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TAKE-ALL DISEASE OF CEREALS

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TAKE-ALL DISEASE OF CEREALS

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ABSTRACT

This review comprises eight chapters, the first six of which attempt to develop a modern concept of take-all in the UK by providing a general background and discussion of the problems that face farmers and researchers and the issues that arise from them. These first chapters contain the justification for the practical advice to farmers given in the seventh chapter and the reasons for the recommendations for future research found in the eighth chapter. A system of cross-referencing has been used to allow a more open presentation of the information and there is an extensive reference section in which the majority of entries relates to the last decade.

Take-all: background and current perceptions

Take-all is the most damaging root disease of wheat world-wide and among the most important cereal diseases in the UK. It represents a major challenge in plant pathology a) because of the losses it causes and the constraints it imposes on rotational practices, b) because, being caused by a soil-borne, root-infecting fungus, it does not respond reliably to conventionally-applied fungicides and c) because no important cultivar resistance exists. There has been much research on many fronts over the last sixty years and this has contributed to take-all becoming an important model for the study of soil-borne diseases generally. Some relatively recent research from abroad, notably on the use of bacteria as biological control agents and on particular forms of nitrogen-containing fertilizers and chloride-containing fertilizers to control take-all has been much publicized in the UK, but the optimism created has not been supported by the performance of such treatments in British farming conditions. Such geographical differences are therefore discussed and emphasized in relation to the behaviour of take-all and its response to treatments.

The geographical distribution of take-all is determined largely by climate, as is the growing of its host cereals. Its incidence and severity are determined principally by the proportion of susceptible crops in rotations and by environmental factors such as soil type and moisture content. Other farming practices such as sowing date and methods of cultivation, the nutritional status of the soil and application of fertilizers also affect the disease, but usually to a

lesser extent. Because significant take-all does not normally occur in a susceptible crop (wheat, barley, rye or triticale) which is grown after a non-susceptible crop in a rotation, it could be mostly avoided, but there are often economic reasons why such rotations are not practised. Therefore the risk of take-all imposes constraints on the husbandry practices of farmers growing sequences of cereals. The ways in which these are manifested are discussed in detail.

Some of the agronomic options open to the farmer for controlling take-all are decreasing inoculum by growing a non-susceptible crop in a rotation, minimizing the effects of take-all by growing a more tolerant cereal host than wheat, delaying sowing, or judicious use of fertilizers. Potential additions to the armoury of control measures are fungicides and biological control agents (BCAs). The most obvious chemical approach is to apply fungicides to the soil. Fungicidal compounds need appropriate physico-chemical properties to be effective in soil; whilst these are reasonably well understood, suitable compounds for use in the complex soils found in the UK are not presently available. Biological control using resident micro-organisms in the soil is already practised, knowingly or unknowingly, on many farms where soil suppressiveness is exploited either by inducing take-all decline (TAD) in long sequences of cereal crops (this usually involves a severe attack of the disease to induce the phenomenon), using fields known not to favour take-all, or inducing the build up of antagonistic *Phialophora* spp. under preceding grass crops (which delays the onset of severe take-all). On the other hand, BCAs suitable for application to control the disease in high risk situations are not available, despite much research. Bacteria, including fluorescent pseudomonads and *Bacillus* spp., have offered most promise, whilst an experimental fungus introduced at the beginning of a cereal sequence is of current interest in the UK. Problems that have to be resolved, and are at the centre of much foreign research concern, the unreliability of BCAs because of their environmental requirements, poor root colonization, lack of persistence, stability and probable regional adaptation of the organisms. There is also much ongoing research (again mostly abroad) on proposed modes of action, including antagonism, competition for nutrients, root stimulation, siderophores and various mechanisms of antibiosis. Integrated control using combinations of agronomic factors has been investigated in the UK. Whilst the importance of delayed sowing was paramount and single fungicide or fertilizer treatments were more or less effective, combinations of treatments rarely achieved better control than the best of the constituent treatments.

Control strategies are unlikely to be implemented successfully without the ability to assess risk, which depends on a fundamental understanding of the epidemiology of the disease. Modelling approaches to explain the spread of infection and rates of epidemic development are described, emphasizing spatial and temporal aspects and the importance of host development. Detailed information from long-running field experiments is a scarce and valuable resource, useful for validating models and provoking ideas. Recent developments in computer graphics have helped the visualization of such large sets of data, showing trends in disease over decades and making seasonal comparisons clearer. This approach using disease progress curves has revealed a manifestation of TAD in the latter part of the growing season, which calls into question TAD studies based on seedling work only. Much more information is still needed on disease build up and decline in relation to crop sequences and sowing dates. The ability to identify the pathogen is also fundamental to the study, and ultimately the control, of take-all. The take-all fungus, *Gaeumannomyces graminis* var. *tritici*, is one of a complex of similar root-infecting fungi, including *Phialophora* spp. Modern serological and molecular biological techniques are being used to study the taxonomic relationships among these fungi and may prove useful for accurate diagnosis of taxa and quantification of infection.

Field experiments on take-all which rely on naturally-occurring inoculum are beset by problems of unreliability because of the patchy distribution and unpredictability of the disease. Current research to overcome these problems concerns experimental design and use of artificially-produced inoculum. Artificial infestation of field soil can also be used to evaluate losses in grain yield and reductions in grain quality without many of the confounding factors relating to crop sequences and soil conditions. Such results in conjunction with survey data (which are few) help in assessing the importance of the disease. Mathematical models for yield loss can be developed from such data and analysis of disease-yield relationships emphasizes the importance of timing of infection, host growth, and factors influencing both.

Throughout this review a need to assess the importance of take-all nationally and regionally emerges. This requires monitoring of disease and measurements of yields throughout the UK over a series of contrasting seasons and should be supported by a complementary series of field experiments. Take-all has changed, presumably in response to changing farming practices and weather trends. Continued research is required to understand these changes so as to achieve a more reliable assessment of risk. Similarly, understanding the complex nature of the disease demands continued epidemiological, ecological and biological research involving more coordinated and less fragmentary effort from the relevant research groups than hitherto.

Advice to farmers

Recommendations for minimizing losses from take-all are given. In summary, these are: 1) avoid damaging take-all by using short rotations or growing continuous cereals to exploit TAD; it may be possible to achieve TAD without serious losses by using a more tolerant cereal (e.g. barley) in the year of greatest risk; 2) ensure adequate availability of nitrogen and avoid phosphate deficiency; 3) sow second, third and fourth wheats (i.e. those most at risk) later than first and other wheats; 4) ensure adequate drainage and avoid loose seed beds; 5) apply lime to prevent acid patches, preferably before a break or first cereal, and do not overlime; 6) avoid the build up of perennial grass weeds, some of which are hosts to the take-all fungus.

Research recommendations

In the following summary; topics recommended for further research are listed in four groups. In parentheses against each topic is a) the authors' assessment of its importance to achieving the objective expressed in the title of its group, b) an indication that there is an existing project (which may need funding for continuation or expansion) or that a new one is required and c) suggestions of organizations to undertake the work.

<u>Establishing the importance of take-all</u>

i.	Surveys	(high; new; ADAS, IACR)
ii.	Disease-yield relationship	(high; existing; IACR, ADAS)

iii. Diagnosis (medium; existing; IACR, Universities
new; Universities)

iv. Economic evaluation (high; new; Universities, ADAS, IACR)

<u>Improving forecasting and risk assessment</u>

i. Data storage and availability
(high; existing; IACR, Universities, ADAS)

ii. Forecasting (medium; existing; IACR)

iii. Agronomic and edaphic factors
(high; existing; IACR and ADAS)

<u>Understanding take-all biology</u>

i. Epidemiology (high; existing; IACR, Universities)

ii. Field work methodology (medium; existing; IACR, Universities)

iii. *Gaeumannomyces-Phialophora* complex
(medium; existing; IACR
new; Universities)

iv. Ecology of pathogen and antagonists
(medium; existing; ADAS and Universities)

<u>Controlling take-all</u>

i. Rotations (medium; existing; IACR and ADAS)

ii. Natural biological control phenomena
(high; existing; IACR and ADAS)

iii. Introduced BCAs (medium; existing; ADAS and Universities)

iv. Resistance - breeding (low; ?; ?)

v. Resistance - cross-protection (medium; new; IACR and/or Universities)

vi. Fungicides (low; existing; ?)

vii. Integrated control (medium; existing; IACR, ADAS)

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NOTES AND ABBREVIATIONS

Much extra background information is available in Asher & Shipton (1981) and Kollmorgen (1985).

Growth stage terminology is according to Zadoks, Chang & Konzak (1974), unless otherwise specified.

Cross references are given as numbers with or without parentheses, e.g. (see 2.) refers the reader to Chapter 2; in 4.2.1. refers the reader to Chapter 4, section 2, sub-section 1.

The following abbreviations are used:

ADAS,	Agricultural Development and Advisory Service
AFRC,	Argicultural and Food Research Council
AUDPC,	area under the DPC
BCA,	biological control agent
cfu,	colony-forming units
CSG,	Chief Scientist's Group
DPC,	disease progress curve
Gga,	*Gaeumannomyces graminis* var. *avenae*
Ggg,	*Gaeumannomyces graminis* var. *graminis*
Ggt,	*Gaeumannomyces graminis* var. *tritici*
IACR,	Institute of Arable Crops Research
RES,	Rothamsted Experimental Station
SW,	spring wheat
TAD,	take-all decline (explanation 3.4. and 5.3.)
TAR	take-all rating (Dyke & Slope, 1978)
TI	take-all index
WW,	winter wheat

CHAPTER 1. INTRODUCTION

1.1. Historical background

The name take-all was first applied to a devastating disease of cereals in Australia about 150 years ago. Lawes and Gilbert (1870), ignorant of the cause of the disease, commented from Rothamsted on Australian experiences as follows: "Take-all... appears to flourish under as wide a range of circumstances as to soil, and a much wider as to climate. ... it occurs on the more as well as the less fertile soils, and on newly broken-up as well as on exhausted land." This comment is still true and today the disease is regarded as the most damaging root disease of wheat world-wide (Heim *et al.*, 1986).

The causal agent, an ascomycete fungus, was not fully proven until the first quarter of this century, when it was known under the misapplied name, *Ophiobolus graminis*. About that time the first unequivocal reports of take-all were made in the UK, although earlier, less certain, reports do exist. Until the name *Gaeumannomyces graminis* var. *tritici* was published in 1972 there had been no valid name for the wheat take-all fungus.

In farming circles take-all has always been notorious and this reputation now owes much to the continuing lack of economic chemical controls and resistant wheat cultivars for commercial use. Yet, paradoxically, take-all has played a leading role in advancing our knowledge of diseases caused by soil-borne plant pathogens. In the UK it can be largely avoided by not growing susceptible crops consecutively, but for decades a significant proportion of UK cereals has been grown as second or subsequent cereals and has therefore been at risk from take-all. The disease is usually a problem only under these conditions in Britain, yet this is the basis for a widely promulgated, general impression of take-all as an intractable disease. Undue emphasis on certain aspects of the disease has coloured opinions and attitudes concerning the achievements of, and prospects for, take-all research and has led to the perception by some that, because take-all still exists as a problem, there has been no progress. Neither has cosmopolitan generalization in the take-all literature helped understanding of the disease as it occurs in Britain. Some of these issues and their interactions are summarized in Figure 1.

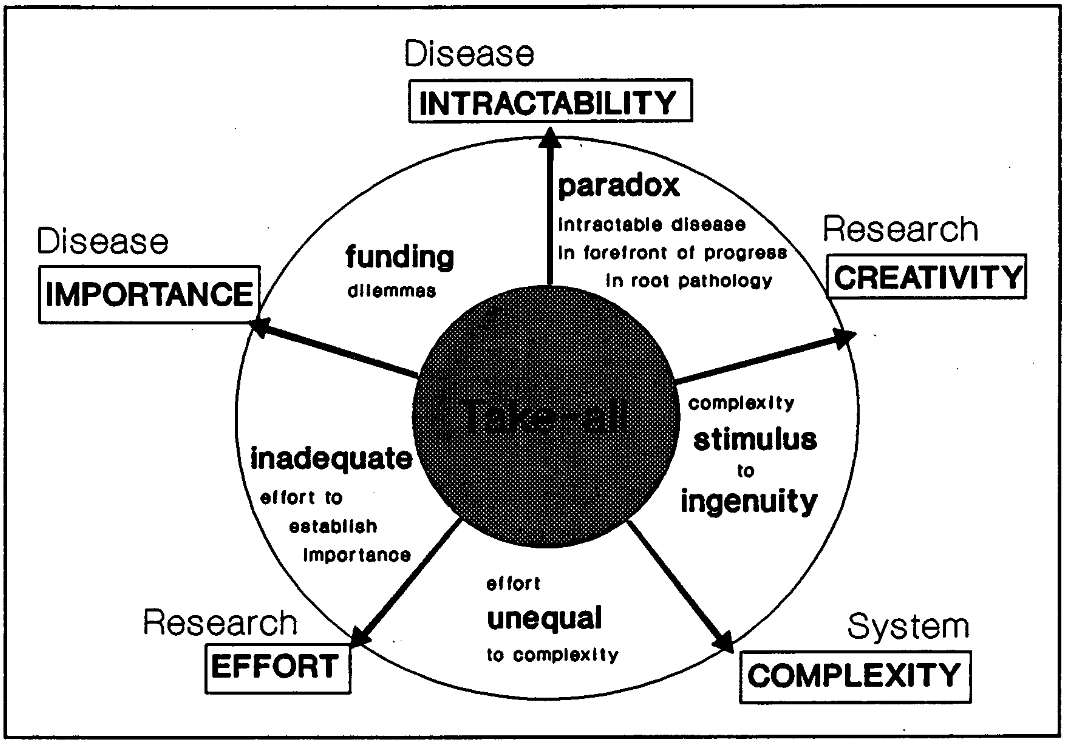

Figure 1. Five major concerns in take-all studies and how they interact.

It should be appreciated that many of the problems of take-all research are common to other soil-borne diseases that are difficult to control. The following observations were made in the context of a study of phymatotrichum root rot of cotton (Jeger & Lyda, 1986), but are mostly familiar ground for those conversant with take-all:

> Apart from avoidance of infested areas, management options are more strategic [i.e. available only before the start of the growing season] than tactical [i.e. available during the growing season], involving rotation, choice of early-maturing cultivars, organic and inorganic amendments of the soil and deep chisel ploughing. Each cultural practice has on occasion provided some level of control, but no one approach has consistently proved effective and economic. There are no resistant host varieties and no economic fungicide or fumigant treatments. The development of basipetally-translocated systemic fungicides may offer new opportunities for control. Despite the lack of control options, weather-based forecasting schemes would be beneficial in alerting

farmers to potential losses.

1.2. Take-all in the UK today

1.2.1. The disease and its control

Take-all is changing. In the 1980s patches of take-all were more apparent in crops than in the 1970s. Patches ranged from a few infected plants to extensive swathes and occurred on a variety of soils. Second and third wheat crops were particularly affected. Some first wheats suffered, which is uncommon, and even some continuous winter wheats (e.g. a ninth wheat on London clay, July, 1987) developed patches: usually a form of natural biological control, called take-all decline (TAD), suppresses the disease in wheat monocultures. Patches were seen, but less frequently in winter barley crops. In July 1990, on a trip to Gleadthorpe EHF, the Cereal Root Pathology Group was shown severe and widespread take-all on this typical sandland farm in Nottinghamshire. Particularly surprising were first wheats and some barley crops suffering badly from the disease, severely-infected rye volunteers in a winter wheat crop, and all plants in some triticale and oat crops with similar levels of slight infection. Apart from dramatically exposing the limitations of our generalisations, this experience raised many questions about geographical location, soil type, different cereal species, irrigation, sowing dates, weed control and previous cropping that remain to be answered.

The disease was most severe in the first half of the 1980s. The reasons suggested have ranged from weather changes to different rotations. (Such observations draw attention to the fact that even if it were possible to predict weather sufficiently in advance, it is still not known in any detail which seasons are likely to favour take-all.) There have been many reports of severe infections occurring in second wheats after oilseed rape (see Table 9 and associated text for a possible explanation), whereas in the 1970s second wheats were less often severely infected. The upsurge in disease has renewed interest in its control, but there seems to be relatively little research effort going into breeding and fungicides. Biological control now holds centre stage, after a change in emphasis from exploiting resident antagonistic micro-organisms to the introduction of biological control agents (BCAs), a research topic that has generated much enthusiasm and optimism, but as yet no product for farmers.

Although farmers often inquire about novel methods of control, fungicides, and resistant or tolerant cultivars, in practice they can do no more than pay attention to good husbandry, assess risks (e.g. of breaking a long run of cereals, or taking a third crop) and consider options. Advisors too, deprived of the usual plant protection arsenal, are limited to advice on a) how to avoid take-all or b) how to minimize its effects by correct husbandry, and to weighing the pros and cons of a limited number of options, such as shortening rotations or exploiting TAD by staying in continuous cereal cropping.

1.2.2. Importance

Tables 1-4, incorporating data from a variety of sources, are an attempt to establish some measures of the importance of take-all in UK farming in the absence of critical data. They should not be regarded as anything more than what currently seems a reasonable starting point for discussion. Apart from the actual losses from take-all (see 4.), there is the question of whether crops at risk from the disease need to be grown at all. At present this seems unavoidable, bearing in mind the shortfall which would otherwise occur, the decreasing world grain stocks, an increasing UK export market and an insufficient variety of economically-viable, alternative crops.

At ADAS Experimental Husbandry Farms on contrasting soils, second winter wheats yielded, on average, 3% (Bridgets, 1982-89), 6% (Boxworth, 1969-89), 13% (High Mowthorpe, 1974-89), 14% (Rosemaund, 1978-89) and 16% (Arthur Rickwood, 1974-89) less than first wheats. In the same periods third wheats yielded 8% less than first wheats at Boxworth and continuous wheats yielded 11% (Boxworth and Bridgets) and 20% (High Mowthorpe) less than first wheats. At Arthur Rickwood in 1982-85 third and subsequent wheats yielded 16% less than first wheats. In explaining these yields there are many confounding factors other than take-all. The area of first wheats was greater than that of second wheats, which exceeded that of continuous wheats. Cultivars usually did not have a uniform spread throughout the crop sequences. In later years second crops were probably sown later; Baytan seed treatment was probably used for second and continuous wheats. Continuous wheats were likely to have suffered grass weed problems. Further information for Boxworth is given in Table 9; in

Table 1. UK cereal supplies in Mt per annum (Source: MAFF)

	1986	1987	1988	1989
Cereals				
total home production	24.5	21.6	21.1	22.7
total home use	20.6	20.4	19.8	20.1
Wheat				
total home production	13.9	11.9	11.7	14.0
total home use	12.0	11.9	11.6	11.6
home-grown use				
milling	3.6	3.5	3.8	4.2
animal feed	6.0	5.5	5.1	5.3
industrial	0.4	0.5	0.6	0.5
seeds & sundries	0.6	0.6	0.6	0.6
total	10.7	10.1	10.1	10.7
total (% of production)	77	85	86	76

Table 12 there are some data on the effect of N fertilizer on the relative yields of first and subsequent wheats and in Table 17 the effects of seasonal variation are shown for Rosemaund.

In experiment CS212 at Rothamsted first wheats yielded 4.5% (1986), 12.3% (1987) and -4.4% (1988) more than subsequent wheats.

1.2.3. Points arising

Estimates of the importance of take-all are elusive because:

i. It is difficult to establish whether growing wheat in rotations where there is a high risk of take-all is absolutely necessary to meet requirements. The implications of a move away from specialization and avoiding intensive cereal production need studying. Some matters that need taking into consideration here are the limited number of acceptable break crops; the uncertainty over the future of global wheat production in what appears to be a period of unprecedented climatic change; and the possible turn round in markets should an industrial use be found either for wheat itself, or for one of the major alternative (break) crops.

ii. The implications and feasibility of replacing wheat with

Table 2. Percentages of UK wheat fields growing first or consecutive wheat crops and estimates of the percentage of the national wheat crop at risk from take-all and the percentage of the national wheat harvest coming from crops not at risk from take-all

	Years (19-)											
	76	77	78	79	80	81	82	85	86	87	88	89
Wheat crops												
First (a)	70	60	63	55	51	52	48	47	56	45	49	57
(b)	18	19	20	14	16	11	14	12	13	11	9	11
Second	23	33	27	31	31	28	28	32	20	32	31	25
Third	4	4	5	7	11	9	10	10	10	10	9	7
Fourth & subsequent	3	3	5	7	7	11	14	11	14	14	11	11
% at risk from take-all	48	59	57	59	65	59	66	65	57	66	60	54
% of harvest from crops not at risk	55	44	46	44	38	44	37	38	46	36	43	49

(a), all first wheats. (b), first wheats after a cereal other than wheat.

Notes

i. Source, 1976-88, Polley & Thomas (1990); 1989 Wheat Disease Survey for England and Wales (D.J. Yarham, pers. comm.)

ii. Crops at risk from take-all are taken here to be all wheat crops grown as second or subsequent cereals, but this is a slight overestimate because oats often behave as a non-susceptible break.

iii. The percentage of harvest from crops not at risk assumes first wheat crops after non-cereal breaks yield 15% more than other wheats.

iv. Consecutive wheat crops have a regional distribution

barley, which yields less and is still less profitable than wheat, at periods of risk are not well-understood.

Table 3. Estimated contributions to UK grain production of wheat grown after wheat or another cereal

	1986[1]			1987[2]			1988[3]		
	I	II	III	I	II	III	I	II	III
Yield of wheat as 2nd & subsequent cereals (Mt per annum)	6.1	7.9	7.5	6.5	8.0	7.9	6.0	7.0	6.7
Balance of national grain production (Mt)	18.4	16.6	17.0	15.1	13.6	13.7	12.1	11.1	11.4
Balance shortfall (note ii) (Mt)	-1.6	-3.4	-3.0	-4.9	-6.4	-6.3	-7.2	-8.9	-8.6
(%)	-8.0	-17.0	-15.0	-24.5	-32.0	-31.5	-36.0	-44.5	-43.0

Notes

i. Based on percentages of wheats not grown as a first cereals (Table 2). Column I, excluding all first wheats; column II, including wheat after a cereal; column III, as II, but corrected for greater yield of first wheats (15%)

ii. Assumes UK needs 20Mt of home-grown grain (Table 1)

iii. Could be made up by using surplus barley as animal feed?[5]

iv. Shortfall of 10%[4] suggested

v. Takes no account of value of exports[4]

vi. [1] HMSO (1989a), [2] HMSO (1989b), [3] HMSO (1990), [4] D. Yarham (pers. comm.), [5] Jim Orson, National Cereals Specialist, (pers. comm.)

iii. Take-all survey data are inadequate and usually not comparable (see Table 7). Adequate surveys would require disease data from different wheat sequences in different seasons in different locations.

iv. Estimates of loss suffer from a lack of standardization. The following measures of disease have all been used:

% plants infected

SW, RES, 0.4% loss in yield for each 1% of disease

% plants with moderate and severe take-all

% tillers infected (results probably refer to % shoots)

WW, Rosser & Chadburn (1968) 0.35% loss in yield for each 1% of disease. Feekes growth stage 10.5, N range 64-102 units, average incidence of take-all, 23.2% (incidence means moderate and severe categories only)

WW, Slope & Etheridge (1971) 0.6% loss in yield for each 1% of disease

% shoots infected

% roots infected

SW, RES, 0.44% loss of yield for each 1% of roots infected

% whiteheads

% area of prematurely-ripened shoots

SW, experiment at RES suggests relationship very dependent on soil conditions

Take-all rating (TAR) (Dyke & Slope, 1978)

WW, Gutteridge *et al.* (1987) 1.4t/ha loss per 100 TAR units (max TAR=300).

Take-all index (TI)

WW, (R.W. Clare, I. Ap Dewi and D.J. Yarham, unpublished). 1.1 t/ha loss of yield for each 10% increase in TI recorded during Nov.-Jan. A 0.56 t/ha loss of yield for each 10% increase in TI during grain filling (max TI=100).

v. Losses have varied considerably amongst years, but the characteristics of years which favour take-all are not well understood.

vi. Dates on, or growth stages at, which take-all has been estimated have varied, making comparisons of disease/yield relationships difficult.

vii. The effect of slight take-all on yields seems variable and may range from depression to stimulation.

Besides Australia and Britain take-all is a serious problem in many other cereal regions, such as the Pacific Northwest of America, other parts of Northern Europe and parts of South America. There are few cereal-growing regions from which it has not been reported. In the

Table 4. Estimates of losses in 2nd and subsequent wheats due to take-all

	1986[6]	1987[2]	1988[3]
National average yield of wheat (t/ha)	6.96	5.99	6.22
Estimated loss in crops (% of all wheat)	1	4	3
National loss (Mt)	0.139	0.476	0.351
Average price (£/t)	117	115	116
Loss (£M)	16	55	41

Notes

i. Estimated losses based on a) the only national (England and Wales) figures available, which are 0.9% for 1977, 2.6% for 1978 and 2.8% for 1979[7] and b) average loss for WW in East Midlands 1963-65 of 3.8% (Rosser & Chadburn, 1968).
Monitoring at Woburn and Rothamsted, and ADAS disease intelligence reports suggest rankings for take-all: 1988>1987>>1986. However, the *Eastern Region Crop Intelligence Report* for 22 July 1988 suggested that although disease levels were greater in 1988, patchiness (see Table 7) and yield losses were greater in 1987.
Estimates of average loss are the weakest link in this kind of exercise.

ii. £/t is mean of prices for 3 kinds of wheat (bread-making, other milling and feeding): proportions of each kind not accounted for.

iii. [6] HMSO (1988), [7] Polley & Clarkson (1980); see Table 3 for other references denoted by superscripts

Pacific Northwest it is estimated that the effective control of take-all would increase winter wheat yields by 10-50% (Heim *et al.*, 1986). Losses in Western Australia have been put at 36-40% of yield in moderate-high risk areas and 5-10% of yield overall in South Australia (Cotterill & Sivasithamparam, 1989).

Table 5. A summary of some practical concerns of farmers and environmentalists

Issues	Problems	Comments and references
Nitrate	Nitrate leaching from soil and entering water supplies	Leaching may be greater where where plants have take-all (Mielke, 1988); conflict between minimizing leaching of nitrate (Anon., undated) and take-all, e.g. sowing date for WW.
Straw disposal	1992 burning ban in UK; disposal problems become acute, particularly on heavy land	One option for farmers, is is to change the rotation and use more break crops. If a five-year rotation such as WW/beans/winter cereal/WW or WB/rape were adopted, there would be fewer second and no third wheats (Long, 1990).
Set-aside	Returning to normal cropping after land has been withdrawn from agricultural production may result in disease problems	Little or no evidence to support view that rye-grass would preserve TAD (see *Farmers Weekly*, 19 May 1989 and 2.1.)
Manganese	Many reports from overseas indicate manganese deficiencies as an important factor in take-all severity (see 2.2.)	No strong evidence to support this as a major factor in UK outbreaks (Hornby, 1985)
Couch grass	Treatment of couch-infested land with glyphosate (Roundup) associated with increased take-all in following cereals	See sections 2.3.5., 4.3.5. and Mielke (1988)
Disease as a tool	Identifying soil problems on heavy land	Take-all may highlight soils in need of management (ADAS, 1989)
Cold and frost	Plants with take-all sensitive to cold and susceptible to frost	Claimed for autumn-sown plants in Germany (Mielke, 1988)

1.3. Current research issues

The more important of these are tabulated either as issues arising out of the practice of cereal growing (Table 5), or issues arising mostly out of ongoing research (Table 6). Most of these issues are discussed

Table 6. A summary of some current research issues

Issues	Problems	Comments
Biological control	No resistant cvs or chemical controls	A popular and attractive alternative which is proving erratic and difficult to manage
Epidemiology	Not fully understood	Incomplete knowledge makes it difficult to interpret data and compare regional findings
Factors affecting take-all	Many recorded, but relative significances unclear	Dominant factors need to be identified and interactions explored
Generalizations	All too often scientists discuss take-all without regard to regional differences	There is growing evidence and experience to show that many findings are not generally applicable throughout the world
Artificial inoculum	Severe, natural infection in soil cannot be achieved to order in field work	Artificial infestation may overcome some difficulties, whilst creating others
Yield-disease relationship	Not fully understood	One reason why it is difficult to be precise about the importance of take-all
Host damage	The way in which take-all causes root dysfunction is thought to be straight-forward	This affects yield through the interaction of remaining functional root and environmental conditions
Diagnosis and identification	Traditional methods are time-consuming and laborious	Serological (e.g. ELISA) and molecular biological (e.g. DNA probes) methods are under investigation

in more detail subsequently.

Hornby (1990) drew attention to the involvement of the rhizosphere in take-all and outlined the significance of host-specific effects, physico-chemical changes, changes in the microbiota, ectotrophic growth of Ggt and fungicides in the rhizosphere.

CHAPTER 2. FACTORS AFFECTING TAKE-ALL

2.1. Rotations

Since take-all in the UK is usually a problem only where cereals are grown frequently, it can be avoided quite easily. Slope (1966) stated that losses from take-all, eyespot and cereal root eelworm could almost be prevented when the proportion of cereals was not more than 40% of the total acreage in the rotation. In Germany, Mielke (1988) recommended that susceptible cereals should not exceed 60% of the arable acreage if rotation is to control take-all.

The traditional rotations such as the Norfolk four-course - wheat, roots, barley, ley (Weston, 1944) - were well-balanced rotations which limited diseases. In the 1970s lower returns on grassland enterprises resulted in land being put into more profitable cereal production. Crops such as potatoes, sugar beet and peas are grown under contract and have limited acreages and so an alternative to growing cereals continuously was sought. Field beans provided a good break, but yields were disappointing and by the mid 1970s oilseed rape had become the preferred alternative. A three-course rotation of rape, winter wheat, winter wheat or winter barley emerged and is widely used today. The search for break crops continues; sunflowers, linseed and lupins are being evaluated and field beans, oats and rye re-evaluated.

Changes in rotations affected take-all and the intensification of cereals put more fields at risk. In the late 1970s and 1980s severe take-all was reported increasingly in second, third and fourth wheat crops. There is an impression that take-all is more severe in second wheats after rape than after other break crops. This may be because minimal cultivation (which would encourage volunteers from a previous cereal crop) used before sowing rape and the fertilizer regime used on the rape crop may favour the survival and/or increase of inoculum. Usually only slight infections occur in first wheats after oilseed rape and it may be that inoculum under first wheats after rape increases more than inoculum under wheat after other crops (see 4.1.).

A current alternative to break crops is 'set-aside', where permitted crops such as clover or rye-grass may affect take-all in subsequent cereals. Work at Rothamsted has shown that rye-grass, alone or in combination with lucerne or clover, is a better break than a ley of lucerne or clover alone. An experiment to look at diseases of winter wheat grown after a set-aside programme is already in progress at Rothamsted and take-all is also being monitored in ADAS 'set-aside' trials. There is, however, still a need to assess new and conventional break crops experimentally.

In the 1860s Lawes and Gilbert demonstrated that winter wheat could be grown continuously at Rothamsted. Since then continuous cereal growing has become a part of the agricultural scene, although it was another 100 years before the take-all decline (TAD) phenomenon was fully demonstrated. Yield losses during the peak take-all years before TAD is established constitute a major risk and may not be economically justifiable or possible for many farmers. Recent work at Rothamsted suggests that a major manifestation of TAD may occur for a short period only well into the growing season. Also, it seems that an early onset of severe take-all in consecutive cereals is linked to the soil developing TAD more quickly, thus supporting the hypothesis that the phenomenon is a consequence of take-all rather than previous cropping. When winter barley was grown as a third cereal, earlier sowing resulted in more severe take-all. In following winter barley crops, take-all decline was more evident in sequences of early-sown crops than in sequences of later-sown crops. ADAS experiments in 1986-87 on the combination of drilling dates in consecutive wheat crops revealed that the second wheat in a sequence with early drilling had about twice the percentage of roots infected in April than the second wheat in a sequence with late drilling. This was thought to reflect inoculum levels consequent upon the date of drilling the first wheat and the earliness of disease establishment consequent upon the date of drilling of the second wheat. By July 1987, however, a reversal of this relationship, with a lower take-all index for the second wheat in the early drilling sequence, suggests that TAD was already beginning to operate in that sequence. Grasses may interfere with the TAD phenomenon and this may explain patches of the disease in sites reported to be in decline (see also 4.3.5.). At Rothamsted, after two years of *Holcus lanatus*, a carrier of the take-all fungus, severe take-all developed in a subsequent first wheat and continued in the next two wheat crops.

It is assumed that a one-year break in a sequence of cereals showing

TAD will not totally destroy the decline factor(s), but it is not known what frequency of breaks would eliminate TAD.

2.2. Host resistance

Hollins *et al.* (1986) found little difference in susceptibility to take-all amongst currently available winter wheat cultivars. One report suggests that cultivars may differ in how much they aid increases in small populations of the take-all fungus (Widdowson *et al.*, 1985): at Saxmundham in Suffolk there was twice as much inoculum after cv. Avalon (bread quality) as after cv. Norman (feed quality).

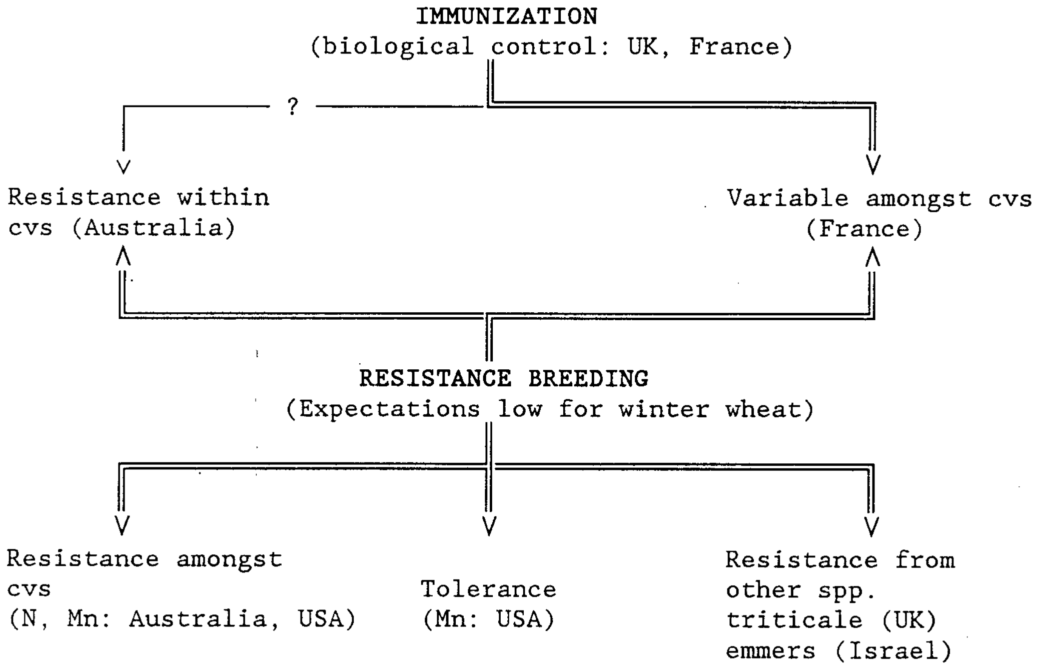

Figure 2. Some connections with the effects of minerals and locations that exist in reports of resistance to take-all (further explanation in text).

Expectations for finding useful resistance in winter wheat are small in Britain (Scott *et al.*, 1989), although resistance from other cereals is feasible (Figure 2). In the USA higher levels of Mn in tissues of take-all-tolerant wheat are correlated with smaller populations of Mn-oxidising bacteria in the rhizosphere. In Australia and the USA resistant cultivars are efficient users of Mn and in the world wheat collection there is a graded response to N of plants with severe take-all. Immunization or induced resistance by avirulent root parasites apparently varies amongst cultivars, according to French work (Lemaire *et al.*, 1982). This immunization is a biological control phenomenon originally researched in France and Britain and may have been responsible for the better plants seen in the field in Australia and selected as 'resistant lines' on the basis of fewer lesions.

Decreased cortical cell senescence in oats may be a contributory factor in their relatively low susceptibility to root invasion by *G. graminis* (Yeates & Parker, 1986). Other factors that have been considered are the production of a fungitoxic glucosidic compound, avenacin, and (for barley) disease escape by a more vigorous production of secondary roots.

The exploitation of known resistance in other cereals would require the collaboration of breeders and/or molecular biologists. An example is the possibility of transferring the ability to produce avenacin, thought to be a cause of resistance to the wheat take-all fungus, from oats to wheat, or to root-inhabiting microbes. Much research into biosynthetic pathways and creating transgenic wheat plants will be required to develop this approach. The subsequent behaviour of the oat take-all fungus, which currently has a restricted distribution in Britain, would be a major factor in the eventual use of such engineered organisms. Australian reports of oat-attacking wheat take-all fungi are also worrying in this context.

Triticale is intermediate between wheat (susceptible) and rye (resistant) in its susceptibility to take-all (Hollins *et al.*, 1986). Work at Rothamsted showed that in the presence of severe take-all, wheat, barley and triticale were all severely infected, but rye was not (but see 1.2.1.). The differences between barley and wheat in the effect of the disease may be explained by different rates of crop development. Under wheat, take-all increases rapidly between May and July and is most strongly related to yield at host growth stage 69-71. Barley reaches this stage in early June, whilst wheat is usually in boot (growth stage 45), and most of the grain filling in winter barley is completed before take-all reaches its peak. There is approximately a three-week period between barley reaching growth stage 69 and wheat reaching the same stage, during which time the take-all rating on wheat may double. This is one reason why barley has been proposed and tested as a 'bridge' over high risk periods in sequences of wheat. This hypothesis, extended to include other less susceptible cereals, is currently under test in a large, long-term field experiment at Rothamsted.

2.3. Disease-environment interactions

2.3.1. Introduction

Take-all is able to develop where the soil pH is between 5.5 and 8.5, where soils are between 5° and 30°C (although severe infection is restricted to a narrower range, given as 5-15°C (Cook, 1981) and 12-20°C (Hornby, 1981)), near to field capacity and sufficiently well-structured for aeration to be good. In many regions these conditions either occur naturally or are created artificially by liming, irrigation and cultivation, for the benefit of the crop (Cook, 1981). As a result, the disease is widely distributed throughout the temperate wheat-growing regions of the world and has been recorded on wheat at high altitude in sub-tropical or even tropical areas (Garrett, 1981).

The effect of take-all on crop yield is dependent on the balance between disease development and host growth. Certain seasonal weather patterns, as described in 2.3.2., are often associated with severe 'take-all years'. These weather patterns exert their effect by encouraging pathogen growth and/or by reducing the plants' ability to tolerate root loss. This general example of a disease/environment interaction illustrates the need to consider both the environment encountered by the pathogen and the environment encountered by the host.

Environment can therefore be taken to include below ground (soil temperature, pH, texture, structure, nutritional status and water status) and above ground (air temperature, humidity, wind speed and sunshine) conditions. Many of these factors can be controlled to some extent by man as part of normal crop husbandry and can therefore offer a method of disease management (see 4. and 7.). Underlying these man-made effects, however, are the natural variations in soil type, weather and climate that occur among different seasons, different areas of the UK and different countries.

2.3.2. Weather and seasonal effects (UK)

'Take-all years', when visible effects of take-all are widespread, represent the most severe end of a spectrum of disease intensity that is weather-dependent. As weather patterns determine, to a large extent, the national loss suffered through take-all in a given year, an understanding of the weather/disease relationship would be desirable.

In 1948 take-all was described as " ... more widespread and destructive in England than it has been at any time since the disease was first recognised here some thirty five years ago" (Moore, 1949). Moore attributed the severity of the epidemic to early planting in the autumn of 1947 (the soil being dry) whilst the fungus was still active in the stubble residues, and the following mild winter which permitted active growth of the fungus along the seminal roots. Exceptionally heavy rain in January 1948 caused much soil nitrogen to be leached and root growth was retarded. This favoured the disease, but the balance was restored a little by dry weather in early spring; which checked fungal growth along the roots and helped prevent a general occurrence of the true take-all symptom (i.e. plant death). With the onset of wet conditions, however, the fungus renewed its activity and whiteheads were prevalent well before harvest in most parts of the country.

In 1948, many crops which followed a one-year break without cereals were affected by take-all. Moore traced the origin of this to the wet summer of 1946 and the severe winter that followed. Stubbles were not ploughed under until late in the spring of 1947 or, if they were, the stubble residues remained frozen and unrotted in the ground. The cold winter was followed by a hot dry summer with very dry soils and in many districts the stubble was still unrotted when autumn sowings began. This almost nullified the effect of a one-year break.

Thus it seems that weather conditions well in advance of sowing can influence the take-all that develops subsequently. Today we are little further ahead in relating weather to take-all development - due primarily to a lack of quantitative information on take-all severity, collected on a national basis. As in Moore's time, much of our understanding is based on qualitative information or field experience.

Hornby (1978) studied the inter-relationship between seasonal weather and take-all levels, using descriptive information on take-all severity from 33 years of the *Report of Rothamsted Experimental Station*. Take-all levels were described as 'rare', 'prevalent', 'damaging' or 'severe'. After dividing the weather data into autumn, winter, spring and summer and ascribing values above or below the long term mean for temperature, rainfall and sunshine, certain trends were apparent. Both 'prevalent' and 'damaging' take-all years occurred when summers were warmer and drier than average, but 'prevalence' was associated with cold, bright springs and 'damage' with warm, dull springs. He suggested that it was a host response to weather that determined the difference between the two categories of years. The picture is confused, however, by those years when take-all was categorized as 'severe', as these were generally associated with below average temperatures and rainfall during the summer. Clearly, a finer breakdown of the cropping cycle would be desirable.

During the spring and summer, winter wheat goes through a number of developmental stages within a few weeks; as a result, short-term weather effects could be critical. For example, 1987 was generally wet during the spring and summer, but a short, hot, dry period in late May/early June was sufficient to put crops under moisture stress at a critical point in their development. Even winter wheat with modest levels of take-all had patches of disease.

Hornby & Henden (1986) reported on take-all data collected from 16 years of continuous spring barley grown on sandy loam at Woburn, Beds. Although changes in cultivar, nitrogen rates and sowing dates may have accounted for some of the changes in disease level seen, it was suggested that the epidemics recorded were weather-determined and reflected a general, long term, trend in the UK and Ireland. The dry years of 1975 and 1976 may have decreased inoculum and wholly or partially eliminated take-all decline, so that a build up of disease followed, similar to those after breaks from cereals.

The ADAS Cereal Disease Survey has collected data on take-all severity from a random sample of winter wheat fields (stratified by region to reflect the area of wheat grown). In 1977 to 1979, root systems were assessed and the percentages of plants with slight, moderate or severe take-all recorded. In 1985, 1987, 1988 and 1989 the disease was assessed on a field scale by crop growth and premature ripening, using the following scale: 0 = no take-all seen; 1 = a scatter of plants showing premature ripening; 2 = occasional small patches (less than 5m across) showing premature ripening and/or stunting affecting less than 1% of the field; 3 = many small or few large patches affecting 1% to 10% of the field; 4 = many large patches, affecting more than 10% of the field. Roots were checked to ensure that take-all was associated with the symptoms.

(Patches of prematurely-ripened plants are often referred to as 'whiteheads', an imprecise term which covers symptoms ranging from bleached, unfilled ears, often occurring singly and often of origins other than take-all (e.g. *Fusarium*) to stunted plants with small, but not bleached, ears, ripening early.)

Table 7 shows the results of the ADAS survey from 1977 to 1989 (Polley & Thomas, 1990; 1989 data unpublished).

Table 7. National take-all severity at growth stage 73-75.

	Percentage plants				Percentage fields			
	1977	1978	1979		1985	1987	1988	1989
Severity rating on roots				Patch rating in crops				
Slight	8.9	29.8	24.9	1	13.7	24.9	16.8	16.3
Moderate	1.6	8.1	7.1	2	7.0	22.8	5.4	8.5
Severe	1.3	2.4	3.1	3	4.3	13.2	6.1	5.4
				4	4.7	9.1	0.7	3.5
% crops affected*	58	91	93		29.7	70.0	29.0	33.7

*, 1977-79 data are not comparable to 1985-89 data.

There are a number of problems in interpreting these data because:

i. data were collected for a limited number of years (ten years is probably the minimum to allow valid analysis of weather effects),

ii. the two methods of assessment cannot readily be related,

iii. take-all severity was not compared with visible crop effects or yield. Nevertheless, the severity of take-all in 1987 is readily apparent (as discussed in 4.3.6., where more detailed effects of weather at a single site are also discussed).

2.3.3. Temperature and soil water potential

According to work from the USA, Ggt cannot grow in wheat tissue at a water potential below about -45 bars (4.5 MPa) and its growth rate is halved below -20 bars (2 MPa). Wheat plants in dryland conditions in the USA are reported to be commonly at -25 to -35 bars between the tillering and heading stages. Wheat at -50 bars was recorded during an exceptionally dry season in the Pacific North-West of the USA (Cook, Papendick & Griffin, 1972; Papendick & Cook, 1974). Under dry conditions therefore, growth of the pathogen within the root tissue can be halted. If this occurs at a time when further root development can still occur then the effects of the disease may be reduced. If, however, the development of the crop is too advanced for substantial root growth to occur then the additional stress of dry conditions may combine with the restricted root system to exacerbate crop loss.

The use of soil and plant tissue water potential data would appear to offer a useful means of interpreting the effects of weather on take-all development and yield loss, as it is a direct measure of water availability. Unfortunately such data are both scarce and difficult to interpret. Soil water potential varies with depth down the profile, and plant tissue water potential fluctuates diurnally and is dependent on the crop canopy, sunshine, temperature and wind speed, amongst other factors. Furthermore, calculation of the soil water potential from the more commonly recorded rainfall or soil moisture deficit data is fraught with difficulty.

Although little or no firm information is available on the relationship between soil water potential and take-all development in the UK (but see 4.3.6. and 5.6.), field experience in Eastern Region in 1989 suggests strongly that take-all development was arrested in dry soil conditions from April onwards. Many similar observations have been made in the past.

In predicting the extent of fungal growth towards host roots in soil, Heritage *et al.* (1989) took into account the effect of different soil water contents. Percentage water-filled pores (% WFP) was used as the measure of soil saturation (40% WFP corresponding to approx. -1.0 bar on the sandy soil used). In glasshouse experiments growth towards roots was not affected in the range 40 to 70% WFP, but was less at 80% WFP. This reduction in growth of the take-all fungus as the soil approached saturation was attributed to an increase in anaerobic activities (such as denitrification) and a decrease in aerobic activity due to decreased soil-gas exchange. An indirect effect of an antagonistic microflora, reduced susceptibility of roots to infection, or the production by the roots of a fungal inhibitor under diminished soil oxygen conditions may also have been involved. It was calculated that all growth of the fungus would cease at 86% WFP.

There has been a considerable amount of study on the saprophytic survival of the take-all fungus (Shipton, 1981). Temperature and water potential are important in determining microbial activity, and hence inoculum survival. Shipton (1981) cited Australian work in which survival of the take-all fungus was tested in naturally-infested soil subjected to a range of temperature and moisture regimes. Viability remained almost unaltered for 45 weeks if the soil was maintained either dry (-250 to -980 bars soil matric potential) and cool (15°C) or moist (-4.0 to -7.0 bars) and cool. Considerable viable inoculum still remained after soil was kept very dry (-980 bars or less) and hot (35°C) or wet (-0.1 to -0.2 bars) and cool. Only in hot, wet soil was the fungus eliminated within 4 weeks.

Wong (1984) in Australia studied the saprophytic survival of the take-all fungus and three avirulent fungi in soil under controlled temperature and moisture regimes. In general all of the fungi tested survived longest in cool (15°C) dry (< -10 MPa) soil, followed by the warm (30°C) dry soil. All the fungi were eliminated from warm, moist (-0.3 MPa) soil within 3 months. Survival was intermediate under cool, moist conditions, which favoured Ggg more than the other fungi tested. There were also differences in survival between different isolates of Ggg and of *Phialophora graminicola*. These findings have implications for the maintenance of TAD as well as for the selection of potential BCAs.

2.3.4. Soil type

The texture, structural stability, depth, available water capacity, pH and nutritional status of the soil can all affect take-all severity.

Nutritional status and pH are manipulated routinely by man and are discussed elsewhere in this review. Soil pH may interact with soil structural stability and an example of this is found on the chalky boulder clays of East Anglia. These are soils of a texture (clay or heavy clay loam) that would normally be prone to structural problems. However, in some series (notably the Hanslope series) the high pH maintained by the soil's natural calcium carbonate content encourages stable aggregates to form. The combination of good soil structure, allowing uninhibited rooting, and adequate available water makes take-all problems rare. In contrast, the boulder clays of the Ragdale series are often deeply decalcified and can suffer from poor structure and waterlogging in winter; take-all problems are more frequent on these soils (Catt, Gutteridge & Slope, 1986). This effect of pH in relation to soil structure contrasts with the normal situation in which high pH is associated with severe take-all.

Moore (1949), drawing on earlier work of Garrett at Rothamsted, stated that "... the fungus travels along the roots more quickly when the soil is of a light texture, alkaline, moist and warm .... Thus the light textured, alkaline soils of the Yorkshire and Lincolnshire wolds, the East Anglian ridge, the Chilterns, the chalk downs of Hampshire and Wiltshire, and the Cotswolds are the chief danger areas for take-all in this country." This statement covers several aspects of the soil environment and its effect on take-all. "Light texture" can have two effects: firstly, by tending to produce a loose seed bed which favours spread of the fungus and secondly, by having poor water availability which subjects plants with damaged root systems to water stress late in the season. Furthermore, such soils are often shallow due to erosion by water and wind, thus restricting rooting depth. The relationship of texture to "moist and warm" soil conditions is more complex. In 'normal' seasons even light soils can be assumed to be near field capacity in the early spring. Lack of water is therefore unlikely to limit growth of the pathogen until late spring or early summer. Even if its growth is halted early, sufficient root damage may already have occurred for the ensuing moisture stress on the plant to have a severe effect. Ggt is likely to be more active in light soils than in heavy soils in the spring because they warm more rapidly. The damage caused to the crop depends on the balance between the growth of the root system and the growth of the fungus. Crop growth increases as the temperature rises in the spring and the ability of increased plant growth to compensate for increased pathogen activity depends partly on the effect of temperature on partitioning between root and shoot growth. This subject has been discussed in detail by MacDuff (1989) and is complicated by inter-relationships between soil temperature and soil moisture effects and by transient and acclimatization responses by the plant. Nevertheless, there is some evidence that increasing soil temperature towards the optimum for root growth results in an increase in the shoot:root dry matter ratio. The plant may therefore be diverting more of its resources into shoot growth just at the time when root growth is required to overcome the effects of increased pathogen activity.

2.3.5. Soil type and climatic effects world-wide

The severity of take-all in different countries is determined by cropping patterns (which may be determined by take-all) as well as by climate and soil type. This section briefly summarizes experience in other countries and is based partly on a report by Yarham (1981).

In Australia the disease is reported to be worse on calcarious sands and sandy loams than on clay loams and clays. Severe attacks can also occur on acid sandy soils in Western Australia (WA) (cf. acid old pasture sites in England, 4.2.4.). Take-all is worse in Southern Australia than in the northern wheat belts: north of latitude 32°S it does not constitute a major problem to wheat growers. Severe attacks are usually associated with above-average rainfall in winter and spring and in the wetter parts of Australia (rainfall above 450mm) the prevalence of take-all and *Septoria* results in little wheat being grown. Recently, Cotterill & Sivasithamparam (1989) compared the behaviour of the take-all fungus under the Mediterranean-type climate of WA with that reported from cool, temperate regions such as the UK. It seems that inoculum of the take-all fungus is present at a greater density and is more infectious in WA than in the UK because of differences in climate, soil type and agricultural practice. It was postulated that hot dry summers promoted the survival of the fungus and that the sandy and nutritionally-poor soils favoured the disease. Because of the nutritional status of the soils, wheat is commonly rotated with pasture or legumes in order to build up soil nitrogen. Unfortunately, pasture grasses in WA are predominantly of a type which carries the take-all fungus and they effectively maintain the disease between crops. Low microbial activity in the soil may also favour survival of inoculum.

In Indiana, USA, take-all was considered to be of limited importance until the early 1970s, when the availability of cultivars resistant to the Hessian fly allowed wheat to be sown earlier in the autumn, which greatly increased take-all, such that in 1977 root diseases (primarily take-all) were estimated to have reduced the Indiana wheat crop by 30%. TAD occurs in wheat, although its effect is less apparent on light sandy soils than on silt loams or clays. Occasional, severe attacks of take-all have been recorded in first wheat crops after pasture, lucerne or, more especially, soya beans. There is a controversial report of isolates of *Ggg* from soya beans which are highly virulent to wheat. In the Pacific North-West of the USA, take-all has long been recognized as a problem in intensively-grown cereals west of the Cascade mountains. The drier areas of the Columbia basin account for over 90% of the region's wheat acreage and take-all was of little importance until the 1960s when irrigation of wheat increased dramatically. The combination of virgin (previously desert) soil, the lack of antagonists and abundant water resulted in losses of as much as 50% of yield in recently reclaimed fields. Farmers in the irrigated areas now practice rotation, or utilise TAD in continuous wheat. Where annual rainfall is 200-400mm, wheat is alternated with fallow. Take-all seldom, if ever, occurs, although brown foot rot (*Fusarium*) can cause severe damage (Yarham, 1984).

Take-all is less of a problem in the spring-sown crops of Canada than in the predominantly winter-sown crops of the mid-western states of America. It does however cause occasional losses, chiefly on the black soils of the prairie provinces.

In the late 1970s take-all began to pose serious problems for the major wheat growing states of Brazil. Wheat is sown in the autumn and harvested in the spring to be followed by soya bean as a summer crop harvested in the autumn. In general, this double cropping is repeated year after year and, combined with high soil moisture levels, temperatures of 12-20°C and heavy dressings of lime (to benefit the soya bean crop), it results in severe take-all. There is no evidence of TAD in this system, perhaps because the soya bean crops prevent the establishment of an antagonistic microflora.

Within Europe, take-all is not considered to be particularly damaging in Belgium, where wheat monoculture is rarely practised. One-year breaks normally provide effective control, except on light or acid soils where a two-year break is recommended. In contrast, take-all is found almost throughout France and in 1981 it was considered to be a major obstacle to the desired intensification of wheat production. TAD has been reported to occur in France (Lemaire & Coppenet, 1968). Experience in the Netherlands is similar to that of the reclaimed silt land of eastern England, where because of intensive sugar beet and potato production potato/wheat/sugar beet/wheat rotations are practised. Take-all problems are therefore rarely seen. Switzerland has some of the longest runs of intensive cereal cropping in the world, with some high altitude fields cropped with spring barley for over 200 years. Take-all in these fields is negligible, yet it does occur in barley grown in rotation at lower altitudes in the same area. The soil from monocropped high alpine fields has been shown to be extremely antagonistic to take-all, although this is not necessarily the usual TAD effect. Not a single example of TAD had been recorded in monocropped wheat in Switzerland.

In Germany take-all occurs on good, aerated soils (e.g. loamy sands, sandy loams and peaty soils) where wheat follows wheat (Mielke, 1988). Measures to prevent or decrease take-all are a) rotation with 'leaf' crops; b) not exceeding 60% of susceptible cereals in the arable acreage; c) one-year breaks to minimize risk; d) utilizing microbial antagonism through using green manure; e) sowing cereals after grass-clover mixtures to utilize biological control by *Phialophora*; f) controlling couch; g) using cultivars with better rooting; h) using rye in preference to wheat or barley; i) careful working of stubble from diseased crops; j) deep ploughing; k) late sowing; l) shallow sowing and lower seed rates; and m) an additional 60kg N/ha early in the year. Because of saprophytic growth of the take-all fungus on couch rhizomes following glyphosate application, the herbicide should be used in the non-cereal rotation crops. Oilseed rape is claimed to be a carrier of the take-all fungus and so cereal volunteers should be controlled after sowing rape. The most effective measures in controlling take-all in Germany are choice of site, rotation and previous cropping.

Severe attacks of take-all were common in Sweden in the 1950s and 1960s, but during most of the 1970s the disease was of minor importance. This change may have been due in part to the increased usage of nitrogen fertilizer, but the main reason seems to have been a change to warmer, drier summer weather. A return to wetter conditions in 1978 and 1979 led to a resurgence of the disease.

In South Africa, the severity of take-all is related to soil type and climate; it is most serious in areas of winter rainfall in the Cape Province and in the eastern Free State where monoculture of wheat is practised on light-textured soils. The disease has been reported to be very severe in wheat following lucerne or lupins and in rotation with soya beans or groundnuts.

Factors influencing take-all world-wide are discussed further in 5.4.3.

2.4. Recommendations

2.4.1. For take-all control

Some soils with an intrinsically high risk of take-all (e.g. peat soils) are suited to intensive vegetable and root cropping, making wheat/break/wheat/break rotations possible, whilst others (e.g. shallow sandy soils) that are marginal for wheat may support barley cropping despite the presence of take-all. Such cropping decisions which decrease risk of losses from take-all are made on financial grounds and are well established. Husbandry practices can and should be used to ameliorate the effects of take-all (see 4.).

2.4.2. For research

i. A structured national survey over a number of years is needed to provide qualitative and quantitative information about take-all. There should be supporting agronomic and weather data and the weather should be recorded during all phases of cultivation (e.g. harvest of the previous crop, sowing) and stages of crop growth (e.g. seminal root development, crown root development, cessation of root growth and grain filling).

ii. Further investigation of the relationship between water tension (in soil and plant), take-all development and root growth is needed.

CHAPTER 3. THE DISEASE PROGRESS CURVE

An epidemic is defined as a change in disease intensity in a host population over space and time (Kranz, 1974). The study of plant pathogens in populations of plants may take several forms:

i. qualitative, e.g. where do epidemics of take-all occur?,

ii. quantitative, e.g. estimating amounts of disease and changes in disease over time and/or space and

iii. analytical, e.g. description of relationships among disease, time and/or environmental and biological variables.

Such descriptions are frequently empirical, but can also be mechanistic, using a mathematical equation (the 'model') to predict disease or some component of the disease cycle.

The DPC is central to the study of plant disease epidemiology, presenting a picture of disease dynamics and a summary of the interactions among the host population, pathogen population and environment.

3.1. **Description**

DPCs may be plotted as disease intensity against a measure of time or host growth, or described in terms of a mathematical function of time. To determine whether certain aspects in the 'shape' of the DPC are significant usually requires fitting the disease progress data to a mathematical function such as a simple polynomial regression equation. Except for some controlled environment experiments (e.g. Asher, 1972; Wildermuth & Rovira, 1977) and detailed studies of the dynamics of inoculum in soil over several years (Hornby, 1975), the take-all progress curve has been somewhat neglected in the past and it received no mention in the index of Asher & Shipton's (1981) book. Recently it has received more attention in:

i. first, second and longer sequences of winter wheat at Rothamsted (Hornby & Gutteridge, 1988; Werker *et al.*, 1991),

ii. analysis of selected agronomic variables in multi-factorial experiments (Bateman, 1986; Christensen *et al.*, 1987; Werker & Gilligan, 1990) and

iii. comparison of different models to describe take-all epidemics in first and longer sequences of wheat (Brassett & Gilligan, 1989).

Models to describe DPCs range from a simple straight line relationship to a series of linked equations incorporating host growth and inoculum decay. Linear models are easily calculated by regression and are very flexible in terms of shape (Gilligan, 1985). Non-linear models require iteration to fit and are less flexible, but appeal intuitively because of biological-like properties with respect to shape and the parameter values which describe these properties such as the upper or lower asymptote. There are however very few examples where disease progress data for take-all have been fitted to either linear models or non-linear models. The cost of obtaining disease progress data for take-all and the variability in the shapes of disease progress curves may have contributed to this. Linear models may be useful in smoothing out oscillations in the data which are not real statistically and in separating out long term trends in inoculum or disease from shorter fluctuations within growing seasons (Werker *et al.*, 1990).

3.2. **Interpretation**

Whilst there is a lot of flexibility in how DPCs can be described, the models frequently reveal little of the underlying biological mechanisms responsible for the shapes of the curves. Quantitative relationships between the various components of the infection chain, such as inoculum density, inoculum decay, the rate of new primary infections and subsequent spread of the fungus, are often such that shifts in the balance may cause significant changes in shape of the DPC (Brassett & Gilligan, 1988). Jeger (1987) noted that including root growth and inoculum density as variables in a model of a monocyclic root disease often leads to a sigmoid curve, so if certain data are well described by a logistic function (non-linear model), it cannot be concluded that the disease is polycyclic, or that the intrinsic rate of disease increase is constant. Biological properties under consideration must have an experimental basis from which models may be developed and tested.

It is known that the amount of initial inoculum of the take-all fungus is important and that this is determined primarily by cropping history, the severity of disease in the previous crop and the rate of inoculum decay. It is also known that the amount of inoculum at sowing is not always correlated with the disease at harvest and that certain environmental and biological properties of the soil, such as moisture and suppressiveness, significantly influence the rate of disease progress.

Werker *et al.* (1991) ascribed the differences in shape observed amongst take-all epidemics in first, second and continuous wheats to differences in the initial inoculum densities and rates of disease spread (secondary infections). It was proposed that the primary mechanism of TAD, manifested by a reduction in disease severity between the fourth and sixth years of continuous cereal growing, was a reduction in the rate of disease spread caused by unknown biological factors (certain groups of fluorescent pseudomonads have been proposed by workers outside Britain). This decrease in the rate of secondary infection may occur relatively early in a sequence of consecutive cereals, but may be camouflaged by the presence of high inoculum densities following second and third wheats (Werker *et al.*, 1991). More detailed analysis has revealed that continuous wheats may show more disease towards the end of the growing season than do second wheats. This may be a seasonal effect where a predominance of primary infections rendered secondary infections significantly less important. The absence of TAD, therefore, is not necessarily the explanation, but this cannot be discounted. Brassett & Gilligan (1989) fitted data for the progress of take-all in first wheats and in second and subsequent wheats to:

i. a linear model (third order polynomial),

ii. standard non-linear models (the logistic and logistic with allowance for host population growth) and

iii. custom-built non-linear models (incorporating parameters for primary and secondary infection and with allowance for host-population growth and decay of inoculum).

The last group yielded a description of the data that was consistent with biological constraints and fitted the data equally as well as the polynomial.

3.3. Analysis

There are sophisticated methods available for comparing DPCs (e.g. Madden, 1986; Gilligan, 1990a), but these have rarely been applied to take-all, where separate analyses of variance for each sampling occasion have been usual. The effect of treatments on the dynamics of the disease have not therefore been subjected to statistical rigour. Werker & Gilligan (1990) used the AUDPC and the linear and quadratic contrasts (equivalent to the slope and amount of curvature below or above the line) to distinguish between categories of effects of treatments and interactions on disease progress. Later sowing typically caused an initial decrease in disease, but by harvest, after subsequent increases, the differences in disease among sowing date treatments was small or insignificant. In one year, however, the DPCs diverged, perhaps because later sowing resulted in a decrease in primary infections and high soil moisture caused a decay of inoculum, so that there was a greater dependence on existing infections for subsequent disease development.

3.4. Some practical problems

It is not easy to explain how relatively small amounts of infection in one year can give rise to severe disease in the following year. Slope *et al.* (1979) showed that soil infectivity, measured by wheat-seedling bioassay, differed after the harvest of different crop sequences and that this difference was reflected in take-all in the following crops. In first and second wheats grown after 'clean' breaks, soil infectivity increased from May to harvest and the more infective the soil in April the more rapid the increase in soil infectivity. If 20% of roots or more are infected in a soil bioassay in September, that field should be regarded as having a high risk of take-all for a following susceptible cereal. Severe take-all in winter wheat in summer may be related in some cases to the amount of autumn infection and, in general, the earlier severe take-all occurs, the greater yield losses will be.

The importance of primary and secondary inoculum in models has been emphasized, but measuring these in practice has so far proved to be impossible.

In the last 20 years large sets of disease data have been collected from long-running field experiments at Rothamsted and Woburn. These and computer graphics allowed epidemics to be pictured in ways hitherto impossible. Graphical displays provide the best summaries of data, simplify the aspect of the data by appealing to our natural ability to absorb visual images, and (hopefully) provide a global view of the information, thereby stimulating possible explanations (Greenacre, 1988). Figure 3 shows a take-all epidemic in an experimental site in terms of the interaction of cropping, season and one measure of disease. It shows a complexity that is all too often ignored. Perhaps one of the most obvious features of this representation is the fluctuation in the

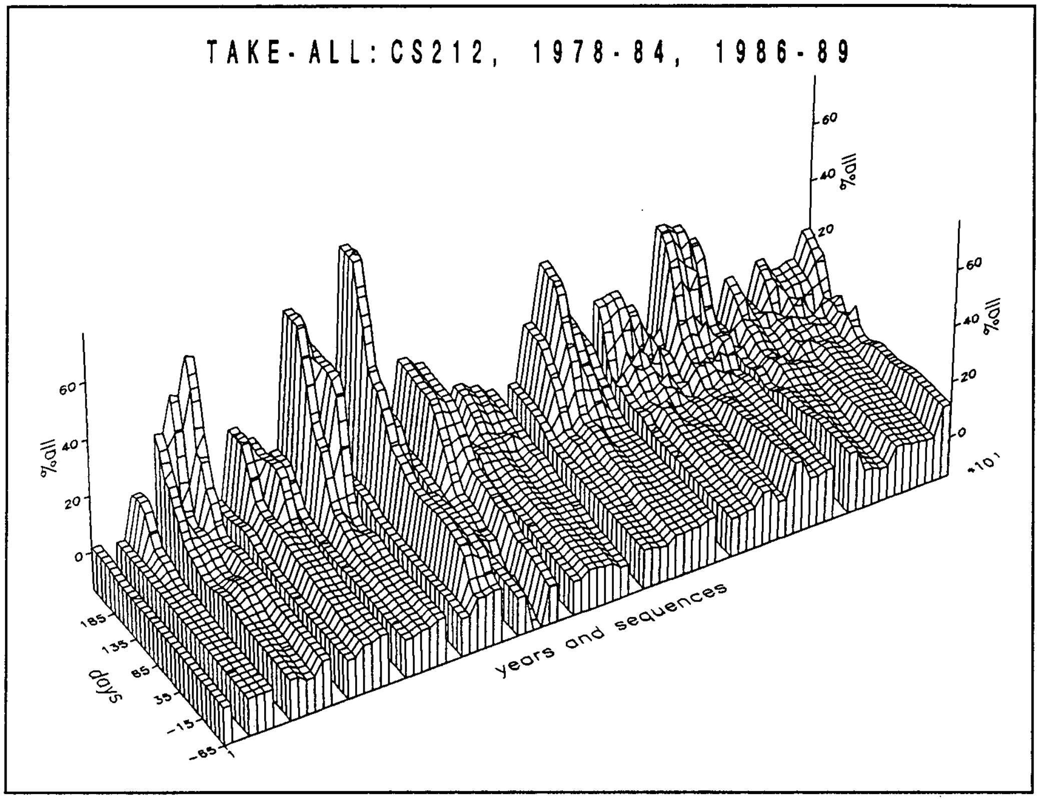

Figure 3. Take-all in CS212, a phased sequence experiment on winter wheat at Rothamsted.
%all = % total roots infected; days = number of days from 1st January (range is approximately a few weeks after emergence to a few days before harvest); years and sequences = each block represents a year and the slices represent disease progress in different wheat crops starting from the left as follows:

Year	Wheat crops compared					
1978	1st only					
1979	1st, 2nd					
1980	1st, 2nd, 3rd					
1981	1st, 2nd,	4th				
1982	1st, 2nd,		5th			
1983	1st, 2nd,			6th		
1984	1st, 2nd,				7th	
1986	1st, 2nd, 3rd,					9th
1987	1st, 2nd, 3rd,	4th				10th
1988	1st, 2nd (x3)	4th	5th			11th
1989	1st, 2nd, 3rd (x2)		5th	6th		12th

Fourth and subsequent crops assumed to be in TAD. Non-vertical lines in the walls and twisting in the tops of the slices are due to interpolation.

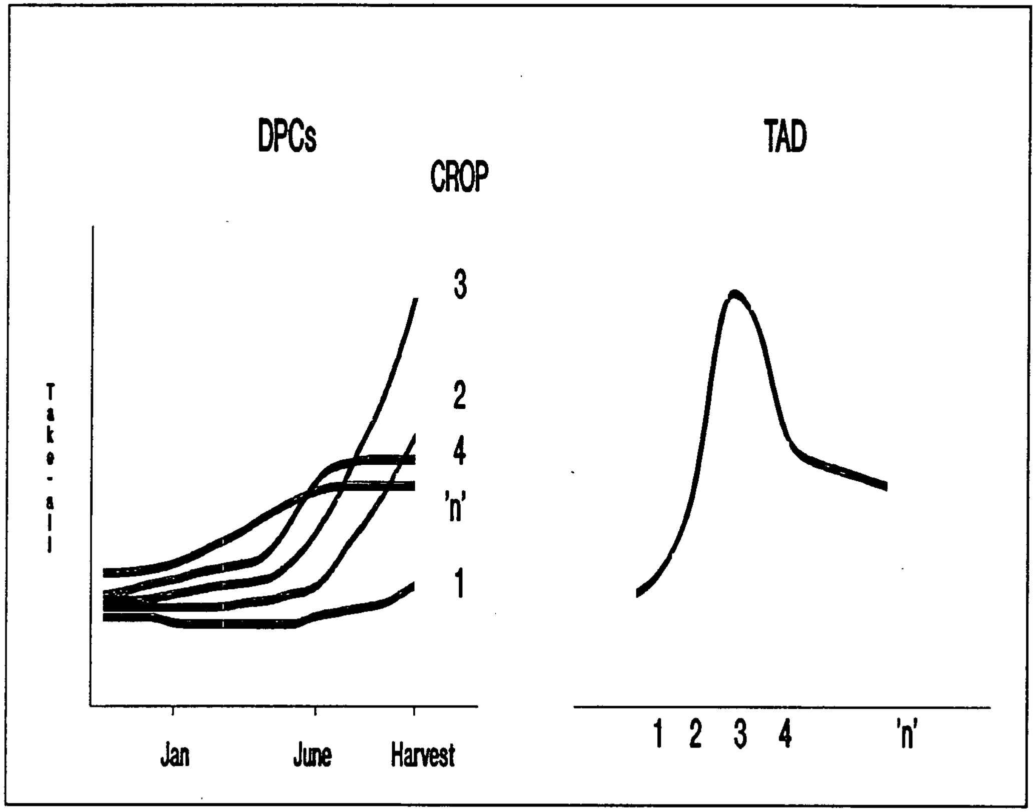

Figure 4. A sketch illustrating DPCs in successive crops. Curvatures increase until after the third crop, then disease ceases to develop at about anthesis. The classical TAD relationship amongst the sequences in July is to the right.

amount of disease through the years, which to some extent reflects what happened nationally. There was little disease generally in the mid 1970s, which led to premature relegation of take-all to an unimportant problem in cereal production. By 1983, a resurgence of the disease necessitated the reinstatement of take-all as a priority research objective in the AFRC. Such studies of the 'anatomy' of epidemics provide new insights. For example they have suggested that the rate of disease increase increases annually in the first few consecutive crops, but then, usually in a fourth crop, it is dramatically capped in June (Figure 4). This may be a major manifestation of the take-all decline phenomenon that has previously been overlooked. Normally TAD is visualized by comparing disease in different crop sequences once in the summer. Most of the research into the mechanisms of take-all decline, as well as on suppression by introduced BCAs, has concentrated on seedlings and young plants, for the obvious reasons of ease and convenience. Results from such work may not explain effects occurring later in the season.

To avoid naive and uncritical adoption of foreign ideas a global framework for take-all is needed to help in:

i. reconciling data from the high input systems of Britain with data from the low input systems in places like Western Australia;

ii. understanding the discrepancies in reported behaviour of host, pathogen and disease and

iii. assisting in unravelling complex natural phenomena such as take-all decline.

Unjustified generalization and simplification have created expectations which continue to be unfulfilled.

3.5. Conclusions and future research

No one model describes the progress of take-all in all or even the majority of situations. Exponential, monomolecular or logistic models contribute little towards explaining the biological mechanisms that generate the DPC. The long duration of a take-all epidemic, infections arising from two sources of inoculum (a dwindling reservoir of infested plant remains and an increasing reservoir of infected roots) and the sensitivity of the pathogen to changes in the soil environment (expressed as a variable infection rate) do not lend themselves to conventional modelling. However, epidemics in which some of the variables predominate may be satisfactorily described by, for example, models that incorporate components for primary and secondary infection (Brassett & Gilligan, 1988), additionally allow for inoculum decay and host growth (Brassett & Gilligan, 1989), or alternatively allow for variable infection rates as a function of seasonal factors such as temperature and moisture (Waggoner, 1986). Whilst such models increase in sophistication, validation of the individual components with experimental data lags behind, because of problems such as the infrequent attainment of an asymptotic level of disease prior to harvest. The appeal of many models lies in their equilibrium behaviour, but the stability properties of epidemics of plant pathogens in general have received little attention and it is not apparent that these should dictate the structure of models for disease progress (Gilligan, 1985). Interpretation of parameter estimates of DPCs relies on the fact that these apply throughout the sampling unit and that the associated errors amongst them are independent (C.A. Gilligan, pers. comm.). It is widely recognized that diseases are not distributed randomly throughout the crop, and indeed that the spatial distribution of disease is an integral part of the dynamics of host and pathogen in which initially small and well defined disease foci grow and coalesce (e.g. Hornby *et al.*, 1989). When dispersal of a pathogen is localized, as in soil-borne diseases, heterogeneity in inoculum density and in the disease conduciveness of the soil environment may obscure the interpretation of epidemiological mechanisms where disease progress is derived from a process of averaging.

"Despite the undisputed influence of mathematics and the computer on the thinking approach to research problems of epidemiologists, epidemiology remains an experimental discipline. Experiments provide the data bases for models and in turn help to test them. It is from this mutual interplay of theory and empirics that epidemiology derives its scientific thrust and charm." (Kranz & Rotem, 1988).

CHAPTER 4. TAKE-ALL AS A COMPONENT OF PRODUCTION CONSTRAINTS

4.1. Introduction and literature review.

It has been estimated from the results of ADAS trials and disease surveys that the leaf and stem base diseases of wheat cost growers in England and Wales about £244M p.a. (£113M in lost yields + £131M in the cost of fungicides without which yield losses would be much greater) (Cook & Polley, 1990). These figures serve to put into context the losses caused by take-all, against which we have no reliable fungicidal control and which (at a conservative estimate) is costing the nation around £40M p.a. (Table 4) as a result of its effects on the second and subsequent wheats which with some seasonal variation make up about 50% of our wheat acreage (Table 2). A single root disease, which affects only half the acreage, is thus having an effect on farm incomes a sixth as great as all the other diseases put together.

The importance of the disease extends, however, beyond this simple yield loss statement. In the absence of chemical controls, the risk of serious yield losses in intensive wheat situations imposes significant additional constraints on arable farmers relating to:

- flexibility of cropping,
- fertilizer practice (particularly nitrogen usage),
- flexibility of sowing date,
- choice of cultivation technique,
- weed control practices,
- the sensitivity of crop yield to climate.

4.1.1. Rotational practices

The effects of rotational practices on take-all have been discussed by many authors and are introduced briefly in 2.1. Their effects on inoculum and saprophytic survival of the fungus have been reviewed also (Hornby, 1981; Shipton, 1981). The disease builds up during the first few years of a sequence of susceptible cereals but if a non-host crop is introduced into the sequence inoculum levels are normally so reduced that a subsequent wheat or barley crop will escape severe infection. In three years of experiments at Rothamsted, for example, wheat after barley suffered severely from take-all and yielded, on average, 2.2 t/ha less than wheat after an oat break (Prew *et al.*, 1986). However, while intensification of cereal production aggravates take-all, growing cereals continuously can reduce its effects as a result of TAD (a topic reviewed by Rovira & Wildermuth, 1981). Crops are at highest risk from the disease between the 2nd and 4th years of a cereal sequence.

Ley farming can reduce the risks of severe losses in second wheats as the antagonist *Phialophora graminicola*, which develops on the roots of the ley grasses, suppresses the development of the pathogen in the early years of any subsequent sequence of wheat crops (Deacon, 1981; Prew, 1981).

The relative susceptibility of the major cereal crops to take-all has been reviewed by Scott (1981). The pathogen reduces the yield of wheat more than barley. Rye shows a measure of resistance to the disease and the susceptibility of triticale is intermediate between that of its two parent species. Oats are little affected by Ggt though they can be damaged by Gga which occurs in some areas of western Britain.

4.1.2. Crop nutrition

The influence of crop nutrition on take-all has been reviewed by Huber (1981) and Hornby (1985). Deficiencies in both major and minor nutrients can increase infection and exacerbate yield losses caused by the disease.

Deficiencies of P (see 5.1.1.), K and Mg have all been shown to exacerbate take-all; although of the three, P is the most important in this respect (the effect is a complex one and excessive application of K to a P deficient soil can actually increase disease levels). It is, however, the effect of nitrogen which is usually seen as being of greatest practical significance to the UK farmer.

In the absence of a host crop high nitrogen levels favour the saprophytic survival of the pathogen. An infected cereal crop, however, generally benefits from additional nitrogen as this helps the plants to cope with the root losses caused by the disease. The practical significance of this will be immediately apparent - the higher the disease risk the higher will be the cost of nitrogen fertilizer to offset its effects.

The form of nitrogen can also influence disease development. There is evidence from many countries that use of NH_4^+, rather than NO_3^-, as a source of nitrogen will decrease the severity of the disease (e.g. Cook & Reis, 1981; Macnish & Speijers,1982). Pot experiments have shown, however, that NH_4^+ can actually increase take-all (Darbyshire *et al.*, 1979). Hornby and Goring (1972) suggested that there was an optimum ratio between the NH_4^+ and NO_3^- forms of nitrogen for minimizing the effects of take-all. Christensen & Brett (1985) suggested that the use of chloride-containing fertilizers could help to maintain this optimum ratio by slowing down nitrification - i.e. the conversion of NH_4^+ to NO_3^- in the soil. [The authors have subsequently rejected this hypothesis and postulate that the chloride effect is more likely to be due to the fact that Cl^- uptake lowers the osmotic potential of the leaf tissue thereby enabling the plants to retain turgor despite root loss due to the disease (Christensen *et al.*, 1990).]

Deficiencies of certain minor nutrients can also exacerbate the disease. The effects of copper deficiency, for example, have been investigated by Wood & Robson (1984), and the effects of manganese have received considerable attention especially in America and Australia (e.g. Rovira *et al.*, 1985; Wilhelm *et al.*, 1988). In the Australian experiments foliar application of Mn had little effect on disease but application of $MnSO_4$ to the seed or, more particularly, to the soil effectively reduced take-all.

4.1.3. Early sowing

That early sowing can increase the severity of take-all has been shown in many trials (e.g. Powelson *et al.*, 1985; Clare *et al.*, 1986; Prew *et al.*, 1986; R.W. Clare, I. Ap Dewi and D.J Yarham, unpublished). The interaction between sowing date and rotational position on the yield of winter wheat has been pointed out by Yarham (1986). At Rosemaund EHF a 2-3-week delay in sowing until mid-October decreased the incidence of take-all and increased yield by 1.4 t/ha.

4.1.4. Cultivation technique

The effect of cultivation technique on take-all has been reviewed by many authors (e.g. Neate, 1988; Yarham, 1981). The effects recorded have been very variable both between and within the countries where trials have been carried out. In the Pacific North-West of the USA, for example, direct drilling has been found to increase take-all (Moore & Cook, 1984) while in Czechoslovakia it is said to decrease the severity of the disease (Novotny & Herman, 1981). In the UK, trials carried out in the 1970s (most of them on sites where straw had been burned) failed to show any strongly consistent effect of cultivation technique on take-all (Yarham & Norton, 1981) but in more recent work the disease has often been observed to be more severe after tine cultivations than after ploughing, although the effect was generally small (Jenkyn *et al.*, 1988).

The effect of a loose seedbed in aggravating the severity of take-all is well documented and was recognized by Australian farmers even before the true cause of the disease was known (Garrett, 1981).

4.1.5. Herbicides

The effects of herbicides on root diseases has been reviewed (Altman, 1985). Several authors have dealt more specifically with the effects of weeds and herbicide use on take-all and this literature has been reviewed briefly by Yarham (1981). Perennial grass weeds such as couch grass play an important role in carrying infection through non-susceptible break crops and, by competing for nitrogen and other nutrients, weeds can increase crop susceptibility to the disease. On the other hand the application of certain herbicides (e.g. mecoprop and benzoic acid derivatives) have been shown occasionally to exacerbate the effects of the disease (Nilsson, 1973a,b; Tottman & Thompson, 1978). Mekwatanakarn & Sivasithamparam (1987) found that trifluralin, diquat+paraquat, and (more particularly) glyphosate increased take-all on unsterilized, but not on sterilized, soil. They attributed this to the herbicides causing 'a shift in soil microbial populations away from those antagonistic to the pathogen'.

4.1.6. Weather

The findings of various authors on the effects of weather on take-all were summarized by Clarkson & Polley (1981) (see also 2.3.2.).

4.2. Current perception in the UK

4.2.1. Rotational policies

Farmers' rotational policies are certainly influenced by the knowledge that take-all can cause significant yield losses during those years in a cereal sequence when the disease is at its peak. Farmers with soils most conducive to the development of the disease are most likely to take this into account.

Table 8 shows recent estimates by ADAS of the costs of rotations suitable for farms on heavy land in East Anglia (K. Butterworth, ADAS, Cambridge, pers. comm.); it illustrates some of the rotational options available to the arable farmer, and highlights the fact that take-all is not the only disease that has to be considered in planning a rotation. The figures are based mainly on data produced at Boxworth EHF where crops on boulder-clay soil (Hanslope Series) seldom suffer severely from the disease (see 2.3.4.).

Table 8. Approximate gross margins for rotations based on combinable crops

	Total gross margin (£) on a 600 acre farm
1. OSR^{sc}/WW/WW/WW/WBa	118,560
2. WBe^{tf}/WW/WW/Li^{s}/WW/WW/WBa/OSR^{sc}/WW	124,450
3. Pe^{sf}/WW/WBe^{tf}/WW/WW/WBa/OSR^{sc}/WW	124,725
4. WBe^{tf}/WW/SBe^{sf}/WW/Oa/WW/WBa/OSR^{sc}/WW	124,050
5. WBe^{tf}/WW/WW/OSR^{sc}/WW/WW	126,000
6. WBe^{tf}/WW/WW/WBa/OSR^{sc}/WW	126,500
7. WBe^{tf}/WW/WW/OSR^{sc}/WW	130,200
8. WBe^{tf}/WW/OSR^{sc}/WW	133,950

WW = winter wheat, WBa = winter barley, WBe = winter beans, SBe = spring beans, OSR = oilseed rape, Oa = oats, Li = linseed.

Crops susceptible to take-all are underlined.

^{c} susceptible to club root, ^{f} susceptible to fusarium/phoma foot rot

^{s} susceptible to *Sclerotinia sclerotiorum*, ^{t} susceptible to *S. trifoliorum*.

The relative profitability of these rotations will obviously be determined by the relative prices received for their various components. To maintain his overall gross margins a farmer needs to retain such flexibility of cropping as will enable him to adjust his rotation to take account of price changes. Take-all losses greatly limit this flexibility.

Of the rotations listed, the most profitable is so short that, in the longer term, it increases the risks of *Sclerotinia sclerotiorum* and club root in the rape, and of *S. trifoliorum* and the fusarium/phoma foot rot complex in the beans. While fungicidal control of *S. sclerotiorum* is possible in rape it increases the costs of production and, once the pathogen is present in a field, it puts at risk most other non-cereal break crops. Although *S. trifoliorum* attacks few crops other than winter beans and clover, its presence limits the choice of non-cereal break crops to species susceptible to *S. sclerotiorum*. If the fusarium/phoma foot rot complex develops in beans grown in too short a rotation it limits the opportunity of introducing spring beans or, more particularly, peas into the system. Thus even when a range of break crops is available it is often judicious (to reduce disease risks on those crops) to lengthen the rotation by the introduction of short runs of wheat or barley. Take-all reduces the profitability of introducing such measures.

On light land or on the more poorly-structured heavy soils, where take-all losses in the 2nd and 3rd wheats are likely to be much greater, the relative profitability of the various cropping sequences would be markedly different from the Boxworth-based figures quoted in Table 9. On light soils in particular, winter barley is often grown as a second cereal in place of the more vulnerable wheat. On very light land such as that of the East Anglian Brecklands triticale or rye offer even safer alternatives.

Recently, an additional rotational concern has been provided by the implementation of the Government's "Set Aside" policy. If land is set aside for one year as part of an arable rotation how should it be managed during the set-aside year to reduce take-all risks in any subsequent wheat crop? How important are cereal volunteers in carrying a) the pathogen and b) the take-all decline microflora through the uncropped year? What are the effects on the disease of the currently recommended cover crops and how should they be managed?

4.2.2. Nitrogen application

That sub-optimal rates of nitrogen can exacerbate the effects of take-all is widely recognized by the farming community. However, not only does the need for extra nitrogen add to the costs of growing second and third wheats but, if supra-optimal rates are used, the risks of nitrate pollution of ground water are increased. The problem of matching nitrogen application to crop requirement is exacerbated by the disease and is further aggravated by the difficulty of predicting disease severity in any particular year (so much will depend on weather conditions after the main nitrogen dressing has been applied).

The use of ammonium, as opposed to nitrate, as a source of nitrogen has been less important in this country than in Australia and the USA. It has been argued (L. V. Vaidyanathan, ADAS, Cambridge, pers. comm.) that on many UK soils the rate of nitrification is likely to be so rapid as to convert the NH_4^+ ions to NO_3^- before they can have much effect on the disease. In practice most farmers continue to use ammonium nitrate as their nitrogen source (though in recent years increasing use has also been made of urea). Ammonium sulphate is, however, becoming more widely used because manufacturers producing it as a by-product are beginning to exploit the agricultural market and extraction of SO_2 from power station emissions is leading to an increased need for sulphur-containing fertilizers.

In 1983 a lecture given in the UK by Dr Neil Christensen of Oregon State University caused considerable interest in the use of chloride-containing fertilizers for reducing the effects of take-all, but experimental work suggests they are likely to have little effect in UK conditions. At least one fertilizer company explored the possibility of marketing a chloride-containing product. There has also been considerable interest (both farmer and commercial) in the possible use of manganese for decreasing the effects of the disease.

4.2.3. Sowing date

It is on the poorly structured heavy soils that the effect of sowing date on take-all is likely to be of particular importance. Early sowing increases the risks of severe attack, but to delay sowing if conditions in September are good is to court the risk that a wet October will so delay drilling that yields will suffer despite the lower level of disease.

The recent trend towards the autumn sowing of spring cultivars of quality wheat has led to an increasing interest in the use of late sowing to reduce take-all.

4.2.4. Cultivations

There is general recognition amongst farmers that good drainage, good soil management and the preparation of a good firm seedbed are important if take-all losses are to be minimized. In this respect the method of cultivation has generally been perceived as being of less importance than excellence of cultivation, though at least one consultant has advocated direct drilling as a means of reducing the severity of the disease.

Soil management practices include the maintenance of suitable pH levels as well as cultivations. Severe attacks of take-all are not infrequently associated with acid patches in fields and one consultant is known regularly to advocate liming for the control of the disease. Since take-all is normally considered a disease of alkaline soils (Reis *et al.*, 1983) this appears at first sight to be anomalous. 'Acid patch take-all' has, however, been reported from Australia and Sivasithamparam & Parker (1981) pointed out the great variability amongst *G. graminis* strains in respect of their tolerance of pH ranges. Careful assessment by ADAS of a sandy clay loam site ploughed out of old pasture in East Suffolk showed a negative correlation between pH and take-all (log transformation of % roots with take-all) at pH values above 5.4 (below pH 5.4 the pathogen is likely to be inhibited). The correlation accounted for 35% of the variance. It was considered likely that a third factor (e.g. soil organic matter) was influencing both pH and disease.

4.2.5. Weed control

Farmers often fail to recognize the importance of linking their weed control and rotational practices so that action for the control of couch infestations is taken before, and not after, a break crop.

4.3. **Recent UK experience**

4.3.1. The effect of take-all on flexibility of cropping

Field data accrued over a number of years at Boxworth EHF have shown a relationship between the rotational position of a winter wheat crop and the yield of grain achieved (Table 9).

The marked difference between the yields of first wheats following oilseed rape and those following winter beans is due to a number of factors including the effects of residual nitrogen (which is greater after rape than after beans) and the fact that wheat after beans will tend to be later-sown and often, therefore, will not achieve its full potential. The differences may also reflect, at least in part, the differences in root disease levels in the two rotations. Because of the different herbicide programmes used in the two crops, cereal volunteers (potential carriers of Ggt) are more likely to survive in rape than in

Table 9. Yields of wheat at Boxworth Experimental Husbandry Farm (Bowerman, 1989)

Yield as % of continuous wheat
(continuous wheat yields 7.2 t/ha)

	After oilseed rape	After winter beans
1st wheat	117	109
2nd wheat	102	107
3rd wheat	101	99

beans. Moreover, the higher levels of nitrogen under the rape will favour the saprophytic survival of the fungus which will then build up rapidly in the following early sown wheat. Taken together, these factors are likely to lead to a greater level of inoculum following a first wheat after rape than following a first wheat after beans. In neither case will the first wheat itself suffer greatly from the disease, but the higher level of inoculum present at the end of the first season will lead to greater losses in the second wheat after rape than in the second crop after beans.

Given that continuous wheat on the Boxworth farm yields 7.2 t/ha and knowing the yields, prices and marginal costs of other crops grown on the farm, one can readily estimate the costs of a range of alternative rotations for use at Boxworth. Making certain assumptions about the yield losses caused by take-all, it becomes possible to recalculate these figures to ascertain what the gross margins would be in the absence of the disease. Although it is seldom very severe at Boxworth, take-all may be responsible for more than half of the differences in yield between 1st wheats and 2nd/3rd/4th wheats. On many soils the effects of take-all will be considerably greater than this, so in the cost estimates of the 'worst case scenario' (Table 11) it is assumed to be responsible for 75% of the yield differences. The other assumptions made in calculating the gross margins are as given in Table 10.

Assuming that take-all is responsible for 75% of the decrease in yield, and that a price of £110/t is obtained for the wheat, then on a

Table 10. Yields and growing costs of arable crops at Boxworth EHF.

	Yield t/ha	Price £/t	Marginal costs			
			Seed	Fertilizer	Agro-chemicals	Contract windrow
First wheat	(see tables 8&9)		32	64	77	
Second wheat	(.. ..	..)	32	80	77	
Third wheat	(.. ..	..)	32	80	93	
Fourth wheat*	(.. ..	..)	32	80	93	
Oilseed rape	3.21	220	22	105	106	33
Winter beans	1.35	148	45	18	27	

*, assuming some recovery of yield in the 4th year due to TAD.

Table 11. Gross margins of arable rotations with and without take-all.

Rotation	Gross margin (£/HA)					
	Feed wheat @ £100/t			Milling wheat @ £110/t		
	Actual	Theoretical in absence of take-all		Actual	Theoretical in absence of take-all	
		I	II		I	II
1. R/W/B/W	537	537	537	578	578	578
2. R/W/W/B/W/W	546	556	561	598	609	615
3. R/W/W/W/B/W/W/W	538	557	567	595	616	627
4. R/W/W/W	540	570	585	597	630	646
5. R/W/W/W/W	535	565	581	595	629	645

B = winter beans, R = oilseed rape, W = winter wheat.

I and II assume take-all responsible for 50% and 75%, respectively, of the loss in yields.

200 ha farm the disease would be costing the farmer £10,000 p.a. (equivalent to the cost of employing a tractor driver).

While barley remains the most popular alternative to wheat as a second cereal on soils where take-all risks are high, trials on the peat soils of the Arthur Rickwood EHF have shown the value of triticale in this situation. Experience on the light soils of Gleadthorpe EHF has shown that rye may be cropped with impunity as a second cereal but has underlined the fact that, despite its relative resistance to the disease, it cannot be used (as oats may be used) as a break crop in a cereal sequence.

The use of rye as a catch crop to reduce nitrogen leaching in the autumn and winter is also likely to increase the risk of take-all in any subsequent cereal. Catch crops of non-susceptible species could reduce the severity of the disease in the following crop by using up in the autumn the nitrogen necessary for the saprophytic survival of the fungus and by subsequently releasing that nitrogen to the benefit of the crop during the following season (cf. Garrett & Buddin, 1947).

The as yet limited data from the current series of ADAS fallowing trials suggest that there is a link between the number of volunteers surviving through the set-aside year and the severity of the disease in the subsequent wheat crop.

4.3.2. The effect of take-all on fertilizer practice

Data obtained from trials carried out by ADAS Soil Scientists between 1981 and 1986 are in Table 12.

Note that in both the 'no N' and the 'optimal N' treatments yields fell and then recovered as the fields passed through what would have been the peak take-all years, but the yield decreases were not so great where optimal levels of nitrogen were given. The amount of N necessary to achieve optimal yields was greatest during the peak disease years.

While additional nitrogen will usually decrease the losses caused by take-all the effects of this nutrient on the disease are complex and variable. Werker & Gilligan (1990) noted that this variation was particularly high in high input crops such as those they monitored at Boxworth EHF (on the chalky boulder clays of west Cambridgeshire). In three years of these trials they found no significant effect on disease of increasing nitrogen rates from 160 to 200 kg/ha.

Table 12. Yields of successive wheat crops (as % of yields of first wheats) in relation to N fertilizer

	1st wheat	2nd wheat	3rd wheat	4th wheat	>20th wheats
No of crops in sample	57	34	8	2	2
No N applied	6.43 t/ha	70%	62%	57%	79%
Optimal N	9.40 t/ha	87%	86%	78%	90%
Optimal rate of N (kg/ha)	156	183	220	196	188

The effect of nitrogen (at least of NO_3^-) on the ability of a crop to withstand an attack of take-all may be due more to its increasing the numbers of healthy roots than to its decreasing the numbers of diseased ones, as illustrated by data from ADAS Soil Science Department trials carried out in the Eastern Region (Table 13).

Table 13. Effect of nitrogen on take-all and root production (1983)

Nitrogen rate (kg/ha)	% roots with take-all	Roots per tiller	Tillers per m^2	Roots per m^2	Healthy roots per m^2
0	43	13	461	5802	3290
120	33	15	702	10252	6910

(Data in Tables 12 and 13 from L. V. Vaidyanathan, ADAS Cambridge, pers. comm.)

Recent experiments at Rothamsted have revealed no significant effect on take-all of ammonium sulphate, ammonium chloride or urea, as compared with the commonly-used ammonium nitrate. At one of seven ADAS trial sites take-all levels were significantly higher with calcium nitrate + ammonium nitrate + urea than with ammonium nitrate + urea + 'Didin' (a nitrification inhibitor). The application of chloride-containing fertilizers had no more than slight and transitory effects on disease levels in the ADAS trials, some of which were monitored by Werker & Gilligan (1990).

Experiments at Rothamsted have shown the benefits, especially after wet winters, of applying an early dressing of nitrogen (40 kg/ha) in late February/early March (Hornby *et al.*, 1987). Werker & Gilligan (1990) found no significant effect of delaying this treatment from mid February to early April, but in some seasons the application of 40 kg N/ha in the autumn did lead to a transitory reduction in disease levels.

Severe attacks of take-all associated with phosphate deficiency occur often in farm practice (see also 4.1.2. and 5.1.1.).

Limited experimentation in the UK has failed to find a close link between manganese and take-all (cf. Table 25 and associated text).

4.3.3. The effects of take-all on flexibility of sowing date

Because the autumn labour peak, especially on an arable farm on heavy land, can be very high; it is obviously of great importance to sow autumn crops before the weather breaks. Many farmers like to sow as much as possible of their cereal acreage in September. Whilst such early sowing can be an advantage in first and long term wheats, it can have a negative effect in the peak take-all years (Table 14) and result in losses (Table 15).

At the Arthur Rickwood Experimental Husbandry Farm early sowing of first wheats appeared to increase the risk of take-all in the following wheat crop. At Rosemaund EHF early sowing of second wheats tended to decrease the severity of take-all in third wheats, especially when these also were sown early. Early sowing of a succession of wheat crops appears to favour the early development of TAD.

4.3.4. Take-all as a constraint in cultivation practice.

Quality of cultivation. Wheat in the first year after a break will often produce a good crop, despite faulty in husbandry. In the second year, however, with take-all destroying part of its root system, a much higher standard of soil management is required to produce a satisfactory yield.

Table 14. Effects on wheat yields of sowing in September compared with sowing in the first half of October in East Anglia

Yields in t/ha
(number of crops in the sample)

	1st wheats	2nd wheats	3rd wheats	4th wheats
September-sown	7.64 (108)	7.07 (83)	6.96 (42)	7.33 (94)
October-sown	7.44 (103)	7.32 (115)	7.09 (81)	7.17 (140)

(data from Cousins, cited by Yarham, 1986)

Table 15. Effect of sowing date on the severity of take-all and the yield of infected wheat at Rosemaund EHF (R.W. Clare, I. Ap Dewi and D.J. Yarham, unpublished)

	Take-all index				Grain yield t/ha	
	November/January		Harvest			
Sowing date:-	Sep	Oct	Sep	Oct	Sep	Oct
Second wheats						
1983	70	22	93	72	2.07	5.05
1984	19	1	22	17	10.38	10.51
Third wheats						
1983	33	20	77	53	8.08	8.57
1984	18	5	93	59	7.35	9.41

Figure 5 is an aerial photograph, taken in 1987, of a field on the

Essex boulder clays. For some years the farmer had neglected the drainage of the field and the mole drain channels had become blocked. A first wheat crop in 1986 had appeared satisfactory but, as the photograph shows, the second wheat performed very badly except in the immediate vicinity of the underlying tile drains (good crop appears dark on the photograph). Examination of the root systems showed them to be severely infected with take-all.

Figure 6 shows the result of poor husbandry prior to an outbreak of take-all. Two years before the photograph was taken the field had carried peas at the top end and potatoes at the bottom. The potatoes had been irrigated, after which it had rained. When potato lifting began the soil was still too wet to work easily and lifting was abandoned until the soil had dried out. As in the previous case the first wheat presented no problems, but the second wheat showed a large area of severe take-all where the potatoes had been harvested under wet conditions and where soil structure had, in consequence, been damaged.

These examples underline the need for good soil management to minimize losses from take-all. In the past few years, however, ADAS has encountered a number of severe attacks in situations where the farmer has been justly proud of his cultivations and seedbed preparation. It seems that it is possible to prepare a fine, friable seedbed which is ideal for sowing with a modern air drill, but which is also ideal for the spread of Ggt on roots. The use of the para-plough to improve soil structure also has been associated occasionally with increased severity of take-all.

Method of cultivation. That direct drilling produces a firmer seedbed than traditional cultivation techniques may explain why, since the first UK trials in the 1960s (Brooks & Dawson, 1968), there have been reports of less take-all after direct drilling than after mould-board ploughing. However, in a large series of ADAS trials in the 1970s (mainly on heavy soils and on sites where straw had been burned) no consistent effect of cultivation on take-all was found and, averaged over 29 comparisons, final levels of disease (% plants infected) were: plough 35%, reduced cultivation 37%, direct drill 36% (Yarham, 1981).

In recent investigations by ADAS and Rothamsted the effects of straw incorporation on take-all have been rather inconsistent, but the

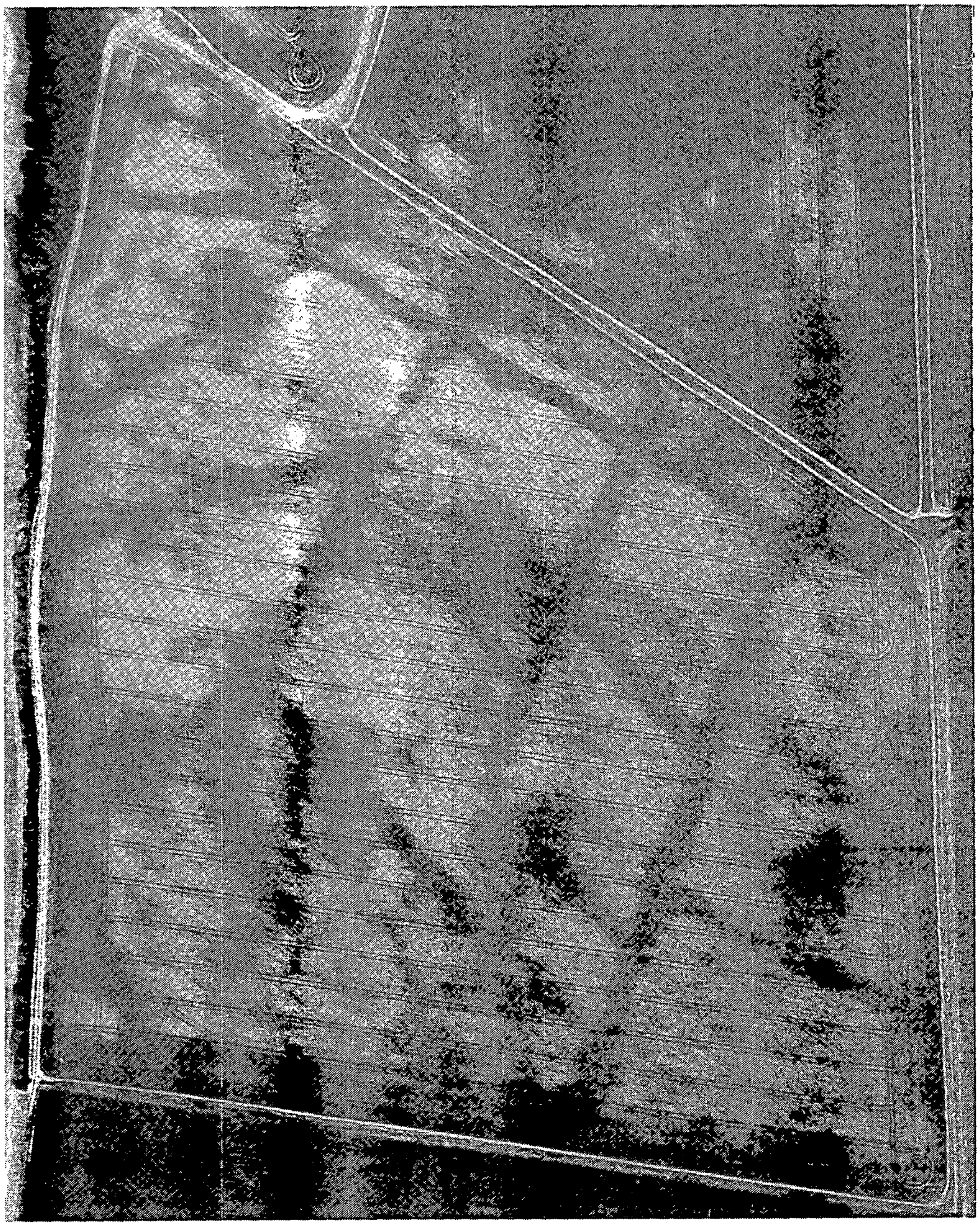

Figure 5. Take-all showing as pale areas in winter wheat on poorly-draining chalky boulder clay where moling had been neglected for the last ten years. The dark lines show better growth over the tile drains. Nuthampstead, Herts., 14 July 1987. (Panchromatic)

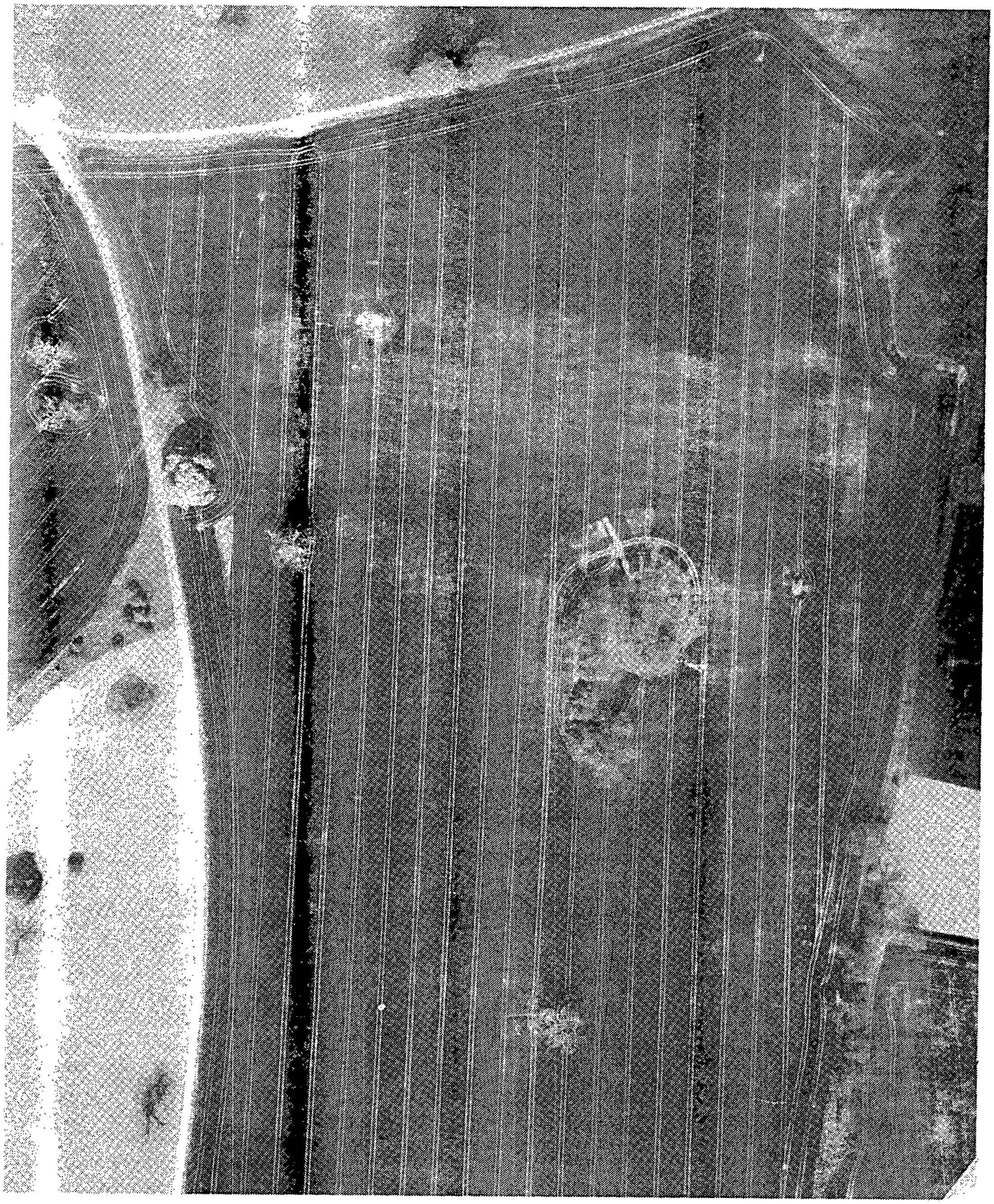

Figure 6. Severe take-all in winter wheat showing as pale areas where soil structure was damaged by lifting potatoes in the previous, wet July. Heveningham, Suffolk, 9 May 1988. (Panchromatic)

incorporation of straw without ploughing has increased the incidence of the disease at some sites. Two trends emerge from a study of the data:-

i. Where straw was incorporated there was a tendency for take-all to be less in ploughed than in minimally-cultivated treatments. The fact that no such effect had been detected in earlier trials on similar soil types where straw had been burned suggests that this was not simply the result of burial of inoculum in the ploughed treatment.

ii. Straw burning sometimes, though not invariably, decreased the disease compared with tine incorporation.

In a cultivation trial at Boxworth EHF take-all in ploughed treatments (with or without the addition of a 'straw digester') was marginally less than in tine cultivated treatments. In the following season (1987/8) the blocks of a seed treatment trial were coincident with the earlier cultivation treatments and although there was no effect of seed treatment on take-all, there was a highly significant block effect which reflected the previous year's treatments (Table 16).

Table 16. Residual effects of cultivation on plant growth and take-all

	Plant and disease data, 22 April 1988			
Block cultivations, autumn 1986	Mean number tillers/plant	Dry weight of 10 plants (g)	Mean % plants with take-all	Mean %roots with take-all
Cultivate	2.93	12.97	18.3	2.81
Plough + D	2.57	6.11	37.2	6.69
Plough + D	2.44	5.70	41.7	6.62
Plough	2.30	3.11	37.8	7.08
Plough	2.88	4.12	42.8	7.70
Cultivate	3.15	6.68	24.9	3.88
VR	7.51	12.86	3.8	4.1
SED	0.168	1.36	6.88	1.37

D= digester

As yet there have been very few cases where a severe attack of take-all could be attributed to the incorporation of straw. It is not impossible, however, that the widespread adoption of 'non-plough' straw-incorporation techniques following a ban on burning could lead to more problems on certain soil types.

4.3.5. Take-all as a constraint in weed control practice

In the spring of 1989 a wheat crop in Kent was so severely affected with take-all that the farmer ploughed up part of it and sowed maize instead. The wheat was the first crop after beans which had been heavily infested with couch grass, the field had been sprayed with glyphosate before the wheat was sown.

Cases of severe take-all in first wheats on couch-infested fields are not uncommon. Figure 7 is an aerial photograph of a field in Bedfordshire carrying a first wheat crop after a two-year ley. Because the ley was known to be infested with couch it had been sprayed with glyphosate before the field was cultivated in preparation for the wheat. The take-all patches obvious towards the bottom of the photograph coincide with the worst area of couch infestation.

ADAS advice is that couch control should be carried out before a break crop rather than before a cereal. Even this, however, does not always solve the problem. In March 1990 severe take-all patches occurred in a first wheat after oilseed rape in the Weald of Kent. The crop before the rape had been infested with couch but the field had been sprayed with glyphosate before the rape crop was taken. Nevertheless, the take-all patches in the 1990 wheat crop were coincident with the couch patches sprayed off in 1988, and the remains of the old, dead rhizomes could still be found in them (J. Batchelor, ADAS, Maidstone, pers. comm.). Test plants grown in compost amended with fragments of the dead rhizomes became severely infected with take-all.

Couch grass not only serves to carry the pathogen through break crops, but also appears sometimes to prevent the development of TAD. Figure 8 shows a series of fields on boulder clay in west Cambridgeshire. The farmer had experienced take-all in the fields in the previous two years in the 3rd and 4th wheat crops. He had continued to crop wheat on the land, assuming that by the 5th crop TAD would be decreasing the severity of the disease. The fields were, however, infested with couch

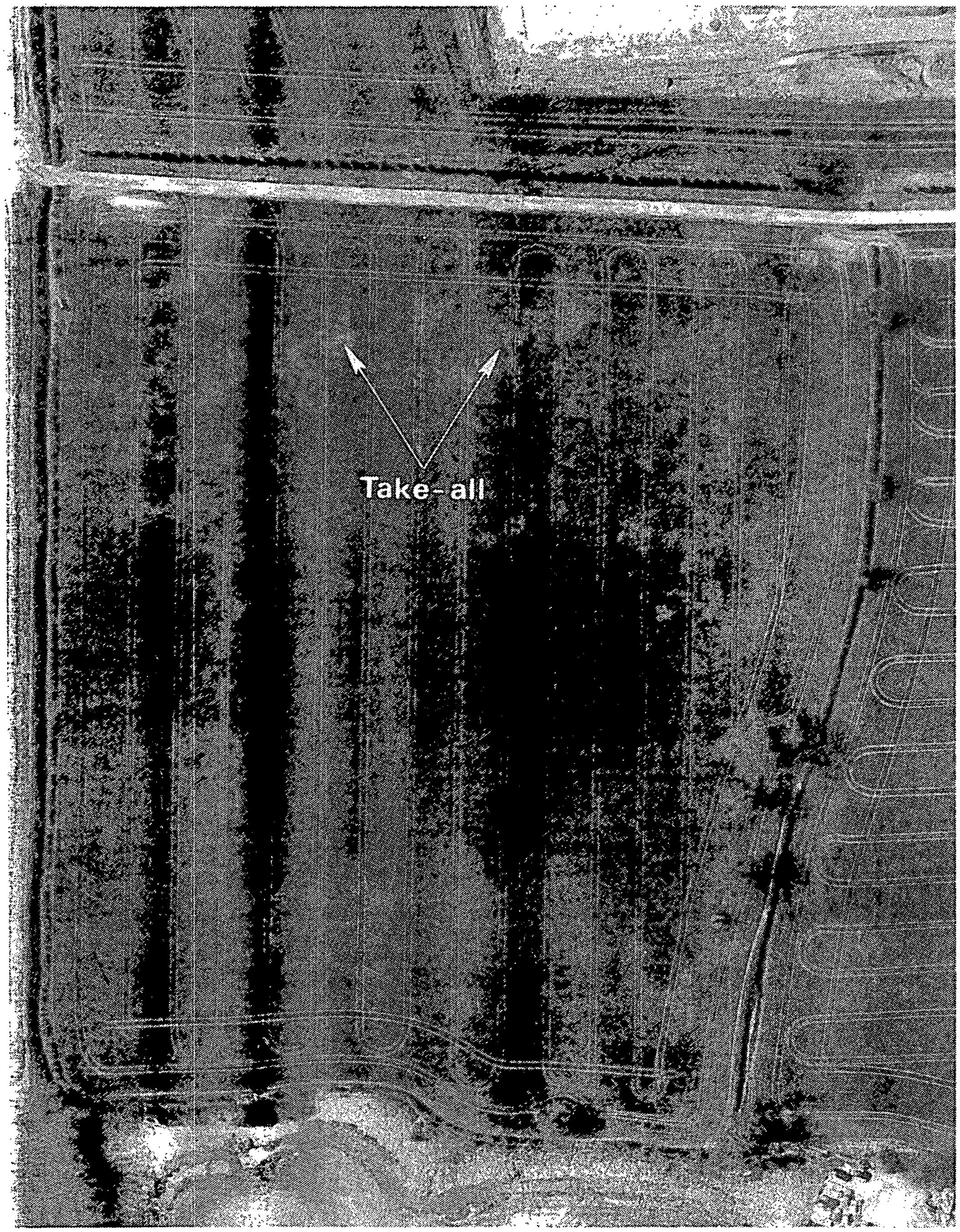

Figure 7. Take-all in winter wheat showing as pale areas which coincide with areas infested with couch grass in the previous two-year rye-grass ley. Billington, Beds., 16 April 1983. (Panchromatic)

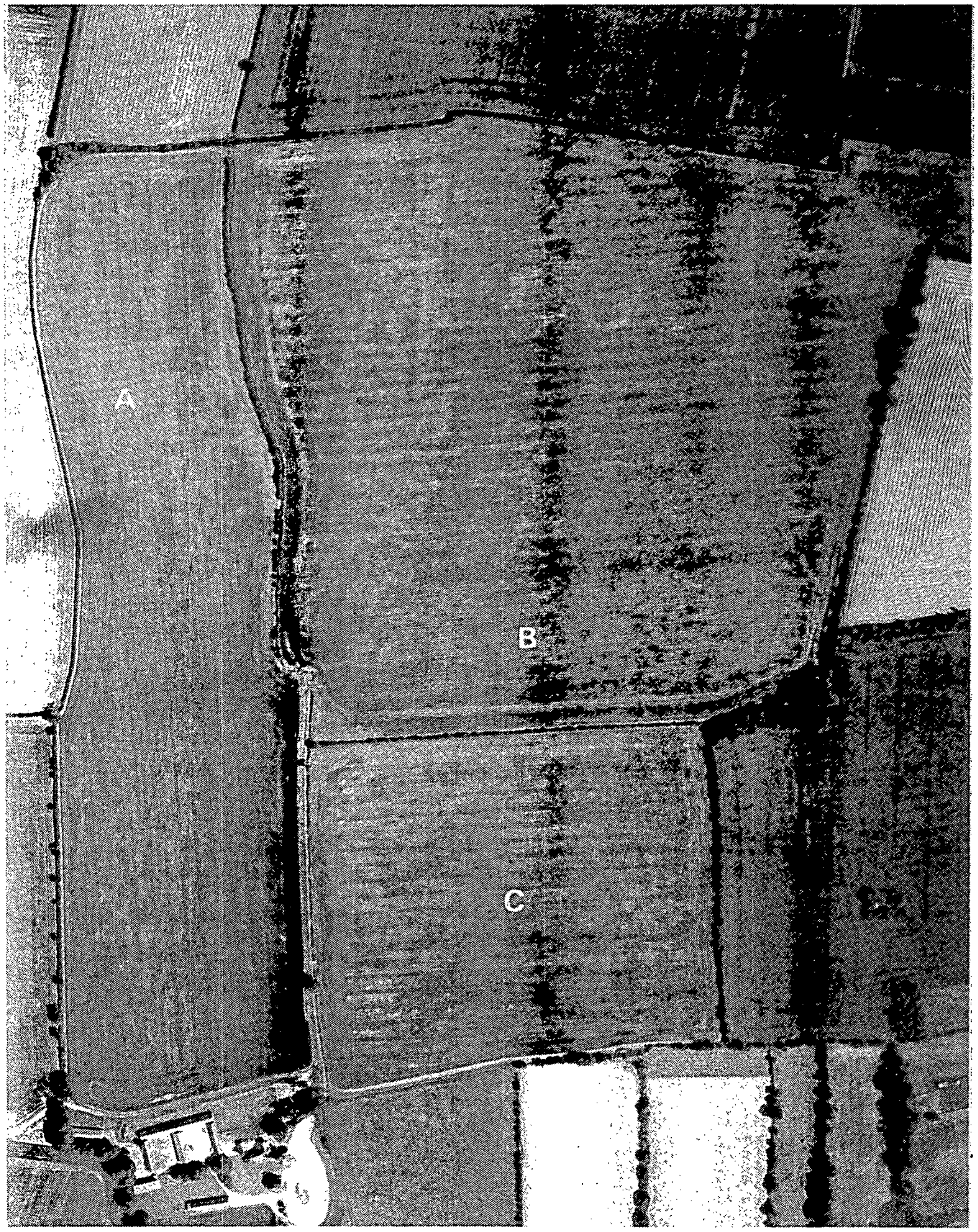

Figure 8. Severe take-all in a fifth wheat infested with couch, showing as pale areas where glyphosate was used to control couch in the previous season. Comberton, Cambs., 16 July 1988. (Panchromatic)

and part of the area had been treated with glyphosate in the autumn before the 5th crop was taken. The worst of the take-all-affected areas coincided with the areas to which the glyphosate had been applied. The delineation of the area by a straight line in at least one place on the photograph suggests that the glyphosate itself had affected the incidence of the disease.

4.3.6. Effect of take-all on the sensitivity of crop yield to climate

The profitability of arable farming depends on seasonal variations in the weather which affect not only crop growth but also the incidence and severity of diseases. Because take-all cannot be controlled by fungicides, it acts as a very significant factor in increasing the vulnerability of crop yields to the vagaries of the climate. Making the justifiable assumption that much of the difference in yield between 1st and 2nd wheats is due to take-all, the data presented in Tables 17 and 18 serve to illustrate this point.

Table 17. Seasonal variation in yields of first and second wheats at Rosemaund EHF

Harvest year:-	1982	1983	1984
1st wheats (t/ha)	8.2	8.8	10.8
2nd wheats (t/ha)	6.6	5.8	9.4
2nd as % of 1st	80%	66%	87%

The greatest difference between 1st and 2nd wheats was recorded in 1983, a year characterised by weather which was (see Table 18):

i. Mild and wet in late autumn, which would favour infection of the seminal roots by the take-all fungus.

ii. Wet and dull in April and May, which would favour infection of the developing crown roots.

iii. Hot and dry in June, which would exacerbate the effects of earlier root loss.

Thus, while 1983 was potentially a higher yielding year than 1982, the yields of 2nd wheats in that year were substantially less than the

Table 18. Rosemaund - meteorological data for the years 1982-1984.

Parameter	Year	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul
Temperature	1982	8.1	7.1	-0.6	2.0	4.8	5.7	8.1	11.0	15.2	16.0
- mean °C	1983	9.9	7.6	4.1	6.7	1.5	6.3	6.5	10.1	14.1	18.9
	1984	9.9	6.9	5.3	3.6	3.2	4.4	7.9	14.3	16.5	17.5
30-year mean		9.9	6.1	4.4	3.2	3.5	5.3	7.7	10.8	13.8	15.5
Rainfall	1982	67	30	100	57	34	78	24	24	175	28
mm	1983	53	78	62	43	18	43	100	86	16	81
	1984	77	25	91	87	35	52	6	63	47	6
30-year mean		54	67	65	62	47	50	43	55	49	53
Sunshine	1982	3.5	1.9	1.2	1.5	1.2	4.4	5.5	6.9	5.1	5.0
h/day	1983	2.4	2.1	1.0	1.6	2.4	2.8	5.0	3.1	5.5	7.2
	1984	3.8	1.1	2.0	2.0	1.7	1.6	7.4	5.6	7.4	8.5
30-year mean		3.0	2.1	1.5	1.6	2.3	3.5	5.0	6.1	6.6	6.1

1982 yields. Note the comparison with 1984 when the very dry April would have checked disease development and (although July was very dry) rainfall in June was not much less than average.

Equally instructive is the comparison between the weather recorded in East Anglia in 1987, when take-all caused much damage, and that in 1989 when there was much take-all in late winter/early spring, but comparatively few crops which suffered severely from the disease later in the season (Figure 9). The apparent soil moisture deficit (SMD) in April was actually rather lower (and hence more conducive to take-all development) in 1989 than in 1987. However, in 1989 the SMD rose very rapidly in May - a time when the production of adventitious roots would still be very active. Since moisture deficits would be greatest in the upper layers of the soil where the pathogen would be most active, the

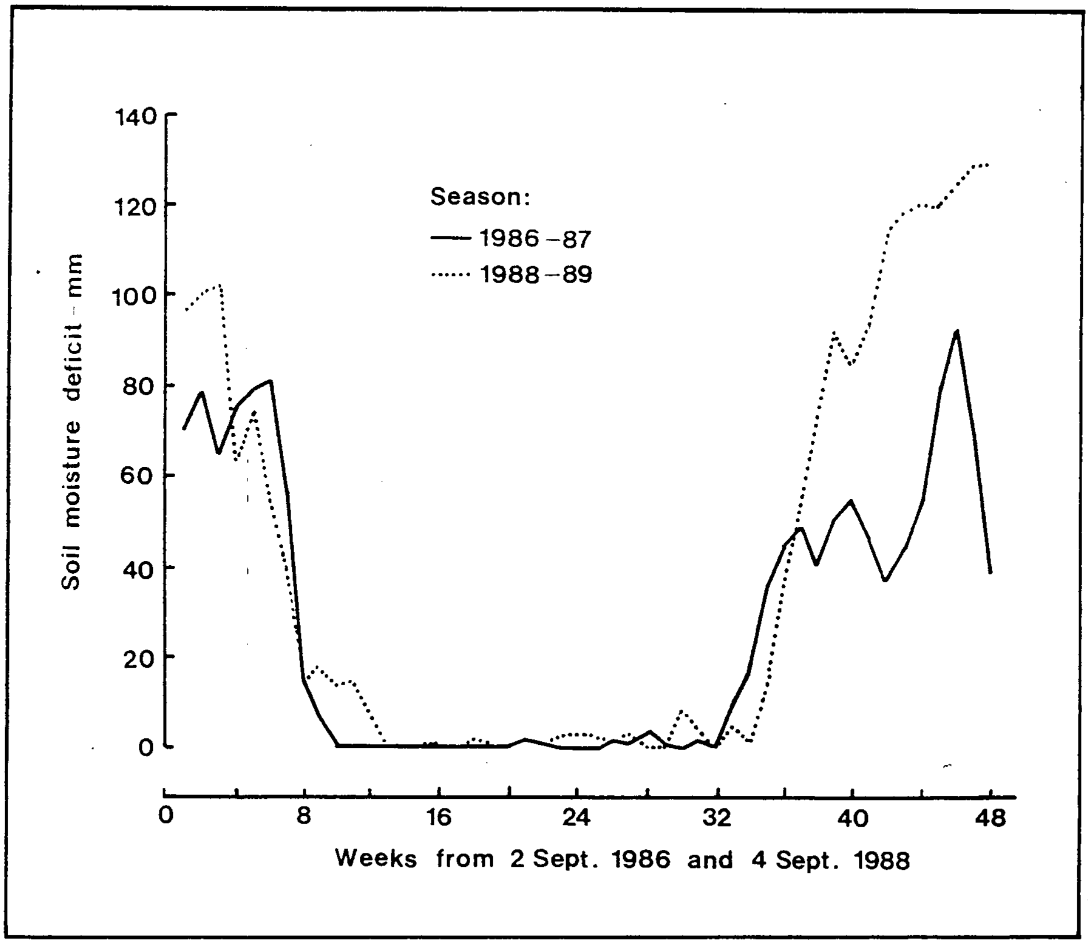

Figure 9. Soil moisture deficits recorded in the two years at Honnington in Suffolk. Meteorological Office Excess Calculation System (MORECS) square 141 (Mid Suffolk).

drying out of the soil would check disease development before it affected root production and crops would thus be enabled to grow away from the disease. Exceptions would be provided by crops which had been so badly damaged earlier in the season that they were unable to produce enough new roots to replace those that had been destroyed. This would explain why, while most crops showed little evidence of severe take-all in 1989 a few crops suffered very severely from the disease.

The situation in 1989 should be compared with that experienced in 1987 when the soil remained moist throughout much of May but crops were then subjected to severe moisture stress in June when it was too late for the crops to replace roots destroyed by the disease.

Such observations on seasonal variations in the severity of take-all illustrate why it has not been possible to predict the severity of the disease in any particular season or to find any consistent relationship between disease levels in late winter and yield.

4.4. Recommendations for further research

The needs are:

i. More information on a) the effects of different break crops on the yield of first and second wheats and b) whether the effectiveness of a break crop in decreasing disease incidence in the second wheat can be improved by manipulation of the husbandry (e.g. delaying the sowing date) of the first wheat.

ii. To continue current investigations of less susceptible species such as rye and triticale to see if they affect the development of TAD and how soon afterwards it would be safe to return to wheat.

iii. To continue current work on the effects of set-aside management and to initiate studies on the effects of catch cropping on take-all.

iv. To look more closely at effects of different sources, timings and rates of nitrogen under UK conditions. Some important questions are a) On how wide a range of UK soils is the use of ammonium sulphate likely to be beneficial? b) Would the use of a urea-based product with a nitrification inhibitor offer a possible alternative? c) Can nitrogen rates be adjusted to take account of take-all risks? Are disease levels in late winter or spring a guide to making such adjustments, and by how much should our standard recommendations be increased if take-all levels are high?

v. More information, over a range of soil types, on the long-term effects of straw incorporation.

vi. More information on possible effects of recently introduced herbicides on crop susceptibility to take-all.

CHAPTER 5. STRATEGIES FOR MANAGEMENT

5.1. Agronomic

Factors that affect take-all are interlinked (see 2., Figure 2, 4., and 5.4.2.) and there is often no strong reason for regarding any one as more significant than any other. The search should be for the key, or keys, to this interlinked structure. In high input systems like that in the UK, changing any of these factors within the normal range of husbandry practices achieves only a fine tuning of disease control (Hornby, 1985).

5.1.1. Host nutrition

There is much work spanning many years to show that nutrient deficiency exacerbates take-all. Recent pot experiments in Australia (Brennan, 1989a) showed that wheat severely deficient in N and P had 60% of roots infected in infection tests, whereas with 'luxury' levels of P no roots were infected and with 'adequate' levels of N only 10% were infected. Increasing N and P decreased the length of lesions proximal to the seed. Pot experiments with wheat on P-deficient soil showed that plants with a vesicular-arbuscular mycorrhiza developed less take-all than non-mycorrhizal plants: the decrease in take-all by the mycorrhiza was indirect and resulted from improved phosphorus nutrition (Graham & Menge, 1982).

5.2. Fumigants and fungicides

5.2.1. Background and literature

Soil fumigants will eliminate the take-all fungus, but amongst other drawbacks they are costly and therefore not commercially practicable (Heim *et al.*, 1986). They are non-selective and following the year of treatment there may be a rapid build-up of the take-all fungus, probably because of a decreased antagonistic microflora in the soil, so that severe infection often results if another cereal crop is grown without re-application of the chemical. The large volumes and high concentrations needed, and hence the risk of contaminating ground water, also preclude fumigation as a practical treatment.

A trickle of reports about successes with fungicides has kept this, albeit relatively narrow, avenue open. A disease such as take-all, caused by a soil-borne, root-infecting fungus, is a difficult target for control by fungicides. It is out of reach of most fungicide applied by conventional means, and no treatments are available specifically for controlling take-all. However, some research has been aimed at achieving control by fungicides, and work published up to 1988 has recently been reviewed (Bateman, 1989). The following summary is taken mainly from that review, direct reference being made only to later publications.

Seed treatment. The only fungicide which has shown promise for controlling take-all when applied as a seed treatment is the sterol biosynthesis-inhibiting compound triadimenol, which was found to be useful in experiments in the USA by providing early protection of the seminal root system in early-sown winter wheat. In British conditions, prolonged protection from later infection of the nodal root system, until late spring at least, is likely to be more important. This may have been achieved in France, where improved control resulted from the application of a high dose of triadimenol to seed using an experimental coating process. Some current research also concerns the use of seed coatings to allow controlled release of various fungicides.

Experiments at Rothamsted have identified specific conditions in which triadimenol plus fuberidazole (Baytan) can be beneficial as a conventional seed treatment: namely, when a winter wheat crop is sown very early and severe take-all develops subsequently and causes premature ripening. Table 19 shows how a yield benefit can result in such conditions. The poor control of take-all symptoms on the roots (shown as TAR) suggests that the fungicide may have induced a physiological change which allowed the plants to tolerate the root infection so that patches of early-ripened plants did not develop. The results from a number of ADAS trials have shown a positive association between the response to triadimenol seed treatment in t/ha and the take-all index of untreated plots. The effects on root infection itself may be improved in more densely sown crops, but generally the treatment is unreliable.

Soil fungicides. Recent research at Rothamsted has concentrated on soil treatment with conventional fungicides which are more selective than the fumigant treatments investigated earlier. A principal objective was to determine how the fungicide should be distributed in the soil, and subsequently how to achieve redistribution from the site of application to the location of the inoculum or the site of infection. Most recently, the importance of the physico-chemical properties of soil fungicides has been emphasized (Bateman, Nicholls & Chamberlain, 1990). Experiments using pot-grown wheat plants and naturally-infested field plots suggested that soil-applied fungicides, as well as being highly fungitoxic with minimal phytotoxicity, should have moderately low lipophilicity. This would avoid excessive sorption to soil particles and allow some mobility and redistribution via the soil water. Moderate persistence is also required. While no fungicide with all the appropriate properties has been identified, it should be possible to synthesize new molecules which have a balance between mobility and persistence. Where persistence limits are dictated by registration requirements, the need for persistence may be better met by the use of slow-release formulations.

Table 19. Effects of seed treatment with triadimenol (as Baytan) on take-all in winter wheat

Sowing date	Seed treatment	Take-all rating (0-300)	% Area prematurely ripened	Yields (t/ha)
8 Sep.	None	268	70	5.72
	Triadimenol	248	43	8.44
7 Oct.	None	218	44	7.43
	Triadimenol	213	44	7.75
SED (15 d.f.)		16.1	9.5	0.655

Recent research in Australia (Ballinger & Kollmorgen, 1988; Coventry *et al.*, 1989; Brennan, 1989b) has identified the fungicide flutriafol as a potential in-furrow treatment, especially when formulated as a coating on superphosphate granules. In the very different growing conditions in Britain, flutriafol has not proved useful after soil-incorporation (Bateman, unpublished); as an in-furrow treatment it decreased take-all in some trials in which grain yields were increased at three out of seven sites, but establishment was severely delayed and yield decreased at two sites (Clare, unpublished).

Foliar treatment. More accurate predictions of severe take-all than is possible at present are required if unnecessary application of fungicides to the seed or seed bed are to be avoided. The availability of a foliar-applied, phloem-translocated fungicide would decrease the need for early prediction, possibly decrease the problem of persistence and avoid much of the wastage which is inevitably associated with applying pesticides to soil. Although there are no phloem-translocated fungicides currently available which are active against the take-all fungus, there is an increasing understanding of the physico-chemical properties required by such fungicides which raises the possibility that they can be synthesized. Even so, the value of phloem-translocation in the control of any root-infecting pathogen has yet to be proved.

5.2.2. Recent research in the UK

From a practical point of view, current interest in fungicides still centres on seed treatment because this, unlike soil treatment, uses existing methodology and equipment. Whilst the conditions needed to achieve significant effects of triadimenol on yields of winter wheat have been identified as early sowing and extensive patch development for UK situations, they are to a large extent unpredictable (i.e. sowing date can be controlled, but the epidemic of take-all in a given crop and the contributory weather conditions can not).

Factorial experiments on winter wheat at Rothamsted (see 5.4.) confirmed the unreliability of seed treatment with triadimenol plus fuberidazole as a control measure against take-all. Similarly, the treatment sometimes, but not always, decreased the incidence and severity of take-all in winter wheat in ADAS trials from 1984 to 1986 (Jones, 1987). In these trials, yield increases sometimes occurred where take-all was negligible in the crop or did not appear to be controlled. In an ADAS trial in 1985 in which there was a large yield response (from 4.21 t/ha with organomercury to 6.78 t/ha) with triadimenol, take-all was decreased but analysis of yield using incidence of take-all as covariate indicated an effect on yield additional to that which resulted from controlling take-all. An increasing yield response to seed treatment with triadimenol plus fuberidazole in ADAS trials as sowing date became earlier (R.W. Clare, I. Ap Dewi and D.J. Yarham, unpublished) may have been associated with the effect on take-all of earlier sowing.

Detailed analysis of data from factorial experiments on winter barley at Rothamsted and Woburn are beginning to add further information (J.F.

Jenkyn & R.J. Gutteridge, unpublished). Although the effects of triadimenol plus fuberidazole on the root symptoms of take-all on barley are not great, they are often significant, usually persist until June, and appear to be more consistent than in wheat. When results of seven experiments over 3 years (1984-6) are combined (which then necessitates cautious interpretation), there was no overall effect of sowing date on disease, but the effect of seed treatment in decreasing take-all was greater with earlier sowing (Figure 10). Increasing take-all in untreated plots and increasing effectiveness of treatment were each associated with an increasing effect on yield.

5.3. Biological control

In the last twenty-five years, biological control has emerged as a possible solution to the control impasse and much has been promised. However the promises have not materialized, questions are repeated and scepticism reigns. It needs to be asked whether the expectations were realistic for the UK in the first place, and whether there has been an uncritical expectation that foreign findings translate readily to Northern Europe.

Raised expectations of biological control of take-all by introduced BCAs is a world-wide phenomenon. Many of the claims have come from the USA and Australia, although there are a few European ones. Patents have been taken out on some organisms and processes, but as yet nothing has emerged that reliably and sufficiently decreases take-all in our fields.

In the USA fluorescent pseudomonads have been applied as seed treatments to wheat to control take-all and pythium root rot (Thomashow & Weller, 1990). In wheat suffering from take-all, yield increases averaged 17% in experimental plots and 11% in commercial-scale tests. Performance in the field has, however, been inconsistent and significant improvements in yield have occurred in only 60% of treatments. This is seen as a major impediment to wide-scale commercial use. It is explained as follows:

i. inoculum density of the take-all fungus was often too low;

ii. environmental conditions were unsuitable for disease development;

iii. BCAs have no ability to stimulate growth directly;

iv. non-target pathogens offset beneficial effects;

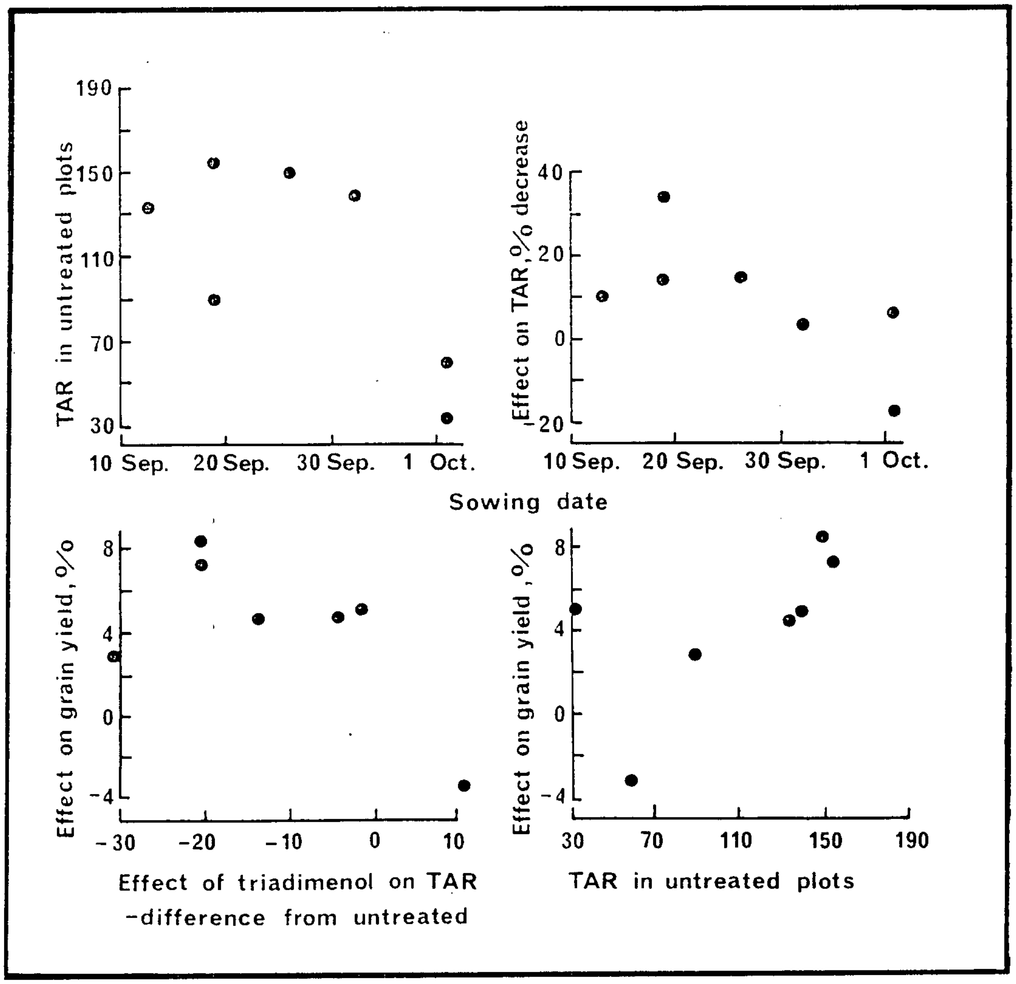

Figure 10. Relationships among take-all rating (TAR) in June samples, effect of triadimenol seed treatment and yield in field experiments on winter barley at Rothamsted and Woburn.

v. variable colonization of wheat roots may be a critical factor.

In the Pacific North-West of America it was estimated (Heim *et al.*, 1986) that some 624,850 acres (252,877 ha) were affected by take-all, 43.4% of which had moderate or severe disease. If seed coating technology, using *Pseudomonas fluorescens*, were introduced, yield increases between 3-25% (mean 5-10%) would be expected. It was assumed that overall this would generate $13.6M (maximum $37.9M), but it was also noted that if yield responses and economic values of wheat were low, then farmers could actually lose money by adopting this technology.

In take-all research an upsurge in biological control interest starting in the 1960s has been marked by the demonstration and naming of take-all decline, the discovery of *Phialophora* spp. which seemed to suppress the onset of take-all and an infatuation with introduced BCAs. The pendulum is already swinging back: a tactical withdrawal from the promotion of single BCAs in the face of inconsistent and small effects to a more realistic position is being forced on the enthusiasts. The BCAs for take-all show unwelcome traits like not working in soils with high clay content. There are possibilities that genetic engineering, new application strategies, the use of biological control as part of integrated control, and new information about mechanisms, such as evidence for antibiotic production *in situ* will give a new lease of life to the subject. At the moment biological control is perceived as more environmentally acceptable for controlling diseases than are fungicides.

TAD soils are the best-known of several types of take-all-suppressive soil. TAD develops after severe infection, but is then an effective form of natural biological control and has been exploited in long runs of cereals for decades by some farmers in the UK. Much work has been done since the early 1960s to try to explain TAD and several different types of mechanism have been proposed. Some evidence suggests changes in the pathogen population. For example, some isolates of the take-all fungus produce a diffusible fungal growth inhibitor on buffered media at pH 3.5-5.0 (Romanos *et al.*, 1980): TAD soils seem to produce more of these isolates than non-decline soils. However, the most popular explanation is microbial antagonism. Many have searched for specific antagonists and, with much publicity, several micro-organisms have emerged that have decreased take-all build-up when introduced as BCAs. However these BCAs rarely reach the level and consistency of control achieved by TAD. This may be because TAD is the expression of a collection of BCAs and control mechanisms which ensures operation over a wider range of conditions than that within which single BCAs operate. Analyses of disease progress curves at Rothamsted, based on large data sets (see 3.4.), have recently revealed a manifestation of TAD in crops near anthesis that is affected by changes both in inoculum of the pathogen and in the environment.

The now considerable literature on the biological control of plant diseases has a very shallow pyramidal structure, with numerous laboratory studies of limited value at the base and a handful of commercial products for specific use at the apex. These products constitute a minute fraction of the sales value of plant protection products. Nobody doubts the enormous antagonistic potential amongst micro-organisms in or on dead substrates and on plant surfaces, but with one or two notable exceptions success in realising it to control disease seems to be inversely proportional to the complexity of a crop's environment.

Reliance on one of the current putative BCAs to control disease in the field is at worst naive and at best too optimistic. Future research needs to pay more attention to why natural biological control phenomena such as take-all decline, *Phialophora*, and suppressive soils decrease take-all more reliably and effectively than the vast majority of introduced BCAs. This is likely to reveal that most natural phenomena have several components that together ensure relative robustness and should give pointers on how best to use BCAs. Attention should also be given to the possible exploitation of growth-stimulating rhizobacteria to enable plants to cope better with take-all.

5.3.1. The case for biological control

At present the best control strategy available for take-all is 'damage limitation', i.e. the manipulation of agronomic practices to decrease the effects of take-all, and the hope that the weather will favour crop growth more than pathogen development. The narrowness of this strategy may be a significant constraint to profitable wheat production and sensible cropping patterns (see 4.1.). Biological control is an alternative strategy.

The phenomenon of biological control of take-all has been known for many years (Sandford & Broadfoot, 1931) but before a BCA can be a commercial proposition it must meet several requirements. There must be a market opportunity. The absence of an effective chemical fungicide and of a wheat cv. with resistance suggests that such an opportunity is likely for take-all. A BCA must carry with it a guarantee of reliability, be patentable, registerable and cost-effective. The use of a 'natural agent' may also be seen as environmentally desirable.

5.3.2. Current situation

Much effort since the early 1970s has been devoted to screening and testing micro-organisms, particularly from TAD situations and so-called 'suppressive' soils, for activity against the take-all fungus. 'Specific' suppression is transferable and destructible (Shipton, 1972; Shipton *et al.*, 1973; Cook & Rovira, 1976). It usually occurs in response to the presence of a severely diseased host and virulent Ggt and is thought to be due to a build up of specific, antagonistic micro-organisms. It contrasts with non-transferable, 'general' suppression caused by increased microbial activity associated with organic amendments, improved fertility, high soil temperature and ammonium-nitrogen uptake by roots.

There are a number of hypotheses proposed for the mechanisms responsible for the specific suppression of take-all which have been summarized by Rovira & Wildermuth (1981) with evidence provided for the massive proliferation of 'asporogenous' bacteria on infected roots as a forerunner to TAD. These bacteria are most probably gram negative fluorescent pseudomonads (Weller, 1983). Such organisms are thought to be strong candidates for biological control because of their ecological and physiological characteristics. They grow quickly in the rhizosphere which is their natural habitat (Rouatt & Katznelson, 1961), are nutritionally versatile (Stolp & Gadkari, 1981) and produce antibiotics (Leisinger & Margraff, 1979) and siderophores (Misaghi *et al.*, 1982) which inhibit phytopathogens *in vitro*. Fluorescent pseudomonads quickly colonize roots and are present in lesions caused by Ggt (Rovira & Wildermuth, 1981). Most importantly it appears that they can be introduced and become successfully established in the rhizosphere and on the rhizoplane of wheat (Weller, 1983).

Field results have been variable although there have been some promising reports of suppression with a concomitant 20% increase in yield

(Weller, 1983; Weller & Cook, 1983). Other bacteria have been reported to show antagonistic activity to take-all in the field and Capper & Campbell (1986) observed a 50% yield increase using a *Bacillus* sp. under dry conditions on a very organic soil where take-all occurred naturally.

Biological control of take-all by other micro-organisms has also been reported, e.g. soil amoebae (Old & Patrick, 1979; Chakraborty & Warcup, 1985) and fungi (Wong & Southwell, 1979; Simon, 1989) with promising reports of cross-protection well documented by Deacon (1973).

Considerable public and commercial sector funding is being allocated to biological control of take-all in Australia and the USA, although it is now generally accepted that no single organism or combination of organisms is likely to be effective under all conditions of wheat production, especially in complex, fertile soils such as those in the UK. The main research approaches to controlling take-all by BCAs world-wide are:

i. To elucidate the mechanisms of action of BCAs with regard to root colonization, antibiotic production and genetic control.

ii. To assess the performance of combinations of BCAs, using up to four bacterial strains and possibly fungi.

iii. To study interactions among BCAs in combinations (and the role of 'promotor' strains, which on their own have no apparent biological control activity).

iv. To relate performance of BCAs to a range of soil variables with the aim eventually of identifying optimal combinations for specific situations.

5.3.3. Mode of Action

The mechanisms of suppression and cross-protection have been reviewed by Rovira & Wildermuth (1981) and Wong (1981), respectively, and it is thought unlikely that the same mechanism will be operating in all environments. In a naturally-occurring situation build-up and maintenance of suppression will probably depend on soil fertility, quantity of plant residues and the levels of pathogens and antagonists that they carry, soil temperature and moisture and the length of time between crops.

Several proposals have been put forward as to possible modes of action of the agents involved in take-all antagonism. Some may be non-specific, e.g. factors related to colonization such as competition for sites and nutrients (Weller, 1983) and root stimulation (Weller, 1985) or production by bacteria of siderophores which have a higher iron-binding ability than fungal siderophores (Wong, 1985). Other modes of action may be more specific, e.g. production of secondary metabolites which are specifically antagonistic to certain other micro-organisms (Weller & Cook, 1983; Gurusiddaiah *et al.*, 1986). Antagonists may cause hyphal lysis on the wheat roots (Campbell & Faull, 1979) or even inhibit the trophic response of Ggt to the wheat root (Pope & Jackson, 1973). This work is actively continuing in other countries, e.g. the USA, but not to any extent in the UK.

5.3.4. Factors affecting BCAs

Much of the experimental work which attempts to determine the mode(s) of action of particular BCAs has been carried out under controlled conditions in the laboratory or glasshouse. Whilst it is important to understand how a BCA effects its control it is also important to understand how that control is affected by environmental factors such as temperature, soil texture, pH, soil matric potential and the activity of other micro-organisms. For example, it is known that soil matric potential can affect root colonization by fluorescent pseudomonads, soils with very high available water probably providing inadequate oxygen for bacterial multiplication, whilst in very dry soils there is inadequate water available to maintain cell turgor (Howie *et al.*, 1987). Soil pH in particular has been shown to affect colonization (Weller, 1988) and uptake of ammonium nitrogen, by decreasing pH at the root surface and enhancing the environment for take-all-suppressive organisms (Christensen & Brett, 1985). The degree of toxic activity of antifungal compounds produced by micro-organisms is also affected by pH (Brisbane & Rovira, 1988).

5.3.5. Experimental results

Despite variable results in field trials some successes have been achieved (Weller & Cook, 1983; Capper & Campbell, 1986). In recent ADAS trials, BCAs (suppressive bacteria applied either as a seed treatment, or in alginate beads) have yielded variable results in terms of significant yield benefits. Positive effects (decrease in root infection or increase in yield) were observed in approximately 80% of treatments over a seven year period, but the differences were not always statistically significant. Soil pHs have been generally higher in UK trials than those in the USA, e.g. Weller & Cook (1983).

Seed coating proved to be an appropriate method of application in that the organisms were in intimate contact with the radicle as it emerged. However, problems have been encountered when coating seed already treated with the fungicides triadimenol and fuberidazole (Baytan). Biological and chemical seed treatments need not necessarily be mutually exclusive but the order of treatment was found to be important, e.g. the seed must be coated with bacteria before treating with Baytan otherwise phytotoxic effects in the form of reduced emergence are observed due to fungicide penetrating the seed coat during bacterization. Additionally, asporogenous bacteria such as pseudomonads, if used for seed coating, need protection from desiccation if they are to survive in adequate numbers for any period of time, e.g. up to one month.

Preliminary studies on the colonization potential of BCAs indicated that there may be a differential response between wheat cultivars to such agents.

Results of ADAS field experiments are summarized below.

1983 Promising results were obtained by the addition of *Bacillus pumilus* to spring wheat at sowing on loamy fen peat, pH 7.5. A significant reduction in infection and an increase in yield were observed in this very dry year (Capper & Campbell, 1986).

1985/86 *Bacillus pumilus* and *B. cereus* var. *mycoides* gave slight decreases in root infection and increases in yield: variability was such that yield increases up to 16% were not statistically significant.

1987 *Pseudomonas fluorescens*, strain 13-79, showed a slight but not significant yield increase when applied as a seed coating to wheat sown in London clay soil, pH 6.9-7.5. The use of alginate beads for inoculum delivery was promising in that 50% of alginate treatments out-performed the control.

1988 At Arthur Rickwood EHF the take-all rating was significantly reduced ($P < 0.05$) by *P. fluorescens*, strain 13-79, applied as a seed coating and by *P. fluorescens*, strain 2-79, applied in alginate beads. In a trial in Northamptonshire on loamy drift over Oxford clay, pH 7.0, seminal root infection was significantly reduced by strain 2-79 in alginate beads (with or without strain 13-79), or as a seed coating.

The field trials are continuing.

Related laboratory studies investigated delivery methods for BCAs and their colonization potential on wheat roots. Although applications of BCAs very readily achieve about 10^8 cfu per seed, they afford little protection to the organisms and can interact with seed treatment fungicides (e.g. triadimenol) resulting in increased phytotoxicity and placing constraints on chemical applications. Perlite granules were unsuitable as carriers because they could not be coated with sufficient bacteria. Alginate beads showed more promise, with initial levels of *c.* 10^7 cfu of bacteria per bead, decreasing to 10^4-10^5 cfu after storage at 22°C for six months. The beads also acted as foci of inoculum which gave a sustained, slow release of the organisms. In pot experiments the levels of take-all infection and the reduction in infection achieved with BCAs were greater in cvs Avalon and Wembley than in cvs Axona, Brimstone, Brock, Fenman, Mercia, Minaret or Norman. *P. fluorescens* 13-79 applied either in alginate or as a seed treatment significantly reduced infection in both Avalon and Wembley. Significant ($P<0.05$) decreases in infection were also achieved in cv. Avalon using *Bacillus* spp. in alginate beads.

An ADAS study of biological control in the context of rotation involved the introduction of an experimental fungus at the beginning of a cereal sequence. In the second year the fungal BCA and winter oats, grown as a mixture with winter wheat, significantly reduced take-all during the winter.

In 1989 a two-year investigation integrating BCAs and fungicides to control take-all in sequences of wheat was started. Two bacterial BCAs (*P. fluorescens* biovar D), a fungal BCA and a fungicide are being compared with organomercury seed treatment and a control. In the first year the treatments were applied to a first wheat crop following a break. None of the BCA treatments affected take-all significantly at any of four sites in either year of the sequence.

5.4. **Integrated control**

5.4.1. Background

Integrated control may utilize different methods of control that affect different stages of pathogen development in a cumulative and beneficial manner that may also decrease other diseases such as eyespot and sharp eyespot. For example, the use of ammonium fertilizers to decrease soil receptivity (conduciveness), fungicide treatment of the seed (triadimenol) or the seed bed (nuarimol) to delay infection and the selection of a wheat variety (cv. Arminda) to delay infection and slow lesion development produced promising decreases of take-all in France (Cavelier, 1989).

Precedents for the success of such systems can be found in the literature, e.g. in the control of onion white rot (Abd-El Moity *et al.*, 1982).

The various components in an integrated system must not affect each other deleteriously and should preferably enhance each other. Thus research to develop practical integrated approaches involving BCAs is unlikely to proceed far until field-effective BCAs with established modes of action are developed, and more is known about the effects of agronomic practices and agrochemicals (fertilizers and herbicides as well as fungicides) on the biological balance in the soil. It is important that BCAs remain effective under the normal agricultural practices to which they will be exposed so that further constraints on wheat production are not introduced. From an environmental viewpoint the effects of chemicals and any microbial introductions (particularly of genetically manipulated organisms) on the soil microflora must be ascertained in order to determine appropriate usage and allow for informed legislative control.

5.4.2. Recent research in the UK and France

Despite optimism in the literature for such measures as seed treatment, particular types of fertilizers, or biological controls, no single treatment has emerged for effective universal control of take-all in second or subsequent cereal crops. A series of experiments was begun at Rothamsted in the 1985-6 season to compare some of the most promising treatments (Table 20) and farming practices, separately and in combination, on sites considered to be at risk from take-all. Although the practicalities of applying the treatments on a farm scale were not a consideration at that stage, it was envisaged that any treatments which consistently achieved significant decreases in combination would form the basis of a package of treatments for recommending to farmers.

Table 21 ranks six factors according to their effectiveness against take-all over three seasons in the Rothamsted experiments. The value of

Table 20. Treatments tested in multifactorial experiments at Rothamsted

Factor	Standard treatment	Test treatment
Sowing date	Early (September)	Late (mid-late October)
Soil fungicide	None	Nuarimol (1.1 kg/ha)
Seed treatment	Organomercury	Triadimenol plus fuberidazole
Autumn N	None	60 kg N/ha as ammonium nitrate (Nitro-Chalk) at sowing
N time	Single application of 200 kg/ha in April	Divided application, 40 kg/ha in Feb./Mar., then 160 kg/ha in April
N form	Ammonium nitrate in spring (Nitro-Chalk)	Ammonium sulphate in spring

delayed sowing is emphasized. The soil fungicide (see also 5.2.) was consistently the next most effective treatment, but the seed treatment was more erratic in its effects. Autumn nitrogen was sometimes effective, and other effects of fertilizers were slight and infrequent. There were relatively few significant positive interactions among treatments, and these mostly involved sowing date. Interactions which increased disease were more frequent. Table 22 lists the number of occasions in two seasons in which the test treatment contributed to least disease (measured as TAR) and greatest yield in any three-factor combinations, regardless of whether or not the interactions were statistically significant. (Such interactions were not determined in 1986 because a full replicate of the factorial experiment was not used.) In 1987, late sowing resulted in poor yields because of poor plant emergence; in other years late sowing resulted in greater yields because of less take-all. All test treatments except divided N application in spring contributed to least disease in the majority of combinations, but it is evident from these experiments that recommendations for a package of treatments for minimizing take-all can not be made with confidence.

Table 21. Single factors ranked according to their effectiveness against take-all in experiments at Rothamsted

	Mean ranking - all assessments				Number of significant, positive main effects out of a total of 8 assessments, including % and logits of %		
Test treatment	1986	1987	1988	All years	1986	1987	1988
Late sowing	1	1	1	1	7	8	8
Soil fungicide	2	2	4	2	0	6	0
Triadimenol sd tr	6	3	3	3	0	6	1
Autumn N	5	4	2	4	0	3	6
Divided N*	3	6	6	5	1	0	0
Amm. sulphate	4	5	5	6	0	0	0

sd tr, seed treatment; Amm, ammonium; *, rankings include Feb/Mar samples, taken before divided N applications were made.

The priority recommendation is the avoidance of early sowing of crops at risk from take-all.

A series of related experiments was conducted in different conditions at Le Rheu, France in 1987-9 (P. Lucas, pers. comm.), following somewhat similar experiments with broader objectives (Lucas *et al.*, 1988). These experiments also showed the value of delayed sowing (tested in 1987-8) and fungicides. A late effect of ammonium sulphate, tested as an autumn treatment at Le Rheu, in early-sown plots may have resulted from a gradual build up of antagonistic micro-organisms (P. Lucas, pers. comm.).

Take-all assessments were also made in a similar series of factorial experiments at Boxworth in 1984-6 (Werker & Gilligan, 1990). The results were generally similar, although take-all was less severe and differences between early and late sown plots seen in early samples were not maintained through to the summer.

In a further factorial experiment at Rothamsted in 1988-9, in which take-all in June was on average only slight, the seed treatment, N timing

Table 22. Number of contributions (maximum 10) made by each test treatment to the smallest take-all rating (TAR) or greatest yield in three-factor combinations in experiments at Rothamsted

	1987		1988	
Test treatment	TAR	Yield	TAR	Yield
Late sowing	10	0	10	10
Soil fungicide	10	10	10	1
Triadimenol seed tr.	9	3	10	6
Autumn N	7	10	10	10
Divided N	5	4	0	10
Amm. sulphate	7	1	10	8

tr., treatment. Amm., ammonium.

and N form factors were replaced by seed rate (200 v. 100 kg/ha) and spring N rates (100 v. 150 v. 200 v. 250 kg/ha). The disease was affected less by late sowing than by soil fungicide and reduced seed rate. Late sowing decreased the incidence of infection overall, but moderate and severe infections were decreased only at the higher seed rate. Other interactions were rare.

In a comparison of the control measures that have been tested in the field at Rothamsted, BCAs have been mostly ineffectual and are not therefore ranked with those factors (sowing date > fungicides > fertilizers) that have decreased take-all. TAD on the other hand is one of the more effective and reliable ways of decreasing disease. This conflicts with the impression created by some research reports (mostly from overseas) and popular articles that have promulgated the views expressed in such reports.

5.5. Take-all control in a world-wide context

In Australia there are more reports of successful use of fungicides such as benomyl and triadimefon against take-all than in Britain. Bateman (1989) suggested that similar fungicide effects in Britain's fertile soils with their greater yield and proportionally smaller losses

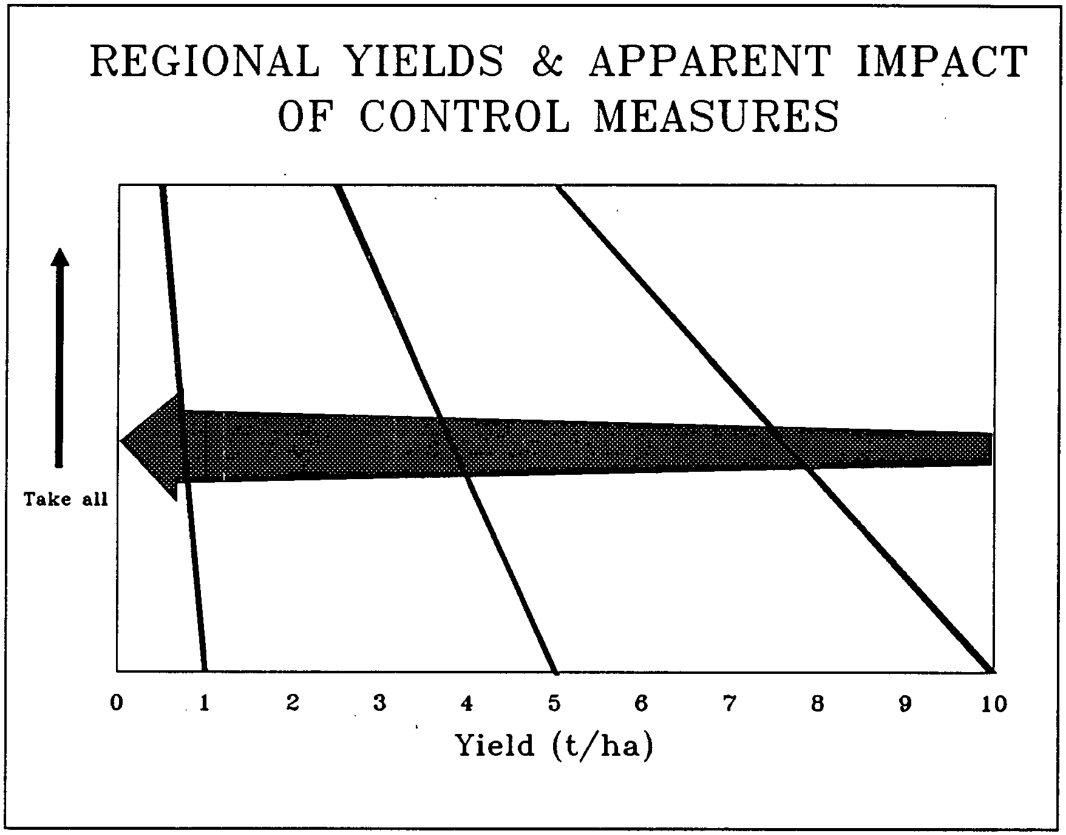

Figure 11. In regions where take-all is a problem its effects on yield tend to be proportionally similar and control measures (stippled arrow) are generally more effective in lower-yielding regions (details in text).

from take-all were less noticeable. The question of whether losses in infected crops in Britain are proportionally smaller is debatable. Figure 11 puts together some ideas arising from work with artificial inoculum on spring wheat. The yields of uninfected crops in Australian experiments were about 1 t/ha and the most infected crops yielded about half that. Work at Rothamsted also showed almost a halving of yield over the range of disease created by using artificial inoculum (see 6.4.2.), when uninfected crops were yielding 7 t/ha. Figure 11 also shows what 50% reductions would look like for a good winter wheat yield and a 5 t/ha cereal. If similar, proportional disease effects occur in different countries, the absolute losses per ha of infected crop will be much greater in high-yielding regions. In the UK generally larger yields, unawareness of a take-all problem in fields not showing patches and recent grain surpluses may have conspired to mask this point. Maas *et al.*, (1989) reported even bigger yield reductions of up to 72% in South Africa using relatively huge amounts of artificial inoculum, but their unusual method of assessing disease makes comparison with other results difficult.

Table 23. A simple scheme showing some characteristics of wheat production in different parts of the world in relation to some factors which affect take-all (full explanation in the text)

System	Trends		
Inputs	High	←→	Low
Fertility	High	←→	Low
Yields (t/ha)	6.0(UK)	2.3(USA) 1.9(S. Am.)	1.5(AUS)
Factors	Effects in relation to trend above		
TAD	Classical		Different or none
BCAs	Weak		Some large
Other*	Small		Some large

AUS, Australia; S. Am., South America

*, Fertilizer treatments (Mn^{2+}, NH_4^+, Cl^-)

The accumulating experience that control measures that work in Australia and elsewhere are ineffective or unimpressive when applied in the UK is worth further consideration (Table 23). Cereal soils in the UK are generally more fertile than in many regions outside Europe. Further, the UK cereal production system uses much greater inputs: e.g. an average of 189kg N/ha for winter wheat in 1989, compared to relatively little or none in Australia; much use of pesticides compared to 52% of wheat produced without pesticides in the USA (Scott, 1990). Because spring wheats may suffer from take-all more than winter wheats and may rely more on their seminal roots, the relative importance of the two kinds of wheat in different countries also needs to be taken into consideration. The national average yields of wheat given in Table 23 are a crude categorization, pooling all sorts of data: the figure for the USA, for example, contains winter, spring and Durum wheat and average winter wheat yields for individual states range from 1.7t/ha in New Mexico to 6t/ha in Arizona. There is some indication that reports of successful control of take-all may be related to this trend. At the high fertility end, take-all decline is well-documented and of the classical kind which follows a peak of disease in consecutive cereal crops. Moving towards lower fertility, TAD becomes weaker, less frequent, ephemeral or is absent. Many of the other factors that affect take-all do so most convincingly in regions that would be located some way along this scale. Forms of N, chloride fertilizers and Mn deficiencies are all factors that have had greater effect in the USA than in the UK. Systems for growing wheat that are mostly alien to British farmers (irrigation, double cropping with soya beans and alternating cereals with self-regenerating legume pastures) are also encountered along this trend. Although long regarded as an ecologically-obligate parasite with a low competitive saprophytic ability, the take-all fungus is now reported to grow through soil in Australia. This is probably because the soils in question are low in organic matter, total nitrogen and have low cation exchange capacities. Western Australian soils seem to support more take-all fungus and the fungus seems to be more infectious than in UK soils (see 2.3.5.). Claims for simple systems that predict take-all and conviction that resistance exists amongst cultivars (see Figure 2) tend not to be associated with the high fertility. It may be that the high fertility-high input system presents a biological buffer that is not easily overcome by single BCAs, which appear to achieve effects in less fertile regions. TAD may be a phenomenon more characteristic of high fertility regions, where only robust, multi-component systems can influence take-all significantly.

Usually liming increases take-all and ammonium sulphate fertilizer decreases it (Table 24). The mechanisms for this are not known, but explanations for the effects of liming are changes in soil pH and predisposition of the host as nutrients such as Cu, Mn, Fe, Zn and Mg become less available at higher pHs. The effect of $(NH_4)_2SO_4$ has usually been explained as an interaction between some or all of these. The following examples will suffice to make the point that many factors interact:

i. In Australia applications of ammonium sulphate favour the antagonist *Trichoderma*, which suppresses the take-all fungus.

ii. In Switzerland certain fluorescent pseudomonads produce HCN, which suppresses take-all. The production of HCN is induced by iron and the availability of iron depends on the type of clay mineral in the soil [Fe is available in vermiculitic, but not illitic soils]. Hence there is a soil type effect.

iii. In the USA dissolution of Mn in soil as Mn^{2+} [manganous ion] is promoted by low pH (H^+), electrons or reducing power and low O_2 tension. These transformations are favoured by NH_4^+-N, superphosphate fertilizer and organic matter, all of which have been reported to affect take-all. Mn may be unavailable to the plant because of microbial oxidation. Mn-oxidising populations increase response to NO_3^--N. Table 25 shows many associations that have been observed for take-all, nitrification and manganese availability. It is now suggested (Huber, 1990) that the concept unifying the effects of pH and forms of nitrogen in plant disease is the availability of Mn.

Table 24. The effects of applying lime or ammonium sulphate

	Lime	Ammonium sulphate
Take-all	Increased	Decreased
Proposed mechanisms	pH Host disposition	Interactions among microbes, nutrients and pH

5.6. Decision making and forecasting

In the last decade take-all has waxed and waned in intensity and has developed a disturbing tendency to reach damaging levels more frequently in second wheats than in earlier years. Weather, early sowing, and oilseed rape in rotations all may have a bearing on this (see 2. and 4.).

Table 25. Conditions affecting take-all and their effects on nitrification and manganese availability (from Huber, 1990)

Condition	Effect on: Take-all	Nitrification	Mn availability
Nitrate nitrogen	I	I	D
Liming	I	I	D
Animal manures	I	I	D
Previous crop - soya bean	I	I	D
- alfalfa	I	I	D
Alkaline soils	I	I	D
Loose seedbed	I	I	D
High soil moisture	I	I*	D*
High plant populations	I	-	D
Short runs of cereals	I	-	D
Plant stress	I	-	D
Ammonium nitrogen	D	D	I
Fertilization - manganese	D	-	I
- chloride	D	D	I
Nitrification inhibitors	D	D	I
Acid soils	D	D	I
Previous crop - oats	D	-	I
- lupins	D	D	I
Tolerant cultivars	D	-	I
Late sowing	D	-	I

I, increased; D, decreased; *, variable with some other conditions
-, unknown effect

Take-all of cereals is an example of an important disease where changes in incidence and severity have occurred over a period of years, but have never been properly explained. During the last two decades epidemics of the disease have been monitored at Rothamsted and Woburn.

The Woburn case is particularly interesting because the observed fluctuations are thought not to be complicated by previous cropping, which means they are likely to be more directly weather-related. Identifying which factors have been important, however, is difficult. Potential soil moisture deficit (PSMD) is often considered important. In the last 20 years annual averages for PSMDs were dominated by a very dry year (1976), otherwise they show a weak trend towards wetter soils. Increased disease in the 1980s may have been affected by changes in PSMD (Figure 12), but there is clearly a need for much more detailed analyses of weather and take-all data.

5.7. Recommendations for research

5.7.1. Fungicides

i. The need for fungicide treatments should be evaluated by: a) surveys to assess the importance of the disease; b) determining the reliability of risk assessments; c) improving estimates of yield loss from take-all, allowing economic evaluation of treatments to be made.

ii. Highly active fungicides with appropriate physico-chemical properties (already identified) need to be found, probably by a programme of synthesis.

iii. Slow-release formulations, for use as seed coatings or soil treatments and preferably using non-persistent soil-mobile compounds, and other methods of application, e.g. in the seed furrow as granules, need to be investigated.

iv. Programmes of synthesis and testing of phloem-mobile compounds need to continue.

v. Relationships among seed treatment fungicides (triadimenol and related compounds), sowing date, host crop and cultivar, nitrogen uptake and other aspects of host plant physiology merit detailed study.

5.7.2. Biological control

Breeding for resistance to take-all is attractive but has not been achieved. Many cultivars have been screened for resistance with little success. The possibility of transgenic wheat needs consideration. The current level of information both from the literature and from practical experience is inconsistent in relation to the benefits claimed to be achievable by the use of BCAs. Promising results have been achieved in environmentally controlled situations or in artificially infested fields

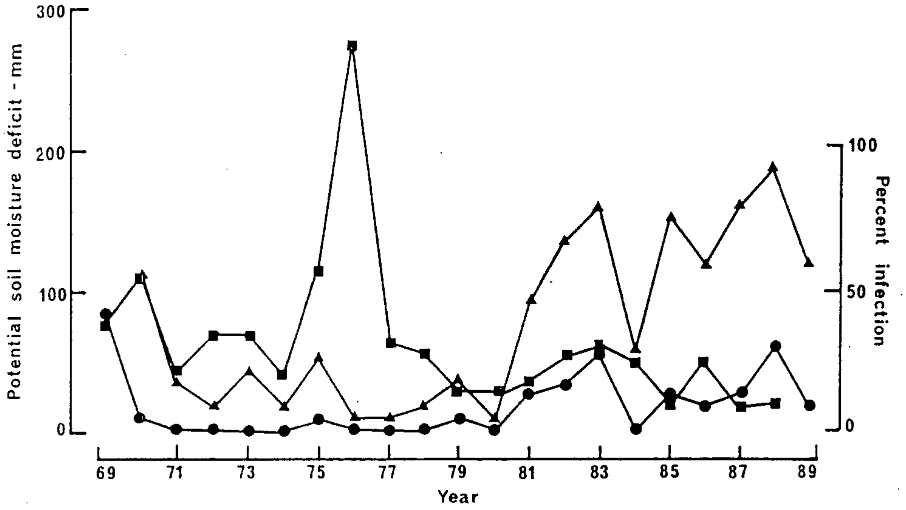

Figure 12. Changes in potential soil moisture deficit (annual averages) and the incidence and severity (in July) of take-all in continuous spring barley in a field at Woburn, Beds., 1969-89. ■ = potential soil moisture deficit, ▲ = % plants infected, ● = % roots infected

but results are more variable in the field with natural infestations. Such conflicting results make it difficult to put forward an unequivocally positive case for the use of BCAs at present.

Inconsistent field results are perhaps to be expected until a) the ecology of BCAs, b) the interactions of BCAs with the root and the pathogen in the rhizosphere and c) the interactions of BCAs with environmental factors, including those which are controllable to some extent (e.g. soil pH) and those which are uncontrollable (e.g. weather patterns) are better understood. Much fundamental work still has to be done in such areas and there appears to be little funding available in the UK at present for such work.

The commercial requirement of 'reliability' will not be achieved until the mysteries of root colonization, host specificity of effective agents, sites of action and the biological characteristics that contribute to the ability of a BCA to suppress the pathogen are resolved for the practical situation. If these characters can be determined it might then be possible to enhance desirable properties in an agent by genetic manipulation techniques and also to tailor organisms to environments because it is unlikely that isolates will be transferrable from one environment to another.

The alternative to enhancing the BCAs that are currently available is to continue to screen potential BCAs in the laboratory and field for antagonistic activity. This is time-consuming and laborious, but it is the method most likely to produce new antagonists in the short term and ideally should be done in parallel with the fundamental work.

Effective delivery systems for the BCAs must also be found. Seed coating, although effective, can be restrictive and alternative means of delivery may be needed to provide easy handling and an acceptable shelf-life.

Finally, there is a need to investigate the use of root-stimulating organisms to decrease the effects of disease, rather than to control it, and to study manipulation of the soil environment to stimulate the development of antagonistic organisms (e.g. Lennartson, 1990).

CHAPTER 6. EXPERIMENTAL AND PRACTICAL PROBLEMS

6.1. The pathogen

This section describes the practical problems of differentiating the take-all fungus (Ggt) from fungi in related taxa and briefly summarizes the taxonomic background.

6.1.1. Background and literature

Gaeumannomyces is a genus of ascomycete fungi which has four known species which infect roots of grasses and cereals, or sedges. They produce characteristic ectotrophic mycelial growth and hyphopodia (appressorium-like hyphal swellings). The taxonomy of *Gaeumannomyces* was reviewed thoroughly by Walker (1981) and only a brief summary will be given here. The visual appearance of members of this complex of fungi on host plants and in culture were discussed respectively by Deacon (1981) and Cunningham (1981).

G. graminis and *G. cylindrosporus* infect cereals and grasses and *G. caricis* occurs on sedges. Other poorly defined taxa are known, including two more from sedges. A fourth species, *G. incrustans*, isolated from turf grass roots in the USA, was recently described (Landschoot & Jackson, 1989). The species are differentiated mainly by ascospore morphology.

The three varieties of *G. graminis*, vars *graminis* (Ggg), *tritici* (Ggt, the take-all fungus of wheat and barley) and *avenae* (Gga) are differentiated by ascospore size and hyphopodial structure (the hyphopodia of Ggg are characteristically lobed) as well as having different host preferences. Ggg is widespread on grasses and causes a sheath rot in rice; Ggt is most commonly associated with wheat and barley and Gga with oats and turf grasses. Some oat-attacking isolates of *G. graminis* with ascospore characteristics of Ggt have been described from Australia (Yeates, 1986a).

Whilst rye is generally less susceptible to Ggt than are wheat or barley, isolates with increased pathogenicity to rye seedlings (R-isolates) have been identified in cereal crops in Britain and other parts of Europe (Hollins & Scott, 1990). They seem not to show particular preference for rye crops, however, and occur in mixed populations with normal, or N-isolates, and isolates with intermediate pathogenicity. The taxonomic and ecological significances of their distinctness from the N-isolates are unknown. Some of these isolates have been shown to be distinct in their effects on disease and yield in the field (T.W. Hollins, pers. comm.).

A variety of *in vitro* and *in vivo* methods are available for inducing perithecial production by these fungi, but different methods are suited to different fungi and some isolates, which fail to produce perithecia, remain of uncertain affinity (Holden & Hornby, 1981).

The conidial (asexual, or anamorphic) state of *Gaeumannomyces* is *Phialophora*. *P. graminicola*, frequently found on grass and cereal roots and often associated with natural biological control of take-all, is the conidial state of *G. cylindrosporus* (the full demonstration of this relationship has recently been completed at Rothamsted). In Australia and South Africa *Phialophora* isolates with lobed hyphopodia are regarded as anamorphs of Ggg and some produce perithecia. Perithecia of Ggg have been induced less frequently on plants inoculated with English isolates of *Phialophora* sp. (lobed hyphopodia) (R.J. Gutteridge, unpublished). Scott (1989) suggested that South African isolates of *Phialophora* sp. (lobed hyphopodia) from Italian millet are states of Ggg in which the ability to produce perithecia has been lost as a result of adaptation to dry conditions; this is unlikely to be the case for British non-perithecial isolates. Other *Phialophora* spp., e.g. *P. zeicola*, identified from South Africa and Brazil, do not have perithecial (teleomorphic) forms in the genus *Gaeumannomyces*.

Phialophora sp. (lobed hyphopodia) and *P. graminicola* can often be differentiated additionally on the plant by vesicles in the root cortex; these are smaller in *P. graminicola* (Deacon, 1981). However, vesicles of intermediate size have been observed in cereal roots from some fields at Rothamsted (R.J. Gutteridge, D. Hornby, unpublished) suggesting that vesicle size may not always be diagnostic, or that intermediate or otherwise different forms exist.

Serological and molecular biological techniques are being used increasingly to assist in establishing taxonomic relationships among fungi and other organisms. Fungi in the *Gaeumannomyces/Phialophora* complex are amenable to these techniques. Diagnostic kits based on serological reactions of fungal (and viral) pathogens are an increasingly realistic prospect since the development of ELISA and related techniques, and some are already available commercially for certain pathogens, but not the take-all fungus. Molecular techniques would be less amenable as a means of providing rapid diagnoses in crops, but have potential for identifying fungi in laboratory work.

The close relationship amongst varieties of *G. graminis* was demonstrated by their similar serological reaction (Abbott & Holland, 1975). Abbott (a pers. comm. in Walker, 1981) also found that the serological reactions of *Phialophora* sp. lobed hyphopodia from Britain and Ggg were identical.

Electrophoretic methods to produce soluble protein patterns have indicated a closer relationship between Ggt and Gga than between either of these and Ggg (Abbott & Holland, 1975). In more recent work, similar protein patterns were found for different isolates of Ggt, but isolates of *Phialophora* spp. with similar colony morphology in culture produced patterns which differed from those of Ggt to different extents (Maas *et al.*, 1990).

Another molecular technique, that of comparing restriction fragment length polymorphisms (RFLP) using DNA probes has shown similarities among isolates of *G. graminis* which infect the same cereal (wheat, rye or oats) (O'Dell *et al.*, 1987), but this work apparently did not progress beyond the preliminary stages.

6.1.2. Identifying the fungi in the UK

Walker's (1981) detailed studies demonstrated that much remains to be learned about the evolutionary relationships among fungi of this group. They are root pathogens and ectotrophs of turf and other grasses and cereals and can occur on other plants; some, notably Ggt, are damaging pathogens and some suppress the pathogenic activity of Ggt. Their identification in culture and on the host plant can be difficult and their symptoms on roots can be confused. Our understanding of the biology of take-all would benefit from clarification of the taxonomic and ecological relationships among the fungi in the complex and by improved methods of identifying them.

Ggt is the fungus which causes take-all in wheat and barley in the UK and other cereal-growing areas of the world. It is commonly found in association with other taxa in the complex. The present status of Gga in the UK is unknown, although it has been found in the past, notably in

Wales (see 6.2.). There is no evidence for the presence of virulent oat-attacking isolates of Ggt in the UK, although take-all lesions are occasionally found on oat roots early in the season, but seem not to develop further, and some Ggt isolates clearly infect oat seedlings in pot tests. *P. graminicola* is common in the UK and is thought to be a major cause of the delayed onset of take-all in sequences of cereals following leys. *Phialophora* sp. (lobed hyphopodia), although by no means rare, is apparently less common in the UK. Tests on pot plants, however, suggest that it has even greater potential for suppressing take-all than *P. graminicola*, as well as an ability to stimulate root production.

6.1.3. Recent research in the UK

The relationships within the *Gaeumannomyces/Phialophora* complex are being investigated currently by ELISA and DNA methods at Rothamsted, using a common range of isolates for both approaches. Although in the early stages, both of these are proving to be promising lines of research.

Reactions on ELISA plates to polyclonal antiserum raised to an isolate of Ggt have suggested a closer relationship between the varieties of *G. graminis* than between *G. graminis* and other species.

A mitochondrial DNA fragment cloned from Ggt in the USA (Henson, 1989) is being used to compare RFLPs of the isolates. Whilst Ggt and Gga isolates are clearly different from Ggg, *Phialophora* spp. and *G. caricis*, there are indications of slightly varying DNA patterns among isolates of Ggt.

6.2. Host-parasite interactions

The concept of a wheat take-all fungus (Ggt), which does not attack oats and an oat take-all fungus (Gga, or OTAF) which does, has been shaken by the discovery in Australia of oat-attacking isolates of the wheat take-all fungus (OATAF). In the UK oats serve as a non-susceptible break, but in Australia they are a carrier. In the UK the OTAF has traditionally predominated where oats are grown (Wales, Scotland and Cumberland: Garrett & Dennis, 1943), but it has been reported only infrequently in the last two decades. It is also apparently absent in Australian cereal crops, perhaps because of annual grasses in the alternating pastures and the climate. It is suggested that the OATAF is a specific race.

Dark mycelial colour is not an essential prerequisite for the functioning of the enzyme avenacinase in oat-attacking *G. graminis* isolates; this and cysteine tolerance are unlikely to be useful in identifying taxonomic varieties of Australian isolates (Yeates, 1986b). The transfer of avenacinase to the take-all fungus is a possible way to test ideas on pathogenicity. The genetic and biochemical basis for pathogenicity is currently being investigated in a study of the properties of avenacinase (Osbourn *et al.*, 1989). The results so far are consistent with the view that the enzyme contributes to the pathogenicity of Gga on oats.

6.3. **Field experiments**

6.3.1. Design

Experimental design is the arrangement of experimental units to optimize error control against a background of environmental variability and practical limitations. In practice, however, experimental designs are more commonly determined by tradition and their suitability is seldom questioned. This is particularly true for the randomized block design and the use of large plots amongst which relative homogeneity of environmental conditions within the blocks cannot be confidently predicted. Hornby *et al.* (1983) demonstrated significant effects of systematic field variation and interactions between field variation and weather on yield of spring barley in years when take-all was slight. The decision to adopt one particular experimental design may involve a number of specific considerations (Gilligan, 1990b), e.g. the number of treatments, replication, plot shape, plot size and block size. Possible designs range from the simple complete randomized block to more complex incomplete blocks, nested and fractional replication designs. The use of any particular design should be determined by the number of treatments and the scale of important environmental heterogeneity (if known).

Treatment effects are tested against the residual variation amongst the experimental units, which may include imprecise plot estimates, caused by inadequate sampling techniques (see 6.3.3.) and lack of environmental uniformity amongst the experimental units. Simple blocking will not account for interactions between environmental differences and treatments, which are indicated by a high residual mean square.

Treatments which are particularly sensitive to inoculum density and variation in the soil environment, or which have small effects, may be tested in micro-plots in incomplete block designs to minimize within block variability (see later this section). Variability arising from a patchy distribution of inoculum may be overcome by use of artificial inoculum (see 6.3.2.). Alternatively estimates of inoculum density and distribution before treatment application may be used as covariates, presupposing an unlikely linear relationship between inoculum density and disease which may be resolved by logarithmic transformations. Such covariates may be used also to allow for variable initial inoculum densities and variable rates of disease increase in estimating and describing disease progress. It may, however, be more appropriate to use covariates pertaining to systematic field variation in soil fertility, soil type and soil moisture (Hornby *et al.*, 1983), hitherto unexplored in relation to take-all. Whilst it remains to be demonstrated that traditional blocking techniques can successfully and reliably account for a significant amount of the environmental heterogeneity observed in take-all experiments, it may be rewarding to explore the use of nearest neighbour models in take-all research.

Field experiments are frequently laid out in plots the same width as the seed drill (often 3m) and several times this in length. This area is suitable for combine harvesting to determine grain yields per plot. However, the unreliability of take-all epidemics and the distribution of the disease in patches means that average disease levels may be too slight to achieve a result (e.g. to show the effects of putative control treatments) or that disease occurs at greatly different intensities in different plots leading to ambiguous results. Sufficient replication of plots and of sites to overcome these problems is usually impractical when such large plots are used.

Novel procedures for field experiments have therefore been developed to test candidate biological and chemical control treatments against natural infections of take-all (Hornby *et al.*, 1989). Small plots (31x37cm) were grouped in two adjacent complementary clusters of four (allowing six treatments plus two control plots) in a single replicate 'block-pair' (2x1m). It was argued that the area of each of these replicates would be sufficiently small that the likelihood of a uniform disease status of the plants occurring within it would be increased and consequently the precision of the experiments increased. In each year there was multiple replication on each of two sites and some sites were used in successive years by avoiding the re-use of block-pair positions. An additional advantage of this approach is that only small amounts of test materials are required. The disease assessment data for small plots (as opposed to block-sized areas) consistently had a smaller variance in the crop where take-all was at a maximum (i.e. the third cereal), but small plots were less effective as a means of decreasing variability after this peak. Comparing the variability of small plots, blocks within block-pairs and block-pairs scattered throughout the experimental sites in different seasons revealed evidence of changing disease patterns and suggested more than one scale of disease pattern (summarized in Figure 13). This scheme fits sites at Woburn better than Rothamsted.

To provide further information on the optimum size of sampling unit, take-all was assessed on all plants in blocks of 16 x 8 small plots in a third and two fourth wheats at Rothamsted and Woburn (unpublished). Differently-sized sampling units were obtained by a progressive doubling of the plot unit and the variance for each size calculated. Preliminary analyses have shown that in the third wheat the variance increased from that for small plots up to a maximum in the 2x2m sampling unit, which, since the variance progressively decreased in sampling units larger than this, may have been close to the average size of the take-all patches. In fourth wheats variances decreased as sampling unit size was increased from small plots to 2x1m areas and thereafter increased steadily for bigger areas. This suggests a change in the scale of patchiness resulting in both smaller and larger disease patches than were discerned in the more severely diseased 3rd crop. Patch size was predicted better from the number of consecutive cereals in the rotation than from the severity of take-all in the patches.

Sampling all the plants from very small plots often resulted in less variable results than sampling areas four (where block-pairs were scattered throughout a site) to sixteen (disease uniformity tests) times larger, especially in crops in which take-all was severe. Sampling units up to eight times larger than small plots tended to produce the smallest variances after there had been a peak of take-all in a cereal sequence. All these areas are much less than conventional plot areas.

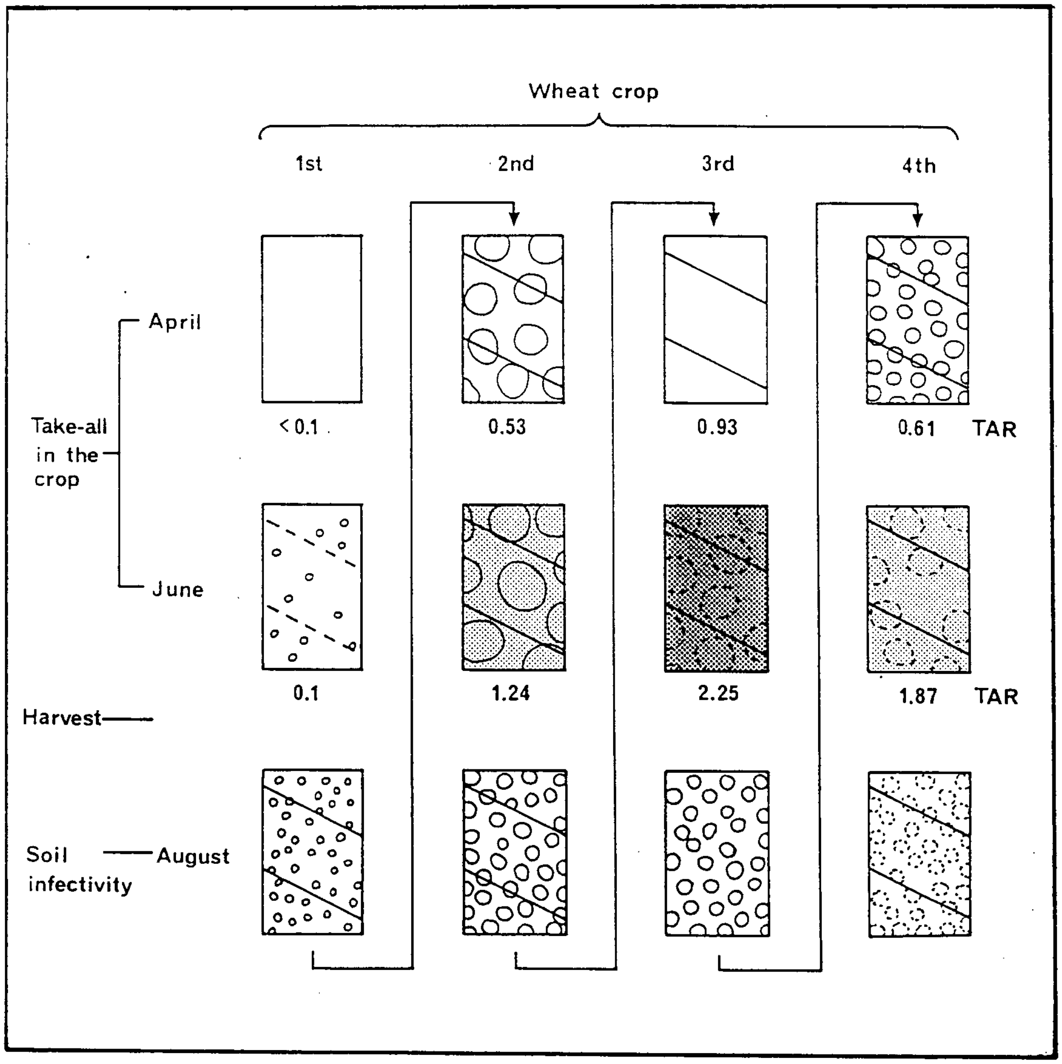

Figure 13. A scheme which incorporates the changing patterns of take-all suggested by data from successive wheat crops at Woburn during 1982-86. The rectangles represent a field at three sampling times in four consecutive crops. Medium-scale and small-scale patterns attributed to disease foci, spread from foci and changes in disease intensity are represented by circles. These occur on a background of a large-scale pattern (represented as the three major divisions of the rectangle) which is probably a site factor and is nearly always detected. ○ , strong pattern. ◌ , weak pattern. ↴ , discontinuity in hosts, i.e. 'between-crop' period. TAR, the take-all rating here has been divided by 100, giving a range 0-3; ☐ <1 (slight), ░ 1-<2 (moderate), ▓ 2-3 severe). From Hornby *et al.* (1989).

6.3.2. Artificial inoculation

Artificial infestation of plots and fields has been used in research on take-all of cereals, notably for testing the resistance of host cultivars and for testing fungicide treatments. The intention usually has been to create predictable and uniform disease. Whereas stubble and roots infected naturally with the take-all fungus have been transferred from one field to artificially infest another (Prew, 1980), artificially-produced inoculum has been used more frequently for infestation. It has been prepared on suitable media such as agar, sterilized seed, meal or straw, sometimes with an inert carrier such as vermiculite, and often dried before use. Killed and colonized oat grains have been very popular as a convenient inoculum, but Simon *et al.* (1987) considered them less realistic than smaller grains because of their larger food reserves.

Cunningham (1981) described the requisites of artificially-produced inoculum, emphasizing the need for virulent isolates of the pathogen, the importance of the nutrient status of the medium and the tendency for staling products to be formed in nutrient-rich media. The medium should not influence greatly the performance of the host plant, either by providing abundant nutrients, or unfavourably through toxins. The inoculum may need to be in a form suitable for application by farm machinery.

When used in testing putative control treatments, biological or chemical, artificially-produced inoculum should be placed so as not to influence unduly the performance of the candidate treatment in favour of control, unless the objective is preliminary screening or the investigation of relationships between infection sites and effects of treatments (e.g. Garcia & Mathre, 1987). The close proximity of inoculum and seed treatment fungicides may result in good disease control when treated seed is planted after being mixed with inoculum, but the performance of the seed treatment against natural infection can not be predicted reliably.

Artificially-produced inoculum is used to test the pathogenicity of isolates of the take-all fungus and for infection studies and epidemiological research. There is, however, some evidence of differences between natural and artificially-created epidemics; artificially-produced inoculum can cause earlier disease as well as retardation of growth, shoot yellowing and wilting not present in naturally-infected plants in the same location (Jensen & Jørgensen, 1973). The survival of natural inoculum tends to be greater than survival of the take-all fungus on artificially-colonized straw in soil (MacNish, 1976). Cotterill & Sivasithamparam (1989) found that after an artificially-inoculated first wheat crop there was more infection, which was more evenly-distributed, in a second crop than in wheat which followed a non-inoculated crop. Much of the infection in the crop after the inoculated crop would have arisen from infected root remains (i.e. natural inoculum) and this use of artificially-produced inoculum to create more uniformly-infested sites for experimentation in the following year may overcome some of the objections to experiments on artificially-inoculated crops. It is an approach that has been used by others for fungicide testing and screening cultivars for resistance (Kollmorgen, 1985).

Artificially-produced inoculum has also been used to investigate the relationship between amounts of take-all and grain yield (see 6.4.).

6.3.3. Sampling

Sampling strategy is concerned with the choice of sampling unit (e.g. single tillers, 10cm lengths of plant row), the number of sampling units (frequently determined by the availability of resources, in particular the time taken for disease assessment) and the sampling procedure (e.g. random or systematic). When the distribution of disease is patchy it is desirable that as much of the area is sampled as possible. The most accurate assessments of soil-borne disease result therefore from taking large numbers of small samples rather than from taking small numbers of large samples from a given area (Gilligan, 1982). However, the use of numerous random sampling positions is often impracticable. Where relatively few samples are taken from a large area, a 'W' pattern is usually better than other patterns of sampling positions, such as parallel diagonal transects, which achieve a lesser degree of randomness or greater variance (Delp *et al.*, 1986).

Guidance on numbers of samples to take is frequently sought by fieldsmen and advisers both for trials aimed specifically at take-all and for other relevant trials where plot size and experimental design are determined by factors other that phytopathological requirements. For monitoring combinable plot trials ADAS plant pathologists take 30 plants from 0.01ha plots where there is six-fold replication, but only 10 plants per plot on very large trials where factorial designs ensure much higher levels of replication for individual treatments. There is currently no simple general guidance against which to check in advance the adequacy of such choices. In estimating the number of sampling units for a desired level of confidence, it is advisable that some functional relationship between the variance and the mean is used to obtain reliable sample sizes (Gilligan, 1990b). Not all field experiments require the same degree of precision for estimating treatment differences and alternatively sampling strategy may be based on management costs or decision making criteria (Gilligan, 1990b).

6.4. **Disease-yield relationships**

Estimates of yield loss from take-all on a national scale have been made for England and Wales (see Table 4 and section 4.1.), but their reliability is doubtful because of the absence of detailed survey data and the problems of associating take-all with yield loss in individual fields (see below). There are also observations that some years which favoured take-all also favoured high yields nationally. This section describes attempts to determine losses attributable to take-all and outlines some of the difficulties that beset such endeavours.

6.4.1. Theoretical background

Disease-yield relationships are concerned with the quantification of loss in yield (dependent variable) per unit increase in disease (independent variable). They may be simple, with the rate of yield loss constant over a range of disease intensities estimated by a single disease variable (single point models), or complex, with several explanatory variables such as estimates of disease, host growth and environmental factors (multiple regression models). A number of independent variables may show correlation with yield and, more problematically, amongst themselves, so choice of disease variables, timing of the measurements and the statistical methods for selecting a minimum number of variables to explain the maximum variability in yield are important. However multiple regression models are multidimensional and therefore difficult to visualize and interpret. They are frequently concerned solely with explaining as much of the variation in yield as possible. The complex interactions, including the effect of disease on host growth, the response by the host to disease and how these are mediated by the environment, are undoubtedly reasons why reliable and repeatable disease-yield relationships are difficult to obtain.

Models for disease-yield relationships. James (1974), James & Teng, (1979), Teng, (1985), Teng & Johnson (1988) and Campbell & Madden (1990) have reviewed disease-yield relationship models.

Only single point models (Y=B0+B1.D+e, where Y is yield, B0 and B1 constants, D take-all and e a measure of error) have been applied to describe the effects of take-all on grain yield. Efforts to improve the relationship have concentrated on disease measurement and experimental techniques for generating different amounts of disease. Estimates of disease incidence have often been made only once, usually towards the end of the growing season (Slope, 1967; Slope & Etheridge, 1971; Shipton, 1975). Shipton (1975) found that the incidence of severely-diseased plants correlated better with yield than did the incidence of infected plants. Although they are popular, it is questionable whether single, end-of-season estimates accurately reflect the effect of disease at a specific time and the cumulative effect of disease as the crop develops (Teng & Johnson, 1988). The shape of the DPC may be particularly important in epidemics of long duration and where the diseased portions of the plant are distinct from those taken for yield (Teng & Gaunt, 1981), as in take-all. The progress of take-all can vary markedly with cropping history, or with season and may be variable within seasons (Werker *et al.*, 1991).

Extensions of single point models utilize one or more disease variables which describe selected aspects of disease progress. Thus, in the multiple point models yield loss is a function of disease estimated at regular intervals throughout the growing season (Y=B0+B1.D1+B2.D2+...+Bn.Dn+e, where D1,D2...Dn are estimates of disease at times 1,2...n and B1,B2...Bn are the associated parameters). These models have been recommended for long-duration epidemics with variable infection rates (James, 1974). Decreasing the time interval between successive observations is likely to lead to increased correlation amongst the independent variables, but using the difference between successive observations, or disease variables which summarize the relationship between the successive observations (e.g. the mean rate of disease increase) may overcome this. These models identify high correlations with yield loss and may therefore point to future models that would need fewer samplings. A critical point model describes yield in terms of the time of onset of the epidemic and the subsequent rate of disease increase. In take-all, the time of onset of the epidemic may be more difficult to determine than the time at which a certain critical level of disease incidence and/or severity occur.

Whilst the derivative of the DPC provides an estimate of the rate of disease increase, the integral provides an estimate of the total amount of disease the host has been exposed to throughout the growing season. The integral of the function of disease progress between times t1 and tn is an estimate of the AUDPC for that period. It takes no account of the shape of the disease progress curve and gives equal weight to disease occurrences at all stages during the growing season. Including a rate parameter, or partitioning the AUDPC into 'critical' stages in relation to host growth are refinements. Alternatively, the AUDPC may be described in terms of a function of both disease and time (Shaw & Royle, 1987), but such surface response models require much data (Teng, 1985).

The form of the yield-loss function. Without transformations of the disease variables and use of multiple regression models it is unlikely that a straight line relationship is appropriate (Werker & Gilligan, unpublished). A constant rate of yield loss is an over-simplification of interactions between host, disease and environment. Disease tolerance (surplus root function), stimulation of new roots and compensation by non-diseased tillers result in a range of disease intensities for which there is little or no loss in yield, otherwise termed minimum thresholds (Teng, 1985). There is some evidence for a threshold in the take-all results presented by Prew *et al.* (1986). It is not known what the yield loss function is between total absence of disease and a minimum threshold. There may be a small but significant amount of yield loss before compensation occurs, or there may be yield enhancement as in other systems (Burleigh *et al.*, 1972; Gaunt, 1980; Teng, 1985). Non-linear models can incorporate explicitly parameters to estimate both lower and upper threshold levels (Seinhorst, 1965; Madden *et al.*, 1981; Madden, 1983), but evidence of an upper threshold above which no further loss occurs is weak. If root function is destroyed completely prior to grain filling, then 100% yield loss may be expected, but a similar disease severity achieved during grain filling is not likely to cause 100% loss. In addition, what is perceived as 100% diseased roots may not mean the total absence of a functional root system.

Factors which are known to affect yield independently of disease (e.g. weather, soil type, date of sowing and soil fertility) need quantifying. If the dependent variable is represented by the absolute yield, then the disease-yield relationship will vary: the differences may involve only the constant or vertical displacement of the disease-yield relationship and therefore will not affect the estimated rate of yield loss, or they may reflect different disease-yield relationships amongst different weather patterns and agronomic variables. Methods for testing such effects are akin to parallel curve analysis and are relatively simple in statistical terms, but not always meaningful when there is a high correlation between environmental variables and disease. Circumstances may arise in which yield is adequately defined in terms of selected agronomic and environmental factors without reference to disease (Werker & Gilligan, unpublished). An early attempt to quantify the relative effects of environmental factors and crop damage explained 78% of variation in wheat yields in Canada over a 10-year period (Sallans, 1948).

Statistical considerations. In developing a disease-yield model there may be many independent variables to consider, including some which have a significant overlap of information. Procedures for 'picking-out' significant explanatory variables, or 'dropping' least significant variables have been devised (Neter & Wasserman, 1974). The first approach involves fitting all possible models (i.e. 2^N, where N is the number of independent variables) and selecting the best on the basis of statistical tests. If the number of parameters is too large to test all possible models, stepwise regression techniques may be used, either adding explanatory variables to find the ones which cause greatest reduction in the residual mean square, or dropping least significant variables after all explanatory variables have been fitted. These regression techniques are powerful and relatively simple, but no attention is paid to the biological interpretation of the order of variables added on, or to the combination of variables that give rise to a 'best' model. To overcome some of these problems an order of priority in the addition of variables, based on biological, practical or other criteria, may be introduced. Multiple regression models assume that the explanatory variables exert independent effects on yield and that correlation between variables has no significant effect on the validity of using such regression techniques (Teng, 1985). More sophisticated multivariate techniques (e.g. principal components analysis and canonical correlation) have been used to select variables amongst which correlation is minimized and have predicted yields of wheat using 12 explanatory variables and explained 84% of the variation in yield (Stynes, 1980).

6.4.2. Practical approaches to assessing losses in grain yield and quality

Relationships between naturally-occurring take-all and grain yield have been explored in a number of ways:

i. survey or experimental data involving different fields, locations and/or treatments (e.g. Rosser & Chadburn, 1968; Polley & Clarkson, 1980);

ii. data for one year from one field with experimental plots treated differently to influence disease (e.g. Nilsson, 1969; Prew *et al.*, 1986; Gutteridge *et al.*, 1987);

iii. data for one year from a field with take-all patches (MacNish & Dodman, 1973).

None of these is entirely satisfactory and in each case it can be argued that disease was confounded with one or more other factors. Conditions which contribute to poor yield, such as waterlogging, stress caused by drought, or nutrient deficiency can also increase the effects of root infection. ADAS workers have on occasions observed areas of fields where, because poor soil conditions have exacerbated the effects of root loss, the expression of symptoms has been most severe, yet there has been a smaller percentage of roots infected than elsewhere in the field.

Yield loss on farms is usually ascribed to take-all only when growth is visibly poor, or more commonly when patches of prematurely-ripened plants develop. ADAS cereal disease surveys include an assessment of such patches and this is used to indicate take-all severity nationally (see 2.3.2.). Incidence of whiteheads (see 2.3.2. for comments on the use of this term) in experimental plots often relates better than root infection to yield, but yield loss is also likely to occur when disease is severe but conditions are such that whiteheads do not become visible. This means that a farmer may often have no indication of the extent of yield loss from take-all, or even of the severity of the disease in a field. Similarly, some effects of take-all on grain quality can be clearly anticipated when whiteheads are present - grains in the early-ripened patches are small and often have mould growth which results in discoloured flour.

Effects on grain quality occur most directly as a result of decreased grain-filling. Bockmann (1963, summarised in Manners & Myers, 1981) found that thousand-grain weight (as well as total yield, tillering and the number of grains per ear) was decreased by the most severe infection in artificially-inoculated plots of wheat. Thousand-grain weight was also sometimes increased in less severely infected compared with healthy plots.

A recommendation in a previous HGCA Review (Stevens *et al.*, 1988) was for the continuation of experiments to assess the relationship between disease, crop maturation and Hagberg falling number. Take-all can affect crop maturation, as seen by the patches where severe take-all has led to premature ripening (and yield loss). When a prematurely-ripened patch stands for a period of wet weather before the crop is harvested, there may be increased alpha amylase activity.

The optimum time and disease level (i.e. 'critical points') at which take-all should be assessed to achieve the best relationship between the amount of take-all and yield are likely to vary amongst seasons, sites and types of crop. In a survey of farm crops, disease in samples taken at a late growth stage (anthesis) related better to yield than that in samples taken during tillering (Rosser & Chadburn, 1968). Although disease assessments during anthesis and grain-filling are generally accepted as relating best to yields, there was a better correlation between yield and take-all at GS31 than at anthesis where no nitrogen was added in two of a series of ADAS trials between 1981 and 1983; where 120 kg or 200 kg N/ha were applied there were no correlations (L.V. Vaidyanathan, pers. comm.). Another ADAS survey (Polley & Clarkson,

1980) relied on assessments made just before harvest, casting some doubt on the validity of the results. However, disease assessments made at frequent intervals in an artificially-inoculated spring wheat crop showed that the relationship between take-all and yield was strong up to growth stage 85 (Bateman & Hornby, 1989 and unpublished), suggesting that very late assessments made for this purpose are sometimes acceptable.

The use of artificial inoculum to clarify the disease-yield relationship has been little explored, although application of different amounts of inoculum has resulted in different amounts of disease and yield (Rovira, 1978; Rothrock, 1987). Such differences may sometimes result from differences in disease incidence rather than from different severities of infection on individual plants. In recent work at Rothamsted (Bateman & Hornby, 1989), the relationship between take-all severity and yield of spring wheat was investigated using different methods of applying inoculum (see 6.3.2.). The procedures followed were intended to achieve uniform infection within field plots, but different severities among treatments, by using a sequence of cultivations that allowed inoculum to be placed at different depths. In this experiment, incidence (% plants infected) and severity (% roots infected) of take-all were related similarly to yield. The incidence of whiteheads was less well correlated with yields than were root disease assessments where cultivation treatments had created slightly different soil conditions. In other experiments (Gutteridge *et al.*, 1987) whiteheads were correlated better with yields than was root infection.

Assuming that a root infected in the upper part of its main axis becomes blocked and non-functional, then 100% roots infected should result in the smallest possible grain yield (but depending on the timing of infection). Published disease-yield relationships are given in Section 1.2.3. and extrapolating from the best regression lines in the Rothamsted spring wheat experiment gave an intermediate value, i.e. each 1% increase in roots infected led to a decrease in yield of 0.44%. These estimates seem to accord with results from plots of spring wheat and spring barley which became severely diseased after artificial inoculation; yield losses of 50% and 24% respectively for the two crops were estimated by comparison with uninoculated crops (Cunningham *et al.*, 1968).

Cunningham *et al.* (1968) also made a detailed comparison of grain quality in artificially-inoculated and uninfected spring wheat and spring barley in Ireland. Although disease levels were similar in the two crops, spring barley was more tolerant, with a smaller yield loss than wheat (see above). Flour colour was poor (caused by mould growth on prematurely-ripened ears) and thousand-grain weight and bushel weight (formerly used as the equivalent of specific weight) were decreased by disease in both crops. Take-all also caused an increase in the protein content and in diastase (barley only) in the grain. This is a dilution effect, smaller grains containing relatively more protein as the carbohydrate content decreases. Take-all also increased the gluten slightly in wheat, but not sufficiently to affect baking. Protein quality and dough characteristics were not affected in wheat and there was little or no effect on alpha amylase activity. These results relate only to one season (1964) in which good harvesting conditions prevailed, but as the authors pointed out, this approach can yield more information than surveys where there are many factors, such as soil conditions and rotations, influencing disease levels and grain yield and quality.

In an experiment in which take-all in winter wheat, assessed at growth stage 59, was decreased significantly by seed treatment with triadimenol plus fuberidazole, the percentage of plants infected in different plots was negatively correlated with yield, thousand-grain weight and specific weight (Jones, 1987).

6.4.3. Recent research in the UK

Oat breaks have been used in experiments to determine yield losses because the nutritional status of the soil is similar after each cereal and the oat-attacking variety of the take-all fungus has a limited distribution within the UK. In experiments at Rothamsted during the 1980s losses from take-all were 2.2 t/ha (3-year mean) for winter wheat and 1.0 t/ha (6-year mean) for winter barley when comparisons were made with crops grown after oats. In years when take-all was severe the losses were 3.0 t/ha for wheat and 1.5 t/ha for barley.

A series of factorial field experiments on winter wheat at Rothamsted (1986-89) were used to investigate the effects of different husbandry and chemical treatments, applied separately and in combination (see 5.4.). Because of the ranges of disease levels and the relatively large number of plots (up to 64), results from these experiments were used to examine the relationships between amounts of take-all infection and grain yield (Figure 14) and quality (Figure 15). The main factor affecting take-all was sowing date (September v. October), and grain yield was affected additionally to a large extent by plant density, a consequence of sowing date and seed rate; relationships for different sowing dates and seed rates are therefore often shown separately.

Grain yield. In the 1986 factorial experiment, in which disease was slight to moderate, regressions of take-all rating in June (TAR; scale 0-300) on yield were not significant for either early or later sowing. In 1987, disease was moderate and there were significant regressions for early-sown and later-sown plots, but with only 17% and 9%, respectively, of the variance accounted for. In 1988, when some plots were severely infected, there was a stronger association between TAR and yield in early-sown plots (64% of the variance accounted for in the regression model) than in the less severely infected later sown plots (14% of the variance accounted for). Disease levels were similar in 1989 when a moderate association was indicated (38% of the variance accounted for). However, these significant regressions may be misleading as there is often an indication that the yield response to increasing TAR was negligible at TARs less than 100. In each of the last two years of the experiments, yields in the most severely diseased plots were 35-45% less than in those least severely infected, although the different treatments mean that not all of this difference can be assumed to result directly from take-all.

The work of (R.W. Clare, I. Ap Dewi and D.J. Yarham, unpublished) referred to in 1.2.3. showed that in the years 1983-86 there was a significant relationship between TI and yield of winter wheat, irrespective of whether TI was assessed during November-January, or at harvest. The amount of yield loss per unit of TI was about twice as much for November-January assessments as for assessments at harvest.

Grain quality. The main effects of take-all on grain quality in the factorial experiments resulted from a direct effect on grain size, indicated by the negative correlations between TAR from June assessments and specific weights in 1988 and 1989. These paralleled to some extent the correlations between TAR and grain yield in those years, i.e. the

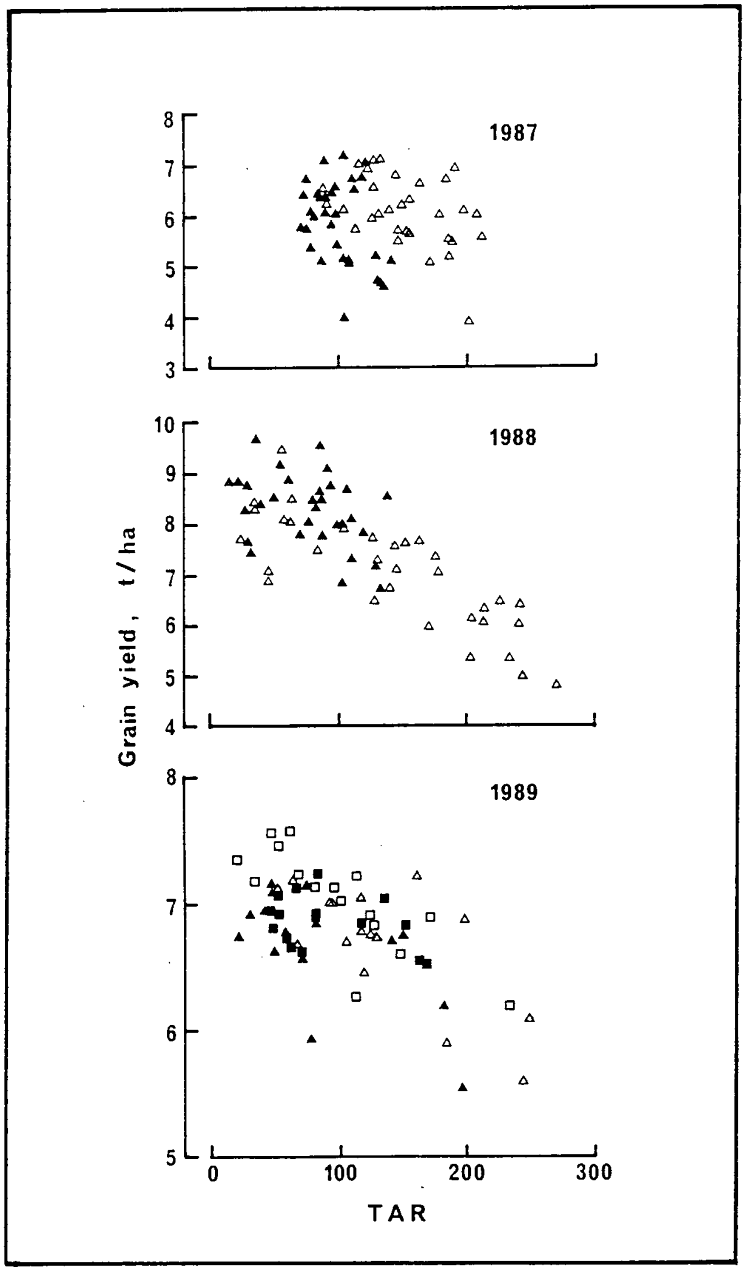

Figure 14. Relationships between take-all rating (TAR) in June and grain yield in three factorial experiments at Rothamsted.

▲= October-sown (1987, 1988) or September-sown at 100kg/ha (1989); △= September-sown (1987, 1988) or September-sown at 200kg/ha (1989); ■ = October-sown at 100kg/ha (1989); □ = September-sown at 200kg/ha (1989).

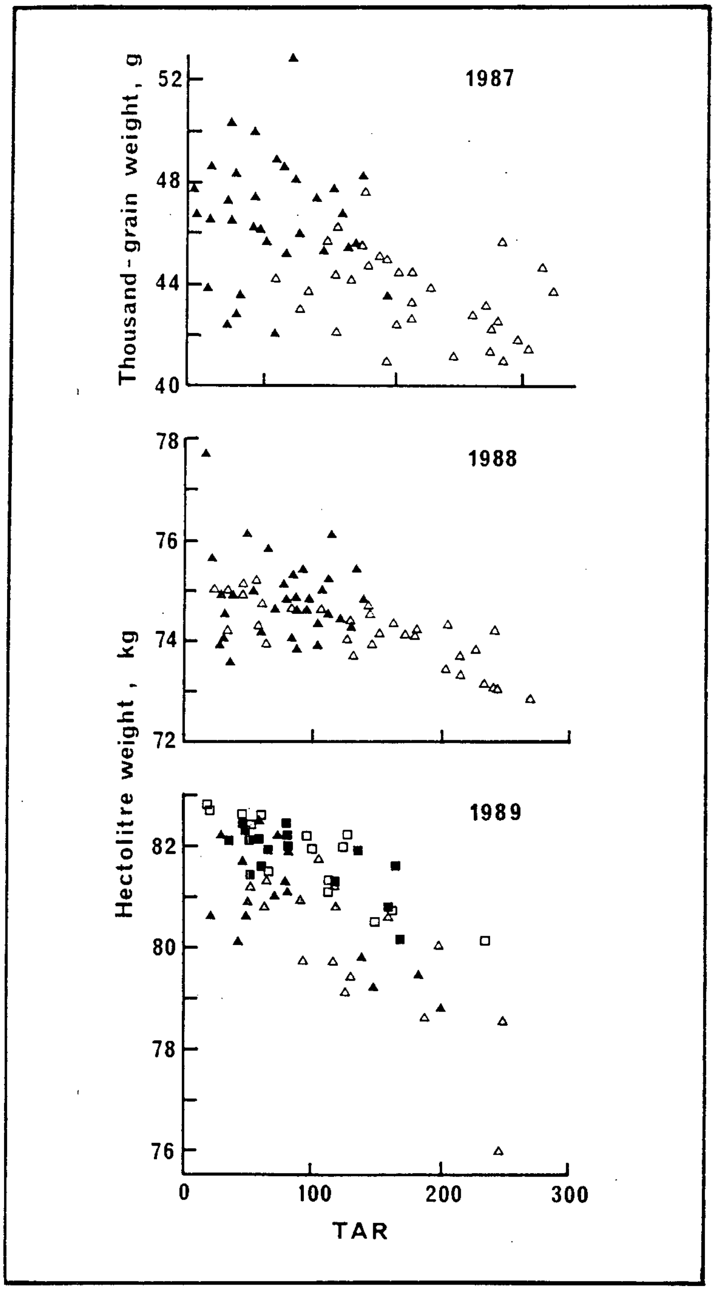

Figure 15. Relationships between take-all rating (TAR) in June and thousand-grain weight or hectolitre weight in three factorial experiments at Rothamsted. For key, see Figure 14.

relationship was strongest at TARs greater than 150 in 1988, but less clearly so in 1989. As with yields, specific weights were not correlated with TAR in the low disease experiment of 1986, but in 1987, a decrease in thousand-grain weight (specific weights were not measured) with increasing TAR was clearer than expected from the yield response. There was no clear relationship between take-all and %N in the grain, measured in 1987 and 1988. There was a negative association between take-all and Hagberg falling number in 1988, indicated by a significant regression, although the percentage of the variance accounted for was small (11.2%); surprisingly, the association was closer for the later-sown plots, which had less disease, than for those sown earlier. The Hagberg falling numbers were acceptably high in 1988, but were excessively high in 1989, when warm dry weather continued throughout the ripening and harvesting period. There was no association between Hagberg falling number and take-all in 1989.

In a factorial experiment on winter barley at Rothamsted in 1987 (J.F. Jenkyn, pers. comm.), take-all affected yield, and as is often the case for wheat, the effect was greatest in the moderate to severe disease range (Figure 16). Thousand-grain weight was similarly affected but there was no effect on %N. An indication of decreased hot water extract with increasing TAR was confirmed when the values were plotted as residuals, i.e. after removing the effects of treatments.

6.5. Recommendations for research

6.5.1. Diagnostics and taxonomy

i. Continuation of detailed comparisons of isolates, from the UK and elsewhere, using all the appropriate serological and molecular techniques, to further our understanding of the taxonomic relationships within the *Gaeumannomyces-Phialophora* complex.

ii. Development of a serological kit for rapidly and reliably identifying different taxa, especially Ggt.

iii. Application of appropriate techniques developed in i. to increase our understanding of the ecological relationships and significance of the taxa, for example the N- and R-isolates of Ggt, and the role of *Phialophora* in take-all epidemics.

6.5.2. Field experimentation

i. Much has still to be achieved in the area of epidemic prediction

Figure 16. Relationship between take-all rating in June and grain yield in a winter barley experiment at Rothamsted, 1987.

and manipulation, and the continuation of artificial inoculation studies at Rothamsted is necessary in this respect. Dependence on natural inoculum in field work has drawbacks: there is no certainty that epidemics will develop and, if they do, the relationship between diseaseand loss of yield is not often clear-cut. There is doubt that artificially-produced inoculum produces epidemics which simulate those occurring naturally and it could therefore be misleading, e.g. in testing BCAs. On the other hand, it may be useful for exploring disease/yield relationships, eliminating patchiness and, if it is uniform in size and infectivity, producing reproducible levels of disease.

ii. The development of disease patches, naturally and artificially-created, needs further study in order that the best use can be made of field sites for experimentation.

6.5.3. Yield loss studies

i. Detailed farm surveys over at least three seasons are needed to relate root infection (and prematurely-ripened patches in the crop) to yield.

ii. The effects of low levels of take-all need to be elucidated.

iii. Many empirical disease-yield relationships lack repeatability and have poor predictive powers. There is a need for alternative mechanistic approaches (Teng, 1985) using crop growth models and simulators incorporating the effects of disease on root and shoot function. In considering alternative models the relationship between the effects of disease on the yield of individual plants and on plant populations may need to be determined in advance. Quantification of the spatial distribution of disease in relation to yield loss is of recent interest (Ferrandino, 1989; Hughes, 1990;), notably amongst nematologists (Seinhorst, 1973; Noe & Barker, 1985).

CHAPTER 7. SUMMARY OF BEST ADVICE TO FARMERS

Current ADAS advice on minimizing losses due to take-all can be summarized as follows:

i. *Local knowledge* It is important that a farmer should know his soils and be able to assess the risks of take-all on them. Whilst data are difficult to come by, experience suggests that soils can be ranked tentatively with regard to their disease risk as follows:

Highest risk - fen peats
- 'black sands' low in manganese
- mineral soils where long-term cropping with grass has resulted in a high organic matter content
- light, alkaline soils
- sandy silt loams
- non-calcareous or decalcified clays (serious problems can occur when a wet season aggravates structural problems)
- silt loams/silty clay loams

Lowest risk - well-structured calcareous clay loams

ii. *Avoid highest risk* On the highest risk soils wheat should never be grown as a second or third cereal, on the lowest risk soils careful attention to husbandry practices will enable such crops to be grown with relative impunity. The higher the risk the greater is the importance of adopting the control measures outlined below.

iii. *Rotation* Short rotations which prevent the field from ever developing severe take-all, or continuous cereal growing which exploits the phenomenon of TAD, are preferable to the intermediate rotations that are so often practised. If, for example, a break crop is taken every fifth year then at least two of the four cereal crops in the rotation are likely to suffer from moderate to severe attacks of the disease.

Because barley suffers less severely from take-all than wheat does, it is safer than wheat where cereals have to be grown in high risk situations. For the highest risk soils, triticale or rye offer even safer options. Oats, being resistant to Ggt, make an acceptable break crop except in areas where Gga is known to be a problem.

Leys, free from perennial grass weeds, also make acceptable breaks. Although ley grasses may carry Ggt, they also carry a fungal antagonist, *Phialophora graminicola*, which is able to suppress the pathogen's development in a subsequent cereal crop. It is the latter property that seems most often to influence matters. It offers an explanation of why second wheats are safer after clean, two-year leys than after non-grass breaks which are likely to decrease inoculum of Ggt, but do not build up the antagonist.

iv. *Weed control* Perennial grass weeds should be controlled before a break crop is taken, because control before a cereal may actually increase the risk of infection. Ggt can survive on dying rhizomes and it is also reported that it can build up on them. Severe infection frequently occurs in first wheats on couch-infested land, irrespective of spraying-off couch with glyphosate in the previous autumn. Spraying before a break does not always have the desired effect if a dry season follows. This is attributed to dead rhizomes, colonized by the pathogen, surviving unrotted through the break year. It is sensible never to allow a field to become seriously infested with couch.

v. *Soil Management* Drainage and/or structural problems that may restrict rooting should be corrected. Firm seedbeds will hinder ectotrophic spread of the pathogen's mycelium over the roots. Ploughing is preferable to tine cultivation for the incorporation of straw.

vi. *Sowing date* First wheats should be sown first, long-term wheats next and the high risk wheats (second, third and fourth wheats) left until last and never sown before October.

vii *Sowing rate* High seed rates which reduce root development by interplant competition and favour the disease should be avoided.

viii. *Crop nutrition* Fields should not be allowed to become deficient in major nutrients, particularly phosphate. If it is intended to take a second wheat on high risk soils a phosphate index of at least 2 should be achieved before the first wheat is grown and then maintained.

Adequate nitrogen is important and an early application of part of the nitrogen in late February/early March, providing at least 40 kg/ha, is often beneficial. In high risk situations ammonium sulphate is very likely to decrease take-all more than other sources of nitrogen.

ix. *Control of pH* Liming to prevent the development of acid patches is important, but overliming should be avoided. Lime should be applied before a break crop or first cereal, rather than before a second or third wheat or barley crop.

x. *Chemical control* Although no fungicide is reliable, triadimenol seed treatment will sometimes decrease infection and increase yields in the presence of high levels of the disease.

CHAPTER 8. THE FUTURE

8.1. Resources

Behind the intractability of take-all is a complex problem, which has not yielded to inadequate and fragmentary investigation. Experience has shown repeatedly that isolated exercises are inefficient and unlikely to succeed. In the formation of the IACR/ADAS/Universities Cereal Root Pathology Group there has now been recognition that in the face of dwindling resources it is important to pool experience and effort to achieve progress. More attention should be given to co-ordination of research and collaboration within the UK, and further afield if possible. Such endeavours would need targeting at what are identified as the major practical and research issues by a consensus of those concerned.

The build up of take-all and development of TAD in experimental sites takes several years. Experiments that phase in sequences of cereals so that different runs of susceptible cereals are available for comparison in one year are extremely valuable scientifically, but uncommon. The long-term field experiment has a vital role to play in take-all research and should not be underestimated. A well-planned, well-documented, long-term experiment therefore constitutes an important resource that once discontinued is not readily replaced.

8.2. Recommendations for research

Research recommendations are placed into four groups. One or two of these groups will have more immediate appeal to the farmer, but it is stressed that work in all the groups is required if the complex problem of take-all is to be understood sufficiently to plan critical research and to improve our chances of significant progress in controlling the disease.

In parentheses after the title of each recommendation are qualifications to:

i. rate it as of *high*, *medium* or *low* priority for achieving the objective expressed in the title of its group;

ii. indicate whether it requires the start of *new* work, or concerns an *existing* project that needs further funding to continue or expand;

iii. identify appropriate organizations for undertaking the work. In lists separated by commas the lead organization is placed first.

Sections in the preceding chapters provide extra information about most of these recommendations.

8.2.1. Establishing the importance of take-all

i. *Surveys (high; new; ADAS, IACR)*

There has been only one extensive survey and that was undertaken in the late 1970s in years when levels of take-all were not generally high. Surveys are required to assess the national importance of the disease, its importance on different soil types at different pHs and under different climatic conditions and the effects of rotational position and agronomic practices (e.g. cultivation, cv. and sowing date).

Continuous winter wheat on a sandy clay loam in North Yorkshire seemed not to be affected by soil-borne diseases in the years 1979-85 (Hodgeson *et al.*, 1989). Such reports draw attention to the perennial question of localities and soil types in Britain which appear not to suffer from take-all. Usually the reports contain insufficient information about disease, previous cropping and typical crop sequences for the district, so there remains some doubt about the disease situation and, if little or no disease is the norm, few clues as to the explanation.

A survey of take-all should use an agreed procedure based on the best information available. This may require a pilot study to optimize sampling and data collection strategy, which in turn might also provide the guidance on sampling take-all sites that is so badly needed (see 6.3.3.). The simplest survey would also need to record take-all and yields in crops throughout the country in a series of contrasting seasons. It might possibly be linked to the existing ADAS cereal disease survey.

ii. *Disease-yield relationship (high; existing; IACR, ADAS)*

This is not well-understood and is usually confounded by other factors. New models of the relationship need exploring and the use of artificial infestation to create artificial epidemics may prove to be a useful tool. Many factors will influence the effect of a given level of disease on yield through their effects on the vigour of the root system. Consequently information will be needed for a range of soil types over a number of years and agronomic factors such as nitrogen, fungicide (seed treatment etc.) and method of cultivation. Much of this could be obtained from monitoring trials laid down to explore effects of these factors on disease incidence. Other approaches would be a) the use of large numbers of small plots (half of each to be destructively sampled to assess disease and half harvested) scattered throughout areas of interest and b) harvesting the grain from single tillers with known levels of disease.

iii. *Diagnosis* *(medium; existing; IACR, Universities*
new; Universities)

Take-all research continues to be hampered because of the time taken to achieve reliable diagnoses by traditional methods. Because of the similarities between Ggt and some of its close, but less pathogenic relatives, it is also quite possible that where Koch's Postulates are not carried out fungi may be identified wrongly. New diagnostic methods are much needed and amongst the most promising areas of research in need of support is the use of serological and molecular biological techniques to identify and quantify the pathogen. At our present level of expertise it is unlikely that these methods could be used routinely in the surveys suggested in i.

iv. *Economic evaluation* *(high; new; Universities, ADAS, IACR)*

Information on the effect of take-all on the profitability of various rotations on different soil types is urgently needed for the proper evaluation of the financial constraints the disease imposes on the flexibility of cropping. A paper exercise using information from a national survey and work on yield loss prediction would indicate for a range of soil types the profitability of second to fourth wheat crops compared to a range of break crops. Data from the ADAS 'Arable Crop Recording System' should form the basis of another desk study to evaluate the effects of soil type and agricultural practices on the comparative yields of first and subsequent wheats, which by inference would indicate the importance of take-all. An economic survey of intensive cereals in the UK should also consider whether the present intensity is unavoidable, or whether adjustments in rotations could be made to minimize take-all.

8.2.2. Improving forecasting and risk assessment

i. *Data storage and availability (high; existing; IACR, Universities, ADAS)*

Much information on take-all in field experiments, trials and surveys is collected annually, but does not become generally available. Some of it is idiosyncratic and would have benefitted from conforming to some general standard for the collection of take-all data. To overcome these inefficiencies the establishment of a central database and data archive is proposed. Such a project should help to systematize the collection of data and provide a powerful tool for re-examining data and trying out new hypotheses. A pilot study has been carried out by Cambridge University and IACR, Rothamsted under the AFRC Linked Research Group Scheme.

ii. *Forecasting (medium; existing; IACR)*

The question of forecasting take-all is a vexed one of long-standing. Although changes in the cereal production system have contributed to the difficulties, it is the relationship between weather and the disease that is at the centre of the problem. For the first time in take-all research long runs of reliable take-all data are becoming available and need investigating in relation to detailed meteorological data which are available for many localities. Initial analyses have revealed long-term trends in the occurrence of take-all and such understanding is vital to predicting national losses over time. Much work on weather relationships is necessary before explaining or forecasting disease trends within crops will advance beyond its current rudimentary status.

iii. *Agronomic and edaphic factors (high; existing; IACR and ADAS)*

Research is required to rank the relative importance and interactions of agronomic and edaphic factors on the development of take-all. Of the few factors that both influence take-all and are under the farmer's control, sowing date is the most important. The use of cultivars least sensitive to sowing date (Sylvester-Bradley & Scott, 1990, pp. 123-136), including rapid-developing, autumn-sown spring wheat cultivars, which allow further delay in sowing date without yield or quality penalties, needs to be investigated in situations where the risk from take-all is high. Information restricted to a list of sowing dates, cultivars and yields limits interpretation and trials including other factors are needed to decide on a cultivar's suitability for early or late sowing (Sylvester-Bradley & Scott, 1990, p. 125). Trials with second and third wheats on sites prone to take-all would, with sufficient disease monitoring, allow interpretation of sowing date x cultivar interactions in the presence of significant take-all.

8.2.3. Understanding take-all biology

i. *Epidemiology (high; existing; IACR, Universities)*

There is much in the epidemiology of take-all that remains unknown. Because an understanding of the epidemiology of take-all is required for a) the proper interpretation of most field work on the disease and b) the realistic extension of laboratory and glasshouse studies to the field, it is a study that should not be overlooked or under-resourced. Further epidemiological work (including work on artificially-created epidemics) is essential for better risk assessment and proper testing of putative controls. Work on models for spatial and temporal development of disease will aid our understanding of the disease system.

ii. *Field work methodology (medium; existing; IACR, Universities)*

Take-all occurs naturally in patches. This heterogeneity has meant that disease in many traditional large plot experiments has been so variable that the precision of the test of any treatments has been low. Various ways of tackling this problem, such as many small plots or more even artificial infestation of soil are emerging, but more work is required to develop new designs and procedures for field work .

iii. Gaeumannomyces-Phialophora *complex (medium; existing; IACR*
new; Universities)

Over the last 20 years the number of fungi in this complex has steadily increased. There are several outstanding and intriguing taxonomic problems and whilst some members of the complex do not complicate the pathology, others do, being potential BCAs or being mistaken for the pathogen. Clarifying the relationships within this complex may be helped by exploiting serological and molecular biological techniques.

iv. *Ecology of pathogen and antagonists (medium; existing; ADAS and Universities)*

Ecological studies of the pathogen and potential BCAs on the root surface and in the soil are needed. These could lead to more practical issues such as a) delivery of BCAs to the root zone, b) enhancing the natural suppressiveness of field soil by such procedures as incorporating organic matter and c) the use of root-stimulating bacteria to alleviate the effects of disease even though not suppressing infection.

8.2.4. Controlling take-all

i. *Rotations (medium; existing; IACR and ADAS)*

This is a topic that has been the subject of much research, but many questions remain to be answered and older work needs to be repeated under the conditions of modern husbandry. More information is required on:

i. effects of different break crops on the survival and subsequent build up of Ggt;

ii. effects of introducing different break crops into long runs of wheat in which TAD is well established;

iii. effects of less susceptible cereals such as triticale and rye on the development of TAD;

iv. effects of the sowing dates of sequential wheats on the development of TAD;

v. effects of the various systems of management of set-aside on take-all;

vi. effects on take-all of catch crops introduced to decrease the leaching of nitrogen.

Items *v.* and *vi.* are already under investigation in CSG-funded trials.

Some attention should be given to long-term experiments aimed at accumulating information about the effects of potential future changes in wheat production, such as lower inputs and organic systems. Cuts in subsidies and changes in consumer demands may cause control strategies to shift in the long-term.

ii. *Natural biological control phenomena (high; existing; IACR and ADAS)*

Research on exploitation of natural biological controls should include assessment of the effects of early sowing on TAD. Detailed assessment of biological and other factors implicated in TAD in one site may help to establish which control mechanisms predominate during TAD, and when. It will also be necessary to follow variations in soil suppressiveness through seasons to establish when the phenomenon is strongest. Such insights should be relevant to, and may be necessary to, the development of effective uses of biological control for soil-borne diseases of field crops.

iii. *Introduced BCAs (medium; existing; ADAS and Universities)*

Although the introduction of specific biological control agents has met with little success in this country the search for BCAs and the assessment of combinations and formulations and their evaluation under a range of conditions should continue, and prospects for integration with other control methods explored. A low priority rating for this research would reflect the view that the search for BCAs should be largely the province of agrochemical companies, but the wide-ranging studies envisaged (see 5.3.) suggest a need for continued involvement of the public sector.

iv. *Resistance I (low; ?; ?)*

Since the demise of the Plant Breeding Institute, public sector research in this area seems to have been discontinued. However, it would be prudent to continue to look for resistance in new wheat genotypes produced by traditional (breeding) methods. Since the British view is that there is little of interest currently to work on, this is an activity awaiting developments. The development of genetically-engineered cultivars with resistance to disease would offer a new and exciting method of biological control which, should it materialize, would need evaluating in the field.

v. *Resistance II (medium; new; IACR and/or Universities)*

Cross-protection, or immunization, is one form of resistance that has never come to the forefront of UK research on take-all. Now, using molecular biological techniques to study cross-protected and non-protected plants it may be possible to detect resistance-related substances which could be exploited.

vi. *Fungicides (low; existing; ?)*

No fungicide has given consistent, satisfactory and economic control of take-all. Certain triazoles (particularly triadimenol seed treatment) have sometimes suppressed infection and sometimes increased the yield from severely-infected plants without any obvious effect on disease.

The physico-chemical properties of the ideal soil-applied fungicide for take-all are known, but synthesizing and developing new fungicides should now be funded by the agrochemical companies. Field trials by others will be required if and when promising fungicides and delivery systems emerge.

vii. *Integrated control (medium; existing; IACR, ADAS)*

It is unlikely that any single material or technique will ever give a satisfactory and consistent control of take-all. Successful disease control strategies will almost certainly depend on combining treatments which favour root development and treatments which act against the pathogen. Some work has already been done by IACR and ADAS to identify best 'packages' based on current treatments and procedures, but such work will be ongoing as long as new factors are identified and promising new treatments emerge.

Attempts to get integrated control by combining the methods that are currently the best would include re-examining the use of fertilizers, such as ammonium sulphate, to control take-all. Non-nitrate sources of nitrogen, nitrification inhibitors, chloride-containing fertilizers and soil-applied manganese have decreased take-all in Australia and USA, but not in experiments in the UK. They, and the currently available phloem-mobile formulations of phosphate for foliar application, need more careful evaluation over a range of UK soil types.

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