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EYESPOT DISEASE OF CEREALS

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ABSTRACT

Eyespot (*Pseudocercosporella herpotrichoides*), a serious disease of winter wheat and barley, has increased in importance in the 1980s because 1) pathogen populations have become resistant to the fungicides which were used to control it; 2) changes in cropping practices, such as earlier sowing dates, have favoured the development of severe epidemics. In 1987, ADAS national surveys suggested that, of the diseases surveyed, eyespot was the most serious disease problem on winter wheat, with losses estimated at *c.*£30M despite the widespread application of fungicides against eyespot (cost *c.* £23M). These figures are underestimates since they include neither the losses caused by eyespot-induced lodging, nor the costs of fungicide application. Furthermore, it is likely that eyespot has been an important factor in reducing the quality of milling wheat and malting barley crops so that they have to be sold for animal feed. Since the formula used by ADAS to estimate losses for winter wheat was derived both varieties and eyespot populations have changed, so experiments are needed to re-evaluate it. A national estimate of losses from eyespot-induced lodging is needed and a formula needs to be derived for winter barley.

The disease takes its name from the characteristic oval brown-bordered lesions which form at the base of the shoots. When severe, lesions may weaken the stem bases so that a crop may lodge. Eyespot attacks all commercially grown varieties of wheat and barley although they vary greatly in resistance. Rye and triticale are susceptible to some strains of the fungus; oats and grasses may be infected but lesions are not damaging. It is a disease of temperate cereal crops, and occurs throughout Europe, in North America, Australasia and South Africa. In the UK it is particularly damaging on autumn-sown crops. Stem bases of cereal crops may also be affected by sharp eyespot (*Rhizoctonia cerealis*) or brown footrot (*Fusarium* spp.) but these diseases are considered to be less serious than eyespot,

although it can sometimes be difficult to distinguish the different cereal stem base pathogens present on plants sampled from crops.

The eyespot fungus, *P. herpotrichoides*, has two main pathotypes. W-type (wheat-type) isolates are generally more damaging to wheat than to barley and much less damaging to rye. They produce colonies with smooth edges when grown in culture on potato dextrose agar. R-type (rye-type) isolates are about equally damaging to wheat, barley and rye. They produce colonies with feathery edges and grow more slowly than W-types. However, it is not clear how these pathotypes relate to two varieties of *P. herpotrichoides* described in West Germany and distinguished on the basis of spore characteristics. Furthermore, another related species, *Pseudocercosporella anguioides*, can be isolated from leaf sheath lesions but does not colonize the stem and appears not to be damaging. However, it may confuse identification of eyespot lesions, and result in unnecessary spray applications. Since the eyespot fungus has now developed resistance to the MBC fungicides which were used to control it, isolates from lesions on crops may be MBC-sensitive or MBC-resistant. It is important to distinguish quickly between eyespot and other stem bases pathogens and between the different strains of the eyespot fungus since spray decisions may be determined by the identity of the fungus present on stem bases of a crop. There is an urgent need for rapid diagnostic methods for use on the stem base pathogens to be developed.

There has been a dramatic change in populations of the eyespot fungus in the UK over the last decade. Formerly MBC-sensitive W-types were predominant but now MBC-resistant R-types are predominant. The development of MBC-resistance has occurred because MBC fungicides were used routinely by growers but is less clear why the predominant pathotype should have changed. However, surveys suggest that the composition of eyespot populations in other EEC countries is different and that different population changes have occurred (e.g. MBC-resistant W-types are predominant in France). A series of comparative surveys in different countries might indicate why these differences between populations in different countries have occurred and suggest methods of manipulating eyespot populations for the benefit of European agriculture.

Epidemics of eyespot can be considered in five phases: survival on infected straw from previous crops, sporulation, dispersal by rain-splash, infection of plants in new crops and lesion development.

In the UK conditions are often favourable for sporulation, dispersal and infection during the winter and, where inoculum is available, lesion development is often the limiting phase which determines whether or not epidemics will become severe. The crucial stage in lesion development is the initial colonization of the stem from the infected leaf sheaths which surround it. If the fungus becomes established in the stem, further lesion development may be a function of temperature but if infected leaf sheaths die before the stem has been colonized lesions may fail to develop further. It is important to forecast the development of severe epidemics so that sprays are only applied when they are economically justified. Yield losses occur only when there is a high incidence of moderate or severe lesions during grain-filling but sprays need to be applied much earlier than this to control the disease. Current methods for forecasting the severity of eyespot epidemics at a time when sprays can be applied have not always been reliable. In some years when sprays have been recommended, eyespot has not become damaging and in others when sprays have not been recommended severe late epidemics have developed. Current work, funded by H-GCA, is aiming to integrate methods for forecasting eyespot and septoria diseases of winter wheat but will not be able to answer all the important questions in the time available. There is, for example, an urgent need to determine more accurately the threshold criteria to be used in deciding whether or not to apply a fungicide spray.

The priorities for future research on eyespot are :

1. To improve estimates of national losses from eyespot.
2. To improve the accuracy of methods for predicting the severity of eyespot epidemics.
3. To compare populations of the eyespot fungus in different EEC countries.
4. To study the comparative biology of the pathotypes of *Pseudocercosporella herpotrichoides*, the eyespot fungus, and of *P. anguioides*.
5. To develop rapid diagnostic methods for distinguishing 1) between the eyespot fungus and other stem base pathogens; 2) between the pathotypes of *P. herpotrichoides*.
6. To develop new varieties with different sources of resistance against eyespot and new fungicides for control of eyespot, and to evaluate methods for improving the efficiency of existing fungicides.

In order to investigate these problems most effectively close collaboration between scientists in ADAS and AFRC will be needed for much of this proposed research. Furthermore, collaborative ADAS/AFRC research will also be needed on other stem base diseases of cereals. To deploy resources most effectively it seems advisable to designate one centre for co-ordination of research on stem base diseases of cereals within ADAS and AFRC.

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GLOSSARY OF TERMS

Disease gradient. The change (usually decrease) in the incidence of disease with distance from a source of infection.

DMI. Demethylation - inhibiting fungicides. Site-specific fungicides including imidazoles (e.g. prochloraz) and triazoles (e.g. propiconazole).

Epidemiology. The study of the factors affecting the outbreak and spread of infectious diseases.

Fungicide resistance. The ability of fungi to grow in the presence of fungicides which previously prevented growth.

In vitro. Means 'in glass'. Generally applied to biological processes when they are experimentally made to occur in isolation from the whole organism.

Fusarium. Cause of brown foot rot disease of cereals.

Leaf sheath. The lower part of a cereal leaf, surrounding the stem.

MBC. Carbendazim-generating fungicides (or benzimidazoles). Site-specific fungicides including benomyl and thiabendazole.

Monocyclic disease. A disease with only one generation (cycle) per cropping season.

Mycelium. A mass of fungal hyphae (filaments of vegetative growth).

Necrotroph. A fungus that kills tissues as it grows through them such that it is always colonizing dead host material.

Pathogenicity. The quality or characteristic of being able to cause disease.

Pathotype. A subdivision of a species distinguished by common characters of pathogenicity, particularly in relation to host range.

Pseudocercosporella herpotrichoides. Cause of eyespot disease.

Regression. A statistical method for studying the relationship between two or more variables.

Rhizoctonia cerealis. Cause of sharp eyespot disease.

Saprophyte. A fungus using dead organic or decaying material as food.

Spore. A general term for reproductive structures in fungi.

Sporulation. Production of spores by a fungus.

Stroma(ta). A mass of vegetative fungal filaments, often on the surface of the host.

1. INTRODUCTION

Eyespot, caused by *Pseudocercosporella herpotrichoides* is a serious disease of cereal crops in temperate climates. It occurs in Europe, North America, South Africa and Australasia, being favoured by intensive cereal cultivation and wet, cool spring weather. The disease is most severe on autumn-sown wheat and barley crops but can affect oats, rye, triticale and spring-sown crops. Losses from eyespot of up to 50% have been recorded in experimental trials on winter wheat, but rarely occur in practice. However, the disease has recently become a more serious problem in the UK, presumably because the eyespot populations have now become almost totally resistant to the MBC fungicides which had previously given good disease control. Other factors have increased the frequency of severe eyespot epidemics, including the replacement of spring cereals by winter cereals and the trend towards early sowing in the autumn. Data from the 1987 Agricultural Development and Advisory Service (ADAS) national survey suggest that, of the diseases surveyed, eyespot was the most serious disease recorded on winter wheat causing losses of 2.4% (£29M); estimated losses on winter barley were 0.7% (£3.3M). However, these figures are underestimates because they take no account of losses caused by eyespot-induced lodging or losses in the quality of grain caused by eyespot.

This review summarizes recent information on eyespot and identifies areas where further research is needed. The emphasis will be on work done in the UK, but reference will also be made to work from other countries.

2. EYESPOT - THE DISEASE

Symptoms

Eyespot takes its name from the characteristic oval brown-bordered lesions (Fig. 1a), between 15-30 mm in length, which have small black dots, sometimes referred to as 'pupils', in the middle, giving them a charred appearance. The symptoms typically appear on the basal leaf sheaths in early spring just above the soil; occasionally the bases of leaf blades show similar symptoms. Eyespot lesions are generally confined to the lower part of the stem but in prolonged damp weather they may occur several centimetres higher. Initially the lesions are rather diffuse with a brown smudgy appearance but as the infection progresses, the fungus spreads in the outer leaf sheaths and penetrates inner leaf sheaths, and the lesions become more defined (Jones & Clifford, 1978; Cook & King, 1979).

Severity of infection depends on the stage of development of the crop and on the rate of penetration. Infection can take place soon after seedling emergence, when decay of the basal parts of young leaves leads to premature yellowing of the blades. If there is a severe infection, as can occur in early autumn-sown crops, diseased shoots or even whole plants can die causing thinning of the crop. More typically, however, the disease develops relatively slowly, penetrating successive leaf sheaths and spreading onto the stem after stem extension has occurred. If lesions become severe they may cause the stem to become ridged, kinked, frayed or otherwise distorted and weakened. The characteristic severe eyespot lesion (Fig. 1b) may cause the straw to bend or, in some varieties, to break at this point. When infected straws are split open the lumen of the hollow stem in the region of the lesion may be filled with a grey fungal mycelial growth although this is not a useful diagnostic symptom since sharp eyespot may also produce mycelial growth in the stem lumen. Eyespot may be distinguished (Appendix 1) from sharp eyespot (caused by *Rhizoctonia cerealis*) because sharp eyespot lesions often have a sharp, dark edge and shredding of leaf sheaths usually occurs; they may spread much further up the plant than eyespot lesions. Furthermore, a watermark-like stain may be apparent on leaf sheaths above sharp eyespot lesions, but is not present above eyespot lesions. *Fusarium* spp. may also cause browning at the base of cereal shoots, but distinctive lesions are not apparent (Booth & Waller, 1973; Gair, Jenkins & Lester, 1987; Cook & King, 1979).

Eyespot weakens the base of the stems and they may fall over (lodge) (Fig. 1c)before harvest. The term 'straggling' has been used to denote the random lodging of individual stems in many directions, which creates a network of untidy criss-crossed stems among the upright ones. If crops of a susceptible variety are severely infected they are more easily lodged by stormy weather when the straws tend to fall in one direction, Storm lodging is more severe than straggling but eyespot need not always be implicated in lodging. A crop may also fall down because over-use of nitrogen makes it too heavy to withstand the strain of wind and rain. This 'non-parasitic lodging' can be distinguished from 'eyespot lodging' because the straws curve down to the ground leaning mostly in one direction, instead of collapsing sharply near the soil level. The two types of lodging merge into each other, and the heavier the crop the less the amount of eyespot needed to cause lodging. The disease increases both the probability and earliness of lodging. Mature crops infected later in the season, or in which infection progresses less rapidly, may fail to lodge, but the ears produced may die prematurely. The grain becomes shrivelled and the ears become discoloured, a symptom known as 'whiteheads', often found scattered throughout a crop. Such ears may also be colonized by secondary moulds and quickly turn black, especially in wet weather (Booth & Waller, 1973; Gair, Jenkins & Lester, 1987; Jones & Clifford, 1978; Cook & King, 1979).

Distribution

Eyespot attacks all commercially grown varieties of wheat and barley, although they differ greatly in resistance. Autumn-sown wheat is most severely affected and spring-sown crops of wheat or barley are not often affected much in England, although most spring wheat varieties are very susceptible to eyespot and spring-sown crops may be badly affected in the wetter climates of Wales, Scotland or Ireland. Rye and triticale are susceptible to some strains of the eyespot fungus. Oats and both wild and cultivated grasses may be infected by *P. herpotrichoides* but lesions are rarely damaging (Booth & Waller, 1973; Cook & King, 1979; Cunningham, 1985).

The disease was first recognised in France and the USA in the early part of the twentieth century but the causative fungus was not identified at the time because it did not produce spores in pure culture. However, in the 1930s Sprague, working in Oregon, USA, showed the disease was caused by *Pseudocercosporella herpotrichoides* (then

called *Cercosporella herpotrichoides*) and it was then recognised in many countries. It was first recorded in the UK at Rothamsted by Glynne in 1935. It is now known to occur throughout Europe, in Canada (Ontario), the USA (Pacific north-west), south-east Australia, New Zealand and South Africa (Anon., 1981). The eyespot disease has a number of different names in different countries: footrot and strawbreaker (USA), piétin-verse (France) and Halmbruchkrankheit (Germany). Furthermore, terms like 'straggling' have been used by British farmers for several hundred years to describe crops with lodging in which straws fall in all directions, presumably as a result of eyespot. In Shakespeare's play when Richard II says "We'll make foul weather with despised tears; our sighs and they shall lodge the summer corn and make a dearth in this revolting land", he may be referring to eyespot. Therefore it seems likely that the disease was common in the UK long before it was identified in the 1930s. It was a serious cause of crop losses in the 1940s and 1950s and, became less important in the 1960s with the introduction of more resistant cultivars such as Cappelle-Desprez. In the 1970s MBC fungicides gave effective control, despite the increase in intensive cereal cultivation. In the 1980s eyespot has become more damaging because changes in cropping practices, such as earlier autumn sowing dates, have favoured the disease and eyespot populations are now mostly resistant to MBC fungicides, although alternative fungicides are relatively less effective.

Interactions with other stem base pathogens

ADAS surveys suggest that eyespot is the most damaging stem base disease in England and Wales; in most years estimated losses caused by eyespot were much greater than those caused by sharp eyespot (*Rhizoctonia cerealis*) and there was little evidence that *Fusarium* foot rot is damaging. Surveys suggest that eyespot is also the most important stem base disease in France and that it is normally dominant in untreated plots where sharp eyespot is also present (Cavelier, Lucas & Boulch, 1985). However, the incidence of eyespot can be reduced by inoculating fields with *R. cerealis* (Reinecke, Duben & Fehrmann, 1979) and *vice versa* (Kapoor & Hoffmann, 1984). In a survey of pathogens associated with stem base disease on West German crops *c.* 40% of eyespot lesions contained *Fusarium* spp. as well as *P. herpotrichoides* (Bruck & Schlosser, 1982). However, *R. cerealis* and *P. herpotrichoides* were rarely present together in the same lesion.

Pathogenicity and *in vitro* tests suggest that *P. herpotrichoides* produces substances which inhibit *R. cerealis* (Bruck & Schlosser, 1982; Kapoor & Hoffmann, 1984; Hoare, 1987). Many field experiments have shown that control of eyespot, with an MBC fungicide applied to a crop with an MBC-sensitive population of *P. herpotrichoides*, or with prochloraz, can increase the incidence of sharp eyespot (e.g. Prew & MacIntosh, 1975; Reinecke *et al.*, 1979; Goulds, 1987; Hoare, 1987). Similarly, treatment with benodanil to control sharp eyespot can increase the incidence of eyespot. Although these field and *in vitro* experiments have demonstrated that antagonism to *P. herpotrichoides* does occur, they provide little indication that methods for biological control of eyespot with microbial antagonists can be developed in the near future. It appears that, once established, *P. herpotrichoides* is a good competitor and that for the foreseeable future chemical control will still be required in crops where severe epidemics seem likely to develop.

3. *PSEUDOCERCOSPORELLA HERPOTRICHOIDES* – THE PATHOGEN

Pseudocercoporella herpotrichoides (Moniliales, Deuteromycetes) was originally classified as *Cercosporella herpotrichoides* and later transferred to the new genus *Pseudocercosporella* (Deighton, 1973). A *Tapesia* sexual stage of the W-type of the fungus, which is widespread in New Zealand (Sanderson, 1988), has just been identified by Wallwork (1987) but the fungus can also reproduce asexually from hyphal fragments and conidia. The vegetative mycelium, composed of elongate cells, is yellow to dark brown and forms thick-walled polygonal stromatic cells. The ultimate ends of hyphae develop into almost colourless sympodial sporophores up to 20 x 3 µm in size and with 2-3 distinct cross-walls. Small sporogenous cells may occasionally form as lateral branches of hyphae. Spores occur singly or in pairs and are colourless, widest at about one third of their length from the base, smooth and straight or slightly curved. Booth & Waller (1973) stated that the spores have 3-7 cross-walls and are 26-47 µm x 1.2 µm in size. However, it is evident that more than one form of the eyespot fungus exists although the taxonomic status of the different forms of the fungus has not yet been clarified.

P. herpotrichoides and related fungi

Two main pathotypes of *P. herpotrichoides* (Fig. 1d) have been distinguished on the basis of seedling pathogenicity tests and cultural

characteristics (Lange de la Camp, 1966a, b; Scott *et al.*, 1975; Hollins *et al.*, 1985; Schreiber & Prillwitz, 1986). W-type (wheat-type) isolates, which were generally more pathogenic to wheat than to barley and much less pathogenic to rye, produce colonies with smooth, even margins in culture on potato dextrose agar. However, R-type (rye-type) isolates, which were about equally pathogenic to wheat, barley and rye, produce colonies with feathery margins and radial growth is typically at about half the rate of W-type isolates. These pathogenicity tests were done in glasshouses at variable temperatures (mean 7-11°C), but in controlled environments at 10-15°C both R-type and W-type isolates were more pathogenic to wheat than to rye (Creighton *et al.*, unpublished), although, on rye, R-type isolates were more pathogenic than W-type isolates. Thus it seems that pathogenicity to wheat and rye is not a reliable criterion for distinguishing W and R pathotypes unless standard conditions and varieties are used. Cunningham (1981) distinguished a third pathotype, C-type (couch-type), which is pathogenic to wheat, barley and couch grass (*Agropyron repens*). There is no evidence that isolates of *P. herpotrichoides* exhibit physiologic specialization to particular cultivars; as with other necrotrophic cereal pathogens pathogenic adaptation appears to be expressed at the host species level (Scott *et al.*, 1976; Scott & Hollins, 1977).

Two varieties of *P. herpotrichoides*, namely *P. herpotrichoides* var. *herpotrichoides* and *P. herpotrichoides* var. *acuformis*, were recognised by Nirenberg (1981), who examined cultures of 18 isolates of each variety. It has been suggested that W-type isolates can be identified as *P. herpotrichoides* var. *herpotrichoides* and R-type isolates as *P. herpotrichoides* var. *acuformis* (King & Griffin, 1985; Sanders *et al.*, 1986). Nirenberg (1981) distinguished the varieties on the basis of spore characteristics. Spores of *P. herpotrichoides* var. *herpotrichoides* isolates were curved or straight, with 4 cross-walls and 35-80 (mean 52) µm in length, whereas spores of *P. herpotrichoides* var. *acuformis* isolates were straight, with 4-6 cross-walls and 43-120 (mean 65)µm in length. On the basis of the shape of spores in suspensions these descriptions fit with the observed characteristics of spores of W-type isolates (straight or curved) or R-type isolates (straight) (Fitt *et al.*, 1987). However, spore shape is not a suitable criterion for distinguishing isolates since straight spores may be either from W-type/*P. herpotrichoides* var. *herpotrichoides* isolates or from R-type/

P. herpotrichoides var. *acuformis* isolates. Furthermore, spores of individual isolates vary in shape and spore characteristics provide less reliable criteria for classifying isolates than cultural characteristics; there were no significant differences between the spores of W-type and R-type isolates in numbers of cross-walls or length in the experiments of Fitt *et al.*(1987).

Another method for distinguishing isolates of *P. herpotrichoides* has been described by Schreiber & Prillwitz (1985), who examined the way in which spores were produced within a minimal sugar nutrient agar medium (SNA). They suggested that, within the medium, spores of *P. herpotrichoides* var. *herpotrichoides* are curved and are in discrete groups with spores produced only on hyphae, whereas spores of *P. herpotrichoides* var. *acuformis* are straight and are borne in chains, with spores produced from other spores. These criteria have been used by Crompton & Thomas (pers. comm.) for classifying isolates obtained in ADAS surveys. When the Nirenberg varieties of *P. herpotrichoides* were classified on this basis they did not correspond respectively to the W-type and R-type categories separated on the basis of cultural characteristics. Further taxonomic work on *P. herpotrichoides* is clearly needed.

Nirenberg (1981) also described two new species of *Pseudocercosporella* which had been isolated from cereals in Germany. Spores of *P. anguioides* had 6-8 cross-walls and were 80-260 (mean 150) µm in length, whilst those of *P. aestiva* had 3 cross-walls and were 15-32 (mean 24) µm in length. *P.* aestiva is rare but *P. anguioides* is widespread in Germany (Schreiber & Prillwitz, 1986) and in the UK (Bateman, 1988). *P. anguioides* was isolated from 3% of *c.* 3000 shoots in a 1987 ADAS national survey of fungi associated with eyespot-like symptoms on winter wheat at G.S. 30-31 (Thomas, pers. comm.). However, although it infects leaf sheaths it does not apparently produce typical eyespot lesions on leaf sheaths or infect stems (Schreiber & Prillwitz, 1986) and it is unlikely that it causes yield loss. When Bateman (1988) investigated the pathogenicity of UK isolates of *P. anguioides*, he was unable to produce typical eyespot lesions and only once was able to re-isolate *P. anguioides* from an inoculated seedling. Nevertheless, further attempts to demonstrate Koch's postu- lates with a range of *P. anguioides* isolates are needed.

Isolates of both the W and R pathotypes of *P. herpotrichoides* (Griffin & Yarham, 1983) and of *P. anguioides* (Bateman, 1988) may be

either sensitive or resistant to carbendazim (MBC) and other benzimidazole fungicides. MBC-resistant isolates can grow on media containing 1 μg ml^{-1} of carbendazim, whereas MBC-sensitive isolates cannot. There are apparently no differences between MBC-sensistive and MBC-resistant isolates in cultural or conidial characteristics or in their pathogeni- city to cereal seedlings (Brown *et al.*, 1984; Hollins *et al.*, 1985; Sanders *et al.*, 1985; Fitt *et al.*, 1987).

It is important to develop reliable criteria for distinguishing the different types of *P. herpotrichoides* and related fungi since much of the work with the eyespot fungus on sporulation, dispersal, infection and lesion development, and relating disease incidence, severity and yield losses has been with the types of the fungus which were previously dominant, rather than those most common now. Limited information suggests that there may be epidemiological differences between the different types of *P. herpotrichoides* which may affect incidence-severity-yield loss relationships and alter criteria for forecasting eyespot severity. Furthermore, if *P. anguioides* were widespread at G.S. 30-31 and caused eyepsot-like symptoms on leaf sheaths which failed to develop further, it might confuse ADAS advice to growers about control of eyespot. Creighton (pers. comm.) is developing a cultural method for distinguishing W-type and R-type isolates. When incubated on maize semolina (40 g l^{-1}) agar (20 g l^{-1}) at 10°C under near-ultraviolet light for 10-12 days, W-type isolates produced a green/ black pigment and R-type isolates produced a pink or light brown colour in the agar. The reliability of the method is being tested further.

Other techniques are being tested for distinguishing isolates of the two pathotypes of *P. herpotrichoides* and of the two related species. The four groups showed consistently different protein patterns when the proteins were separated by gel electrophoresis (Bolik, Casper & Lind, 1987). However, they found it impossible to distinguish *P. herpotrichoides* from other fungi infecting stems by using serological techniques (enzyme-linked immunosorbent assay; ELISA) because their antisera were not specific. A similar method is being developed by M. Dewey (Oxford University), using highly specific monoclonal antibodies that will differentiate *Pseudocercosporella herpotrichoides* from other fungi causing stem-base and leaf sheath lesions such as *Fusarium nivale* and the sharp eyespot pathogen *Rhizoctonia cerealis*. The assay is relatively rapid, taking only a few

hours and in its final format should be easy to perform. She hopes to develop a "user friendly" kit, consisting of a one- or two-step dip-stick assay that requires no laboratory facilities. Preliminary field trials should begin in spring 1988 in conjunction with Rothamsted Experimental Station. The genetic basis of the differences between the types of isolates is being studied using cell protoplasts (Hocart, Lucas & Peberdy, 1987). Application of these and other genetic techiques should lead to a clearer understanding of the taxonomic differences between the types of isolates and may also lead to the development of a simple, rapid technique for distinguishing isolates.

4. EPIDEMIOLOGY OF EYESPOT

Epidemics of eyespot can be considered in five phases: survival on infected straw from previous crops, sporulation, dispersal by rain-splash, infection of plants in new crops, and lesion development (Fig. 2). These five phases overlap considerably during a growing season and may be influenced differently by the same crop and weather factors. In general eyespot epidemics are most severe on heavier, wetter soils. The disease is favoured by mild, wet winter weather and cool, damp spring weather; cold winters and dry, warm springs impede disease progress. Eyespot is most severe in early-sown autumn wheat and barley crops. Spring-sown crops are rarely badly affected in the drier eastern areas of England. However, eyespot can be a problem on spring-sown crops in areas with wet winter and spring weather such as western England, Wales, Scotland and Ireland. Excessive use of nitrogen fertilizer may favour eyespot development which is most rapid in densely sown patches and the more luxuriant parts of crops; also over-use of nitrogen weakens stems and makes them more susceptible to lodging. Eyespot is most severe on land growing continuous wheat or barley crops, and a first cereal crop after several years of grass usually has little or no eyespot. Under intensive cereal cropping eyespot epidemics become severe within a few years. The seasonal increase in the severity of eyespot epidemics is more rapid in wetter regions and after arable break crops, and breaks of less than 2 years are generally ineffective in controlling the disease (Cook & King, 1979; Gair *et al.*, 1987).

Survival

The eyespot fungus survives the period between susceptible crops as mycelium on stem bases which were infected during the growing season.

Infected straw on the soil surface is the main source of inoculum for development of new epidemics although self-sown wheat and barley may carry over the disease from one crop to the next, and grass species may also be infected. In the UK sporulation occurs on the infected straw throughout the winter but declines rapidly in the spring (Hollins & Scott, 1980;,Jordan & Tarr, 1981); in many years the straws have been exhausted as a source of inoculum by April although sporulation can continue until July in some years (Fitt & Bainbridge, 1983b).

The fungus survives for much longer on buried straws. Buried stubble remains highly infective for at least 3 years and buried inoculum survives for much longer (Macer, 1961). Although the eyespot fungus is a poor saprophyte and colonizes straw more slowly than competing saprophytic fungi, it is effective in excluding other organisms from straws colonized parasitically during the growing season; infected straw decomposes much more slowly than uninfected straw. When infected straw is brought back to the soil surface, for example, by ploughing, sporulation occurs and the straw again becomes a source of inoculum.

Sporulation

Pseudocercosporella herpotrichoides sporulates abundantly on infected crop debris remaining after harvest. Experiments with naturally infected wheat stem bases suggest that sporulation may occur over the temperature range 1-20°C, with an optimum at *c.* 5°C. A higher optimum temperature for sporulation (10-15°C) has been observed in pure culture (Rowe & Powelson, 1973a), but on naturally infected debris a temperature of 10-15°C stimulates growth of competing fungi and 20-25°C stimulates multiplication of bacteria (Higgins & Fitt, 1984). Rowe & Powelson (1973a) developed, for pure cultures, a 'daily thermal sporulation coefficient' (DTSC) to assess the level of sporulation on debris in crops from meteorological information but its relevance to natural epidemics is uncertain.

Most information from natural epidemics is observational rather than experimental. For example, it has been observed that periods of fluctuating temperatures with frosts at night, and periods of alternating wetting and drying of the debris, appear to favour sporulation (Glynne, 1953). Water is essential for sporulation and, in experients, sporulation only occurred on straw after water had been absorbed (Glynne, 1953; Rowe & Powelson, 1973a). However, evidence on the role of light in sporulation is conflicting. In some pure culture experi-

ments *P. herpotrichoides* sporulated under near-ultraviolet light (NUV) but not in darkness (Chang & Tyler, 1964). In other experiments with pure cultures (Reinecke & Fokkemma, 1979) or infected straw (Rowe & Powelson, 1973a) sporulation has been induced on material kept in darkness. It is, however, possible that this material was exposed to light for a short period before being transferred to darkness and that this was sufficient to induce sporulation. In practice, most scientists working with *P. herpotrichoides* use NUV to induce or enhance sporulation.

Eyespot epidemics are unlikely to be limited by a shortage of inoculum since in many areas where winter wheat is grown conditions are favourable for sporulation of *P. herpotrichoides* for long periods. Evidence from field experiments in the UK (Glynne, 1953; Hollins & Scott, 1980; Jordan & Tarr, 1981; Fitt & Bainbridge, 1983b; Higgins & Fitt, 1984), France (Ponchet, 1959), the Netherlands (Van der Spek, 1975) and North America (Rowe & Powelson, 1973b) suggests that viable spores are produced on infected debris (primary inoculum) throughout the growing season, with a peak in sporulation in March/April followed by a decline as the temperature increases, but with some spores still being produced by June/ July. By comparison with this primary inoculum, the secondary inoculum produced by sporulation on infected plants seems unimportant (Rowe & Powelson, 1973b; Nelson & Sutton, 1988a).

Spore dispersal

Both direct and indirect evidence suggest that spores of *P. herpotrichoides* are normally dispersed from infected debris to plants of the new crop in rain-splash droplets. When Glynne (1953) passed dry air over infected straw no spores were detached but when water drops were allowed to fall on to this straw the resulting splash droplets contained numerous spores. This result has been confirmed in several later experiments with simulated raindrops falling on to infected debris or spore suspensions (Fatemi & Fitt, 1983; Fitt & Nijman, 1983; Fitt & Bainbridge, 1984; Fitt & Lysandrou, 1984). Spores of *P. herpotrichoides* were clearly visible in traces of splash droplets collected on fixed photographic film, as illustrated by Fitt, Lysandrou & Turner (1982). Furthermore, when pieces of film were exposed near infected debris on a field site during rain, they collected large numbers of spore-carrying splash droplets (Fitt & Bainbridge, 1983). Slides exposed on this site collected no spores during dry periods or when there was only very light rain (< *c.* 0.2 mm h^{-1}), but collected large

numbers of spores in heavier rain (3-23 mm h^{-1}), even in periods as short as 15 min. No spores were collected in the first few minutes of rainfall, suggesting that the mucilage in which they are produced must be dissolved before they are released into a spore suspension and become available for dispersal. In addition, pot-grown seedlings exposed amongst infected debris on a field site during rain of 3-4 h duration collected many *P. herpotrichoides* spores on their leaves; these spores were not removed by subsequent exposure to rain (Higgins & Fitt, 1984).

Indirect evidence that the spores are dispersed by rain-splash is provided by artifical samplers and bait plants exposed near infected debris on field sites. When several samplers were exposed together for weekly periods during a season most spores were collected by samplers appropriate for collecting splash droplets and few spores were collected by samplers appropriate for collecting air-borne spores (Fitt & Bainbridge, 1983). In addition, most spores were collected within 15 cm of the ground, which is consistent with evidence suggesting that most of these spores are carried in the larger ballistic splash droplets (Fitt & Bainbridge, 1983; Fitt & Lysandrou, 1984). Furthermore, in the field experiments of Hollins & Scott (1980) infection of bait plants was correlated with the occurrence of rainfall expressed as the number of wet days/wk.

Eyespot exhibits steep disease gradients (Rowe & Powelson, 1973b; Fitt & Bainbridge, 1983), which reflect the steep spore deposition gradients typical of splash-dispersed pathogens that have been observed in rain tower experiments (Fatemi & Fitt, 1983; Fitt & Lysandrou, 1984). In still air most spores are deposited within 1 m from the source and even in windspeeds of 2 m sec^{-1} few spores travel beyond 2 m (Fitt & Nijman, 1983). Although most *P. herpotrichoides* spores are carried in large splash droplets, small numbers of air-borne spores have been collected above infected debris during rainfall (Fitt & Bainbridge, 1983). Such spores might be carried considerable distances by wind, but their significance in the epidemiology of eyespot depends on how long they remain viable and on how many spores are necessary to initiate a lesion. In experiments where seedlings were inoculated with different numbers of spores, lesions could be initiated by a few spores but developed much more rapidly from a larger inoculum dose (Higgins & Fitt, 1984), which suggests that the small numbers of spores which become air-borne are probably not very important. In any case the

collection of large numbers of spores, and the infection of bait plants, in every week of the growing season (Hollins & Scott, 1980; Fitt & Bainbridge, 1983) suggest that in the UK eyespot epidemics are rarely limited by a lack of weather suitable for spore dispersal.

Infection

Whilst the process of infection by *P. herpotrichoides* on wheat has been studied in detail (Defosse & Dekegel, 1974; Khan *et al.*, 1986), there has been little work to establish the optimum and range of conditions under which infection occurs. In controlled environment room and glasshouse experiments inoculated plants have developed lesions at temperatures from 6-18°C (Lange de la Camp, 1966b, 1967; Scott, 1971; Bateman & Taylor, 1976a, b; Higgins & Fitt, 1985a, b), which implies that infection can take place over this range. However, most of these experiments give no more information about factors affecting infection *per se*, since lesion development was not scored until several weeks after inoculation. Bateman & Taylor (1976a) did examine the infection of the coleoptile and first two leaf sheaths in detail but found few consistent differences between temperatures of 12 and 17°C. Moisture is required for infection to occur, since experimental inoculations with either mycelial or spore inoculum are not successful unless the site of inoculum is kept moist during the infection process.

On seedlings, the coleoptile is the tissue which is most susceptible to infection (Bateman & Taylor, 1976a, b) and in the autumn many leaf sheath lesions are probably initiated from coleoptile infections. However, wheat plants remain susceptible to eyespot throughout their lives. Hollins & Scott (1980) showed that plants exposed as seedlings or as plants of comparable age to the crop developed lesions throughout the season provided that after exposure they were incubated under conditions favourable for infection. This suggests that *P. herpotrichoides* can infect leaf sheaths directly later in the season, when coleoptiles have disintegrated. Whereas plants transplanted from an uninfected to an infected site from November to April developed lesions, plants transplanted in May and June developed few lesions although spore samplers showed that large numbers of spores were still being dispersed. This suggests that the environmental conditions in May/June were unfavourable for infection.

Lesion development

After infection of the coleoptile or outer leaf sheath there is a period of several weeks before the typical eye-shaped lesions of

eyespot are visible at the base of the stem. During autumn and winter eyespot lesions continue to develop in winter wheat as the fungus penetrates successive leaf sheaths. Two processes which may influence the development of eyespot lesions are the production of new inner leaf sheaths by the plant and the death and eventual disintegration of outer leaf sheaths.

The initial stages in the development of leaf sheath lesions in seedlings inoculated with spore suspensions have been studied by Bateman & Taylor (1976a, b). Frequently appressoria develop on coleoptiles at sites of attempted penetration. The development of stroma between the coleoptile and first leaf sheath is evidence that successful penetration of the coleoptile has occurred. The fungus then penetrates the first leaf sheath from this stroma and develops a further stroma between the first and second leaf sheaths. This process continues as successive leaf sheaths are penetrated. Whereas colonization of the coleoptile is generalized and no distinctive lesions are visible, colonization of leaf sheaths is localized and defined lesions may be observed on the first leaf sheath. Frequently, by the time that lesions are visible on the first leaf sheath, stromatal development and penetration of the second leaf sheath have occurred.

It has been suggested that the growth of *P. herpotrichoides* in infected plants is solely a function of temperature because there is always sufficient water at the site of the lesion to support growth (Ponchet, 1959; Rapilly *et al.*, 1979). For the susceptible cultivar Étoile de Choisy, an accumulated temperature function(D) was derived empirically:

$$D = 0.87T + 1.17 \qquad (1)$$

where T is the mean daily temperature and $0 \leqslant T \leqslant 20°C$. As the temperature increases from 20 to 25°C growth of the fungus decreases and no growth occurs below 0°C or above 25°C. Ponchet (1959) suggested that, after infection, an accumulated temperature of $\Sigma D = 240°C$ days is necessary for the appearance of visible lesions and that $\Sigma D = 90°C$ days is necessary for the penetration of each leaf sheath. To account for differences in susceptibility between cultivars Rapilly *et al.* (1979) introduced a factor K1 by which these ΣD values are multiplied. Values of K1 were estimated in pot experiments.

Further evidence that penetration of leaf sheaths by *P. herpotrichoides* is a function of temperature is provided by glasshouse and

controlled environment experiments, where the number of leaf sheaths penetrated increased with increasing temperature over the range 6-18°C (Scott, 1971; Fitt, 1985; Higgins & Fitt, 1985a). However, in the experiments of Higgins & Fitt (1985a) the rate of death of leaf sheaths also increased with increasing temperature.

In UK field experiments, where weekly samples were taken, the progress of eyespot lesions was fitted well by the accumulated temperature formula (equation 1) in some seasons (Fitt & White, 1988). Although the value of K1 for Armada, the cultivar used, was not known, the date on which lesions were visible and the initial rate of progress through the leaf sheaths in the period Nov. 1980 - Jan. 1981 fitted well with those predicted by the equation for the cultivar Étoile de Choisy. Furthermore, a regression of numbers of leaf sheaths penetrated on accumulated temperature for this period accounted for almost 90% of the variance (Fitt, 1985). However, this regression does not prove that lesion development was a function of accumulated temperature since regressions on other accumulated variables and on time also accounted for 90% of the variance. Where a disease is progressing steadily, regression may suggest a relationship between disease severity and almost any accumulated meteorological factor. Thus the method is inappropriate for assessing which factors are important.

The French accumulated temperature equation does not take into account factors which may restrict the penetration of leaf sheaths in UK crops. For example, if the rate of leaf sheath penetration is more rapid than the rate of leaf sheath production, penetration may be arrested because there are no further leaf sheaths available (Fitt & White, 1988). Furthermore, lesions may fail to develop further if the rate of death of outer leaf sheaths is greater than the rate of penetration of leaf sheaths so that outer leaf sheaths die and decay before the fungus has colonized the leaf sheaths beneath them. Both periods of cold (Fitt, 1985) and warm, dry weather (Higgins *et al.*, 1986) may enhance the rate of death of outer leaf sheaths.

A crucial stage in the development of eyespot lesions is the time after stem extension has begun when the fungus is spreading from the innermost leaf sheath to the stem (Higgins *et al.*, 1986). In glasshouse and controlled environment experiments with plants grown individually in lengths of tubing, the most severe lesions developed in plants which received the most water in the five weeks after growth stage (G.S.) 31 (Zadoks *et al.*, 1974) and had the highest root and stem

water potentials. In crops there may be a high incidence of shoots with leaf sheath lesions at G.S. 30-31, but if the weather is hot and dry at this time, infected leaf sheaths may die before the fungus is well established in the stems and severe lesions may not develop. Conversely there may be a low incidence of leaf sheath lesions at G.S. 30-31, followed by a period of weather favourable for infection before the leaf sheaths have died, so that several small lesions become established on many of the shoots at a relatively late stage. Whilst individually these lesions may be unimportant, they may coalesce to form severe lesions.

Assuming that colonization of the stem was a function of accumulated temperature, Ponchet (1959) estimated a value $\Sigma D = 650°C$ days for complete colonization of stems of the French cultivar Étoile de Choisy (Table 2) and Rapilly *et al.* (1979) introduced a factor K2 to allow for differences in susceptibility between cultivars. In the UK it is possible to relate the increase in the severity of stem lesions to accumulated temperature in some seasons (Fitt, 1985), although this does not necessarily imply that lesion development is solely a function of temperature. However, in many seasons severe lesions do not develop although values of ΣD greatly exceed those necessary for the development of severe lesions (Fitt & White, 1988). Unfortunately the formula does not allow for the failure of lesions to become established in stems, and it seems unlikely that it is applicable to UK conditions.

Incidence - severity relationships

When eyespot lesions first become visible on leaf sheaths of plants in winter wheat crops, the incidence of eyespot is assessed as the proportion of plants or shoots with visible lesions. Rowe & Powelson (1973b) assessed the incidence of eyespot (y) in monthly samples from plots in north-west USA, and regressed $\ln(1/(1-y))$ on time (t) to calculate the apparent infection rate (r). They concluded that eyespot is a monocyclic disease, with one cycle per season, because the value of r increased between spring and summer in plots where primary inoculum remained but not in plots from which it was removed in April.

However, evidence from field experiments suggests that in the UK the monocyclic equation describes the increase in the incidence of eyespot only in seasons when conditions favour the disease (Fitt & White, 1988). The equation assumes that the incidence of disease increases but in the UK the incidence may decrease. The incidence of infected plants or infected shoots may decrease if lesions fail because

outer leaf sheaths die and decay before the fungus has colonized the leaf sheaths below them. The incidence of infected shoots may also decrease if infected shoots die or if new shoots are being produced more rapidly than they are being infected. It seems unlikely that spores produced on leaf sheath lesions contribute greatly to the spread of eyespot to new shoots since throughout the season numbers of spores produced on leaf sheath lesions are small by comparison with numbers produced on infected debris (Rowe & Powelson, 1973b). Thus most new shoots are infected directly by splash-dispersed conidia from infected debris (primary spread) or by mycelial growth from infected shoots on the same plant (secondary spread). Rapilly *et al.* (1979) consider that secondary spread is the dominant mechanism for infection of new shoots and that the incidence of shoot infection is fitted by the equation for polycyclic diseases, although Rowe & Powelson (1973b) concluded that their data for the incidence of infected shoots was fitted by the monocyclic equation.

Incidence-severity relationships for eyespot differ from those for many foliar and root diseases because disease severity is assessed not as the area affected but by the depth of penetration of the lesion or lesions at the base of the shoot. Thus for leaf sheath lesions on seedlings, a severity score based on the number of leaf sheaths infected or penetrated was developed by Scott (1971): 1, coleoptile infected; 2, coleoptile penetrated; 3, first leaf sheath infected; 4, first leaf sheath penetrated etc. When the mean number of leaf sheaths penetrated per infected plant is assessed changes in eyespot severity between successive samples may reflect changes in incidence (Fitt & White, 1988). If disease incidence increases and plants with slight or mild lesions are included in the later sample, then the mean severity score may decrease. Alternatively, disease incidence may decrease between samples and the mean severity score may increase. Furthermore, the assessments of eyespot incidence and severity are imprecise because the optimal size of samples and best method of sampling are unclear. Such problems need to be considered when interpreting results of experiments.

To incorporate both incidence and severity data for eyespot lesions on leaf sheaths, a penetration index (PI) was used by Higgins & Fitt (1984):

$$PI = \left(\sum_{1}^{3} n_i x_i / 3n_t + \sum_{1}^{9} n_i z_i / 9n_t\right). 100 \qquad (2)$$

where x_i was lesion severity expressed on a 0-3 scale, z_i the number of leaf sheaths penetrated (0-9), n_i the number of main shoots with a given score and n_t the total number of main shoots in each sample. Since lesion severity x_i and the number of leaf sheaths penetrated z_i appeared to be closely related, this penetration index was simplified by Higgins *et al.* (1986) :

$$PI = \Sigma\, n_i z_i / n_t \qquad (3)$$

(the mean number of leaf sheaths penetrated per infected plant multiplied by the proportion of infected plants).

The increase in the incidence of lesions on stems as the eyespot fungus grows from the innermost leaf sheath to the stem, appears to be fitted by the monocyclic disease equation when conditions favour the disease and there is a steady increase in the incidence of stem lesions (Fitt & White, 1988). However, when conditions are unfavourable for the disease and the incidence of eyespot is low or basal leaf sheaths die before the fungus has become established in the stem, the incidence of stem lesions is not fitted by the monocyclic equation.

The severity of eyespot lesions on stems is often expressed on a 0-3 scale (Scott & Hollins, 1974) :

0, no lesion visible;

1, slight lesion, covering less than half the circumference of the stem;

2, moderate lesion, covering more than half the circumference of the stem;

3, severe lesion, girdling the stem and softening the tissue so that lodging can occur.

This scale gives a rough indication of the proportion of the cross-sectional area of the stem colonized by the fungus. Rapilly *et al.* (1979) attempted to assess this proportion more accurately. However, their method is time-consuming and therefore inappropriate for practical application.

As with leaf sheath lesions, changes in mean severity scores of infected stems are complicated by changes in the incidence of infected stems. To incorporate both incidence and severity a stem severity index (SI) was devised by Scott & Hollins (1974) :

$$SI = \left(\sum_{0}^{3} n_i\, x_i / 3n_t\right) . 100 \qquad (4)$$

where severity scores $x_0 = 0$, $x_1 = 1$, $x_2 = 2$ and $x_3 = 3$. A similar index was used by Higgins *et al.* (1986). These indices give a useful

indication of the severity of an eyespot epidemic to compare it with other epidemics and to estimate when it might be going to cause yield losses.

Comparative epidemiology of different types of *P. herpotrichoides*

Most comparisons between the different types of *P. herpotrichoides* have examined their pathogenicity to wheat seedlings grown in pots in glasshouses or controlled environment rooms, and the severity of eyespot lesions has been assessed as the number of leaf sheaths penetrated. Such experiments have produced apparently conflicting results; no difference in pathogenicity between W-type and R-type isolates (Brown *et al.*, 1984), or R-type isolates generally more pathogenic than W-type isolates (Hollins *et al.*, 1985), or W-type isolates generally more pathogenic than R-type isolates (Higgins & Fitt, 1985b; Sanders *et al.*, 1986; Fitt *et al.*, 1987).

In contrast all experiments showed no differences in pathogenicity between MBC-sensitive and MBC-resistant isolates of either pathotype. The wide variation in pathogenicity between individual isolates of both the W and R pathotypes, which was observed in the experiments of Fitt *et al.* (1987) may, in part, explain the apparent differences between results of these experiments. This suggests that large numbers of isolates must be tested to distinguish reliably between the two pathotypes, but the greatest number of isolates tested was only 77 (Sanders *et al.*, 1986). Furthermore, the experiments were done at different temperatures (from 7-20°C) and used different varieties; both temperature (Lange de la Camp, 1966b) and variety (Bateman *et al.*, 1985) may affect the pathogenicity of isolates. Some experiments used mycelial inoculum whereas others used spores but the form of inoculum seems to have little effect on the relative pathogenicity of isolates (Fitt *et al.*, 1987).

It is not clear how the results of these pathogenicity tests on seedlings relate to the situation in crops. The ranking of isolates was not the same in the field and glasshouse experiments of Scott *et al.* (1975) and the relationship between pathogenicity to seedlings (assessed on leaf sheaths) and pathogenicity to adult plants (assessed on stems) is poor (Higgins & Fitt, 1985b). Few studies have investigated the comparative pathogenicity to adult plants of the two pathotypes. The R pathotype was generally more pathogenic than the W pathotype in the field trials of Schreiber & Prillwitz (1986), but the W-type was more pathogenic than the R-type in the outdoor bucket

experiments of Higgins & Fitt (1985b). However, Higgins & Fitt (1985b) studied only 14 isolates (11 W-type, 3 R-type).

More recently the comparative epidemiology of the W and R pathotypes has been examined in a field experiment (Goulds *et al.*, 1987). In September-sown wheat the incidence of eyespot in April was greater in plots inoculated with R-type isolates (82% of shoots) than in plots inoculated with W-type isolates (70% shoots). However, by August the incidence of eyespot had decreased to 36% in R-type plots but increased to 82% in W-type plots. These differences may have occurred because penetration from leaf sheaths to the stem was arrested more in R-type lesions than in W-type lesions during dry weather in May-June. No differences between the W and R pathotypes were observed in plots which were sown later. However, these results show that there may be differences between the two pathotypes in their epidemiology. Since the R pathotype has now replaced the W pathotype as the dominant pathotype in UK populations of *P. herpotrichoides* and most investigations have been with W-type isolates or W-type populations, further investigation of the comparative epidemiology of the two pathotypes is needed.

5. LOSSES CAUSED BY EYESPOT

It is generally agreed that slight lesions are not damaging and that eyespot reduces yields of winter wheat or winter barley only when there is a high incidence of moderate or severe lesions during grain-filling. Experiments in which ears from stems in different eyespot categories were threshed individually, suggest that eyespot reduces grain yield per ear through reducing both grain number per ear and 1000 grain weight (Scott & Hollins, 1974; Clarkson, 1981). Yield losses of *c.* 40% have been measured for winter wheat in pot and field experiments in which most stems had severe lesions (Glynne *et al.*, 1945; Jørgensen, 1964). Fungicide application to control eyespot may increase both 1000 grain weight and specific weight (Hims, 1987; Jones, 1987). Losses are associated with direct effects of lesions, which interfere with the movement of water and nutrients through the stem base, and with the indirect effects of lesions, which may cause lodging because they weaken the stem. In one series of inoculated trials losses were 11-12% when lodging was prevented and 18% when lodging occurred (Scott & Hollins, 1974). In addition to causing yield losses, it seems likely that eyespot also reduces the quality of grain, although little information is available. A reduction in 1000 grain weight will

probably be associated with an increase in the proportion of small grain and interference with nutrient flow in the stem may lead to reduced amounts of grain protein. Furthermore, when lodging occurs in infected crops, grain discolouration is likely to occur as saprophytic fungi colonize the ears in the moist environment provided by a lodged crop.

To assess the national importance of eyespot from season to season, estimates of national losses, rather than individual crop losses, are needed. Such national loss estimates can be obtained from national estimates of eyespot incidence inserted into formulae relating incidence to yield loss. The necessary disease data are now provided by the ADAS disease surveys for winter wheat and winter barley crops in England and Wales.

ADAS surveys of eyespot incidence

ADAS surveys to assess the incidence of stem base diseases in England and Wales have been made in most years since 1975 for winter wheat and since 1981 for winter barley crops (King, 1977, 1980). Samples are collected from *c.* 300 farms selected at random from MAFF annual census returns. The number of farms to be surveyed in each ADAS region is related to the acreage of wheat or barley grown in the region so that final results require no weighting to transform them into national disease incidences. A single field of wheat or barley is selected at random from each nominated farm, and a sample of 50 shoots is taken from along a diagonal across each field at growth stage 73-77, when grains are milky ripe. All samples are sent to the ADAS Harpenden Laboratory for diagnosis of leaf and stem base diseases present and for assessment of disease severity. The severity of stem base diseases, including eyespot, is assessed as slight, moderate or severe according to the scale of Scott & Hollins (1974). Each sample is accompanied by details of the field location, the cultivar, the fungicide used and other agronomic information.

The effects of sample size (number of farms sampled, number of shoots per sample) on the standard errors of sample means have been examined in detail by King (1980). A sample size of *c.* 300 farms is required to give a reasonable estimate of the national average incidence. Samples with more than 50 shoots per sample would give more precise estimates of the field mean disease incidence but to process such samples on a national scale would be very time-consuming.

Yield loss formulae

Several attempts have been made to quantify the relationship between eyespot incidence/severity and yield loss. Scott & Hollins (1974) integrated areas under disease index progress curves from field trials for the period April to August and related yield loss to the integrated disease index. By extrapolation from a linear regression of yield loss on disease incidence in field trials, Glynne (1963) estimated that if all shoots had severe lesions the % yield loss (L) would be *c.* 50%. Thus, for a given crop:

$$L = (0.5n_3/n_t).600 \qquad (5)$$

Clarkson (1981) modified this formula. He classified lesions on large numbers of individual shoots taken from commercial crops between 1975 and 1979. By linear regression he estimated that severe lesions caused a 36% yield loss and moderate lesions caused a 10% yield loss. Thus

$$L = [(0.1n_2 + 0.36n_3)/n_t].100 \qquad (6)$$

One problem with this formula is that the method does not assess the loss due to lodging of infected crops. Using data from field trials at PBI over a nine year period, Scott & Hollins (1978) regressed yield loss on eyespot severity at G.S. 91 and a lodging index (i, %) measured just before harvest:

$$L = (0.17\ n_3/n_t).100 + 0.41\ i - 0.19 \qquad (7)$$

This equation, which accounted for 79% of the variance, shows that lodging can contribute significantly to eyespot-induced yield loss. However, equation 7 is based on results of experiments at PBI, rather than on representative sites throughout the country. Furthermore, lodging assessments need to be made just before harvest if they are to be accurate and lodging losses are generally not easy to quantify as they are very dependant on variable crop and weather factors.

The single shoot method does not detect the ability of healthy shoots to compensate for infected shoots on the same plant (Scott & Hollins, 1974) or of healthy plants to compensate for infected plants. However, no such compensation was observed by Clarkson (1981). In addition any reduction in shoot number caused by eyespot is not included in this single shoot method; Scott & Hollins (1974) suggest that wheat and barley can compensate to some extent for death of diseased shoots. It seems likely that wheat and barley may be able to compensate for infection or death of shoots when incidence is low, but not when incidence increases. The effect of compensation on the disease-loss relationship needs to be examined in more detail, but

compensation at low incidence would probably result in a curved relationship between disease incidence/severity and yield loss. Thus a linear regression crop loss model may not be appropriate. However, more complex crop loss models have been reviewed by Madden (1983) and could be tested when the relevant data are available.

The Clarkson formula is not strictly applicable to the ADAS survey data since disease assessments were made on plants at G.S. 91-92 because of the need for yield data, whereas survey samples are taken at G.S. 75. Thus the formula assumes that little disease progress occurs in the month between G.S. 75 and G.S. 91, an assumption which is probably unjustified. Since some lesions may develop from slight to moderate and others develop from moderate to severe between G.S. 75 and G.S. 91, this would suggest that use of the formula with survey data will underestimate losses. However, a sample at G.S. 75 seems most appropriate for identifying the eyespot lesions which are most severe during grain-filling, but further experiments are needed to examine how the progress of lesions over the period between G.S. 75 and G.S. 91 affects yield so that the formula can be modified accordingly.

However, Clarkson used equation (6), together with results of ADAS surveys, to estimate that eyespot caused national losses from 0.3 to 1.2% annually in England and Wales between 1975 and 1980 (Table 1). Using this equation, it is estimated that winter wheat losses were 0.05 to 2% in 1981-86 and were 2.35% in 1987. The epidemic was more severe in 1987 than in any other year for which ADAS survey data are available. As no comparable formula is available for winter barley, equation (6) was used to estimate winter barley losses for 1981-87 as 0.2 to 2% (Table 1). When improved yield loss models are available it may be possible to improve these estimates but the methods currently available provide a good basis for comparing seasonal and geographical differences in the severity of eyespot epidemics.

Financial costs

The national costs of eyespot on winter wheat and winter barley crops are composed of the yield losses attributable to the disease together with the costs of fungicide sprays for controlling it. ADAS estimates of these costs for the period 1981-1987 are given in Table 2. The national financial losses from eyespot (F) can be estimated as:

$$F = y/(1-L).L.a.p \qquad (8)$$

where y is the mean national yield (t/ha), L is the estimated yield loss (proportion), a is the area grown (M ha) and p is the price

(£/t). Thus for winter wheat in 1987 ADAS estimated the proportional loss as 0.0235, the area grown as 1.847 M ha, the mean national yield as 5.93 t/ha and the approximate price of feed wheat as £110/t, giving an estimated financial loss of £29M.

This figure is almost certainly an underestimate. Not only are any errors in estimating the yield loss transferred to this estimate of the financial loss, but also there are other sources of error. In calculating the loss of £29M, the mean wheat yield for 1987 (adjusted to allow for eyespot losses) was used. However, if the mean yield for the period 1982-86 (6.7 t/ha) is used to get a better estimate of the potential yield in 1987, the estimated loss is £32M.

Furthermore, the estimate of £29M takes no account of the losses in quality of grain caused by eyespot, which will greatly affect the financial loss. In 1987 almost 40% of the winter wheat area was sown to milling varieties on which eyespot was as severe as on feed wheats, according to ADAS survey data. Eyespot may have contributed to the loss in quality of many of these crops in 1987, particularly when lodging occurred. If milling crops were down-graded and sold as feed wheat, the loss incurred was *c.* £32/t (using monthly average farm prices for milling and feed wheat for the period July-December 1987, *Home-Grown Cereals Authority Weekly Digest* 14 (27), 11 Jan. 1988). If loss in quality of milling wheats was associated only with severe eyespot (3.5%) it would represent a further loss nationally of £5.0M. If, however, there was a loss associated with both moderate and severe eyespot (28.8%), it would represent a further loss of £41.4M. Nationally the loss in quality caused by eyespot may have been more significant than the loss in yield, since it may have contributed to the shortfall in milling wheat production in 1987. Consequently milling wheats are being imported from abroad and the Minister of Agriculture has estimated that the price of bread will be rising by 3p per loaf (Times, Oct. 14 1987), a national cost of £110M (consumption *c.* 10M loaves per day). These alternative calculations of the financial losses caused by eyespot result in estimates for winter wheat in 1987 ranging from £29M to £73M, demonstrating the urgent need to obtain the data necessary to provide more reliable estimates.

The proportion of winter cereal crop treated with fungicides has increased greatly, from about 1% in 1974 to over 90% currently. The costs of fungicides applied against eyespot (Table 2) may be estimated from ADAS survey data. If it is assumed that fungicides applied at

G.S. 31 were applied against eyespot, the survey data give the proportions of crops treated then with MBC fungicides (cost £5.20/ha), prochloraz (£19.30/ha) or MBC + prochloraz (£20.50/ha). From these figures, and the total area of the crop, the total cost of fungicides applied against eyespot can be calculated. Thus it was estimated that in 1987 the national costs of fungicides applied to control eyespot were £15.6M for winter wheat and £7.2M for winter barley. These estimates do not include the costs of fungicides applied against eyespot other than at G.S. 31. Furthermore, they do not include a proportion of the application and wheeling damage costs, which cannot be attributed entirely to eyespot control. In addition to these estimated fungicide costs, there are other long-term costs which are difficult if not impossible to quantify. Repeated use of fungicides may lead to the development of fungicide resistance in the pathogen so that new fungicides have to be produced to control it. The production of a new fungicide may take several decades and cost many £M. Furthermore, excessive use of fungicides may be damaging to the environment, particularly if they affect non-target organisms. Thus for pathological, environmental and economic reasons it is desirable that fungicides be used only when they are needed.

Applications

Estimates of yield losses caused by eyespot and the financial costs of the disease are extremely useful to organisations wishing to assess the national importance of the disease, and the seasonal changes in eyespot severity. Such information can be used to assess the priorities for further research and for developing new cultivars with improved resistance and new fungicides for eyespot control. However, this retrospective information cannot be used by the grower to predict yield and financial losses in crops at times when it is necessary to make spray decisions. For predicting yield losses, and hence the likely benefits of control measures, a simple relationship between some measure of disease incidence and/or severity and future yield loss is needed.

6. CONTROL OF EYESPOT

Control of eyespot in the UK relies on a combination of varietal resistance, fungicides and cultural methods. All three strategies for controlling eyespot are important but, in practice, their relative use has changed greatly in response to socio-economic and political

influences on agricultural practice. Varietal resistance to eyespot has been important in UK cereal cultivation since the 1950s. However, with the intensification of cereal production and the introduction of effective fungicides in the mid-1970s, the use of fungicides increased greatly over the next decade. Correspondingly, the importance of cultural methods for control of eyespot has declined in the UK. Rotations, which were important in eyespot control, have been replaced by continuous sequences of autumn-sown cereal crops because economic factors have favoured cereal production. The existence of effective fungicides has reduced the risks of serious losses from eyespot in such high-input high-output crops. However, in countries where cereals are grown less intensively, it is uneconomic to use fungicides against eyespot, and cultural methods are still important. Furthermore, as the economics of cereal production in the UK change, the relative importance of the three strategies for eyespot control may also change.

Varietal resistance

Varietal resistance is a strategy for eyespot control which is both agriculturally and environmentally desirable. For the grower, it is a cheap method of control; he/she pays a 'fixed cost' towards the variety breeding costs when buying seed at the beginning of the season. Furthermore, use of a resistant variety imposes no great constraints on methods for growing the crop and leaves options open. It reduces the need for application of chemicals, which may affect non-target organisms, either in the crop or in the surrounding environment if chemical is dispersed by spray drift or run-off water.

Resistance to eyespot may take the form of direct resistance to the growth of the pathogen in the stem base or of indirect tolerance to eyespot through resistance to lodging (Scott & Hollins, 1985). Commercial winter wheat varieties differ in their resistance to eyespot with National Institute of Agricultural Botany (NIAB) ratings from 4 (Brock, susceptible) to 8 (Rendezvous, resistant) on a 0-9 scale (Anon., 1988). Commercial winter barley varieties are less severely attacked, in general, and eyespot resistance ratings of 5-7 were recorded in 1983 NIAB trials (Bayles, pers. comm.).

Resistance to lodging, which is widespread in modern varieties with short, stiff straws, reduces damage from eyespot. In experiments at the Plant Breeding Institute (PBI, now a part of Unilever PLC) tall-strawed, lodging-susceptible varieties yielded less when lodging occurred in infected plots than when lodging was prevented by netting,

but nets had no effect on yield of short-strawed, lodging-resistant varieties (Scott & Hollins, 1974). Lodging resistance, which confers tolerance to eyespot indirectly, does not necessarily confer resistance to growth of the eyespot fungus in the stem base. However, the stem base characteristics which are important in lodging resistance may also be important in eyespot resistance.

Most of the current commercial UK varieties of winter wheat incorporate resistance to eyespot, discovered in the 1950s, derived from the French variety, Cappelle-Desprez (Batts & Fiddian, 1955). Cappelle-Desprez dominated the UK wheat crop for over 20 years and was officially recommended in the period 1953-1976. Its resistance to eyespot was a major factor in its success, and allowed it to continue in cultivation as cereal production intensified and more cereal crops were grown in continuous sequences. The resistance of Cappelle-Desprez is incomplete; eyespot infects Cappelle-Desprez and varieties with this resistance, but disease severity and yield losses are generally less than in susceptible varieties (Scott & Hollins, 1985; Murray & Bruehl, 1986). For example, in PBI/ADAS trials eyespot and lodging were less severe and yield was greater for the variety Norman which has Cappelle-Desprez resistance than for Armada, which does not (Table 3). The Cappelle-Desprez resistance to eyespot is readily introduced into new varieties and appears to be durable since it has not been overcome, despite widespread exploitation for over 30 years.

The new variety, Rendezvous, which is provisionally recommended by NIAB (Anon., 1988), incorporates more effective resistance to eyespot than that of Cappelle-Desprez. This new resistance is from a wild goat grass, *Aegilops ventricosa*, and was first transferred into the French breeding line VPM 1. In PBI/ADAS field trials over 6 years, using both artificial and natural eyespot inoculum, Rendezvous has been more resistant than other winter wheat varieties, many with resistance from Cappelle-Desprez (Hollins *et al.*, 1988). Although Rendezvous can be infected by the eyespot fungus, symptoms are less severe at the start of grain-filling (G.S. 71), lodging is less and yields are greater than in moderately resistant varieties such as Norman (Table 3). Furthermore, these trials suggest that Rendezvous is more resistant than its parent, VPM 1, implying that it may have eyespot resistance from both *A. ventricosa* and Cappelle-Desprez. Sequential sampling from infected plots showed that eyespot lesions develop more slowly in stems of Rendezvous than in stems of other cultivars, although severe lesions

may be present at the end of the season (Hollins *et al.*, 1988). Consequently, in several experiments differences between varieties in disease severity (assessed by an eyespot index) were much smaller in pre-harvest samples than in samples taken earlier. This illustrates the importance of taking several samples prior to the end of grain-filling from field trials on eyespot to identify the factors influencing yield differences between varieties. Although there has been no evidence from field trials to suggest that the resistance of Rendezvous will break down, the durability of this resistance will only become apparent when it is tested by extensive exposure to the pathogen in commercial agriculture.

The genetics of the cereal-eyespot host-pathogen interaction are not clearly understood. However, it is known that the Cappelle-Desprez resistance is coded by one or more genes on chromosome 7A (Law *et al.*, 1975) and that the *A. ventricosa* resistance is coded by a single dominant gene on chromosome 7D (Hollins *et al.*, 1988). *P. herpotrichoides* has the ability to adapt to different host species; variants have been described which are pathogenic to rye (Scott, Hollins & Muir, 1975), couch grass (Cunningham, 1981) and *Aegilops squarrosa* (Scott, Defosse, Vandam & Doussinault, 1976). This expression of pathogenic adaptation at the host species level is a common feature of many necrotrophic cereal pathogens (Scott & Hollins, 1980). However, there is no indication that *P. herpotrichoides* exhibits physiologic specialization with races consistently adapted to different varieties, although varieties of wheat, barley and rye differ in susceptibility and isolates of *P. herpotrichoides* differ in pathogenicity in seedling pathogenicity tests (Scott *et al.*, 1976; Scott & Hollins, 1977).

Many workers have attempted to explain the nature of resistance to *P. herpotrichoides* by studying seedling infection, but the results have not been consistent. In the seedling tests of Macer (1966) with different cereal species, the pathogen grew more slowly in resistant hosts and he correlated the results with lodging and yield loss data from field trials. However, Higgins & Fitt (1985b), comparing the pathogenicity of different isolates of *P. herpotrichoides*, found that pathogenicity to seedlings was poorly related to pathogenicity to adult plants. Furthermore, Scott (1971) concluded that the rate of penetration of seedling leaf sheaths was independent of variety after an initial lag phase, possibly resulting from differences in the rate of colonization of the coleoptile between varieties (Bateman & Taylor, 1976a,b). Since the stem phase in the development of eyespot lesions

appears to be more important than the seedling phase, the approach taken by Murray & Bruehl (1983), who examined the cross-sectional structure of the first node of the stem, seems more likely to identify the reasons for differences in resistance between varieties. They found that in healthy plants the width of the hypodermis and the number of cell layers in the hypodermis were greater for resistant wheat varieties than for susceptible varieties. Furthermore, cell wall thickening and lignification occurred earlier in resistant than in susceptible varieties. When plants were infected, lignified cell wall appositions (lignitubers) were larger and formed in greater profusion at penetration sites in cells of resistant then in cells of susceptible varieties. Properties such as early cell wall thickening and lignification would also contribute to lodging resistance, so some cultivars might be resistant to both the direct and the indirect effects of eyespot.

Priestley & Bayles (1988) have estimated the economic value of resistance to eyespot and other pathogens, using data from NIAB trials and ADAS surveys in the period 1980-83 (Table 4). The varieties used in that period have been classified as :-

susceptible: the most susceptible varieties grown, with the greatest disease score in trials;

popular: the most popular varieties grown by farmers, which indicate the level of resistance used in commercial agriculture;

resistant: the varieties with the lowest disease score in trials indicating the best resistance available at the time.

The formula of Clarkson (1981) was used to estimate the national loss from eyespot from ADAS survey data on the incidence of moderate and severe lesions. The estimated national loss was then used to estimate the financial loss from 1983 data for the price and area of wheat grown. Thus Priestley & Bayles estimate that £0.8M was being saved by growing the most popular varieties and that a further £0.8M could have been saved by growing the most resistant varieties. However, these are probably underestimates since the most susceptible varieties probably had some resistance to eyespot. Furthermore, national losses from eyespot in the period 1980-82 were small by comparison with losses in seasons such as 1983 (no survey data available), 1985 and 1987 (Table 1). In addition, the resistance of Rendezvous is much greater than that of cultivars available in 1983. Assuming that Norman is a typical 'resistant' variety and using comparative eyespot scores from PBI/ADAS

trials (Table 3), one might estimate that growth of Rendezvous would save an additional £3.1M (estimated national losses £4.7M). However, these figures do not include the saving through reduced fungicide usage by growing resistant cultivars.

Fungicides

Until the mid-1970s it was uneconomic to use fungicides against eyespot on cereal crops in the UK and no effective fungicides were available for control of eyespot. However, with the introduction of the carbendazim-generating (MBC) fungicides and the increase in cereal prices in the mid-1970s, usage of fungicides on cereals against eyespot (Table 5) and other diseases has increased greatly. Whereas only 1% of winter wheat crops were sprayed with fungicides in 1973, 75% were sprayed in 1982 (Cook & King, 1984) and 90% were sprayed in 1987. According to the ADAS survey, in 1987 60% of winter wheat and winter barley crops were sprayed at G.S. 31, presumably against eyespot (Table 5).

When they were introduced, MBC fungicides gave excellent control of eyespot and good yield increases, even when amounts of eyespot were small in crops. Since their cost was small by comparison with the potential benefit, they were used routinely by many growers as an 'insurance' against possible eyespot development. Resistance to MBC fungicides in the eyespot pathogen, *P. herpotrichoides*, was first identified in West Germany (Rashid & Schlosser, 1975) but was thought to be unimportant because the incidence of resistance apparently increased little where fungicides continued to be applied (Fehrmann *et al.*, 1982). However, in the UK in 1981 failure of MBC fungicides to control severe eyespot in two crops was found to be associated with a high incidence of MBC-resistance in *P. herpotrichoides* isolates taken from them (King & Griffin, 1985). Subsequently ADAS surveys showed that MBC-resistance was widespread in UK *P. herpotrichoides* populations (Griffin & King, 1985; King & Griffin, 1985) and by 1987 over 70% of isolates from a survey were MBC-resistant.

The dimethylation-inhibiting (DMI) fungicide prochloraz, first recommended for control of eyespot in 1980, is now used on more than 35% of the winter cereal area for control of eyespot, either alone or in a mixture with MBC fungicides. Whilst it may be less effective than MBC fungicides against MBC-sensitive isolates (Hoare *et al.*, 1986), prochloraz is effective against both MBC-sensitive and MBC-resistant populations and in recent trials on commercial winter wheat and winter

barley crops, prochloraz, alone or in a mixture with carbendazim, reduced the incidence of moderate or severe eyespot and increased yields substantially (Table 6). Furthermore, carbendazim did not control eyespot, and increased yield little, suggesting that it should not be used against eyespot in the UK although it may give effective control of eyespot and increase yields in countries (e.g. Canada, USA) where MBC-resistance is not yet a problem (Hermann & Wiese, 1985; Nelson & Sutton, 1988b). However, evidence from the UK and other European countries suggests that if MBC fungicides are widely used against eyespot, these populations will also become MBC resistant (King & Griffin, 1985; Cavelier *et al.*, 1985; Schreiber & Schlesinger, 1985). Furthermore, when MBC fungicides are used against an MBC-resistant population of *P. herpotrichoides* they may increase the severity of the eyespot epidemic and decrease yield (Griffin & King, 1985). It also seems unwise to use the prochloraz/carbendazim mixture against eyespot in the UK since it does not provide better control of eyespot or increase yield more than prochloraz alone (Table 6), whilst inducing the development of MBC-resistance (Hoare *et al.*, 1986).

There is no evidence that resistance to prochloraz has developed in UK populations of *P. herpotrichoides* despite extensive use over the last few years (Birchmore *et al.*, 1986; Gallimore *et al.*, 1987). A suggestion that resistance to prochloraz was developing in *P. herpotrichoides* populations in New Zealand (King *et al.*, 1986) was not substantiated by later work (Birchmore, Buckley, Browning & Russell, 1987). Another advantage of prochloraz is that it may give effective control of eyespot when applied between G.S. 30-37, whereas it was necessary to use MBC fungicides at G.S. 30/31 to obtain good control of eyespot. The greater flexibility in spray timing for prochloraz may give growers the opportunity to delay treatment until the weather is optimal for spraying, or until the risk of a severe eyespot epidemic can be ascertained more accurately.

It is not clear why prochloraz is effective at the later growth stages (e.g. G.S. 37) when the crop canopy is well developed and most chemical is deposited on upper leaves, since downward translocation of prochloraz in the phloem is limited (Jordan, pers. comm.). However, 30 days after spraying, substantial amounts of prochloraz and its metabolites are sometimes present at the stem base; it has been suggested that the chemical may be redistributed from the upper leaves by rain. To investigate methods of application of late spray

treatments, Bateman (1987), using hand-held sprayers, compared conventional sprayers with sprayers using nozzles trailed through the crop near ground level which could apply fungicide directly to stem bases; prochloraz applied at G.S. 34-37 decreased the severity of eyespot when applied with trailed nozzle sprayers but not when applied with conventional sprayers, suggesting that it is not always redistributed from upper leaves. Deposition of fungicides and control of cereal foliar diseases has been improved by displacing the crop during spraying with a bar attached below the spray boom (*Farmers Weekly* 106, p.33, 1987); this method might also be useful for improving deposition of prochloraz at the stem base for eyespot control. Improved control of eyespot and increased yield may sometimes be achieved by using a split rather than single application of prochloraz (Hoare *et al.*, 1986). However, it is doubtful whether the increase in yield would justify the increased application costs incurred by introducing this extra spray.

The costs and economic benefits from the use of fungicides in UK cereal crops have been reviewed by Cook & King (1984) and Cook & Jenkins (1988). Using 1982 prices and data from a 1982 ADAS survey of pesticide usage and from disease surveys for 1978-82, it was estimated that the national increase in yields of cereal crops attributable to use of fungicides (cost £60M) was £118M, a net benefit of £58M *per annum* (Cook & King, 1984). By another method, using 1984 prices, the national benefit was estimated as £41M for winter wheat and £13M for winter barley (Cook & Jenkins, 1988). It is not easy to estimate the overall benefit from fungicide used to control eyespot since MBC fungicides used in the last few seasons have probably been ineffective. However, from ADAS data for 1987 presented in Table 5, it can be estimated that 0.98M ha of winter wheat or winter barley were sprayed with prochloraz at a cost of £18.8M. Field trial data suggests that the average yield benefit from prochloraz treatment is 0.58 t ha^{-1} (Table 6), estimated to be worth £62.5M nationally, giving a net benefit of £43.7M.

However, in 1987, growers spent an estimated £4.1M on MBC fungicides (£5.20 ha^{-1}) or on adding an MBC fungicide to prochloraz (£1.20 per ha^{-1}, the estimated additional cost of using MBC + prochloraz as opposed to prochloraz alone); it is likely that these MBC fungicide sprays did not increase yields and they may have decreased yields (Griffin & King, 1985), so this money was wasted. Furthermore,

some 42% of the area of winter wheat or winter barley received an MBC fungicide spray, maintaining the selection for MBC-resistant strains in the *P. herpotrichoides* population. This inappropriate use of fungicides highlights the need to communicate to growers the results of work by the AFRC, ADAS and the agrochemical industry to improve farming practice. It is essential to identify crops where application of fungicides will be cost-effective, and to ensure that they are treated with the most appropriate chemical at the best time.

Cultural methods

Whilst the importance of cultural methods for control of eyespot has declined in the last decade when cheap, cost-effective chemicals for controlling the disease have been readily available, both economic and environmental criteria suggest that this may change. Glynne & Salt (1958) have reviewed cultural methods for control of eyespot, especially crop rotation. Two year breaks with non-susceptible crops reduce eyespot damage in the first wheat crop to negligible levels, provided that volunteer cereals have been controlled to prevent carry-over of the disease. With the current trend for farmers to grow increasing areas of non-cereal crops, it seems likely that two-year breaks can be used more often. However, it is probable that winter cereals will be grown more often than one year in three on most of the arable land and one-year breaks are insufficient to control eyespot, although application of fungicides to control eyespot after a one-year break may not be cost-effective (Cook, pers. comm). Furthermore, eyespot can be a serious problem in second wheat crops, particularly in wetter areas of the country. Thus rotation is unlikely to become a very significant strategy for controlling eyespot in the foreseeable future.

The review of Glynne & Salt concluded that eyespot is less likely to be severe in late-sown crops. However, early sowing of winter cereal crops will continue to be desirable for other reasons in the UK although control of eyespot by late sowing may be appropriate in Canada (Nelson & Sutton, 1988b). Nevertheless growers should be aware that if crops are late-sown (for example, because of a late harvest) the risk that serious eyespot epidemics will develop is much reduced. Excessive use of nitrogen fertilisers and very high seed rates are both likely to produce very lush crops and to favour eyespot, so should be avoided, if possible. In the Pacific north-west of the USA, where cultural methods for control of eyespot are very important because use of fungicides is

often uneconomic, less eyespot developed in crops with minimal cultivation before sowing than in crops sown in ploughed land. This suggests that although there has been an increasing use of minimal cultivation in some areas of the UK, it is unlikely that this will increase the severity of eyespot.

Another trend has been for straw residues to be incorporated rather than being baled (uneconomic) or burnt (environmentally undesirable). In Rothamsted experiments testing the effects of straw residues, eyespot has typically been less severe where straw has been chopped and incorporated than where it has been burnt despite the fact that burning must destroy at least a proportion of the infected stem bases. The reasons for this effect are not known but there is some evidence that sporulation is inhibited in the presence of straw residues, perhaps as a result of competition by other faster-growing fungi (Jenkyn, pers. comm.). Research to study the effects of changing cultural practices on the severity of eyespot epidemics remains important and may show how cultural methods can be used to reduce reliance on fungicides in the light of current economic and environmental pressures on the agricultural industry.

Integration of control strategies

It seems likely that there will be an increasing emphasis on use of resistant varieties and cultural methods for control of eyespot to reduce fungicide usage. Nevertheless there will continue to be a role for fungicides in the control of eyespot in UK cereal crops, although use of resistant varieties like Rendezvous may reduce the need for fungicide treatments (Hollins *et al.*, 1988). In field trials Rendezvous yielded well when other varieties were severely infected by eyespot. Furthermore, it showed smaller increases in yield as a result of fungicide treatment than other varieties, suggesting that there will be fewer occasions when fungicide treatment can be justified economically. Even if the resistance of Rendezvous does not break down when it is grown widely, there is an urgent need to produce other varieties with similarly high levels of resistance to eyespot derived from other sources of resistance. It would be very unwise to grow varieties with just one source of resistance, however good its qualities, since this would exert tremendous selection pressure on eyespot to produce virulent strains. Furthermore, other resistant varieties are required because a range of varieties with different qualities will be needed for different markets (e.g. for bread-making,

biscuit making, animal feed, etc).

There is also an urgent need for new fungicides to control eyespot, and especially for fungicides with different modes of action from prochloraz. It is unfortunate that control of eyespot in the UK relies almost exclusively on this one fungicide. If the pathogen population were to develop resistance to it at the moment, there might be large scale losses. In practice, strategies for the control of eyespot by a combination of resistant varieties, fungicides and cultural methods need to be coordinated with strategies for controlling other diseases and for managing crop growth so as to maximise the economic yield. Thus ADAS produce recommended management schemes for winter wheat (Anon., 1986) and winter barley (Anon., 1987). Research is needed to refine these schemes and to adapt them to changes in agricultural practice as they occur. A current IACR/ADAS project is examining methods for improving the forecasting of eyespot and Septoria diseases of winter wheat in order to integrate strategies for controlling these diseases and reduce fungicide usage.

7. FORECASTING THE SEVERITY OF EYESPOT EPIDEMICS

There is currently an urgent need for accurate methods to forecast the severity of eyespot epidemics in winter wheat and winter barley crops. Nationally eyespot epidemics cause serious losses in some years, such as 1985 and 1987, but not in others (Table 1). In a given year eyespot epidemics are damaging in some crops but not in others and it is becoming increasingly important to identify both crops which will benefit from control of eyespot and crops which will not benefit. Yield losses are associated with the occurrence of severe lesions during grain-filling (Scott & Hollins, 1974; Clarkson, 1981) but fungicides need to be applied much earlier than this if they are to give effective control of eyespot. Before the eyespot populations became resistant to the MBC fungicides it was possible for growers to routinely apply a cheap 'insurance' fungicide at G.S. 30/31 and there was less need for an accurate scheme for forecasting eyespot severity. However, the only fungicide now available, prochloraz, is much more expensive and it is extremely important to minimize selection for resistance to prochloraz in the eyespot populations, so it is essential that prochloraz is used against eyespot only when it is necessary.

An eyespot forecasting scheme needs to predict, at a time when control sprays can be applied effectively, the occurrence of severe

lesions during the grain-filling period. Ideally it should also assess the yield and financial benefits which can be achieved from control of eyespot in relation to the costs of fungicide treatment. However, since yield losses are associated with severe lesions, an initial step would be to predict the future occurrence of severe lesions. Forecasting schemes currently available are based on risk assessment, weather data (infection periods or accumulated temperature) or disease assessment, alone or in combination .

Risk assessment

A risk assessment scheme for forecasting eyespot severity in winter wheat in Switzerland was devised by Vez & Gindrat (1976) and an element of risk assessment is incorporated in the UK ADAS schemes for managed disease control in winter wheat (Anon., 1986) and winter barley (Anon., 1987). The Swiss scheme, based on the results of field trials in 1971-75, assesses the influence of previous cropping, soil type, winter crop density and variety on eyespot severity. In the spring each factor is a given score from 1 (contributing little risk) to 7 (contributing much risk, e.g. previous crop a cereal, susceptible variety being grown). If the total risk score, obtained by adding scores for individual factors, is <21 no treatment is recommended. If the score is >23, treatment is recommended. If the score is 21-23, treatment is recommended if more than 20% of shoots are infected. The UK ADAS disease management schemes recommend routine application of fungicides against eyespot to high risk crops of susceptible varieties grown after wheat or barley and sown before mid-October (Anon, 1986, 1987). When applied to data from Rothamsted field experiments for 1980-84, these schemes recommended treatment of eyespot in some years when severe epidemics did not develop (Fitt & White, 1988). Whilst they may give a useful indication of crops at risk, spray decisions should not be based on risk assessment alone if fungicide sprays are to be applied only to crops which need them.

Weather-based shemes

Many forecasting schemes for other crop diseases use meteorological data from synoptic weather stations to predict the occurrence of conditions favourable for pathogen sporulation, dispersal and infection; when the weather data suggest that infection has occurred, growers are recommended to spray their crops (Royle & Butler, 1986). Such a weather-based forecasting scheme has been developed for eyespot on wheat in Germany (Fehrmann & Schrodter, 1971, 1972, 1973; Schrodter

& Fehrmann, 1971a, b). This scheme recommends that a fungicide be applied against eyespot after a period of 30-40 days with a high 'infection probability'. The formula for calculating the infection probability from meteorological data was developed using results from field experiments at Geissen in 1966-68. Pots of 1 wk-old wheat seedlings were exposed in field crops for 1 wk, incubated in a glasshouse for 2 months and then scored to assess the incidence of eyespot. Temperature, relative humidity and wind-speed at a height of 2 m and the amount and intensity of rainfall were recorded. From the fluctuations in the incidence of eyespot on the exposed plants they deduced the occurrence of 'infection periods'. However, the term is used rather loosely since these exposed plants did not necessarily assess the occurrence of weather favourable for infection. The failure of symptoms to develop on them subsequently might equally well reflect the absence of inoculum or conditions unfavourable for spore dispersal during the week of exposure. Furthermore, the development of symptoms would imply that infection occurred during the week of exposure only if subsequent conditions in the glasshouse were always unfavourable for infection.

Fehrmann and Schrodter (1971) found no direct relationship between the incidence of plants which developed eyespot and the weekly mean values of accumulated rainfall or temperature, although the graph they present does suggest that little disease developed on plants exposed during weeks when there was little rainfall. They concluded that the relationship was more complex and calculated correlation coefficients to assess whether the incidence of eyespot developing in exposed plants was related to rainfall intensity, windspeed, temperature or relative humidity, with the meteorological variables considered either for the whole week or for periods when other variables were optimal for infection. From their correlation analyses they concluded that temperature and relative humidity were the most important variables and that periods of at least 15 h with temperature between 4-13°C and relative humidity > 80% were necessary for infection to occur. Multiple linear regression was used to estimate an equation relating the observed incidence of eyespot to these variables.

A further conclusion was that dispersal of *P. herpotrichoides* conidia is by wind alone, and not by rainfall. It seems difficult to reconcile this conclusion with other evidence that the spore dispersal is primarily by rain-splash, even if wind also plays some role

(Ponchet, 1959; Hollins & Scott, 1980; Fitt & Bainbridge, 1983), and the basis for it warrants further examination. Fehrmann and Schrödter found some correlation between eyespot incidence and wind velocity at 2 m height but none between eyespot incidence and rainfall intensity. However, it seems unwise to deduce cause-effect relationships from such correlations, particularly when the inference does not appear to be supported by other biological and physical information. As the spores of *P. herpotrichoides* are produced in a sticky mucilage on debris at ground level, it seems highly unlikely that they are removed in large numbers by wind. However, Fehrmann and Schrodter (1971) observed that eyespot symptoms developed on plants exposed in a wind tunnel downwind of infected debris under dry conditions. Unfortunately they did not place any spore samplers in the wind tunnel during the tests and so did not confirm the presence of wind-dispersed spores. Furthermore, they used windspeeds of 2 and 4.5 m sec^{-1}, far greater than those normally occurring at ground level where the infected debris is lying.

Despite these problems in the methods used, Fehrmann and Schrodter obtained a good agreement between the 'infection probability' predicted by their model and the incidence of eyespot which developed on exposed plants (Schrodter & Fehrmann, 1971b). The model has been tested in the UK (Polley & Clarkson, 1978), but has not proved useful for predicting the severity of eyespot epidemics. Furthermore, in Germany this forecasting scheme has not been sucessful (Schrodter, 1983); the agreement between the calculated and observed 'infection probability' is poor when weather data from synoptic weather stations are used rather that data from on-site weather stations. They point out that in Germany weather favourable for infection occurs on many occasions during the growth of a winter wheat crop. This is also the case in the UK (Hollins & Scott, 1980; Fitt & Bainbridge, 1983) and it seems unlikely that such a forecasting scheme, based on weather conditions favourable for sporulation, spore dispersal and infection, will prove useful in predicting whether eyespot epidemics will become severe.

Rapilly *et al.* (1979) developed an eyespot forecasting scheme which incorporates the German criteria for infection periods (Schrodter & Fehrmann, 1971a), and the French formula relating lesion development to accumulated temperature (equation 1). Thus meteorological data from synoptic weather stations are used to determine when the infection criteria (15 h with temperature 4-13°C, relative humidity >85%) have been fulfilled. Starting from these infection periods, the equation is

used to predict the development of lesions and a fungicide spray is recommended when the equation predicts that four leaf sheaths have been penetrated:

$$\Sigma D = 240K1 + (90 \times 4)K1 \qquad (9)$$

A similar scheme has been developed for West Germany by Siebrasse & Fehrmann (1987), using an equation for lesion development derived from results of their own field experiments.

Rapilly *et al.* (1979) also incorporated their formula into a theoretical model to assess the risk of severe eyespot in different parts of France. An arbitrary date (15 April) was chosen and they calculated the risk that eyespot would reach the stem by this date from meteorological data for each year and produced a map to illustrate the calculated risk of severe eyespot in different regions.

However, these forecasting schemes assume that, after infection, eyespot lesions continue to develop whenever temperatures are >0°C. They do not allow for the loss of lesions which sometimes occurs in the UK, both in the leaf sheath lesion and stem lesion establishment stages of lesion development (Fitt & White, 1988), particularly when outer leaf sheaths die before the fungus has become established in the leaf sheath or stem beneath. Thus they seem inappropriate for the UK.

Disease-assessment-based schemes

The forecasting scheme developed by ADAS for UK growers relies mostly on assessment of the incidence of eyespot in crops at a time when spray decisions have to be made (Anon., 1986, 1987). Formerly, when MBC fungicides were commonly used, ADAS advice was to spray at G.S. 30-31 if more than 20% of shoots were infected (Anon., 1984). However, in Rothamsted and ADAS field trials the incidence/severity of eyespot at grain-filling (G.S. 75) was only poorly related to the incidence at G.S. 30-31, when eyespot sprays are usually applied. Two possible explanations are:

1. A variable proportion of the early infections develop into damaging lesions on the stem; thus severe disease may fail to develop when it was predicted.
2. The relationship is obscured by later infections, or by latent infections that are overlooked when the disease is assessed at the early growth stage; thus severe disease may develop when it was not predicted.

In the former case treatment will appear to have been successful, although the grower will have incurred unnecessary expense, but the

financial consequences are likely to be much greater if severe disease develops following a recommendation not to treat.

Furthermore, in a series of trials at the Plant Breeding Institute from 1969-1977, the severity of eyespot at harvest, and yield loss, were not predicted well by assessments of eyespot incidence at G.S. 30-31 (Scott & Hollins, 1978). Such assessments are made before a crucial stage in lesion development, when the fungus is spreading from the leaf sheaths to the stem (Fitt, 1985; Higgins *et al.*, 1986). During this period some infected shoots die and do not contribute to final yield, although other shoots may compensate for their loss (Scott & Hollins, 1974). In addition, lesions may be lost if infected leaf sheaths die and decay before the fungus has colonized the stem (Higgins *et al.*, 1986). Current ADAS advice (Anon., 1986, 1987) suggests that unless lesions have penetrated more than two leaf sheaths on more than 20% of shoots at G.S. 30, a spray decision should be delayed and further inspections made up to G.S.32. However, if spray decisions could be delayed further it seems likely that more accurate predictions of lesion severity during grain-filling could be made. Results of recent trials suggest that prochloraz, the fungicide currently used against eyespot, may sometimes be applied effectively after G.S. 32.

However, it is not clear what is the earliest stage at which accurate predictions of lesion severity during grain-filling and yield loss can be made. Thus further work is needed to improve the reliability of the current ADAS forecasting schemes. In particular experiments are needed to examine the threshold criteria (an incidence of 20%), which appears to be somewhat arbitrary; it may be that different criteria are applicable to different situations. When more biological information is available, it may be possible to incorporate estimates of financial benefit into the forecasting schemes so that the grower can assess the cost/benefit of a particular course of action for any crop.

8. CHANGES IN POPULATIONS OF THE EYESPOT FUNGUS

Two major changes have occurred in UK populations of *Pseudocercosporella herpotrichoides*, the cause of eyespot, over the last few years. Firstly, the frequency of MBC-resistant strains has increased greatly. Secondly, the R pathotype has been replacing the W pathotype as the dominant pathotype. These changes in populations have been investigated in national surveys of *P. herpotrichoides* populations

isolated from eyespot lesions on shoots sampled from commercial crops (King & Griffin, 1985). Field experiments have examined how different populations change under various fungicide strategies in order to investigate why these population changes are occurring (Bateman *et al.*, 1987; Hoare *et al.*, 1986).

Fungicide resistance

The selection for MBC-resistant strains of *P. herpotrichoides* in UK populations has been a direct consequence of the regular use of MBC fungicides by growers. Isolates are regarded as MBC-resistant if they grow on agar containing 1 µg/ml of carbendazim; such isolates are frequently obtained from crops where MBC fungicides have failed to control eyespot. MBC fungicides affect fungal tubulin; MBC-resistance, which involves an alteration in the structure of the tubulin, has developed in a wide range of fungi (Georgopoulos, 1987). MBC-resistance, which involves a single gene mutation, appears to be 'absolute' and resistant isolates can grow on media containing high concentrations of MBC fungicides. MBC-resistant isolates also show no evidence of a reduced pathogenicity to cereals, by comparison with MBC-sensitive isolates (Brown *et al.*, 1984; Fitt *et al.*, 1987). Furthermore, these isolates usually exhibit cross-resistance to all MBC-generating fungicides. However, there is a negative-linked cross-resistance between MBC and MDPC (methyl-N-(3,5-dichlorophenyl)-carbamate) for the eyespot fungus; i.e. isolates which are MBC-resistant in culture are sensitive to MDPC and *vice versa* (Fitt *et al.*, 1984). Nevertheless phenylcarbamates have not been effective in field trials (Hollomon, pers. comm.) and isolates of *P. herpotrichoides* resistant to both MBC and phenylcarbamates have been identified (Leroux *et al.*, 1985; Griffin, pers. comm.).

MBC fungicides were introduced for eyespot control in the 1970s and MBC resistance in *P. herpotrichoides* was first observed in 1974 in isolates from stubble sampled in Germany (Rashid & Schlosser, 1975). Initially, the frequency of MBC-resistant conidia was low (10^{-9}) and it apparently increased little where MBC fungicides continued to be applied, so gave Fehrmann *et al.* (1982) no cause for concern. Of *c.* 60 isolates collected from 1956-1980 none were MBC-resistant when tested by Hollins *et al.* (1985). However, in 1981 MBC fungicides failed to control eyespot on some winter wheat crops in the UK and most isolates of *P. herpotrichoides* from these crops were MBC-resistant (Griffin & Yarham, 1983). Subsequent surveys showed that the highest frequencies

of MBC-resistance in winter wheat and barley crops in the UK were associated with crops from sites which had received several applications of MBC fungicides (King & Griffin, 1985). By 1983 the frequency of MBC-resistant isolates had increased to 50% (Table 8) and UK populations of *P. herpotrichoides* are now almost totally MBC-resistant (Yarham 1986; Hollins & Scott, 1987). An increase in the incidence of MBC-resistant isolates has also been reported in France (Cavelier *et al.*, 1985), West Germany (Fehrmann, 1984; Schreiber & Schlesinger, 1985), The Netherlands (Sanders *et al.*, 1985), Denmark (Nielsen & Schutz, 1985), Eire (Cunningham, pers. comm.) and Belgium (Maraite *et al.*, 1985).

In the UK the incidence of MBC-resistant isolates in wheat crops on sites which had never received MBC-fungicides was 1-4% in 1984 (Bateman *et al.*, 1985, 1987). This incidence is much greater than that observed by Fehrmann *et al.*(1982), but the data were for mycelial isolates rather than conidia and the two methods of assessing incidence may not be directly comparable. In experiments to study changes in populations of *P. herpotrichoides* on such sites under different fungicide strategies the incidence of MBC-resistant isolates rapidly increased to more than 90% when MBC fungicides were applied (Hoare *et al.*, 1986; Bateman *et al.*, 1986, 1987). In the absence of MBC-fungicide sprays on plots inoculated with MBC-resistant isolates the incidence of MBC-resistance declined gradually. The incidence of MBC-resistance did not increase more in plots treated with prochloraz, the fungicide currently used to control eyespot, than in untreated plots but it did increase in plots treated with a mixture of carbendazim plus prochloraz.

Isolates of *P. herpotrichoides* which had a decreased sensitivity to a wide range of DMI fungicides have been identified in France (Leroux & Gredt, 1985). However, these isolates were sensitive to prochloraz and no increase in resistance to prochloraz has been found in surveys of *P. herpotrichoides* populations in New Zealand (Birchmore *et al.*, 1987) or in the UK (Birchmore *et al.*, 1986; Gallimore *et al.*, 1987) where it has been widely used against eyespot for several years (Table 5). Since prochloraz is currently the only fungicide effective against eyespot which is available in the UK , it is essential that surveys to monitor the sensitivity of populations to prochloraz are continued.

Pathotypes

Another change which has occurred in UK populations of *P. herpotrichoides* is that the W pathotype has been replaced by the R pathotype, which is now predominant (Table 8, Yarham, 1986; Hollins & Scott, 1987). A similar population change has occurred in West Germany (Schreiber & Prillwitz, 1985). Whilst isolates which produce colonies with R-type characteristics have been present for many years (Glynne & Salt, 1957), they were formerly rare other than in rye-growing areas (Hollins *et al.*, 1985). It is not clear why the frequency of R-type isolates should have increased. It has been suggested that in the last few years the increase in the area of winter barley (King & Griffin, 1985) or the increase in the use of fungicides (Bateman *et al.*, 1986; Hoare *et al.*, 1986) may have selected in favour of the R pathotype. The widespread use of DMI fungicides for late-season disease control on winter cereal crops may have selected for R-types, which are less sensitive to DMI fungicides (except prochloraz) than W-types (King & Griffin, 1985). Furthermore, under the influence of MBC selection pressure in the field, MBC resistance builds up more quickly in R-types than in W-types (Griffin , pers. comm.).

Both surveys (King & Griffin, 1985; Coskun *et al.*, 1987) and field experiments (Bateman *et al.*, 1986, 1987) have shown increases in the frequencies of R-type isolates between spring and summer samples from the same crop, suggesting that these population changes may occur during growing seasons as well as between seasons. These within-season population fluctuations highlight the need to take samples at similar crop growth stages if population changes between seasons are to be measured. It is not evident how these within-season population fluctuations occur since only 2.7% of eyespot lesions yielded isolates of both pathotypes in a 1987 ADAS survey at G.S. 30-31 (Thomas, pers. comm.). The related species *Pseudocercosporella anguioides* was present in 5.8% of eyespot lesions from which isolates were obtained, which suggests that it does not have a significant role in eyespot epidemics. However, isolates were obtained from only 42% of the eyespot lesions included in the ADAS survey and from only 30% of the lesions in samples taken in the field experiment of Bateman *et al.* (1986) at G.S. 30-31, although they were obtained from 70% of lesions in a sample at G.S. 75. If the lesions from which isolates were successfully obtained were unrepresentative and one pathotype was consistently more difficult to .

isolate at, for example, G.S. 30-31, it might account for some of the apparent population fluctuations.

Although the increase in the frequencies of MBC-resistant strains and of the R pathotype have occurred simultaneously in UK populations (Table 8), they are not necessarily linked directly. In France an increase in the frequency of MBC-resistant strains has not been associated with a change in pathotype and MBC-resistant W-types are now predominant (Cavelier *et al.*, 1985). Climate, fungicide use and cultural practices all differ between France and the UK, which may explain why the populations have evolved differently in the two countries, although there appear to be no intrinsic biological differences between them (Creighton, Cavelier & Fitt, unpublished). The composition of populations of *P. herpotrichoides* and related fungi differs greatly between different countries (Russell & Birchmore, 1988); the frequency of *P. anguioides* isolates is greater in West Germany (Schreiber & Prillwitz, 1986) than in the UK and the frequency of MBC-resistant and R-type isolates is much less in Switzerland (Gindrat, pers. comm.).

Whilst these survey data for different countries are very interesting, it is difficult to know the extent to which national differences result from the use of different methodologies. To investigate why and how populations of the eyespot fungus change, it would be very useful to conduct a survey to compare the populations in different European countries, using standard sampling procedures and isolation techniques.

9. SUMMARY AND RECOMMENDATIONS

There is an urgent need for more research on eyespot (*Pseudocercosporella herpotrichoides*), a serious disease of winter wheat and barley. This disease has increased in importance in the 1980s because 1) pathogen populations have become resistant to the fungicides which were used to control it; 2) changes in cropping practices, such as earlier sowing dates, have favoured the development of severe epidemics. In 1987, ADAS national surveys suggested that, of the diseases surveyed, eyespot was the most serious disease problem on winter wheat, with losses estimated at *c.* £30M, despite the widespread application of fungicides against eyespot (cost *c.* £23M). These figures are underestimates since they include neither the losses caused by eyespot-induced lodging, nor the costs of fungicide application. Furthermore, it is likely that eyespot has been an important factor in reducing the

quality of milling wheat and malting barley crops so that they have to be sold for animal feed.

The priorities for future research are :

1. To improve estimates of national losses from eyespot. Current estimates are based on a formula which assesses direct yield losses, applied to ADAS national disease survey data. However, since this formula was derived for winter wheat varieties, eyespot populations and cropping practices have changed greatly. Therefore new experiments are needed to re-evaluate the formula under current conditions. Ideally a new formula should include a national estimate of losses from eyespot-induced lodging. In addition a formula needs to be derived specifically for winter barley. Furthermore it is especially important for work to be done so that the effects of eyespot on the quality of winter wheat (especially milling varieties) and barley (especially malting varieties) crops can be assessed nationally.

   Work to improve estimates of national losses from eyespot would involve a combination of 1) detailed experiments to derive new formulae, which might be done at the AFRC Institute of Arable Crops Research; 2) experiments at a wide range of sites and surveys of commercial crops, which could be done by ADAS. It could be appropriate for funding by H-GCA.

2. To improve the accuracy of methods for predicting the severity of eyespot epidemics. Yield losses occur only when there is a high incidence of moderate or severe eyespot lesions during grain-filling but sprays need to be applied much earlier than this to control the disease. Current methods for forecasting the severity of eyespot epidemics at a time when sprays can be applied have not always been reliable. In some years when sprays have been recommended, eyespot has not become damaging and in others when sprays have not been recommended, severe late epidemics have developed. A joint IACR (Long Ashton/Rothamsted)/ADAS project, funded by H-GCA, is aiming to integrate methods for forecasting eyespot and Septoria diseases of winter wheat but will not be able to answer all the important questions in the time available. There is a need to improve the forecasting scheme for winter barley and to determine more accurately the threshold criteria to be used in deciding whether or not to apply a fungicide spray.

The priorities for future research on integrated forecasting

of eyespot and other cereal diseases will be determined by results of existing experiments. Future research in this area, which will involve collaboration between ADAS and AFRC scientists, should be appropriate for H-GCA funding.

3. To compare populations of the eyespot fungus in different EEC countries. ADAS and other surveys have shown that populations of the eyespot fungus in the UK have changed greatly in the last few years. Not only have MBC-sensitive strains been replaced by MBC-resistant strains, but also the W-type (wheat-type) has been replaced by the R-type (rye-type). However, surveys suggest that the composition of eyespot populations in other EEC countries is different and that different population changes have occurred (for example MBC-resistant W-types are dominant in most regions of France). Furthermore, the related fungus *P. anguioides* is widespread in both West Germany and the UK early in the season, although its significance is unclear. International surveys of eyespot populations are being made by the agrochemical industry.

   There is a need, firstly, to examine the data from the different surveys. Then a co-ordinated programme of experiments in different EEC countries should be set up to investigate why eyespot populations differ between countries, and how populations are changing in different EEC countries. Such information will help the development of strategies for controlling the disease throughout the EEC. This work will involve collaboration between scientists working on eyespot in different EEC countries (e.g. Belgium, France, the Netherlands, UK and West Germany) and may be appropriate for EEC funding.

4. To study the comparative biology of the pathotypes of *Pseudocercosporella herpotrichoides*, the eyespot fungus, and of *P. anguioides*. Work at Rothamsted is indicating that there are epidemiological differences between W-types and R-types of the eyespot fungus. However, the causes of these differences are unclear. Almost all previous work on the biology of *P. herpotrichoides* has been done with the W-type which is no longer dominant in the UK. Furthermore, the taxonomy of the types of the eyespot fungus is confused. It is not clear how the W-type/R-type categories relate to the *P. herpotrichoides* var. *herpotrichoides*/ *P. herpotrichoides* var. *acuformis* varieties described by Nirenburg. In addition ADAS surveys indicate that the related

fungus, *Pseudocercosporella anguioides*, which can cause eyespot-like symptoms on leaf sheaths, is widespread but the significance of this fungus is unclear.

Thus there is an urgent need for experiments to investigate how epidemiological phases such as survival, sporulation, infection and the latent period differ between the pathotypes of *P. herpotrichoides* and related fungi and to establish reliable taxonomic criteria for classifying isolates of these fungi. A collaborative project between ADAS (Harpenden Laboratory) and IACR (Rothamsted) is being established to investigate the taxonomy of these fungi and an application has been submitted to a trust for funds to investigate their comparative biology.

5. To develop rapid diagnostic methods for distinguishing 1) between the eyespot fungus and other stem base pathogens; 2) between the pathotypes of *P. herpotrichoides*. It is not always easy to distinguish visually between eyespot and other stem-base pathogens, particularly early in the growing season. Isolation from infected tissue is time-consuming and not always reliable, especially where lesions are colonized by saprophytic fungi which grow rapidly in culture. Even when lesions are clearly distinguishable as eyespot on visual examination, it is currently necessary to culture the fungus to determine whether the isolate is MBC-sensitive or MBC-resistant, W-type or R-type. Although W-types and R-types may be distinguished in culture, intermediate types are found. Yet it may be important to know which pathogen or pathotype is present in order to devise an appropriate control strategy. Current work is investigating more rapid cultural methods for distinguishing between the pathotypes of *P. herpotrichoides* in isolation and in mixtures.

There is a need to extend this work to determine whether molecular biological and serological methods can be used to distinguish rapidly between the stem base fungi and between the pathotypes of *P. herpotrichoides*. If rapid diagnostic methods could be developed they would have widespread use throughout the EEC cereal industry. Planned work at IACR (Rothamsted) and Oxford University aims to extend existing projects in order to develop rapid diagnostic techniques for identifying these fungi.

6. To develop new varieties with improved resistance against eyespot and new fungicides for control of eyespot. Many of the winter

wheat and winter barley varieties currently grown in the UK can suffer severe attacks of eyespot and even Rendezvous, the variety with greatest resistance, can sometimes be affected. Yet control of the disease relies almost entirely on one fungicide, prochloraz.

There is an urgent need for new resistant varieties with such high levels of resistance as Rendezvous but with better milling qualities. Furthermore, there is a need for new sources of resistance to eyespot to be identified and incorporated into new varieties. Ideally there should be available to growers a range of varieties with different characteristics (e.g. good milling quality, high yielding, etc.) and different sources of resistance to eyespot. Furthermore, there is an urgent need for new fungicides for control of eyespot and for methods to improve the efficiency of existing fungicides (e.g. use of adjuvants to improve penetration). Whilst the development of new varieties and new fungicides is primarily the concern of the plant breeding and agrochemical industries, new products will need to be evaluated in independent trials.

Much of this proposed future research will involve close collaboration between scientists in ADAS and AFRC in order to investigate problems most effectively. Furthermore, collaborative research will also be needed on other stem base diseases of cereals (the subject of other H-GCA review articles). To deploy resources most effectively it seems advisable that one centre be designated to coordinate research on stem base diseases within ADAS and AFRC. This could be Harpenden where there is currently the greatest concentration of expertise on these diseases within ADAS and AFRC. A new core post, jointly funded by ADAS, AFRC and H-GCA could be created to coordinate research on cereal stem base diseases at the central location and elsewhere in the UK.

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Figure legends

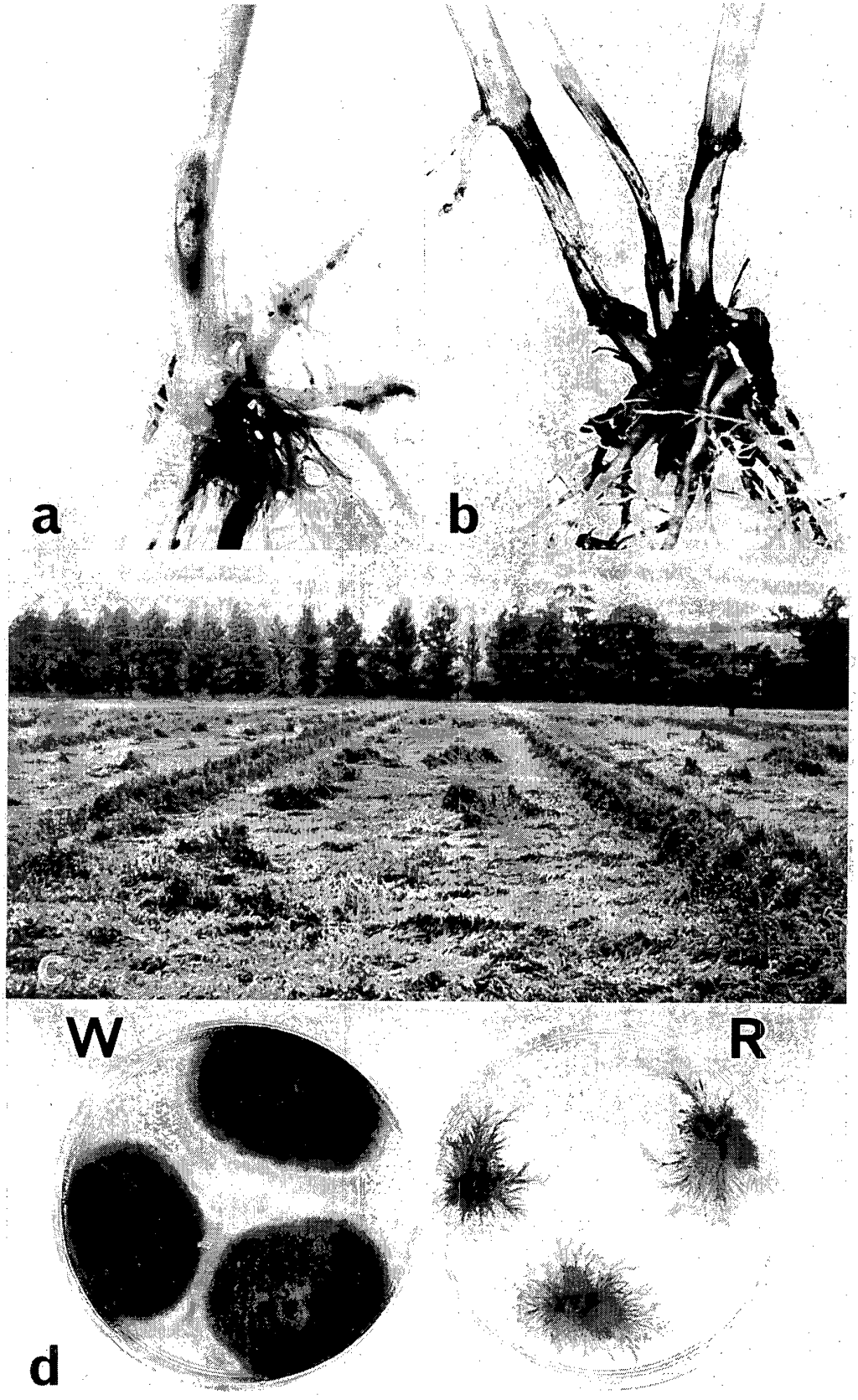
Fig. 1. (a) Slight eyespot lesion (R.J. Gutteridge)

(b) Severe eyespot lesions (M.D. Glynne)

(c) Lodging caused by severe eyespot (G.L. Bateman)

(d) W-type and R-type isolates of *Pseudocercosporella herpotrichoides*.

Fig. 2. Stages in the development of eyespot (*Pseudocercosporella herpotrichoides*) lesions in winter wheat crops. From Fitt, Goulds & Polley (1988).


a
b
W
R
d

7

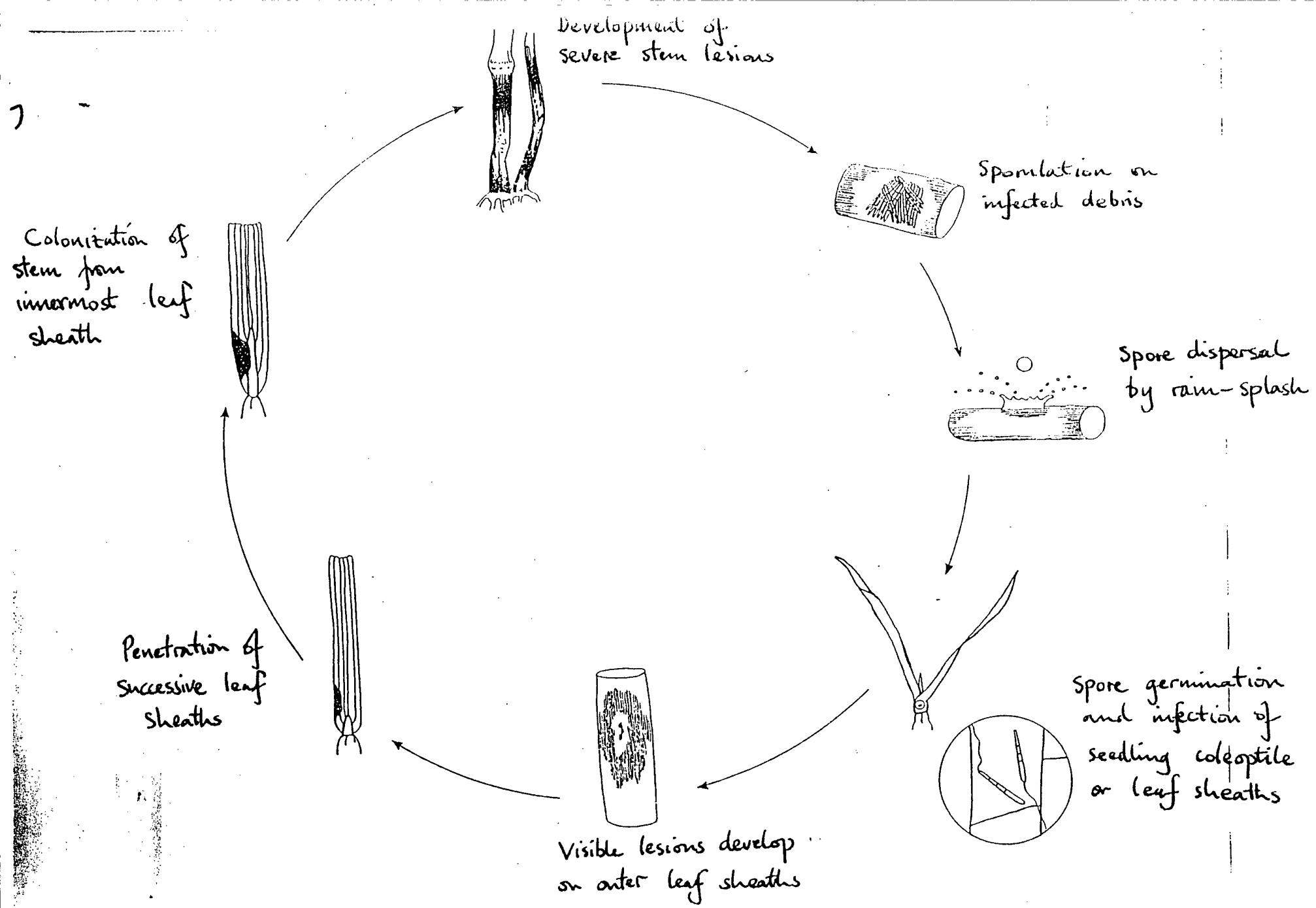

Development of severe stem lesions
Sporulation on infected debris
Spore dispersal by rain-splash
Spore germination and infection of seedling coleoptile or leaf sheaths
Visible lesions develop on outer leaf sheaths
Penetration of successive leaf sheaths
Colonization of stem from innermost leaf sheath

Table 1. National incidence of moderate or severe eyespot lesions on winter wheat and winter barley in England and Wales, assessed in ADAS surveys at G.S. 75 in 1975–1987 and estimated yield losses

Year	Winter wheat			Winter barley		
	Incidence of eyespot (%) Moderate	Severe	Estimated yield loss (%)[1]	Incidence of eyespot (%) Moderate	Severe	Estimated yield loss (%)
1975[2]	2.5	1.8	0.9	–	–	–
1976	1.1	0.4	0.3	–	–	–
1977	4.4	1.7	1.1	–	–	–
1978	5.0	2.0	1.2	–	–	–
1979	1.8	1.3	0.7	–	–	–
1980	1.8	0.2	0.3	–	–	–
1981	4.6	0.8	0.7	5.2	1.6	1.1
1982	0.4	0.04	0.05	1.0	0.2	0.2
1983	–	–	–	8.1	3.6	2.1
1985	9.8	2.9	2.0	–	–	–
1986	5.2	0.5	0.7	6.0	0.9	0.9
1987	16.9	1.8	2.4	4.4	0.6	0.7

[1]. Yield loss estimated by the single stem method of Clarkson (1981):

$$Y = [\ (0.1n_2 + 0.36n_3)/n_t\ ] .100$$

where n_2 and n_3 are the numbers of stems in the moderate and severe categories and n_t is the total number of stems in the survey.

[2]. Wheat data for 1975–80 from Clarkson (1981). Other ADAS survey data from Polley (pers. comm.). No data collected for 1983 (wheat), 1984 (wheat and barley) and 1975–1980, 1985 (barley).

Table 2. Estimated costs of eyespot on winter wheat and barley crops in England and Wales in the period 1981-1987; loss assessments and fungicide costs.

Year	Costs for wheat (£M)		Costs for barley (£M)		Total
	Loss[1]	Fungicides[2]	Loss	Fungicides	
1981[3]	6.7	*	4.8	*	-
1982	0.5	6.6	0.9	2.0	10.0
1983	-	-	10.2	*	-
1985	25.7	14.6	-	-	-
1986	10.3	17.3	5.0	8.3	40.9
1987	29.0	15.6	3.3	7.2	55.2

1. Financial loss estimated : $y/(1-L).\ L.\ a.\ p.$
where y is mean national yield (t/ha), L is estimated loss (proportion), a is the area grown (M ha) and p is the price (£/t).

2. Total costs of fungicides applied at G.S. 31, excluding application and wheeling damage costs.

3. Data from ADAS surveys (Polley, pers. comm.). No survey data for 1983 (wheat), 1984 (wheat & barley) and 1985 (barley). Data for 1981 and 1983 (winter barley) stored on computer at MAFF (Harpenden).

Table 3. Eyespot, lodging index and yield differences in untreated plots from PBI/ADAS winter wheat and winter barley trials

Variety	NIAB rating	Eyespot index (G.S. 71)[1] (0–100)			Lodging index[2]			Yield (t/ha)		
Winter wheat		1984	1985	1987	1984	1985	1987	1984	1985	1987
Armada	4	63	54	70	0	82	5	6.1	6.6	5.1
Norman[3]	5	62	47	71	0	67	2	6.9	7.3	6.1
Rendezvous	8	37	23	61	0	6	1	7.3	7.9	6.8
Winter barley										
Gerbel	-	70	67	69	24	8	15	8.8	7.3	6.9
Maris Otter	-	75	68	69	18	46	11	7.5	5.2	5.5

1. Scott & Hollins (1974)

2. Caldicott & Nuttall (1968)

3. Mardler in 1987

Data from Hollins *et al.* (1988), unpublished ADAS report (Polley, pers. comm.) and unpublished PBI data (Hollins, pers. comm.).

Table 4. Eyespot severity and estimated annual losses in susceptible, popular and resistant varieties of winter wheat, 1980-83.

Varieties	Eyespot index[1] (0-100 scale)	National losses[2] (%)	National losses[3] (£)
Susceptible	73	0.78	9.4
Popular	66	0.71	8.6
Resistant	59	0.68	7.8

[1]. Data from NIAB national trials, 1981-83

[2]. Data from ADAS national disease surveys, 1980-82

[3]. Using 1983 wheat prices, area

From Priestley & Bayles (1988)

Table 5. Use of fungicides for control of eyespot on winter wheat and barley (sprays applied at growth stage 31).

Year	Winter wheat[1]				Winter barley[1]				Total cost[2] (£M)
	Total area (M ha)	% crops treated MBC	P	MBC+P	Total area (M ha)	% crops treated MBC	P	MBC+P	
1981	1.42	*	*	*	0.79	*	*	*	-
1982	1.57	74.2	1.8	0	0.83	26.4	5.6	0	8.6
1983	1.61	-	-	-	0.84	*	*	*	-
1984	1.85	-	-	-	0.92	-	-	-	-
1985	1.78	39.5	5.8	24.6	0.93	-	-	-	-
1986	1.89	34.5	16.0	21.0	0.89	31.2	19.0	19.7	25.5
1987	1.85	24.5	19.0	17.2	0.88	24.0	15.6	19.2	22.8

[1]. Data from ADAS surveys (Polley, pers. comm.). No surveys for winter wheat in 1983/1984 or for winter barley in 1984/1985. Data for 1981 and 1983 (winter barley) stored on computer at MAFF (Harpenden).

[2]. Estimated costs of fungicides per ha: MBC, £5.20; prochloraz (P), £19.30; MBC + P, £20.50; these costs do not include application and wheeling damage costs.

Table 6. Control of eyespot in winter wheat and winter barley crops with more than 20% of tillers infected by fungicides applied at G.S. 30/31.

Treatment	% moderate/severe eyespot					yield (t ha^{-1})				
	1983[1]	1984[1]	1985[1]	1986[1]	1987[2]	1983	1984	1985	1986	1987
Wheat										
Untreated	61	41	59	45	61	7.2	8.2	7.2	8.2	7.9
Carbendazim	67	44	51	44	66	7.5	7.9	7.3	8.3	7.7
Prochloraz	41	24	38	24	34	7.9	8.9	7.7	8.6	8.4
Carbendazim + Prochloraz	42	20	37	25	43	7.9	8.8	7.6	8.6	8.2
No. of sites	6	3	9	8	3	6	3	9	8	2
Barley[2]										
Untreated					57					5.3
Carbendazim					54					5.4
Prochloraz					30					5.6
Carbendazim + Prochloraz					32					5.5
No. of sites					3					3

[1]. Data from ADAS trials (Jones, pers. comm.).

[2]. Data from Schering Agriculture trials

Table 7. Control of eyespot in winter wheat and winter barley with sprays of prochloraz (P) or prochloraz + carbendazim (P + C) applied at different times

Spray timing (G.S.)	% moderate/severe eyespot					yield (t ha^{-1})				
	1984[1]	1985[1]		1986[1]	1987[2]	1984	1985		1986	1987
	P + C	P	P + C	P + C	P	P + C	P	P + C	P + C	P
Wheat										
Untreated	57	39		55	47	8.1	7.3		7.6	7.3
11-21	15	26	29	37		9.2	7.5	7.5	8.2	
22-25	25	29	32	35		8.6	6.7	7.5	8.0	
30	24	27	26	30		9.0	7.6	7.5	8.3	
31	31	28	30	31	18	8.8	7.7	7.7	8.1	7.8
32-33	21	26	25	15	17	9.0	7.8	7.8	8.4	7.8
No. of sites	2	12		4	8	2	12		4	6
Barley										
Untreated					62					5.5
31					27					6.0
33					31					6.0
No. of sites					6					6

[1]. Data from ADAS trials (Jones, pers. comm.).

[2]. Data from Schering Agriculture trials

Table 8. Change in populations of *P. herpotrichoides* in cereal crops in Eastern England, assessed in ADAS/PBI surveys at G.S. 75. Frequency (%) of MBC-sensitive W-type (WS), MBC-resistant W-type (WR), MBC-sensitive R-type (RS) and MBC-resistant R-type (RR) isolates.

Year (no. of isolates	WS	WR	RS	RR
1983 (962)[1]	34.9	6.6	15.1	43.4
1984 (674)[2]	12.2	5.6	9.8	72.2
1985 (644)[2]	8.2	5.7	6.7	79.3
1986 (578)[2]	7.3	4.8	4.3	83.6
1987 (578)[2]	6.8	12.3	2.9	78.0
(113)[3]	12.4	2.7	2.7	82.3

[1]. Data from King & Griffin (1985).
[2]. Data from PBI/ADAS survey (Hollins, pers. comm.).
[3]. Data from ADAS survey at G.S. 30/31 (Thomas, pers. comm.).

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Appendix 1

Assessment of eyespot and other stem base diseases of winter wheat and winter barley

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1. INTRODUCTION

The identification of eyespot in winter cereals is a perennial problem. Disease management plans currently recommend that eyespot assessments be made at the beginning of stem extension (Growth Stages 30-32) when the crop is undergoing considerable change in structure and when much plant material is lost through natural senescence. Assessors commonly confuse eyespot lesions with those of sharp eyespot, particularly during these earlier growth stages. Further difficulties may be encountered if symptoms caused by other fungi such as *Fusarium* spp., *Septoria nodorum*, *S. tritici*, *Gaeumannomyces graminis* or in barley, *Rhynchosporium secalis* are also present on the leaf sheaths and/or stems. Some cultivars of winter barley also have extensive natural pigmentation which can obscure the presence of disease, particularly if this pigmentation occurs on the leaf sheaths.

These notes are intended to supplement MAFF identification cards IC/5, IC/13 and IC/16 (Anon. 1981a, 1981b, 1981c) which are currently used as guides to the identification of cereal stem base diseases. Descriptions based on lesion shape and colour are inevitably subjective and advisors or researchers should confirm diagnoses using reisolation or other *in vitro* techniques until sufficient experience and confidence have been gained. Further information on these and other diseases of cereals is given in the bibliography.

2. DISEASE DESCRIPTIONS

Although the appearance of eyespot symptoms is similar on leaf sheaths and stems, separate descriptions of the disease on seedlings and adult plants are given to reflect differences in the problems encountered at these two stages of crop growth.

2.1 Seedlings. This information can be used for leaf sheath symptoms up flag-leaf emergence. Eyespot and other stem base diseases can be

identified initially by holding infected leaf sheaths up to the light. However, with practice symptoms can be studied by peeling back successive leaf sheaths on individual tillers. In some cases it may be necessary to remove any dead plant material before assessing disease.

Key.

1a. Colouration absent - healthy leaf sheath

1b. Colouration present - 2

2a. Uniform pale green to purple-brown areas - healthy leaf sheaths

This is natural pigmentation which normally occurs at the junction between the leaf blade and leaf sheath.

2b. Brown discolouration - 3

These lesions can be obscured by natural pigments but often have a paler mirror image on the next leaf sheath.

3a. Lesion eye-shaped - 4

3b. Lesion not eye-shaped -

This category will include dirty-brown flecks or thin, elongate lesions which can coalesce to cover the entire leaf sheath. Such symptoms are caused by a number of fungi including species of *Fusarium; F. nivale* is also associated with lesions having dark borders and pale green centres on the leaf blade at the junction with the leaf sheath.

4a. Lesion with a diffuse brown border -

Eyespot (*Pseudocercosporella herpotrichoides*) lesions can occur anywhere on the leaf sheath. The presence of a pupil of black dots either within the lesion itself or below on the next leaf sheath is a useful criterion for identifying eyespot, particularly in the presence of Fusarium seedling blights.

4b. Lesion with a thin, necrotic red-brown border -

Sharp eyespot (*Ceratobasidium cereale*; anamorph *Rhizoctonia cerealis*). The centres of sharp eyespot lesions are whiter than those of eyespot and usually rot, leaving characteristic bullet-shaped holes. In some instances the leaf and sheath above the lesion may be severed leaving a serrated edge with a darkly bordered margin.

2.2 Adult plants. This information can be used from the start of stem emergence through to the end of grain-filling. Whilst viable leaves are present at the stem base follow the guide for seedling disease assessments on the remaining leaf sheaths. For stem disease assessments remove all leaf material and look down the tiller at an angle and in good, but not bright, light. Keys for assessing the severity of stem lesions are given in section 3.2.

Key:

1a. Stems including nodes ("joints") are green - Healthy

1b. Stems and/or nodes with brown lesions - 2

2a. Lesions eye-shaped - 3

2b. Lesions not eye-shaped - Brown foot rot

Identification card 13 (Anon., 1981b). *Fusarium* spp. cause either brown, elongate flecks or a wettish general discolouration of internodal tissue along the entire length of the stem. In the field diseased plants are easily broken at one of the lower nodes. The fungi responsible for this disease are occasionally visible as orange or pinkish-white pustules of spores on the lower nodes.

3a. Lesion with a diffuse-brown border - Eyespot

Identification card 5 (Anon., 1981a). Stem lesions are initially uniformly brown but can become bleached with age, particularly

with cultivars of barley. Lesions commonly occur on the first internode above the soil but in wet seasons eyespot can be found as high as the base of the third internode. On mature plants eyespot lesions give the culm a charred appearance distinct from the superficial, black and shiny growth which develops around the crown and first internode during severe take-all. A distinctive feature of eyespot lesions is the presence of black pupils of fungal growth which cannot be removed by rubbing (cf. sharp eyespot). This character may be the only indication that eyespot is present if the internode becomes completely colonised by *Fusarium* spp. late in the season. In severe attacks of eyespot the stem can become filled with a grey fungal growth (cf 3b). Lodging, which is most damaging to yield, occurs when the stem breaks or twists in the middle of the lesion (cf. Gair *et al.*, 1987).

3b. Lesion with a thin, brownish-purple border - Sharp eyespot

Identification card 16 (Anon., 1981c). Initially the centres of lesions are uniformly brown, becoming paler or straw coloured with age. The sharp eyespot pathogen is also associated with orange-coloured lesions in some cultivars. Although sharp eyespot symptoms usually develop higher up the plant (up to the 4th internode above the soil) than true eyespot, they are equally common near the crown where adventitious roots develop. A dark brown cushion of fungal growth can form in the centre of the lesion but this, unlike the black pupils of eyespot lesions, can easily be scraped away. The centre of the stem can be filled with an ash-white fungal growth, often in association with dense, brown-black resting "bodies" (sclerotia). In some cases this growth results in sharp eyespot lesions on the inside of the stem which are

visible externally as distinctive dark bands. Lodging may occur in severe sharp eyespot attacks, with the stem becoming brittle and breaking cleanly through infected tissue, but is less frequent than with eyespot.

3. SAMPLING AND ASSESSMENT

The ADAS Plant Pathology Discipline's guidelines on cereal disease assessment techniques (Anon., 1987) gives the following instructions for the assessment of eyespot and sharp eyespot.

3.1 At G.S. 30-33. It is desirable that assessments should be based on the percentage on potentially fertile tillers affected. However, this poses problems because prior to G.S. 30 not all tillers will have been formed, and at G.S. 30-32 (-33) tillers will be present which will not come to maturity. In a winter wheat crop there are typically 200-250 plants/m^2 which give a final population of about 500 tillers/m^2. The corresponding figures for winter barley (2-row) are 250 plants/m^2 and 800-1000 tillers/m^2.

In order to compare tillers assessed early in the season with those assessed later, the method to adopt is as follows:

Winter wheat

(a) up to and including G.S. 30: assess % plants infected as a sample of 25 plants per plot; also record the % tillers affected (assessing only the main tiller and the strongest of the others).

(b) G.S. 31-33: assess % tillers affected (strongest 2 tillers only on each plant) on a sample of 25 plants.

Winter barley

Use the same method as for winter wheat, but assess a total of 3 tillers per plant, not 2.

N.B. The number of tillers suggested for assessment can only be a guide, and the numbers should be increased or decreased for thin and thick crops respectively.

3.2 At G.S. 75

3.2.1 Eyespot and sharp eyespot. An assessment is made of eyespot or sharp eyespot as the percentage of fertile tillers in each of four severity categories (Scott & Hollins, 1974).

nil - no lesions

slight - lesions girdling less than half the stem circumference

moderate - lesions girdling more than half the stem circumference

severe - lesions girdling more than half the stem circumference, tissues softened so that lodging would occur

Results can be expressed as the percentage of tillers in each infection category or as an eyespot index (EI) calculated as:

$$EI = \frac{N_1 + (N_2 \times 2) + (N_3 \times 3)}{25} \times \frac{100}{3}$$

N_1 = Number of 25 tillers with slight eyespot.

N_2 = Number of 25 tillers with moderate eyespot.

N_3 = Number of 25 tillers with severe eyespot.

3.2.2 Brown foot rot (*Fusarium* spp.). *Fusarium* should be assessed separately on nodes and internodes as follows:-

Internodes:	0	No infection
	1	Slight streaks on stem base
	2	General browning of stem base
	3	Stem base severely rotted
Nodes:	0	No infection
	1	Staining on one or more nodes

A sample of 25 tillers/plot should be assessed in this way.

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