 0.01 – 0.06 in the early period and 0.02 – 0.16 later. Effects of irrigation were also not consistent, in 1999 TAI was reduced by 2 and PDR by 0.02. In 2000 these figures were 12 for TAI and 0.16 for PDR.
It is not possible to quantify the effects of rotational position of the wheat crop on take-all as a logistic equation could not be fitted to the data. However, it is clear that the shape of the curves in first and third wheats is totally different, and the curves are more qualitatively distinct than any of the other treatment comparisons. It is likely that the upper asymptote C may be affected, this is the subject of ongoing work. Where the curve shape has been quantified it appears that cereal species has the greatest effect on the timing of the infection, followed by silthiofam (with more effect at the higher rate) and finally irrigation. Irrigation has been identified as increasing the rate of infection in one year, but this is confounded by effects of temperature.
In summary, take-all was most affected by growing first wheats, followed by use of barley instead of wheat and then use of silthiofam. Irrigation can increase take-all, though not consistently.

General conclusions

1. Silthiofam consistently reduced take-all levels in winter wheat and winter barley under conditions of high disease pressure at ADAS Rosemaund.
2. Silthiofam delayed take-all progress, probably by reducing maximum distance between inoculum and host at which infection could occur.
3. Take-all epidemics were delayed in barley compared to wheat. This delay could have been due to increased root axes numbers in barley.
4. Increasing soil moisture post anthesis may not favour take-all under the conditions at Rosemaund, but a combining low soil moisture and high soil temperature may reduce the rate at which take-all can infect the crop.
5. Silthiofam only significantly controls take-all in non first wheats where high levels of inoculum exist, first wheats are not significantly affected by use of silthiofam.
6. Epidemics did not start increasing rapidly until consistent soil temperatures above 10^{o}C occur.

APPENDIX 2

RESOURCE CAPTURE

Introduction

Occlusion of the vascular tissues in the root by hyphae of *Gaeumannomyces graminis* var. *tritici* (Ggt) is thought to be the primary cause of yield loss. With the xylem blocked, one would expect water and nutrient uptake through the infected root to be inhibited, whilst blockage of the phloem would be expected to reduce the supply of photosynthates to the roots. The death of roots following infection may also result in a smaller root system, and therefore one less able to explore and exploit the below-ground environment. If a large enough proportion of the roots are infected then the reduction in water and nutrient uptake may be sufficient to reduce above-ground growth, and ultimately yield.

Effects on water uptake

Work in the laboratory by Kararah (1976), measured the water uptake of 12-20 day old wheat seedlings using a micropotometer system. He found that 16 days after infection with Ggt roots could be taking up as little as 1/45th of the water being taken up by an uninfected root. In other infected roots however water uptake was similar to that of control roots. Subsequent microscopic investigation showed these infected roots to have intact steles as yet uninvaded by the fungus. This work, supported by the others clearly demonstrates that water uptake is inhibited in roots infected by Ggt, as long as the stele has been penetrated. Kirkegaard *et al.* (1994) found that soil water depletion between emergence and end of grain fill could be halved in 2nd wheats compared with wheats following brassicas in two out of four experiments. This reduction in soil water depletion occurred along with a reduction in root growth and increased levels of take-all. However the authors did not attribute this directly to Ggt, as effects of brassica break crop residues on wheat root growth could not be excluded. There is no conclusive evidence, therefore, that take-all reduces root function at the crop level.

High levels of rainfall in the spring might have two counteracting effects on root growth in non-first wheats: firstly, through increased levels of Ggt infection in the crop (e.g. Trolldenier, 1981; Murray, Heenan and Taylor, 1991; Cook and Papendick, 1972) and, secondly, through stimulation of growth of roots in the upper layers of soil (e.g. Barraclough, Kuhlman and Weir, 1989; Chaudhary and Bhatnagar, 1980; Zhang *et al.*, 1998). Whether take-all root loss would outweigh any extra root growth, leading to a net reduction in the size of the root system in upper layers is not known. High rainfall early (increasing levels of Ggt), followed by a drought might be expected to have a greater impact on water uptake during grain-fill compared to crops with either healthy root systems or adequate summer moisture availability, due to the combined effects of a smaller root system attempting to capture less resource. This is supported by various works cited in Asher and Shipton (1981).

Differences in water availability with depth will affect the depth at which water extraction will predominantly occur. If the crop has adequate moisture in the top layers of soil, then most of the water extraction will occur from these layers (Barraclough, Kuhlman and Weir, 1989). If however drought conditions are experienced the crop will be more dependent on water from greater depths (Gregory McGowen and Biscoe, 1978). Studies of the influence of soil moisture and effects of take-all on root growth and water uptake with depth are as yet not available.

Effects on nitrogen uptake

Kirkegaard *et al.* (1994) found that plant nitrogen (N) levels at the end of grain fill were reduced in 2nd wheats compared to 1st wheats where take-all levels were higher. This implies that take-all is reducing N uptake by the crop. Echeverría, Navarro and Andrade (1992) found that although wheat crops grown after soyabean, maize or sunflower yielded significantly more when given extra N, wheat following wheat did not, possibly due to a severe take-all epidemic. Widdowson *et al.* (1985) found that uptake of N was greater in wheat after beans than 2nd wheats where it was also observed that take-all severity was greatest in the 2nd wheats. All these studies suffer from the problem of directly relating reduced N uptake to increased levels of take-all and loss of root function, since rotation can itself alter many factors. Possibly one of the most important of these is reduced residual N seen in 2nd or subsequent wheat crops. Although Kirkegaard *et al.* (1994) found that residual N was similar in his study, N uptake significantly differed in wheats following different break crop species. This implies an additional effect of the break crop rather than an effect solely of take-all. Therefore there is no conclusive proof that take-all significantly affects crop nitrogen uptake.

Effects of Ggt on root growth

The effects of Ggt on water uptake may be via effects on total root growth rather than root function, since density of rooting affects water uptake (e.g. Barraclough, Kuhlman and Weir., 1989).

Ggt disrupts the flow of photosynthate to root material below the point of infection (Asher, 1972a; Manners and Myers, 1981 and works cited therein). Therefore root growth should be stopped below the lesion, as long as the stele has been invaded. Clarkson *et al.* (1975) showed that infection with Ggt stopped root elongation in a proportion of infected roots in 2-4 week old wheat plants. Asher (1972b) found in pot experiments that Ggt infected wheat plants had lower seminal root dry weights. Crown root dry weight was not affected, but the study was only conducted up to 47 days after sowing. Deacon and Henry (1978) showed that root death occurred below the infection point in 50% of infected roots in wheat seedlings under laboratory conditions.

There is some evidence that Ggt can affect numbers of root axes on wheat. Davis (1925; cited in Manners and Myers, 1981) noted that some plants artificially inoculated with Ggt were shown to replace crown roots lost to infection. Increased crown root production in infected plants was also seen by other workers (Russell, 1931, 1934; and Defosse, 1959; both cited in Manners and Myers, 1981). More recently modelling work by Bailey and Gilligan (2001) has suggested that in the early stages of infection when disease levels were low root numbers increased, but later on, when the levels of disease increased root number was depressed.

These studies suggest that take-all can inhibit root growth, possibly sufficiently to significantly reduce the size of a whole plant's root system, under laboratory conditions. There is also some evidence (Kirkegaard *et al.*, 1994) of take-all reducing root growth in field grown crop. However, observed rotational effects on crop root growth could not be wholly attributed to take-all, due to confounding effects of rotation, eg residual nitrogen levels, and there is a gap in the literature regarding take-all's quantitative effects on root growth at the crop level.

Summary

It is known that take-all infects and disrupts the xylem and phloem, and that this leads to a reduction in water and nutrient uptake through infected roots. There are also indications that take-all may reduce the total size of the root system which may, depending on soil moisture availability, reduce the capacity of the crop to take up water. Nitrogen uptake similarly seems to be reduced in high take-all situations. However, while laboratory work has suggested how take-all may be responsible for yield losses in wheat, its relevance in the field has not been explored in such a way that quantifiable reductions in root growth and below-ground resource capture can be attributed solely to take-all. In addition the relative importance of soil moisture on root growth, root losses to take-all infection and depth of water extraction have not been investigated.

This study will attempt to address these points.

Hypotheses:

1) Take-all infection reduces size of the crop root system, and thereby reduces water and nitrogen uptake.

2) Take-all infection stops water and nitrogen uptake by an existing root system. Therefore water uptake will relate to the remaining healthy root system.

3) Increased soil moisture during grain-fill will allow the crop to maintain adequate levels of water uptake despite infection with take-all.

It was planned to test these hypotheses by measuring crop root growth under different take-all pressures and soil moisture availabilities. This would be achieved by using early irrigation and a seed treatment to manipulate levels of disease, and late irrigation to manipulate soil water availability.

Materials and Methods

The Irrigation x seed dressing experiment, as described in Appendix 1, was used to assess the effects of take-all on resource capture. Thus the site and experimental treatments are the same. However further experimental measurements were required.

Water uptake

Changes in volumetric soil water content were measured in both years using a neutron probe at fourteen day intervals. In 1999 measurements were taken from two access tubes per sub-plot in half of the replicates from the spring irrigation and unirrigated treatments from the beginning of April to harvest. In 2000 readings were taken from one access tube per sub-plot in all replicates and treatments. Readings were taken at 10 cm intervals down to 1.6m in the first two replicates and down to 1.2m in the remaining two in 1999, and down to 1.2 m in all replicates in 2000. Crop water uptake was assessed as the change in soil moisture content taking account of intervening rainfall and applied irrigation, measured by a weather station located on site.

Root growth

Samples to assess root length density were taken at GS39 and GS65 in 1999 (for definitions see Tottman, 1987) and post-harvest in 2000 in all sub-plots. Soil samples were taken using a split corer with a 2.5 cm diameter internal bore at 20 cm intervals down to a depth of 1 m. Four cores were taken from each sub-plot. Two cores in each sub-sub-plot were taken on a row of crop, the others from between rows. Samples were stored in the freezer prior to assessment. After storage, the samples were washed to clean out soil and organic debris. Root length density (RLD, cm root cm^{-3} soil) was assessed using a line intersect method developed by Tennant (1975). This gave a figure for RLD at 20 cm intervals down to 1m. In order to get an estimate of the functional root system in the soil a value for effective RLD was calculated by reducing RLD at all depths by the proportion of diseased roots (PDR) obtained from disease progress data. It was assumed that all roots in upper layers with disease present were not capable of translocating water past the site of infection i.e. were non-functional, and therefore the PDR value would be applicable at all soil depths. It was also assumed that total RLD did not change significantly between anthesis and harvest, effective RLD could therefore be calculated for any time between these two points by using PDR data from that time.
Due to the labour intensive nature of the processing of root soil cores, the following is based on a sub-set of samples taken which have been processed at the time of writing. The samples include the unirrigated treatment for 1999 the unirrigated treatment in 2000 and half the replicates of the irrigated treatment in 2000.

Biomass sampling

All sub-plots were sampled. Each biomass sample was taken from an area 6 rows wide by 0.25 m long from each of the four sampling sub-sub-plots, giving a total sample area of $0.81m^{-2}$. A sub-sample of 10% on a fresh weight basis from the total area sampled was used to estimate green area of leaves, stems and ears (where present) of the potentially fertile shoots, the individual areas being re-combined to give total GAI. This sample was also used to estimate dry matter biomass partitioning to the various crop components. A second, larger 20% sub-sample was taken and oven dried prior to chemical analysis for N to provide an estimate of N uptake. Biomass samples were taken at GS31, 39, 65, 77 and pre-harvest in 1999 and at GS31, 39, 61, 75 and pre-harvest in 2000.

Results

Root length density

In both years root length density (RLD) decreased (P=<.001 for 1999 and 2000) with depth to 60 cm (Figure 2.1). Below 60 cm there were no significant effects of depth, although RLD values continued to decrease. In neither year were there any significant effects of silthiofam on RLD. In 2000 there were no significant effects of irrigation at any depth~~s~~. Analysis of comparable data from unirrigated treatments from each year showed that RLD was higher in 1999 than in 2000 (P<0.001). This effect was consistent but only significant in the 0-20 and 0-40 cm (P=0.005) horizons.

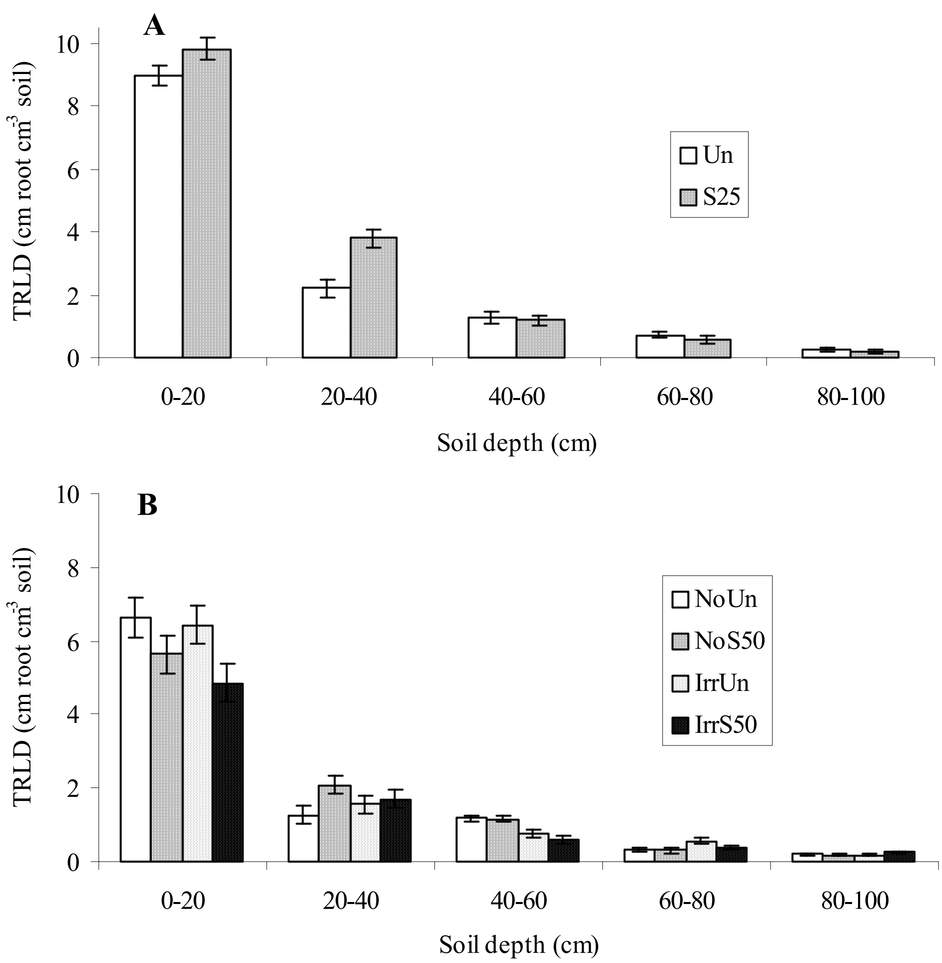

Figure 2.1: Total root length density (RLD, cm root cm^{-3} soil) at different soil depths at GS65 in 1999 (A) or immediately post-harvest in 2000 (B). Data in A(1999) is for unirrigated treatments only. MON25 and MON50 refers to sithiofam used at 25 and 50g of active ingredient (a.i.) 100 kg^{-1}. SEDs are for comparing chemical and irrigation means at individual depths.

Diseased RLD (DRLD)

Measurements of DRLD assessed by counting intercepts of diseased root are shown in Fig. 2.2 A and B for 1999 and 2000 respectively.

Diseased roots were present at all depths down to 100 cm, though in exponentially decreasing levels from the 0-20 cm layer. Disease levels in 1999 were higher than those of 2000, due to changes in the criteria for disease assessment. In both years, ANOVA suggested that DRLD was greater in the 0-20 cm layer than all other layers ($p<0.001$). There were no significant differences between other soil layers.

The irrigation and chemical treatments had no significant effect on DRLD at any of the depths examined in either year. However, in both years the top 20 cm had consistently more DRLD where no chemical had been applied.

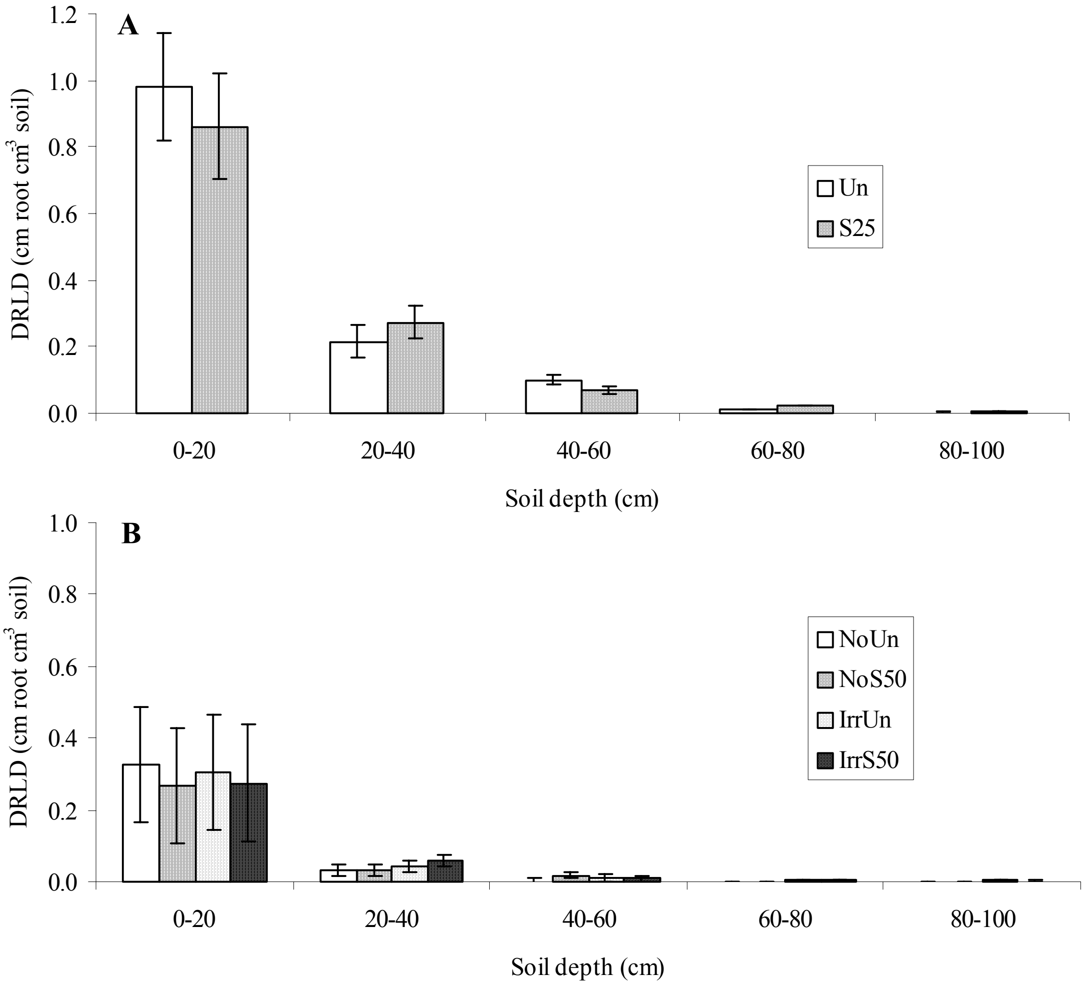

Figure 2.2. Diseased root length density (DRLD) at GS65 in 1999 (A) or postharvest in 2000 (B) at different depths. Data for 1999 are for unirrigated treatments only. Error bars are SEDs for comparing chemical means at individual levels of irrigation.

Effective RLD at mid-grainfill

ERLD at mid-grainfill declined with depth in both years in an exponential manner (Figure 2.3). Where the chemical was present there was consistently higher ERLD at all depths except the 60-100 cm horizon in 1999. There was also an interaction between chemical and depth effects (P=0.001), with the chemical only significantly increasing ERLD in the 0-20 (P=0.026) and 20-40 cm (P =0.025) horizons in 1999.

Irrigation in 2000 also consistently reduced ERLD at all depths, significantly so–in the 0-20 and 40-60 cm horizons (*P*=0.002), analysis showed that irrigation reduced ERLD overall (*P*≤0.05). In 2000 silthiofam again consistently increased ERLD at all depths within the irrigation treatment, significantly so at the 20-40 (*P*=0.035) and 40-60 cm (*P*=0.033) horizons, but did not return it to a value approaching unirrigated levels. There was no interaction between the chemical and depth.
The magnitude of the irrigation effect was slightly larger than the chemical, irrigation decreasing ERLD by 0.437 cm cm^{-3} and the chemical increasing ERLD by 0.291 cm cm^{-3}.

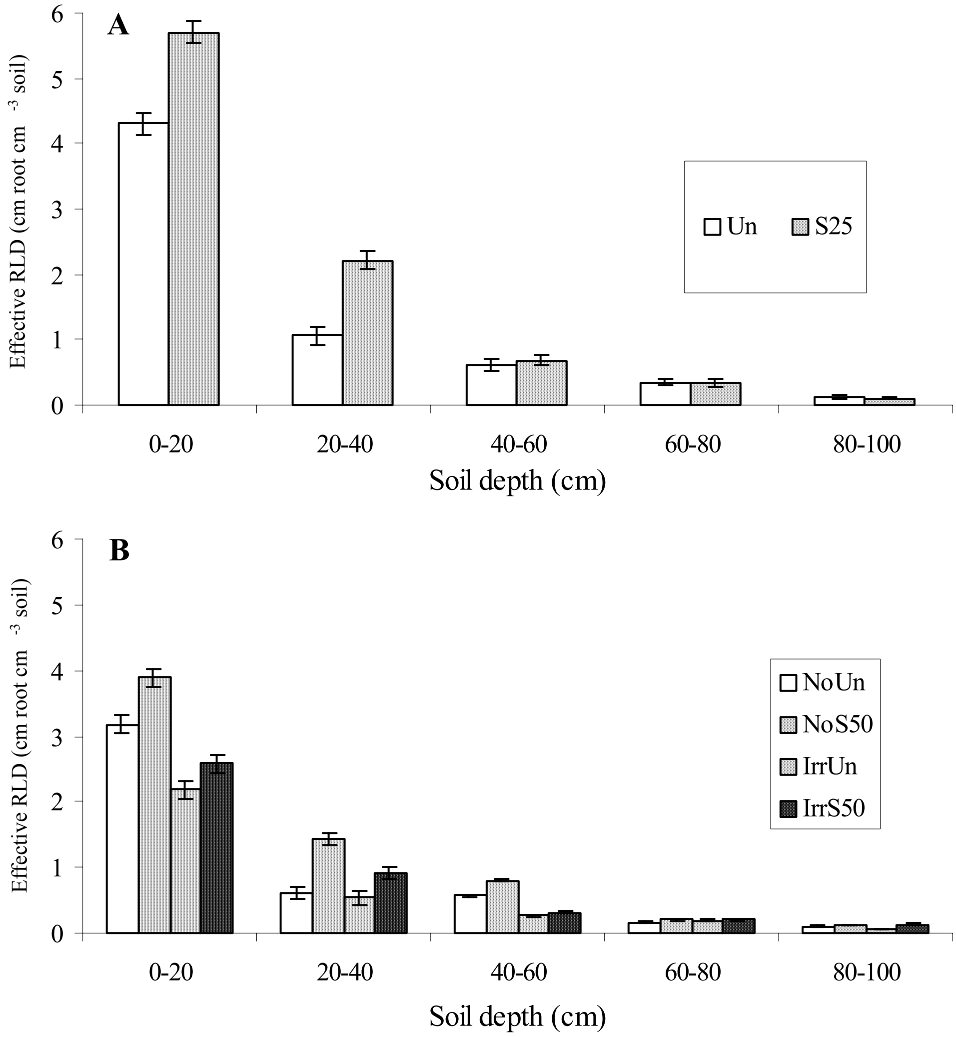

Figure 2.3 Effective root length density (cm cm^{-3}) at mid-grainfill at different soil depths in 1999 (A) and 2000 (B). 1999 data is for unirrigated sub-plots only. Error bars are SEDs for comparing chemical and irrigation means at individual depths.

Water uptake

Soil moisture deficit

Rainfall from October to August was above the long term mean (613 mm) in 1999 (709 mm), but below this in 2000 (543 mm).In both 1999 and 2000 SMDs increased from mid-June onwards levelling off at about 50 mm was reached in irrigated treatments in both years and at 70 mm in 1999, and 80 mm in unirrigated treatments in 1999 and 2000, respectively (Figure 2.4). Where irrigation was applied SMDs decreased for the last three readings (*P*<0.05). In

1999 the chemical had no significant effects on SMD at any point in the season. In 2000 the chemical increased SMD by 10 mm on 20/6/00 (*P*=0.035) and 12 mm on 6/7/00 (*P*=0.030). There were no significant interactions between the chemical and irrigation treatments.

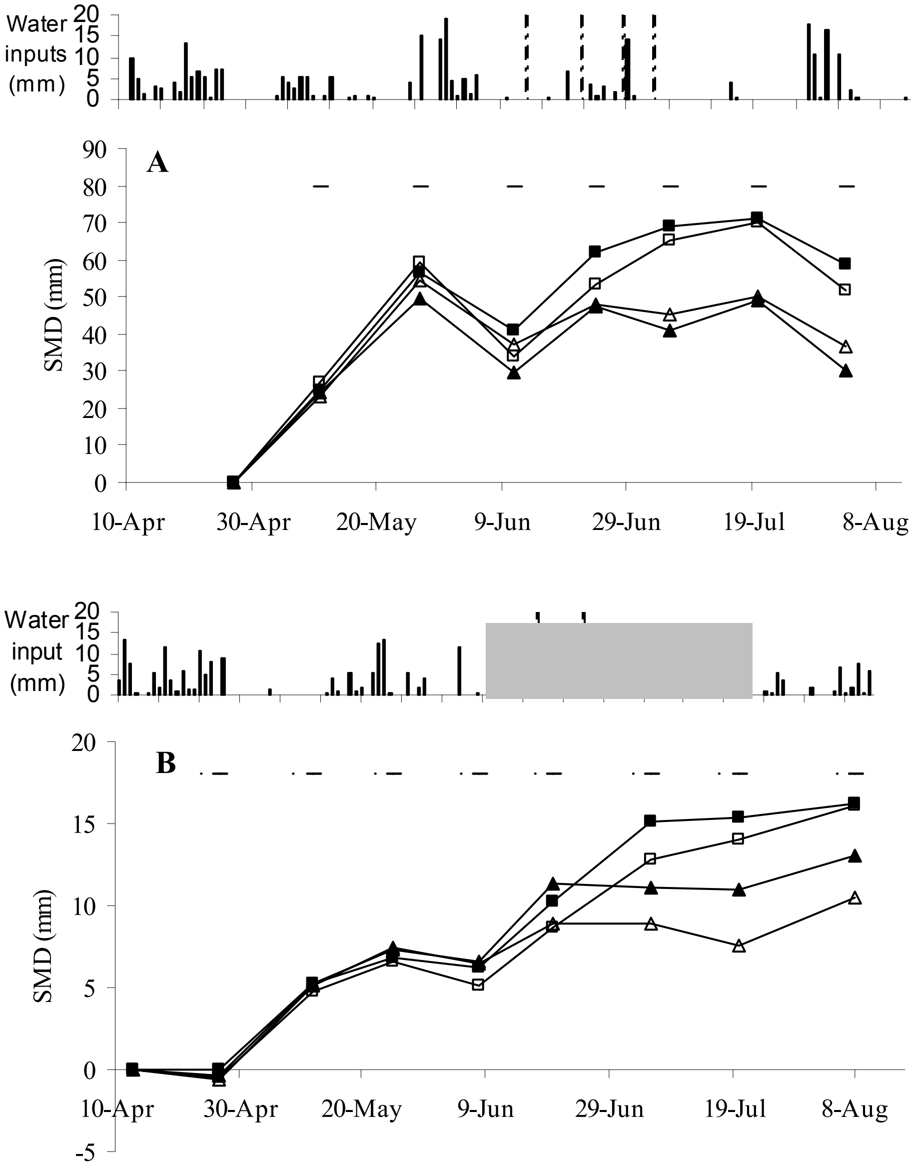

Figure 2.4. Soil moisture deficit (SMD) – GS31 to harvest in 1999 (A) and 2000 (B) in unirrigated (squares),irrigated (triangles),sub-plots without sithiofam (open symbols) or with sithiofam (closed symbols). Water inputs are rainfall (solid) or irrigation (broken lines). The shaded area indicates when a polytunnel covered the unirrigated plots. SEDs are capped error bars for comparing irrigation means and uncapped error bars for chemical means.

<u>Total water use</u>

Water use from the soil profile down to 1.2m was calculated from change in soil water content allowing for irrigation/rainfall contributions, and values were adjusted to allow for between 5-32 mm of drainage (only required in 2000).

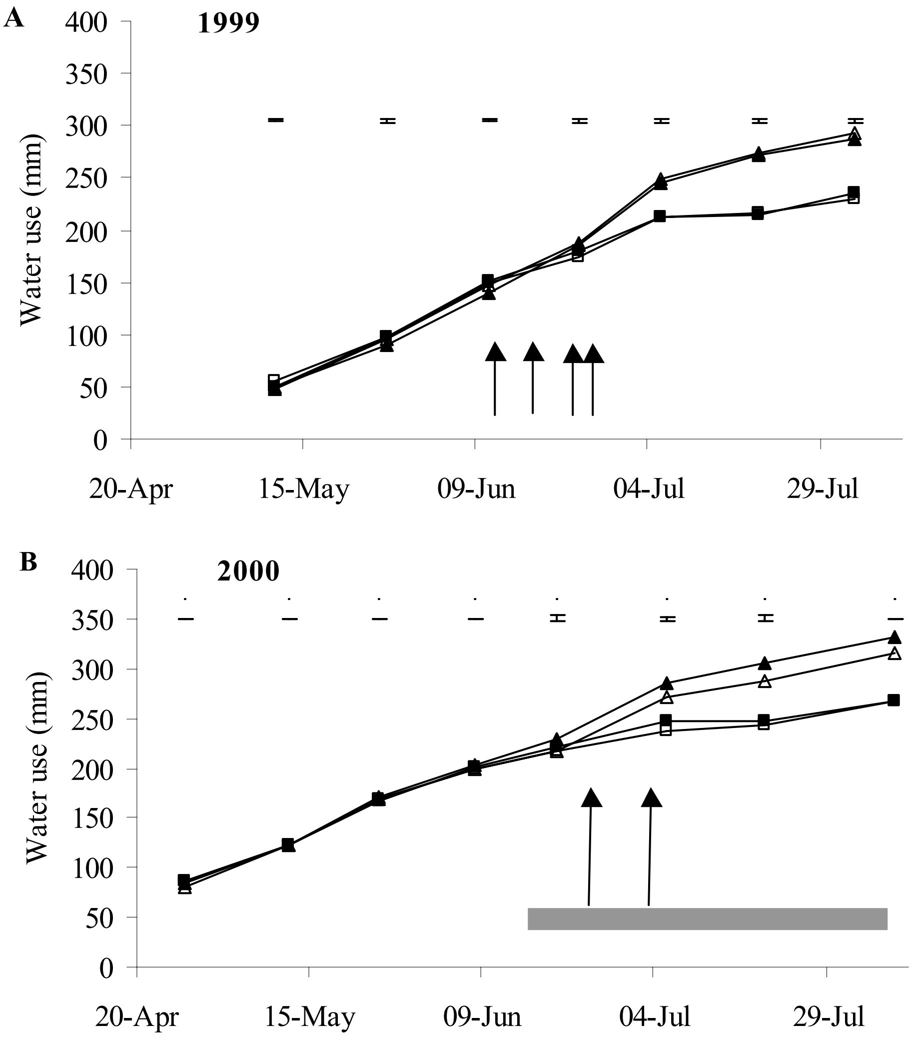

Figure 2.5. Cumulative water use, end of field capacity to harvest, in 1999 (A) and 2000 (B). For symbols see Figure 2.4 above Arrows indicate 20 mm irrigation. SEDs are capped error bars for comparing irrigation means and uncapped error bars for comparing chemical means.

In 1999 irrigation increased water use by 46 mm on 6/7/99 (*P*=0.003) and 59 mm on 20/7/99 and 8/8/99 (*P*=0.001 and <0.001 respectively)(Figure 2.5). There were no significant effects of silthiofam in either irrigation treatment, nor were there any significant interactions. In 2000 irrigation increased water use by 37 mm on 6/7/00 (*P*=0.002), 51 mm on 20/7/00 (*P*=0.001) and 55 mm on 8/8/00 (p<0.001). Sithiofam increased water use by 9 mm on 20/6/00 (*P*=0.013), 11 mm on 6/7/00 (*P*=0.014) and 10 mm on 20/7/00 (*P*=0.037). There were no significant interactions. Averaging across irrigation and chemical treatments, 54 mm more water was taken up in 2000 than in 1999 (*P*<0.001).

Relationship between effective RLD and water uptake.

Analysing data from all soil horizons within all treatment combinations in both years, an increased ERLD was associated with an increase in season-long water extraction from the profile. Within individual soil layers the effects of varying ERLD on water uptake can be examined without the confounding effects of depth.

In 1999 in the 0-20 cm layer a decrease in ERLD from 5.7 cm cm^{-3} with the chemical to 4.3 cm cm^{-3} resulted in a reduction in water uptake of 4 mm. In the 20-40 cm layer a drop in ERLD from 2.2 cm cm^{-3} to 1.1 cm cm^{-3} resulted in a reduction in water uptake of 2 mm.

These relatively small effects of ERLD on water uptake suggest that an ERLD above 1 cm cm^{-3} was sufficient to extract all available water. At lower depths, however, much smaller decreases in ERLD resulted in proportionately larger decreases in water uptake, but because absolute differences were small and error large, these were not statistically significant.
In the unirrigated treatments in 2000 patterns similar to 1999 of ERLD : water uptake relationships were observed. Decreases in ERLD in the top 40 cm of soil had little impact on water uptake, whereas proportionately larger effects of ERLD on water uptake were seen lower down the soil profile. Again however, these differences were not statistically significant. In irrigated treatments reduction in ERLD in the 0-20 cm layer from 2.6 to 2.2 cm cm-3 in the absence of the chemical reduced soil water extraction by 13 mm, and from 0.9 to 0.5 cm cm^{-3} by 7 mm in the 20-40 cm layer. Despite differences not being statistically significant it appeared that crop water uptake was more sensitive to reductions in RLD in the irrigated treatment compared to the unirrigated treatment.

Nitrogen uptake

Total nitrogen uptake for the 1999 and 2000 irrigation experiments is presented in Figure 2.6. In 1999 nitrogen uptake by the crop increased steadily from the start of stem extension and levelled off at around anthesis. Analysis of variance indicated that neither the chemical nor the irrigation treatment had any significant effect on nitrogen uptake at any point in the season. There were also no significant interactions between the two treatments.
In 2000 nitrogen uptake again increased steadily until a plateau was reached at anthesis (the third sampling date). However, N uptake was prolonged by just under three weeks, until mid-grainfill where the chemical had been applied . Analysis of variance indicated that where the chemical had been applied nitrogen uptake was significantly higher on 5/7/00 and 10/8/00, equating to mid-grainfill and preharvest respectively. Irrigation had no significant effect at any point, and nor were there any significant interactions.

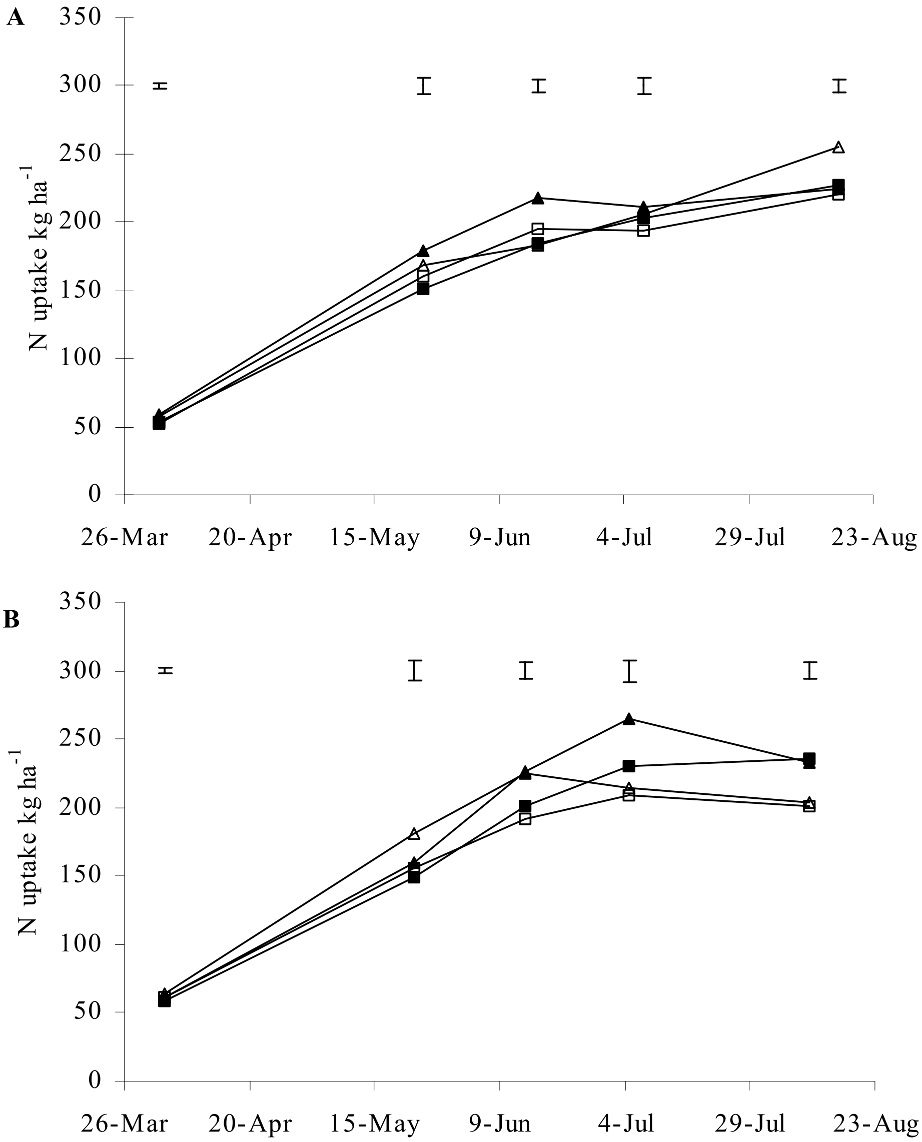

Figure 2.6. Total nitrogen uptake over the season for winter wheat with silthiofam (closed symbols or without (open symbols), irrigated (triangles) or unirrigated (squares) in the 1999 irrigation experiment (A) and the 2000 irrigation experiment (B). Error bars are SEDs for comparing chemical means at individual sampling dates.

Discussion

Effects of take-all on size of the root system

Root length density ranged from 5-10cm root cm^{-3} soil in the top 20 cm of soil, down to around 0.2 cm root cm^{-3} soil in the lowest sampled depth of 80-100 cm. These figures compare reasonably well with values obtained from previous studies (Gregory *et al.* 1978a, Welbank *et al.* 1973).

Previous studies suggested that increased levels of take-all may reduce the size of the crop's total root system (Clarkson *et al.*, 1975; Deacon and Henry, 1978; Kirkegaard *et al.*, 1994). However, these studies were either carried out under laboratory or growth room conditions, or on field sites where studies were confounded by rotational position factors. In this study, take-all levels were manipulated independently of other factors by use of silthiofam. Appendix 1 on disease progress demonstrated the effectiveness of this chemical in reducing levels of take-all.

Despite reduced levels of take-all with the chemical there was no significant effect on the RLD (i.e. sum of infected and uninfected RLD). In addition, in 2000 irrigation significantly increased take-all levels during grain filling, but there were no effects on root growth. These results do not support the hypothesis that take-all reduces the size of the root system. However, since take-all was not completely eliminated by silthiofam there cannot be complete certainty that a root system entirely free of the disease would not be larger than one with take-all.

The timing of the take-all epidemic may have affected the present results. As noted in Appendix 1, the epidemic in 1999 did not start to increase rapidly until mid-to-late April and in 2000 not until the beginning of May. The rate of root growth increases from stem extension onwards (Gregory *et al.*, 1978), which corresponded to early April in the two years of experimentation. However, root growth effectively stops after anthesis. Thus it is possible that root growth was effectively complete before take-all could have a significant effect. Thereafter, take-all can infect the existing root system, but since expansion of the root system is complete at anthesis, this would not have affected its total size.

Rainfall in the spring summer period was above the long-term mean at Rosemaund in 1999 and below it in 2000. The consistency of results across this range of rainfall suggests that effects of take-all on RLD may be relatively insensitive to fluctuations in rainfall on moisture retentive soils in the UK. Mean temperature in both seasons were between 0.5 and 1°C higher the long-term mean at Rosemaund of 9.26°C. As take-all is favoured by warm conditions it seems unlikely that this would have hindered take all progress.

Effects of take-all on root function

When take-all infects a root system one would expect to observe a reduction in root function and therefore a decrease in water uptake per unit RLD. Take-all effectively destroys the vascular system at the point it infects the root, therefore even though only a small portion of the root near the soil surface has been infected, its entire length will be rendered non-functional. With this in mind a figure for 'effective root length density' (ERLD) was calculated from RLD using data for the proportion of diseased crown roots. The relationship between ERLD and season-long water uptake was then examined and compared with that in previous works in the absence of take-all (Barraclough *et al.*, 1989; van Noordwijk, 1983).

In this study increased levels of take-all in the absence of silthiofam did not affect seasonal water use to 1.2 m soil depth or nitrogen uptake by the crop in 1999, but these were significantly decreased in 2000. The difference in treatment effects between the years could have been due to seasonal differences in RLD, effects of silthiofam on take-all, or resource availability. It appears in this case that that water and nitrogen uptake may not have been significantly affected in 1999 mainly because ERLD was generally higher in 1999, even though there was a larger difference in disease levels with and without silthiofam in 1999 than in 2000.

ERLD measurements estimate resource-capture capability. The results in 1999 support the idea that greater RLD allowed water uptake to be maintained despite infection with take-all, as the ERLD remaining was still sufficient to acquire the necessary below ground resources. Given that the difference in ERLD levels with and without silthiofam was much greater in 1999 than 2000, especially in the 0-20 cm layer, it might have been expected that water uptake would be affected more in 1999. However water uptake does not begin to be significantly affected until RLD falls close to 1 cm root cm^{-3} soil (van Noordwijk, 1983; Barraclough, Kuhlman and Weir, 1989). Averaging across treatments, ERLD was around 33% higher in 1999 than in 2000, and therefore despite the greater difference in ERLD due to take-all in this year, an effect on water and nitrogen uptake would be less likely. In 2000 ERLD values were much closer to critical values of RLD, and this could explain why treatment effects on water and nitrogen use were more marked.

Effective RLD was calculated by reducing total RLD values by fitted values of PDR at mid-grainfill. An assumption was made that all roots infected with take-all were non-functional i.e. not transporting any water to the above-ground parts. Kararah (1976) noted that some infected roots translocated water normally, despite infection with take-all, up to 16 days after infection. A second assumption was that PDR observed in the top 20 cm of soil would effect the rest of the root system down to 1m in the same proportion. This assumption would be correct if every infected root are the same length as uninfected roots, if infected roots were shorter than uninfected roots then it would only be correct to use this calculation to the depth to which the root extended. The absence of any treatment effects on total RLD would tend to indicate that the extension growth of infected roots was unaffected, and in this case the assumption is reasonably safe.

The results in this study imply that take-all infects the existing root system of a wheat crop, and by this reduces its capacity for water and nitrogen uptake. Water uptake appeared to be restricted in relation to ERLD in accordance with established thresholds for RLD observed in take-all-free crops (van Noordwijk, 1983; Barraclough, Kuhlman and Weir, 1989). This suggests that estimates of ERLD might offer a means of quantitatively predicting effects of take-all on water capture across a range of environments. The greatest effects of take-all on ERLD are seen in the top 20 cm of soil, however, the greatest impact is likely occur at greater depths where ERLD is close to or below 1 cm cm^{-3} soil, and when the crop is reliant on deeper soil water reserves due to drought. Similarly crops with a small total RLD , are likely to be more vulnerable to loss of root function due to take-all infection.

Effects of soil water availability on water uptake with take-all

The summer irrigation treatment was intended to ameliorate the effects of take-all on water uptake by providing an abundance of resource.
The difference in soil water extraction between irrigated and unirrigated treatments was greater than that between +/- silthiofam (59 mm vs <1 mm in 1999 and 55 mm vs 10 mm in 2000). However, in neither year did the response of soil water extraction to silthiofam differ in irrigated and unirrigated conditions, this reflected the lack of interaction effects between sithiofam and irrigation regime on PDR and similar non-significance for effects on ERLD.

Previous work has shown that as soil dries out, water extraction occurs predominately from deeper within the soil (Gregory, McGowen and Biscoe, 1978; Barraclough, Kuhlmann and Weir, 1989; Weir and Barraclough, 1986). Compensatory root growth may also occur in lower layers in response to drought (Barraclough, Kuhlmann and Weir, 1989; Zhang *et al.*,

1998) although Weir and Barraclough (1986) found that no such extra growth occurred in their droughted treatments.

In this study increased soil moisture did not significantly influence total RLD. It was found to significantly reduce ERLD but this was due to the increased disease pressure in the irrigated plots. It is most likely that water deficits imposed on the crop by withholding irrigation were too late to affect root growth, and insufficient in severity to stimulate uptake from lower layers. This, along with small differences in take-all levels +/- sithiofam, could explain why altering levels of take-all in the crop appeared to have little effect on water uptake below 60 cm soil depth.

General conclusions

From the results in this section the following conclusions can be made on the nature of the effects of take-all on below ground resource capture:

1) RLD is not affected by late epidemics of take-all.
2) Lack of compensatory water uptake from lower soil layers in take-all-infected crops (i.e. without silthiofam) suggests that, where infected, all of the root's length is rendered non-functional.
3) Crops with lower RLD are more likely to be affected by take-all in terms of water uptake.
4) Most of the effects of take-all induced reduction of water uptake occurs in the upper layers of the soil, where take-all is greatest.
5) In these experiments where large soil moisture deficits did not develop in unirrigated treatments, the response of crop water uptake to silthiofam was similar in irrigated and unirrigated conditions. However, if a drought occurred early enough during grain filling in unirrigated conditions it seems possible that the response to silthiofam would be greater in the unirrigated compared to the irrigated crop.
6) Water uptake appeared to be restricted at ERLD around 1 cm cm^{-3} in diseased crops. This is in accordance with established thresholds for RLD in non-take-all-infected crops. The calculation of EFRD from estimates of root growth and PDR, therefore offers a means for improving quantitative predictions of effects of take-all epidemics on water and N capture.

APPENDIX 3

THE EFFECTS OF SOWING DATE ON TAKE-ALL CONTROL WITH SILTHIOFAM.

Introduction

Delaying sowing has been shown to reduce the severity of take-all epidemics (Prew *et al*., 1986); probably by increasing the inter-crop period, during which the pathogen has to survive saprophytically. Experiments at ADAS Rosemaund prior to this study showed that a 2-3 week delay in sowing until mid-October, decreased the severity of take-all and increased yield (J.H. Spink unpublished). Delaying sowing beyond mid-October further decreased disease levels, however the shorter duration for vegetative growth reduced yield potential, overriding the benefits of reduced disease. The optimum drilling date for second to fourth wheat is a compromise between the conflicting requirements to establish canopy and reduce disease severity. This experiment was designed to establish the extent to which take-all control affects that optimum.

Method

In each of the three years a fully randomised and replicated field trial was set up at ADAS Rosemaund, Herefordshire. In the first 2 years a Split plot design was used with sowing date on main plots and seed treatments on sub-plots in four replicates. Sub-plots were 2m by 24 m in size. In the first 2 years seed were treated with either a standard treatment, or standard seed treatment + silthiofam at 25g ai/100 kg or 50g ai/100 kg seed. In the third year seed was treated with either a standard treatment, standard seed treatment + silthiofam at 25g ai/100 kg or fluqinconazole 75g a.i./100 kg + procloraz 14g a.i./100 kg seed. The design was a split-split plot with sowing date on main plots, rotational position on sub-plots and seed treatment on sub-sub-plots.

A single variety with good standing power and relatively intolerant of take-all infection was chosen cv. Equinox was used in all years. In all years 5/6 different sowing dates were used with the first sowing invariably in early October, and subsequent sowings ranged into February (1997-98) early December (1998-99) and mid-November (1999-2000). In 1997-98 the previous crop was winter wheat, in 1998-99 winter barley. In 1999-2000 the experiment was carried out on both first and third wheats with previous crops of oats or wheat.

Results:

Grain yield

The effect of seed treatment on grain yield (Figure 3.1) was significant at the 5% level in 1997/98 (P<0.001), 1998/99 (P<0.001) and 1999/00 (P<0.001). Sowing date also significantly affected yield in 1997/98 (P<0.001), 1998/99 (P<0.001) and 1999/00 (P=0.015). No significant interaction was observed between sowing date and seed treatment with silthiofam in any year. A mean yield response across sowing dates of 0.66, 0.14, and 0.57 t/ha was recorded for 1997/98, 1998/99 and 1999/00, respectively. In both the 1997/98 and 1999/00 seasons yield was reduced across all treatments from sowing in the first week of October. In the 1998/99 season, when the previous crop was Winter Barley, yields of crops not treated with silthiofam also follow this trend however the yield penalty was lower than in the other years and treated crops showed the highest yield at this first sowing. In the 1999/00 season when both silthiofam and fluqinconazole were include both gave a significant yield increase over the basic seed treatment in third wheats. Numerically the yield response to silthiofam was slightly greater although this was not statistically significant.

Grain Quality

<u>Specific weight</u>

The specific weight of grain was significantly affected by seed treatment in 1997/98 (P=0.004). In this year, plots treated with silthiofam (25g a.i.) showed a mean specific weight increase across sowing dates of 1.1 kg hl^{-1}. Sowing date had no effect on specific weight and there was no significant interaction between sowing date and seed treatment. Similarly in 1999/00 specific weight were significantly different (P<0.001). Silthiofam resulted in a mean specific weight increase across all sowing dates of 0.73 kg ha^{-1}, whereas fluquinconazole caused an increase of 0.34 kg hl^{-1}. Delayed sowing was also found to increase specific weight (P=0.03) however there was no significant interaction between sowing date and seed treatment. In the 1998/99 season a statistically significant (P=0.048) increase in specific weight was observed with delayed drilling, however there were no seed treatment differences, and no significant interaction between seed treatment and sowing date.

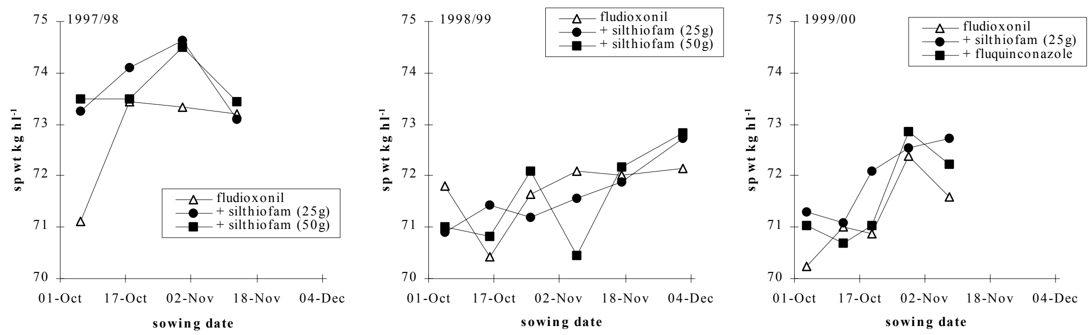

Figure 3.2. Specific weights (kg/hl) of winter wheat across a range of sowing dates with and without take-all control, in the 1997/98, 1998/99, and 1999/00 season. SED for comparing seed treatment differences = 0.300 (24 df), 0.346 (36 df) and 0.128 (60 df) in 1997/98, 1998/99 and 1999/00 respectively.

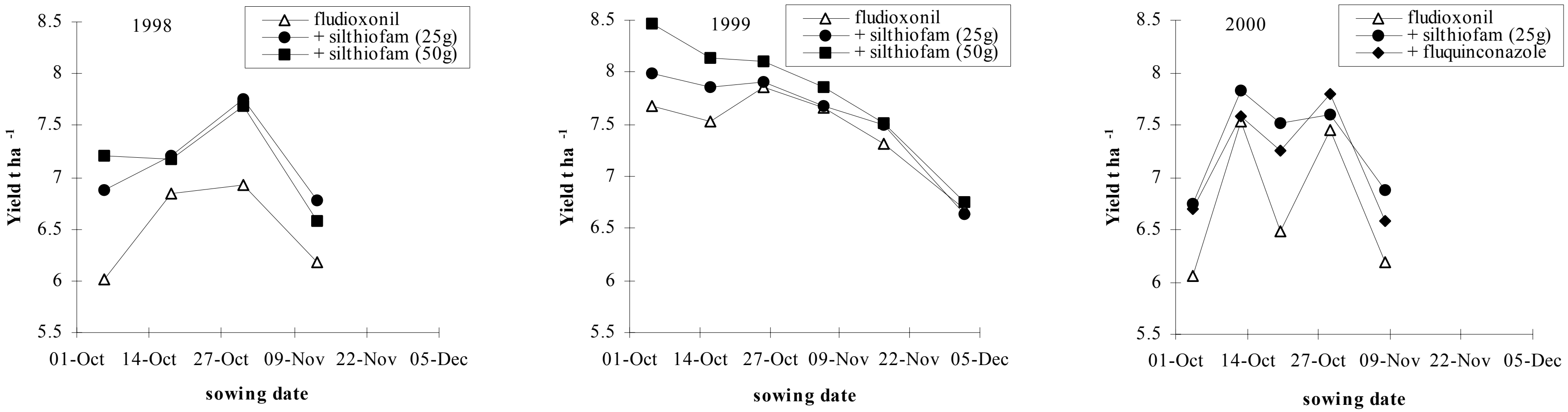

Figure 3.1. Grain yield of winter wheat across a range of sowing dates with and without take-all control, in the 1997/98, 1998/99, and 1999/00 season. SED for comparing seed treatment differences = 0.105 (24 df), 0.077 (36 df) and 0.067 (60 df) in 1997/98, 1998/99 and 1999/00 respectively.

Thousand Grain weight (TGW)

The TGW was significantly affected by seed treatment in 1997/98.(*P*=0.003). In this year plots treated with silthiofam (25 g a.i.) showed a mean TGW increase across sowing dates of 2.04g. Sowing date had no effect on TGW and there was no significant interaction between sowing date and seed treatment. No significant difference in TGW were observed in either of the other two years although there was a trend for seed treatment with silthiofam to increase TGW in 1999/00. In this third wheat situation the mean TGW improvement across sowing dates was 2.36g when silthiofam was used, and 1.47g for fluquinconazole although this was not quite significant at the 5% level (*P*=0.053).

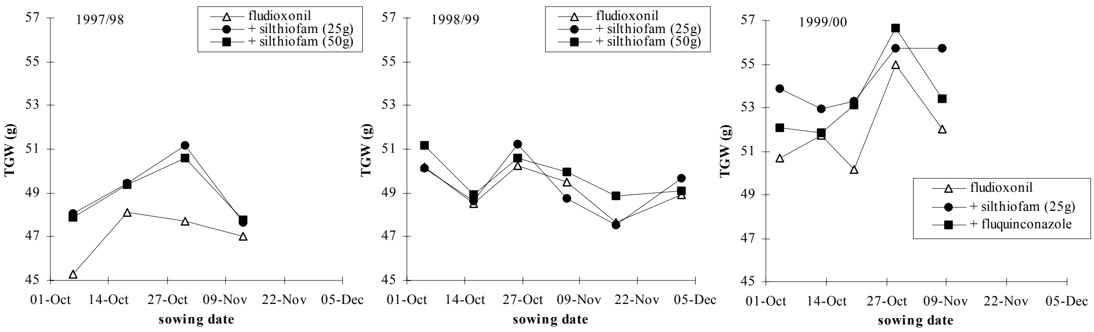

Figure 3.3. Thousand grain weights (g) of winter wheat across a range of sowing dates with and without take-all control, in the 1997/98, 1998/99, and 1999/00 season. SED for comparing seed treatment differences = 0.9 (24 df), 0.395 (36 df) and 0.515 (60 df) in 1997/98, 1998/99 and 1999/00 respectively.

Take-all development

Take-all indices (Figure 3.4) in 1997/98 were significant lower in wheat crops treated with silthiofam (*P*=0.047). Indices were also reduced by later sowing (*P*=0.001), and a significant interaction existed between sowing dates and seed treatments whereby the difference in take-all indices between treated and untreated seed was reduced with later sowing (*P*=0.047). In the 1998/99 season final take-all indices were reduced by later sowing (P=0.003), however indices did not significantly vary with seed treatment and no interaction was present. There were no significant differences in take-all incidence levels across sowing dates and seed treatments in any of the three seasons.

In 1999/00 both silthiofam and fluquinconazole significantly reduced take-all indices. Although there was a suggestion that this reduction was larger at the earlier drilling dates there was no significant effect of drilling date, and there was no interaction between drilling date and seed treatment.

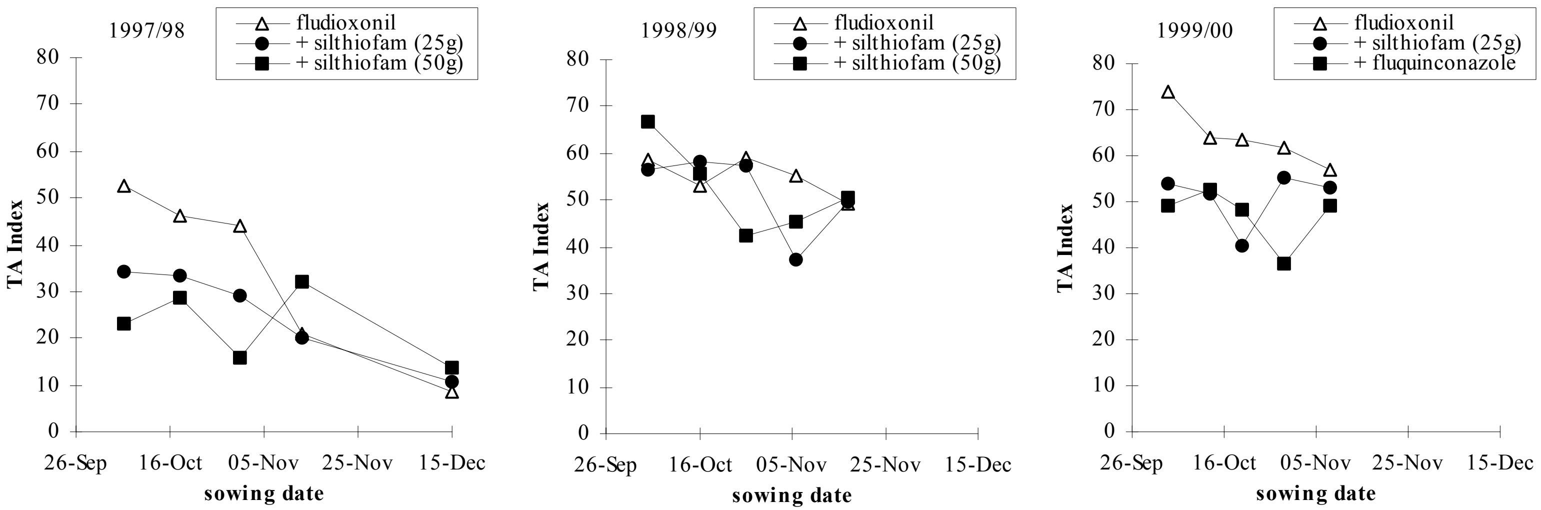

Figure 3.4 . Final Take-all indices of winter wheat grown across a range of sowing dates with and without take-all control, in the 1997/98, 1998/99, and 1999/00 season. SED for comparing seed treatment differences = 3.28 (24 df), 3.580 (36 df) and 2.029 (60 df) in 1997/98, 1998/99 and 1999/00 respectively.

Discussion

In all years grain yield was significantly enhanced by seed treatment. Although sowing date also affected yield, there was no interaction. This suggests that despite yield potentials being reduced as a result of later sowing take-all control still gave a consistent benefit enhancing yield by a similar amount at all sowing dates.

The lack of a yield penalty in early drilled plots in 1998/99 is reflected by the lack of any clear effect of seed treatment on take-all indices in this year. This could be a result of reduced disease carry over due to earlier harvesting of the previous winter barley crop. In both the 1997/98 and 1999/00 seasons the yield improvement can be explained by the reduction in take-all achieved. The convergence of TA Indices scores from the different seed treatments with later sowing does imply that silthiofam has the largest effect on take-all control at the earlier drilling dates, however, despite lower observed differences in take-all control, yield improvements following the use of silthiofam were maintained with later sowings.

Silthiofam appears to have little effect on the optimum sowing date, silthiofam shows a similar level of yield enhancement across the full range of drilling dates in two out of the three years. In the 1998-99 season however the yield advantage with the use of silthiofam appears to decline with later drilling, suggesting that later drilling may benefit less from take-all control. This could be due to a longer period in which take-all has to survive saprophytically, cooler temperatures later in the season would also reduce take-all development in the autumn, diminishing the advantage that take-all control may give compared to earlier sowings.

In terms of optimising the use of silthiofam the general conclusion from this series of experiments is that use should be targeted at the earlier drilled crops. In order to gain the maximum output from a non-first wheat the use of the seed treatment should be combined with the optimum sowing date that would be used in the absence of the seed treatment. Alternatively if drilling dates need to be bought forward for operational or other reasons the use of silthiofam will allow this to be done without suffering the severe yield penalties that would be incurred without its use.

In conclusion, the sowing date experiment was grown in a third wheat situation and showed that silthiofam significantly improved yield in all seasons with a cross season mean yield response of 0.46 t/ha. There was however no significant effect of sowing date on this response in all the three years, although there was a trend in the 1999 season for the yield response to silthiofam to decline with delays in sowing. To obtain the maximum output from and take-all risk wheat the use of silthiofam should be combined with a sowing date to minimise the severity of the disease. If for operational reasons however sowing dates must be bought forward use of the seed treatment will minimise the impact of take-all on the yield.

APPENDIX 4

THE EFFECTS OF ROTATIONAL POSITION ON TAKE-ALL CONTROL WITH SILTHIOFAM.

Introduction

Take-all builds up in the soil through successive cereal crops and usually reaches its most damaging levels in second to fourth cereal crops. Thereafter, disease severity diminishes due to a phenomenon called take-all decline (Rovira and Wildermuth, 1981). The yield of continuous wheats does not, however, return to the level obtained in first wheats. A one year break from susceptible cereal crops reduces the level of the disease, such that it has little or no impact on yield (Wiese, 1987), but also 'breaks' take-all decline.

Rotational strategies have evolved to reduce the impact of take-all, but these strategies limit grower's ability to respond flexibly to changes in market demand and the gross margins of different crops. Typical arable rotations include a non-cereal break crop after 2 or 3 cereal crops, to prevent take-all impacting on the yield of the next wheat crop. An alternative approach has been to grow wheat continuously and rely on take-all decline to minimise the effects of the disease.

The severity of take-all across a rotation depends on a dynamic balance between the pathogen and antagonistic / competitive soil micro-organisms. During a first wheat crop the level of the take-all organism in the soil is low, as it competes poorly in the absence of a susceptible host during the preceding break. Substantial disease development during subsequent crops in the rotation seems to be required before an antagonistic microflora can establish and initiate take-all decline. A more detailed review of the effects of rotational position on take-all can be found in Appendix 1.

For increased take-all levels to have significant effects on yield, resource capture has to be significantly affected. A review of the effects of take-all on resource capture can be found in Appendix 2. This section will review the effects of rotational position on the yield of winter wheat and investigate the implications of take-all control on rotational decisions

Method

This experiment was designed to test the extent to which: (i) the use of silthiofam removes rotational constraints by preventing disease in second to fourth wheat crops, and (ii) control of take-all during the high risk part of a rotation interferes with the development of take-all decline, causing long term dependence on chemical support for continuous wheat. As this is a long term experiment requiring a number of years to phase in the rotational treatments, only the first 3 years are reported here, the experiment continues under HGCA and Monsanto funding.

Three separate rotations were set up using winter wheat, winter barley and oilseed rape.. The experiment is partially phased meaning that all bar 1 year of each rotation is represented in each year. The rotations were continuous winter wheat, a 3 course oilseed wheat rotation and a 4 course rotation with oilseed rape, 2 wheats and a barley crop. In each rotation all cereals were grow either with or without silthiofam.

Table 4.1. Rotational experiment design

Rotation	1997	1998	1999	2000	2001	2002	2003
1	ww1	ww2+	ww3+	ww4+	ww5+	ww6+	ww7
1	ww1	ww2-	ww3-	ww4-	ww5-	ww6-	ww7
1	ww1	ww2+	ww3+	ww4+	osr	ww1+	ww2
1	ww1	ww2-	ww3-	ww4-	osr	ww1-	ww2
1	ww1	ww2+	ww3+	osr	ww1+	ww2+	ww3
1	ww1	ww2-	ww3-	osr	ww1-	ww2-	ww3
1	ww1	ww2+	osr	ww1+	ww2+	ww3+	ww4
1	ww1	ww2-	osr	ww1-	ww2-	ww3-	ww4
1	ww1	osr	ww1+	ww2+	ww3+	ww4+	ww5
1	ww1	osr	ww1-	ww2-	ww3-	ww4-	ww5
2	ww1	ww2+	osr	ww1+	ww2+	osr	ww1
2	ww1	ww2-	osr	ww1-	ww2-	osr	ww1
2	ww1	ww2+	ww3+	osr	ww1+	ww2+	ww3
2	ww1	ww2-	ww3-	osr	ww1-	ww2-	ww3
2	ww1	osr	ww1+	ww2+	osr	ww1+	ww2
2	ww1	osr	ww1-	ww2-	osr	ww1-	ww2
3	ww1	wb+	osr	ww1+	ww2+	wb+	ww4
3	ww1	wb-	osr	ww1-	ww2-	wb-	ww4
3	ww1	ww2+	wb+	osr	ww1+	ww2+	ww3
3	ww1	ww2-	wb-	osr	ww1-	ww2-	ww3
3	ww1	ww2+	ww3+	wb+	osr	ww1+	ww2
3	ww1	ww2-	ww3-	wb-	osr	ww1-	ww2
3	ww1	osr	ww1+	ww2+	wb+	osr	ww1
3	ww1	osr	ww1-	ww2-	wb-	osr	ww1

WW = winter wheat
WB = winter barley including some winter malting varieties
OSR = Oilseed rape
+ = treated with silthiofam

This experiment was designed as a phased experiment to run for seven years looking at a sub-set of rotational combinable crop options with or without take-all control.
Each treatment was replicated four times. Treatments were also fully randomised within blocks, with a plot size of 3.5 m by 24 m.

Results

The large number of treatments and imbalance between cropping types in the early years as treatments are phased in has rendered the data inappropriate for statistical analysis. However the graphs do indicate some interesting trends.
In both 1997-98 and 1999-2000, the 2nd wheats showed a positive response to silthiofam with a 0.58 t ha^{-1} and 0.59t ha^{-1} mean yield improvement respectively. First, third and fourth wheats and winter barley showed little or no positive effects in any of the three years(Figure 4.1).
The effect of rotational position on disease levels has been discussed in Appendix 1. Figure 1.3 indicates that in 1998 silthiofam is effective at delaying the onset of the epidemic in both winter barley and 2nd wheat. The lack of a yield effect suggests that barley avoids a yield penalty either by better disease tolerance or by avoidance through earlier ripening reducing the likelihood of experiencing drought conditions during grainfill.
Take-all progress curves for 2000 illustrate the differences between rotational position in both the level of disease seen and response to the use of silthiofam (Figure 1.4). Third wheats as

well as exhibiting much higher levels of disease also showed a positive response to the use of silthiofam. In first wheats the take-all control chemical had little or no effect on take-all levels probably due to much lower initial levels.

Discussion

This experiment has not been concluded, with the most valuable data yet to be obtained. It appears that where the disease is present in autumn, seed treatment may help prevent the early onset of the infection cycle irrespective of rotational position. The results to date indicate that only second wheats have shown a consistent yield improvement from the use of silthiofam. The years in which this experiment have been carried out have however, tended to be years of severe take-all development, with higher than usual levels of disease in second wheats. Take-all decline was also apparent third wheats, which is much earlier in a sequence of wheat crops than usual for the site. The effects of take-all control in 3rd and 4th wheats has not been fully assessed, as figure 3.5 shows both 3rd and 4th wheat crops have each only been grown in one season (the 1998-99 and the 1999-2000 seasons respectively). The continuation of this field trials should give a clearer indication of the impact of silthiofam in these rotational positions as well as the impact on take-all decline, by the removal of silthiofam treatment in rotations grown with it up to the 3rd and 4th wheat crop.
Although no positive effects on yield have been seen in barley, disease levels appear to be reduced by silthiofam, confirming that barley is generally much less affected by take-all, probably through avoidance or tolerance of the disease reducing the yield penalty.

In conclusion, although the rotational trial is not yet complete the preliminary results suggest that 2nd wheats consistently gain from the use of silthiofam. Although disease levels in barley are reduced, this has had little effect on yield possibly as a result of tolerance or the earlier ripening reducing the exposure to late season drought stress and subsequent differences in resource capture.

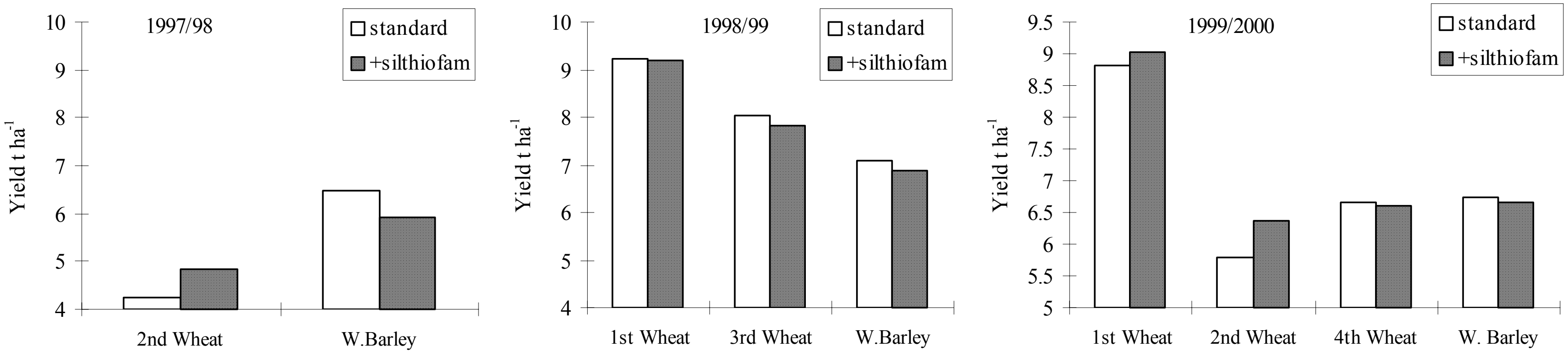

Figure 4.1. The effect of silthiofam on crops at different rotational positions.

APPENDIX 5

THE EFFECTS OF VARIETY ON TAKE-ALL CONTROL WITH SILTHIOFAM.

Introduction

Varietal types described by early date of flowering, economic tillering (low ratio of maximum to final shoot number), low canopy N requirement (ratio of shoot N uptake per m^2 to projected green area per m^2) and high levels of soluble stem reserves, have been shown to minimise yield loss due to take-all (Spink *et al.*, 1996). These varietal interactions have also been observed in NIAB RL first and second wheat trials in 1993-4 and 1994-5 (NIAB, 1995, 1996). Differences amongst varieties in the ability to amass stem reserves at around the time of flowering, which may buffer effects of premature canopy senescence with take-all, were particularly strongly correlated with good non-first wheat performance.

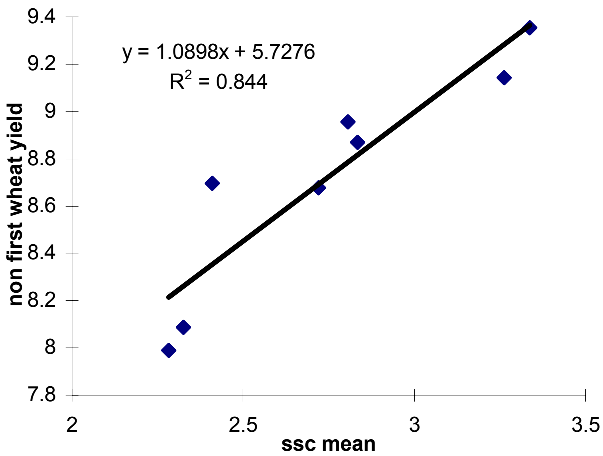

Figure 5.1 Average yield of non-first wheats at ADAS Rosemaund and ADAS Boxworth 1994-96 against level of soluble carbohydrates.

The extent to which desirable varietal traits, and hence varietal choice, are altered by take-all control was examined in field trials at ADAS Rosemaund between 1998-2000.

Method

A minimum of 10 varieties were selected in each of the three season to represent a range of tolerance to take-all, these were sown on third wheat sites, and were grown with either a standard seed treatment (Beret Gold) or with silthiofam (25g ai/kg). Varieties evaluated are shown in Table 5.1.

Table 5.1. Varieties assessed at Rosemaund for the effects of take-all and take-all control.

1997-98	1998-99	1999-2000
Abbot	Abbot	Abbot
Buster	Buster	-
-	Cockpit	Cockpit
Consort	Consort	Consort
Equinox	Equinox	Equinox
Hereward	-	-
Hunter	-	-
-	Hybrid 2	-
-	Madrigal	Madrigal
Maverick	Maverick	-
Rialto	Rialto	Rialto
Riband	Riband	Riband
-	Savannah	Savannah
Spark	Spark	Spark
-	-	Claire
-	-	Napier
-	-	Charger

The experimental design was a two way factorial with four replicates. Treatments were fully randomised within blocks and plot size was 2m by 24m.

Results

Silthiofam did not have a significant effect on establishment in any of the three years. Take-all assessments carried out on Spark showed that take-all indices in each of the three years were similar and substantially reduced were silthiofam was used (see Figure 5.2) This data as with the disease progress experiments in Appendix 1, suggests that silthiofam is delaying the onset of take-all in this experiment.

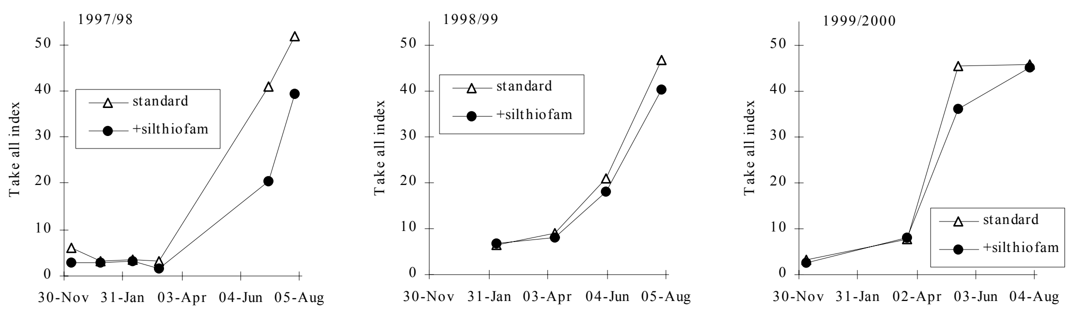

Figure 5.2 The take-all indices (TAI) for winter wheat cv. Spark grown with either silthiofam or a standard seed treatment in the 1997-98, 1998-99, 1999-2000 cropping seasons.

Take-all was assessed across all varieties in each year during early grain filling. There was no significant or consistent difference between the varieties in the level of take-all that developed (Figure 5.3).

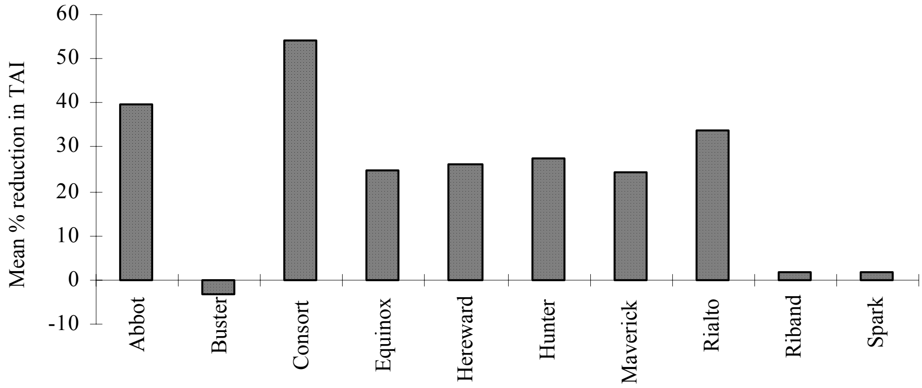

Figure 5.3. The mean percentage reduction in final TAI scores as a result of silthiofam application. SED for comparing seed treatment variety interaction means is 8.99 (*P*= not significant).

Table 5.3 The yield response ($t\ ha^{-1}$) to silthiofam application, for all varieties in all years.

	1997-98	1998-99	1999-2000
Abbot	0	0.18	0.13
Buster	0.76	0.22	-
Cockpit	-	-0.15	0.64
Consort	0.71	0.67	0.34
Equinox	1.53	0.22	0.08
Hereward	0.28	-	-
Hunter	0.21	-	-
Hybrid 2	-	0.19	-
Madrigal	-	0.39	0.12
Maverick	0.69	0.05	-
Rialto	0.63	0.17	-0.1
Riband	0.51	0.41	0.75
Savannah	-	0.31	-0.26
Spark	0.35	0.22	0.22
Claire	-	-	-0.09
Napier	-	-	0.21
Charger	-	-	0.16
Mean	0.57	0.24	0.18

In 1998 silthiofam had a positive effect on yield in all varieties except cv. Abbot. The result also indicate that in 1998 there was a significant difference in varietal response to seed treatment. Equinox, Buster , Consort and Maverick showed the strongest yield response to silthiofam, other varieties such as Abbot, Hunter and Hereward and Spark showed less of a

response. The mean percentage reduction in TAIs by silthiofam for each variety indicates that take-all level was reduced most in Consort, Abbot, and Rialto. However analysis of the data shows that there were no statistically significant differences between varieties in response to seed treatment with silthiofam. It should be noted that the low and sometimes negative responses to silthiofam shown by some varieties in the 1998-99 and 1999-2000 seasons, is in part related to the lower overall yield response.
In 1999 and 2000 although yields varied significantly between varieties, there were no statistically significant differences between varieties in response to seed treatment.

A cross season analysis of variance was conducted for the 6 varieties that were tested in all years (Abbot, Equinox, Consort, Riband Rialto, and Spark). This showed that seed treatment caused a significant mean yield improvement of 0.39 t ha^{-1}. There was however a trend for varieties to differ in there response to seed treatment (Figure 5.4). Although this was not significant at the 5% level it was at the 10% suggesting that varieties such as Abbot, Rialto and Spark may respond less to silthiofam applications than varieties such as Riband Consort and Equinox.

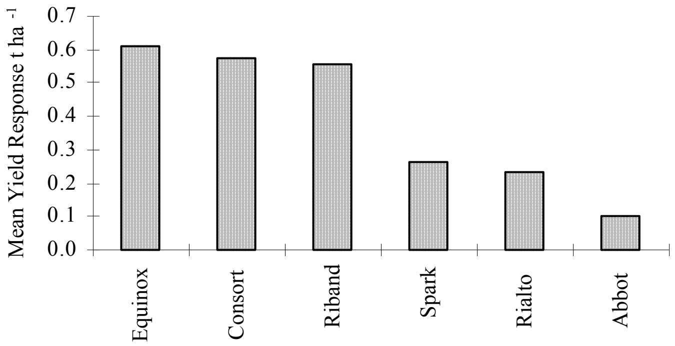

Figure 5.4 The mean yield improvement in t ha^{-1} as a result of silthiofam application across years averaged across years for varieties grown in all three seasons. SED for comparing seed treatment variety interaction means is 0.204 (*P*= 0.076).

Discussion

The effect seed treatment on yield in 1998 does not appear to correlate well with the reduction in TAI achieved (see Figures 5.3 and 5.4). This could be as a result of differences in take-all tolerance between varieties. The varietal difference in response to seed treatment in 1998 was not supported in either of the following two years when analysed separately. However, a cross year analysis of the 6 varieties present in all years showed a trend for varietal differences in response which was close to statistical significance (*P*=0.076).
Take-all indices shown in figure 5.2 suggests that silthiofam is affecting take-all by delaying the point of inflection of the disease progress curve. This is in accordance with the results on disease progress in Appendix 1.
It should be noted that the low and sometimes negative responses to silthiofam shown by some varieties in the 1998-99 and 1999-2000 seasons, is in part related to the lower overall yield response in these years. The water retentive soil at Rosemaund and its location in the West Midlands mean that it can suffer from moderate to severe take-all infections, but may not suffer the same yield penalty as free draining soils or land in drier areas of the country.

In conclusion, significant differences in the response to silthiofam were observed between varieties in the 1997-98 season, in the following 2 seasons average responses were smaller and a varietal interaction was not present. However, a cross year analysis of the varieties that were grown in every season indicates a trend for a varietal effect on the size of the response although this was not quite statistically significant (p=0.076).

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