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Mini review

Epidemiology in relation to methods for forecasting light leaf spot (*Pyrenopeziza brassicae*) severity on winter oilseed rape (*Brassica napus*) in the UK

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Abstract

Pyrenopeziza brassicae, cause of light leaf spot of oilseed rape, has a complex polycyclic life cycle. It can be difficult to control light leaf spot in winter oilseed rape in the UK since it is not easy to optimise fungicide application timing. Early autumn infections are usually symptomless and recognisable lesions do not develop until the epidemic has progressed further by the spring. Light leaf spot often has a patchy distribution in winter oilseed rape crops and estimation of disease incidence can be difficult. There is evidence that epidemics are initiated primarily by ascospores produced from apothecia that survive the summer inter-crop period on infected debris. Subsequent development of the epidemic during the winter and spring is maintained by rain-splashed conidia that spread light leaf spot from initial foci. Understanding the relative roles of ascospores and conidia in the light leaf spot life cycle is crucial for forecasting epidemic severity and developing control strategies. The current web-based regional forecast system provides an autumn forecast of the incidence of light leaf spot that can be expected the following spring. This is based on survey data which assesses the occurrence of disease the previous July, and weather factors, such as deviations from summer mean temperature and winter rainfall. The forecast can be updated throughout the autumn and winter and includes crop-specific elements so that growers can adjust risks by inputting information about cultivar, sowing date and fungicide use. Crop-specific forecasts can be confirmed by assessing the incidence of light leaf spot. Such assessments will become easier when immunodiagnostic methods for detection of the disease become available. Incorporation of information on spore biology (e.g. apothecial maturation, ascospore release and infection conditions) is considered as a component of the interactive, continuously updated, crop-specific, web-based forecasts which are needed in the future.

Introduction: the need to forecast light leaf spot severity

An accurate understanding of the epidemiology of light leaf spot (*Pyrenopeziza brassicae*; anamorph *Cylindrosporium concentricum*) on winter oilseed rape (*Brassica napus*) is essential for forecasting epidemic severity to achieve effective control of the disease. In recent seasons, yield losses of up to 22% of the total potential seed yield were estimated to have been caused by light leaf spot in the UK (Fitt et al., 1997). Light leaf spot epidemics can also be severe on winter oilseed rape crops in other northern European countries (Paul and Rawlinson, 1992). None of the currently grown winter oilseed rape cultivars are completely resistant to light leaf spot (Anonymous, 1998), and fungicides remain the only effective means of light leaf spot control. However, because of great variation in disease incidence between seasons (Figure 1), regions and individual crops within a region (Fitt et al., 1996), different numbers of fungicide applications and dosages are needed for each season, region and individual crop.

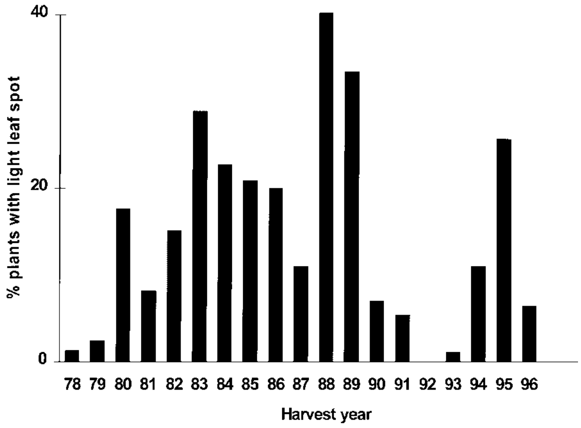

Figure 1. Incidence (% plants with leaves affected) of light leaf spot (*P. brassicae*) in eastern England in March, assessed in a survey of diseases on commercial crops of winter oilseed rape in harvest years 1978–1996. Amended from Fitt et al. (1994).

In practice, fungicide applications in certain regions and seasons were not related well to disease incidence, as fungicides were often applied unnecessarily, for example when the risk of a severe epidemic was low or at times during the season when they were less effective at controlling the disease (Fitt et al., 1996).

In the UK, winter oilseed rape crops are sown in the autumn, during late August and throughout September, although planting date varies with latitude. Planting occurs earlier in more northern latitudes, as cooler temperatures dictate the need for a longer growing season in order to maximise yield potential. Harvest occurs during the summer, from mid-July through to late August, with more northerly crops being harvested later. In Scotland and northern England this creates the potential for overlap of growing seasons, particularly in wet years when growers have to delay harvest and consider an early sowing date (Sutherland et al., 1995). Light leaf spot can infect crops soon after emergence and can cause yield loss at two periods in the season. An early, widespread epidemic can cause plant stunting and sometimes death at the rosette stage of growth during the winter (December–February). Later in the season, following stem extension (late February–April), infection of developing floral structures and seed pods (April–July) can result in malformation of pods/seeds, premature senescence of pods and pod shatter before harvest.

Research has shown that sprays in the autumn are often needed to control light leaf spot effectively in the UK (Rawlinson and Cayley, 1984; Jeffery et al., 1989; Gladders, 1990; Rawlinson et al., 1984; Sutherland et al., 1995; Fitt et al., 1997). However, the visual diagnosis of light leaf spot can be difficult in the autumn because of the long incubation period between infection and appearance of recognisable necrotic lesions (Figueroa et al., 1992; 1993; 1995b; Fitt et al., 1998), and fungicide sprays are often applied after the time that would give optimal control. In general, fungicides need to be applied before light leaf spot symptoms are visible in a crop (Fitt et al., 1997). There is thus a need to accurately forecast, at the time when spray decisions need to be taken, the risk that severe light leaf spot epidemics will develop. The forecasts currently being developed are designed to assist farmers in making decisions about when to apply fungicides, particularly during the early part of the season when symptoms of light leaf spot may not be visible.

A thorough understanding of the processes that contribute to light leaf spot epidemics can be used to develop forecast systems. These processes, such as the survival of *P. brassicae* during the inter-crop period in the summer, maturation and release of ascospores, infection by ascospores, the latent period and cycles of conidial production and infection, are influenced by weather factors. For example, leaf wetness duration and temperature influence the infection of winter oilseed rape leaves by conidia (Figueroa et al., 1995a,b; Gilles et al., 2000). The influence of weather factors on some of these components of light leaf spot epidemics can be described as mathematical functions, which can be incorporated into models to forecast the risk of severe epidemics. This review discusses current knowledge of the critical stages in light leaf spot epidemics and the factors that influence them in relation to development of methods for forecasting light leaf spot severity in the UK.

Epidemiology of light leaf spot: the role of ascospores and conidia

To accurately forecast the onset and severity of light leaf spot epidemics, it is necessary to understand the role that ascospores and conidia play in the disease cycle. Sexual ascospores of *P. brassicae* develop in apothecia during saprophytic survival on oilseed rape debris under favourable moist conditions and are dispersed by wind (Lacey et al., 1987). However, asexual conidia are produced in acervuli during parasitic growth of *P. brassicae* in living plant tissue and are dispersed by rain-splash (Maddock and Ingram, 1981).

Summer survival strategy – sexual or asexual?

The mode of survival of *P. brassicae* over the summer, between successive winter oilseed rape crops in the UK, influences the type of spores that can act as the primary inoculum, although the relative importance of each spore type in eventual epidemic development is unclear. Two main survival strategies have been identified; saprophytic survival on stem, pod and leaf debris after harvest (Lacey et al., 1987; McCartney and Lacey, 1989; 1990) and pathogenic survival on green tissues of late harvested oilseed rape crops, volunteer oilseed rape (McCartney and Lacey, 1990; Maddock and Ingram, 1981), vegetable brassicas (Maddock et al., 1981; Cheah and Hartill, 1985; Staunton, 1967) and cruciferous weed species (Maddock and Ingram, 1981) (Figure 2).

In southern England, the pathogen has to survive an inter-crop period of about two months between harvest in mid-July and emergence of the new crop in September. The most likely mode of survival for the initiation of epidemics in newly sown winter oilseed rape crops, as with diseases of many winter sown arable crops in Europe, is on the stubble and crop debris left after harvest of the previous crop in the summer. *P. brassicae* forms its sexual state on infected debris; the apothecia develop and ascospores are produced within them (Lacey et al., 1987). Senescent infected leaves of volunteer oilseed rape in previously cropped fields and along headlands and pathways and vegetable brassicas have been reported to act as sources of ascospores in several countries (McCartney and Lacey, 1990; Staunton, 1967; Staunton and Kavanagh, 1966; Cheah et al., 1980). However, the frequency of sexual reproduction on senesced leaves of volunteer oilseed rape or vegetable brassicas in the UK is unknown. Recent evidence from population studies of field isolates, collected in spring (Majer et al., 1998) and summer (Ball et al., 1990), indicates that both mating types of *P. brassicae* are present throughout the UK and that the sexual stage occurs frequently. The sexual phase of the life cycle is therefore important in the survival of the pathogen in the UK.

However, in northern England and Scotland, late harvested crops have been known to form a ‘green bridge’ and act as a primary inoculum source for newly sown crops (Sutherland et al., 1995). There is thus the potential for asexual survival of *P. brassicae* in these areas. Conidia, produced during biotrophic growth on these late harvested winter oilseed rape crops, may therefore play a role in the transmission of light leaf spot (Rawlinson et al., 1978), although they are only dispersed over short distances by splash (Fatemi and Fitt, 1983; Rawlinson et al., 1978). It has been suggested that conidia produced on volunteer oilseed rape, vegetable brassicas or other host plants (Rawlinson et al., 1978) could play a role in the transmission of *P. brassicae* to newly sown winter oilseed rape crops on a localised scale (Maddock and Ingram, 1981). Weeds probably play a lesser role in the transmission of *P. brassicae* to winter oilseed rape from one cropping season to the next. Of 19 weed and closely related cruciferae species tested, only a few individuals of *Brassica rapa* (6 out of 21 plants tested), *B. nigra* (4 out of 21) and *B. juncea* (1 out of 17) developed a small number of light leaf spot lesions (Maddock and Ingram, 1981).

Initiation of epidemics in autumn

Considering current rotational practices in the UK, with the winter oilseed rape crop as an important break from cereal crops, and the limited dispersal range of splash-dispersed conidia, light leaf spot epidemics are most likely to be initiated by ascospores in the autumn. As ascospores are wind-dispersed (McCartney and Lacey, 1989), they travel further than splash-dispersed conidia and have a greater opportunity to land on uninfected winter oilseed rape crops. Recently, Evans et al. (1999b) suggested that dispersal patterns of light leaf spot provide further evidence that wind-dispersed ascospores form the primary inoculum source. Early in the season, at low levels of light leaf spot incidence ($< 10\%$), affected plants were randomly distributed. It was suggested that this pattern was caused by wind-borne ascospores arriving from distant inoculum sources (Evans et al., 1999b).

Controlled environment studies have indicated that ascospores may be much more infective than conidia. This provides further evidence that they may play the major role in causing primary infections and initiating epidemics (Gilles and Fitt, 1999). However, the infection conditions for ascospores have not been investigated fully and may differ from infection conditions for conidia (Figueroa et al., 1995a,b; Gilles et al., 2000). If ascospores are more infective than conidia and infect winter oilseed rape under a broader range of infection conditions, ascospores are more likely to cause the primary infections in newly sown winter oilseed rape crops each autumn. Gilles and Fitt (1999) suggested that this may be the case, as infection conditions

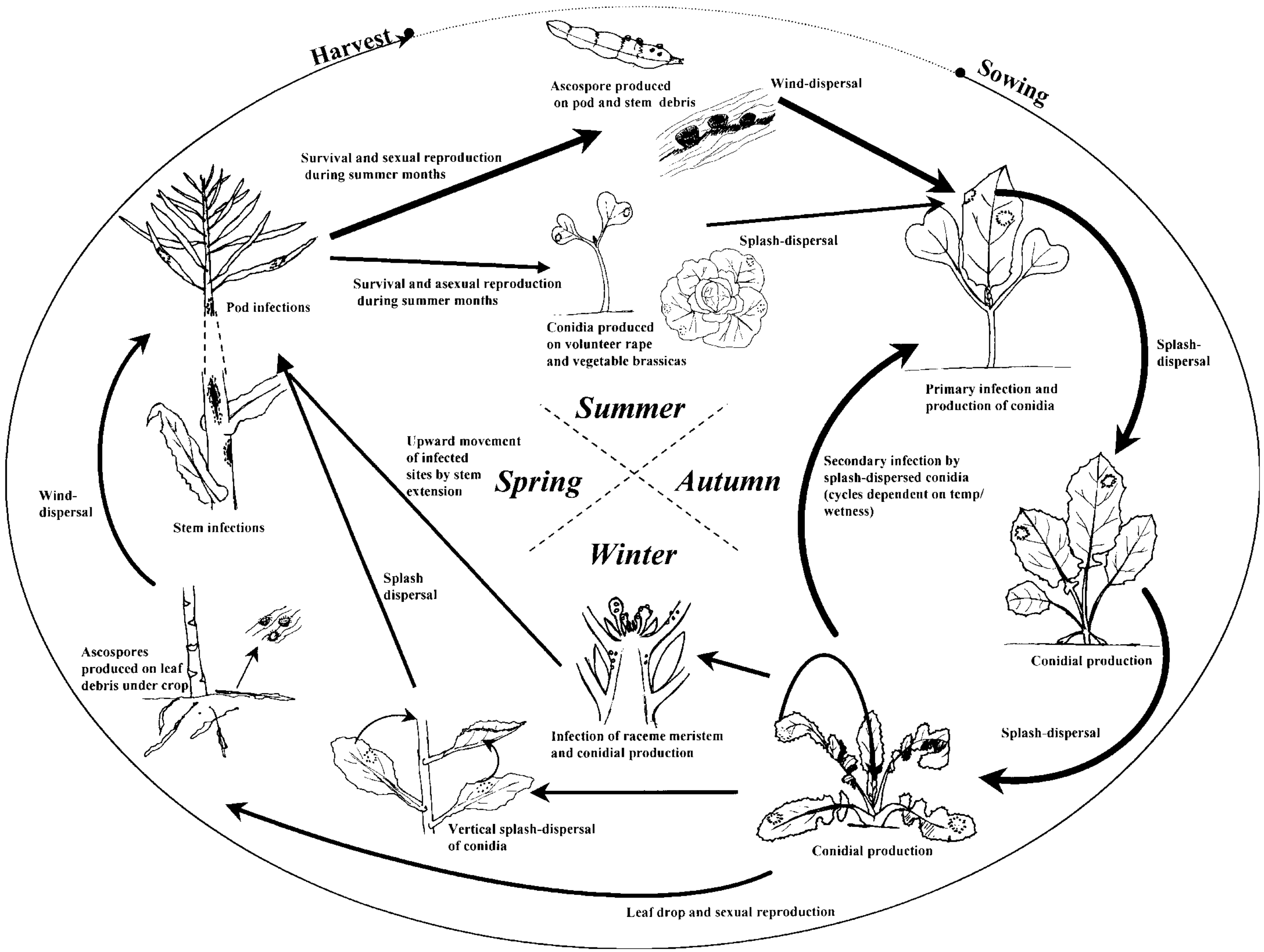

Figure 2. Epidemic cycle of light leaf spot (*P. brassicae*) in winter oilseed rape in the UK, indicating the potential roles of wind-dispersed ascospores produced in apothecia and splash-dispersed conidia produced in acervuli.

would generally be less limiting for ascospore infection and fewer spores would be required for successful infection.

Further evidence for the importance of ascospores was provided by Lacey et al. (1987), who observed apothecia on crop debris from the previous season in the autumn, at the start of the following season. Large numbers of air-borne ascospores have been collected near oilseed rape crops at Rothamsted in the autumn of several seasons (McCartney, unpublished data). Observations from field experiments suggested that there was a requirement for the debris to be moist for apothecial development and ascospore release to proceed (McCartney and Lacey, 1990). Thus, the production of ascospores depends on both the presence of infected debris (colonised by both mating types of the pathogen) on the soil surface and the occurrence of weather conditions favourable for development of apothecia. Indirect evidence for this was provided by Cheah and Hartill (1985) who demonstrated that, in New Zealand, ploughing after harvest greatly decreased both the amount of infected debris on the soil surface and the production of ascospores. Weather conditions favourable for ascospore production and release occur frequently during the autumn in the UK.

Light leaf spot progress in winter

In northern England and Scotland, plant death during winter has been reported to be an important cause of yield loss from light leaf spot in winter oilseed rape (Sutherland et al., 1995). The increase in the incidence of light leaf spot resulting from primary infection in the autumn to the levels observed in March may be determined by the number of cycles of asexual reproduction that have occurred during the winter (Figure 2). Dispersal of conidia, success of infection and the length of the latent period are influenced by occurrence of rain events (Fatemi and Fitt, 1983), temperature and leaf wetness duration (Figueroa et al., 1995b), and temperature (Figueroa et al., 1995a; Gilles et al., 2000), respectively (Figure 2). Evidence for a major role for rain-splashed conidial secondary infection in the increase in severity of epidemics has been suggested by Evans et al. (1999b). Following the observation that light leaf spot has a random distribution early in the season, Evans et al. (1999b) observed that, as the season progressed and incidence increased to more than 10% plants affected, the spatial pattern of light leaf spot showed aggregation. It seemed likely that the observed aggregation was a direct consequence of rain-splashed secondary spread and that this could explain the 'patchiness' of light leaf spot reported by Fitt et al. (1996).

Infection of floral structures/developing pods in spring

Little information is currently available about the most important mechanism for infection of the developing floral and pod structures in the spring and the effect of this on subsequent yield loss. Three possible mechanisms that have been identified for the infection of the floral structures (Figure 2). From fungicide experiments, Rawlinson and Cayley (1984) suggested that infection may take place relatively early in the season, probably through the development of latent infections on leaf and flower primordia, which have been initiated by conidia splashed to the central meristematic tissues of prostrate plants at the rosette stage. Dissection of such meristematic tissues in January showed that they may be infected by *P. brassicae* (Figueroa, pers. comm.). Early infection of these tissues prior to stem extension could explain how the disease progresses from leaf infections at the rosette stage to infections on flowers and pods.

It is possible that the developing floral and pod structures are infected by the ascospores observed during April, May and June, which have been produced on infected leaf debris lying on the ground under crops (McCartney and Lacey, 1990). Alternatively, the presence of abundant conidia on leaves during spring/early summer suggests that infection of the upper stem, flowers and developing pods can take place through the upwards movement of rain-splashed conidia (Pielaat et al., unpublished). Further work is required to characterise the relationship between early infections and the occurrence of light leaf spot on the upper sections of the plant after stem extension. Apart from reducing yield through pod shatter, it appears that light leaf spot on stems and pods in the upper part of the crop canopy provides the majority of the inoculum source for the infection of the crop the following season (Gladders et al., 1995).

Methods for forecasting severity of light leaf spot epidemics

The seasonal, regional and inter-crop variation in severity of light leaf spot is the main reason why a robust forecasting system is necessary if winter oilseed

Table 1. Methods for forecasting, in autumn/winter, severity of light leaf spot (*P. brassicae*) epidemics on winter oilseed rape in the UK

Current and *potential* forecast methods	Advantages	Disadvantages	*Potential for improvement*
Inoculum based: regional risk, crop risk	Advance warning for growers (based on previous disease) Updated in autumn/winter (inclusion of weather data) Not complex; easily delivered Interactive, allowing grower input	Problems in defining 'regions' Likely inaccuracies at crop level Empirical models; not continuous Perturbation over time	*Improve crop forecasts* *Include pathogen/host/ environment information* *Include yield loss and economics*
Disease assessment based: sampling and diagnosis	Crop-specific Provides disease data Improves spray timing	Time-consuming; may need repeating (monthly) Patchy spatial distribution Diagnosis difficult Yield loss thresholds needed	*Improve sampling strategy* *Develop rapid PCR and immuno-diagnostics* *Calculate thresholds*
Spore biology based: apothecial development/ ascospore release, infection criteria	More reliable advance warning Improves spray timing Allows farm/crop specific forecast Potential continuous interactive system	Requires scientific knowledge Difficult to collect ascospore data Time-consuming interpretation Requires up-to-date weather data	*Regional depots for regional forecasts* *Diagnostic automation for crop-specific forecasts* *Incorporate into dynamic models* *Continuous updates with automatic weather data*

rape is to remain economically sustainable as a break crop in the UK (Figure 1). Current and potential future methods for forecasting severity of light leaf spot on winter oilseed rape in the UK are based on pathogen inoculum, disease assessment or *P. brassicae* spore biology (Table 1).

Inoculum-based risk assessment forecasts

Currently the only forecasting system widely available to growers in the UK is an inoculum-based system for forecasting regional risk, with an option to modify the regional risk to produce a crop risk (Fitt et al., 1996). The regional forecasting system (Table 1, Figure 3) has been produced using a number of disease and weather factors; national disease survey data for incidence of light leaf spot on pods in July and deviations from the 30 year mean for summer temperature and winter rainfall (Fitt et al., 1996; Welham et al., 1999). A preliminary light leaf spot risk assessment forecast, based on incidence of light leaf spot on pods and deviations in summer temperature, is issued in the early autumn (in October). The forecast is then updated the following March after the inclusion of winter rainfall data (Welham et al., 1999). The observed relationship between current and past disease incidence may occur because the amount of infected debris on which the pathogen can survive during the summer, and thus the numbers of ascospores produced, is related to incidence of light leaf spot on pods in July. Variation in temperature over the summer period affects the development and maturation of apothecia on the debris (Gilles and Fitt, 1999). The inclusion of winter rainfall allows the updated model to take account of the effects of rainfall on dispersal of conidia and infection of leaves at this time and thus the number of disease cycles that can occur early in the season.

Analysis of the ADAS/CSL winter oilseed rape disease survey data suggests that England and Wales can be divided into specific 'light leaf spot regions' that consist of areas which have similar levels of light leaf spot from season to season (Welham et al., 1999). Weather parameters that clearly predicted the incidence of light leaf spot differed between some of these regions and as a result, the forecast model was regionally specific. Currently, the forecasting scheme has only been used in England and Wales and it needs to be extended to Scotland. The regional forecast has been adapted for delivery via the Internet to growers since 1998. Recently the forecast has been improved by the introduction of active server pages (ASPs) (Figure 4), which can be found at the URL: http://www.iacr.bbsrc.ac.uk/lightleafspot (Evans

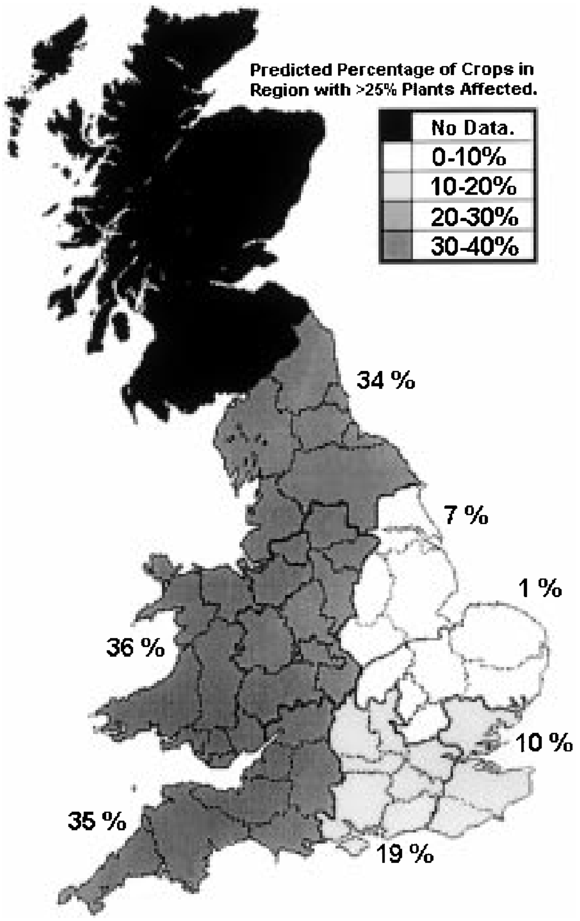

Figure 3. Map of the UK, illustrating, for different forecast regions, the % crops predicted in October 1999 to have > 25% of plants with light leaf spot (*P. brassicae*) in March 2000.

et al., 1999a). These allow the grower to input three crop-specific parameters which influence the risk that a severe epidemic may develop; cultivar (to take account of resistance rating), sowing date and autumn fungicide application information (Welham et al., 1999).

The advantages of the inoculum-based forecasting system are that it provides the grower with an advance warning of the risk of severe light leaf spot, which allows a period of several weeks in which to make a decision about fungicide applications, and the risk can be updated during the autumn/winter period. Furthermore, it is not complex and can be easily delivered to the user via the Internet, press releases and other methods. Although the model is based on large light leaf spot regions, the inclusion of the interactive choices allows the forecast to be more crop-specific. This interaction also allows the grower to carry out role-play scenarios, for example to calculate the decrease in light leaf spot risk for the following spring if an autumn spray application is applied. The interactive system can also be used before the start of the season to assess the decrease in light leaf spot risk if a more resistant cultivar is grown or the crop is sown later in the season.

A disadvantage of the inoculum-based forecasting system is that it is difficult to define the light leaf spot regions or to assess risks for crops near to the borders of regions with different risks. Furthermore, the system is open to inaccuracy, especially at the crop-specific level, because it is based on a few simple empirical relationships which do not fully describe the dynamics of the biological processes influencing light leaf spot epidemics. Although the forecasts can be updated by incorporation of weather information, the risk assessment system is still susceptible to perturbation over time. However, a comparison of predicted regional risks against the actual incidence of light leaf spot the following March over three seasons (1996/97, 1997/98 and 1998/99) indicated that the model provides growers with reasonable information with which to make spray decisions (Figure 5). The light leaf spot risk assessment model appears to have slightly overestimated the percentage of plants that will be affected with light leaf spot the following March. However, the predictions were made before fungicide sprays were applied in autumn; the fact that observed incidences were less than predicted incidences may have been the result of treatments applied in response to the predictions.

Improvements could be made to the inoculum-based forecasting system by incorporating more survey information on agronomic, environmental and crop factors affecting the epidemics. For example, the lengths of the periods between harvest, ploughing, sowing and crop emergence and the weather conditions during these periods influence maturation of apothecia, release of ascospores and potential for disease escape. The value of these factors for prediction of light leaf spot incidence the following March needs to be investigated on a regional basis. The disease data collected in the autumn winter oilseed rape survey could be used to improve the accuracy of the updated risk for each region. Analysis of survey data for light leaf spot severity (as opposed to incidence) might also help to improve the accuracy of the crop-specific component of the forecasting system. To overcome one factor influencing the observed variation between forecasts for regions and for individual crops within a region (Fitt et al., 1996), it should be possible for growers to input their own local weather

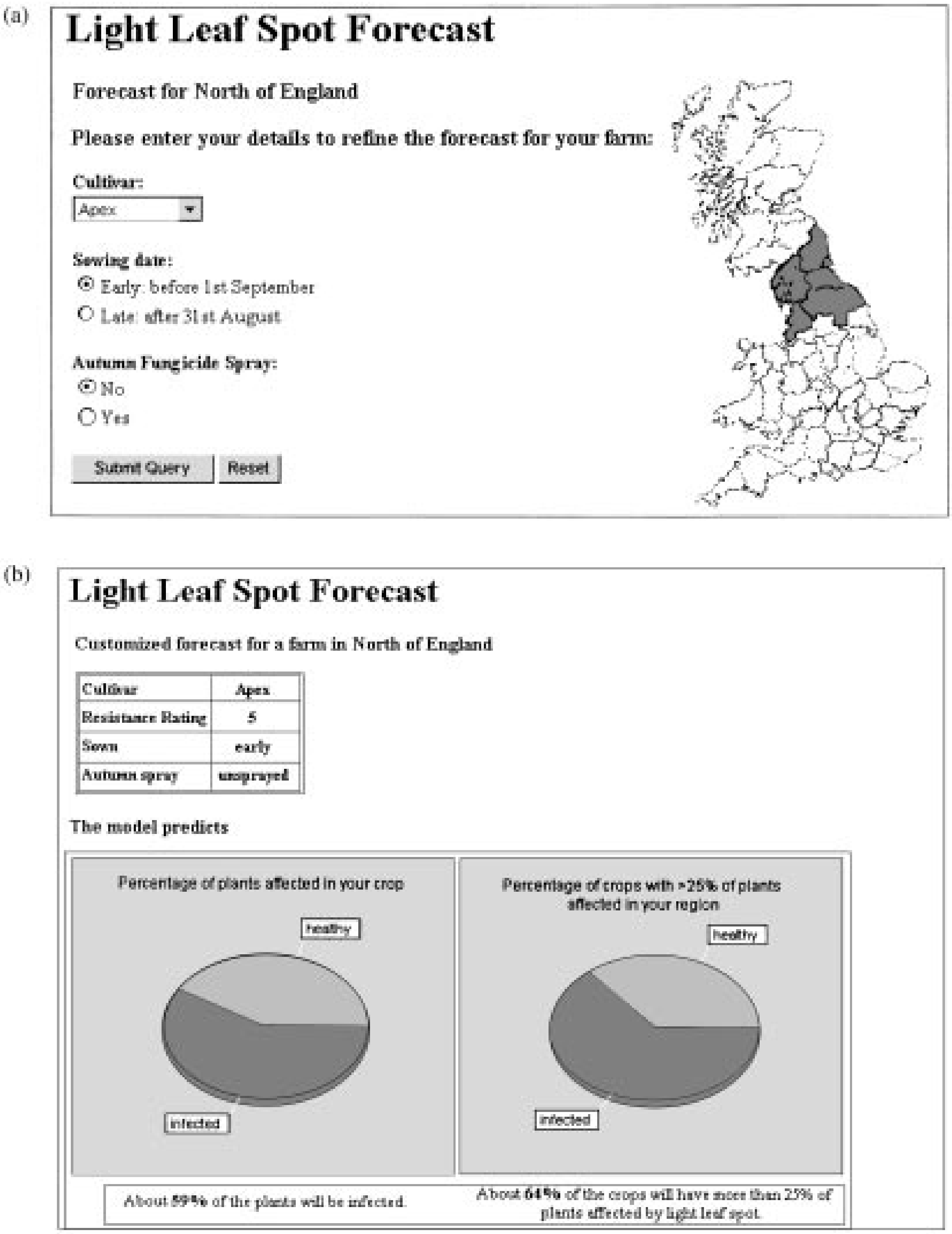

Figure 4. Internet-based, interactive light leaf spot (*P. brassicae*) forecast. (a) Grower input page with cultivar choice, sowing date and fungicide application information. (b) Output page with regional (right pie chart) and crop-specific (left pie chart) light leaf spot risk forecast (Courtesy JA Antoniw).

information to improve the accuracy of predictions for their own crops, using the ASPs on the forecasting web-site. This would move the responsibility for updating the forecast from the scientist to the individual grower and decrease the cost of maintaining it. Since Su et al. (1998) observed that the incidence of light leaf spot at early flowering in March gave a good prediction of yield losses caused by light leaf spot, incorporation of yield loss models into the forecasting system would allow growers to assess more accurately whether or not a fungicide application is justified economically.

Disease assessment based forecasts

Disease assessments are already being used to improve the accuracy of inoculum-based forecasts of the risk that severe epidemics will develop since the light leaf spot forecasting web-site includes a recommended protocol for sampling crops so that growers can confirm the occurrence of the disease (Fitt et al., 1998). Growers are recommended to inspect crops at monthly intervals from October to April and to collect samples to assess the incidence of the disease, if they consider the crop to be at high risk or symptoms are beginning to appear. During the winter, plants need to be sampled in clusters because light leaf spot has a patchy distribution (Fitt et al., 1996) and disease symptoms are not randomly distributed (Evans et al., 1999b). Diagnosis of light leaf spot can be improved by incubating sampled plants in polyethylene bags under humid conditions for 3–4 days (Fitt et al., 1996) because infected leaves are frequently symptomless early in the season. Incubation creates conditions conducive to asexual sporulation of *P. brassicae* and characteristic white spore pustules become visible on infected leaves (Fitt et al., 1998). The assessment of light leaf spot incidence at various times during a season can be used to provide crop-specific information to update and verify risk forecasts and improve the accuracy of spray timing decisions. The relationship between light leaf spot incidence at early flowering in March and yield loss (Su et al., 1998) can be used as a basis for calculating economic thresholds. However, further work is needed to establish detailed relationships between light leaf spot incidence in the autumn/winter, when spray decisions need to be made, and incidence/severity in spring and subsequent yield loss before disease assessment based forecasts can be developed effectively.

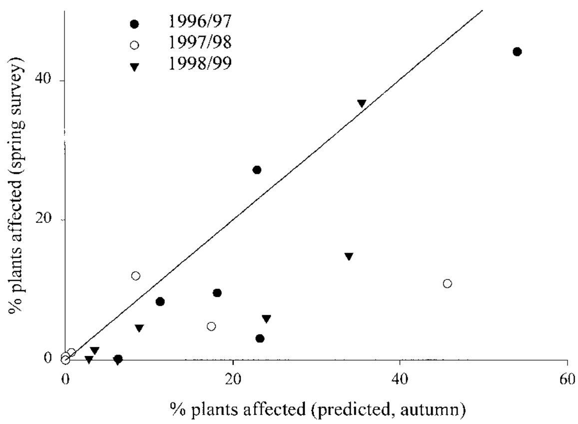

Figure 5. Validation of the regional light leaf spot (*P. brassicae*) risk forecasting system. Figure indicates a comparison of the regional risk (% plants with light leaf spot predicted) in October 1996–1998 against incidence of light leaf spot observed in March 1997–1999 in winter oilseed rape disease surveys.

Such disease assessments are time-consuming, particularly if they need to be repeated on several occasions during the autumn/winter period. Accurate diagnosis of light leaf spot, when infections are symptomless or show ambiguous symptoms which can be confused with frost damage or other diseases, is difficult, even if plants are incubated to induce pustule development. Forrer (1992) cited the requirement for accurate disease diagnosis as the main reason why decision support systems have had little impact on European agriculture. He suggested that the future integration of immuno-diagnostic tests with decision support systems may simplify the process of disease identification and improve the accuracy of assessments and that this would make the decision making process more robust. The effectiveness of the disease assessment based light leaf spot forecasting can be improved by developing novel molecular diagnostic techniques to detect light leaf spot in winter oilseed rape crops before symptoms appear (Foster et al., 1999; Hollomon, 1998). A PCR-based technique that has been developed to detect *P. brassicae* in symptomless leaves is expensive, and requires specialised equipment and knowledge. Whilst it can be used for research purposes, it cannot easily be used by growers. There is a need to develop a simple immuno-diagnostic test specific for *P. brassicae*, which can be used in crops.

However, a light leaf spot forecasting system based only on sampling and disease assessment, whether assessment is based on symptoms, molecular or immunological methods, could be unreliable because the spatial pattern of the disease is not fully understood. There is a need for a robust sampling protocol to effectively assess disease incidence. Procedures that detect nanogram quantities of target DNA or antigen cannot provide meaningful results unless the plant sample tested is representative of all susceptible host tissue from the larger population being sampled (Putnam, 1995). Further research is required to clarify the spatial distribution of the disease and to design specific sampling strategies (Evans et al., 1999b).

Spore biology based risk forecasts

Recent improvements in the understanding and modelling of the epidemiology of light leaf spot, together with improvements in information technology, provide the potential for delivery via the Internet of two-way interactive, continuous, crop-specific forecasts. As light leaf spot epidemics appear to be initiated by ascospore infection (Figure 2), the development of a forecasting scheme based on aspects of apothecial development, ascospore release and/or ascospore infection conditions should provide more specific advance warnings for growers than regional or crop risk forecasts. Subsequently, spore biology based forecasts could be improved by using information about the latent period of *P. brassicae*, production of conidia and infection conditions for conidia. They could also include forecasts of disease spread from leaves to pods, based on apothecial maturation and ascospore release in the spring (McCartney and Lacey, 1990) or vertical splash dispersal of conidia (Pielaat et al., unpublished).

It is likely that such spore biology based forecasts would initially need to be developed on a regional scale. A network of 'depots' of infected oilseed rape debris could be developed around the UK. The debris could be monitored on a weekly basis, at ADAS/SAC regional centres, for example, to provide regional warnings that weather conditions have been favourable for apothecial maturation. A 'depot' system has been used to monitor sclerotinia apothecial development in Sweden (Nordin et al., 1992) for a number of years and has been evaluated as part of a risk forecasting scheme in the UK (Sansford, 1995). Monitoring of apothecial maturation, through the use of depots, could provide growers with a regionally based forecast of the likely onset of the epidemic to allow the first control spray to be targeted more efficiently. Furthermore, ascospore release could be monitored at these depots with a Burkard spore sampler and used to improve the accuracy of warnings. It would not be practical to monitor apothecial maturation and ascospore release in this way on individual farms. Identification of apothecia and ascospores is currently both difficult and time-consuming. Ascospores of *P. brassicae* are very small in size, hard to identify and easily confused with ascospores of the saprophyte *Unguicularia* cfr. *raripila* (Inman et al., 1992).

When models have been developed to describe relationships between weather factors (e.g. temperature, wetness duration) and ascospore maturation (Gilles and Fitt, 1999), ascospore release and ascospore infection conditions, to complement those for conidial infection conditions, the latent period and sporulation (Figueroa et al., 1995a,b; Gilles et al., 2000), it may be possible to use regional weather as a basis for regional warnings. This would be considerably less time-consuming than monitoring apothecial maturation or ascospore release in depots. It seems unlikely that forecasts based on infection criteria alone, such as the Beaumont period (Beaumont, 1947) and Smith period (Smith, 1956) utilised to guide potato blight control, would be successful with light leaf spot since prior knowledge of the presence of ascopores or conidia would be essential. Forecasts based on ascospore occurrence and infection criteria would allow fungicides to be applied at the onset of epidemics. These forecasts could be updated in response to occurrence of conidial infection criteria, the latent period, and sporulation and dispersal criteria (which would allow estimates of the number of asexual reproductive cycles that could be expected). From this, the severity of the epidemic could be predicted much more effectively. The work of Gilles and Fitt (1999) and Figueroa et al. (1995a,b) indicates that the timing of the forecast need not be that precise, as the light leaf spot pathogen has a long latent period (ca. 250 degree-days), which creates a large spray 'window' for effective control. If the relationships between weather factors and these phases in the epidemiology of light leaf spot can be accurately modelled, then it should be possible to produce farm-specific forecasts for farms with local meteorological data available.

In the future, forecasts based on ascospore release may become more practicable as automated systems for sampling and identifying spores become available. Foster et al. (1999) recently developed a PCR-based diagnostic for symptomless *P. brassicae* in infected leaves and an immuno-diagnostic test specific for *P. brassicae* could be developed (S. Foster, pers. comm.). Although current PCR-based diagnostics are not of direct use to growers because of their cost and requirement for specialised equipment, it may be possible to develop a PCR-based diagnostic test to identify *P. brassicae* ascospores in air samples. A similar system has been successfully used for *Penicillium roqueforti* (H.A. McCartney, pers. comm.). If samples could be quickly and efficiently assessed for the presence of *P. brassicae*, it would save time and remove the possibility of misidentification of ascospores. Furthermore, development of immuno-diagnostic techniques for use with simple spore samplers, which could be used on farms, may allow automatic incorporation of spore data with meteorological data to produce more accurate crop-specific forecasts.

Developments in information technology now provide the possibility that epidemiologically based forecasts could be delivered to growers and advisers and updated continuously via the Internet. Unlike a forecast based only on past survey data, such a system would be based on 'real time' epidemiological events and would be less susceptible to perturbation. Monitoring throughout the season could improve the accuracy of forecasts and maximise efficiency of fungicide spray timing. Such a forecasting system will be effective only if it is based on models which accurately describe the progress of light leaf spot epidemics in time and space. Internet delivery could allow forecasts to be updated continuously in response to daily weather data. Two-way interaction would be possible. Warnings could be issued automatically to growers by E-mail. Growers could input their own data, for example assessments of disease in specific crops, from mobile phones used in the field to get instantaneous information with which to make decisions. Furthermore, the cost of maintaining and updating such an Internet-based forecasting system would be considerably less than for systems delivered by traditional methods.

Discussion

This review indicates how improvements in understanding the epidemiology of light leaf spot can be exploited to improve current inoculum-based risk forecasts and disease assessment based forecasts or to develop new forecasting systems based on *P. brassicae* spore biology (Table 1). In combination with improvements in diagnostic and information technology, these improvements offer the prospect of developing more accurate, interactive, crop-specific forecasts of the risk of severe light leaf spot epidemics. Recent advances in understanding the effects weather factors have on progress of light leaf spot epidemics will allow improvements to be made to inoculum-based regional risk forecasts (Fitt et al., 1996). It should be possible to use information about relationships between temperature/wetness and apothecial development, ascospore release (McCartney and Lacey, 1990), ascospore infection conditions (Gilles and Fitt, 1999), the latent period and conidial infection conditions (Gilles et al., 2000) to provide weather-based updates to regional risk forecasts more frequently than at present. Furthermore, this epidemiological information can also be used to improve updating of the interactive, crop-specific component of these inoculum-based forecasts delivered via the Internet (Welham et al., 1999). Nevertheless, the accuracy of these regional and crop risk forecasts will always be limited by the simplicity of the empirical models on which they are based. There is also an urgent need for regional and crop risk forecasts for stem canker to be developed and combined with those for light leaf spot in southern England, where both diseases cause serious problems on winter oilseed rape.

An understanding of the epidemiology of light leaf spot, especially the mechanisms of disease spread, can also be used to improve the disease assessment based forecasts. Since spatial analyses of light leaf spot epidemics indicate that initial infections in the autumn fit a random distribution (Evans et al., 1999b), suggesting that primary infections are caused by wind-blown ascospores, in the autumn samples can be taken as individual plants collected at regular intervals along a transect across a crop. However, later in the season aggregation of light leaf spot is observed, providing evidence for the importance of localised spread of the disease from initial foci by rain splashed conidia (Evans et al., 1999b). This 'patchy' pattern of disease observed in crops (Fitt et al., 1996) suggests that samples then need to be taken as clusters of plants to get an accurate estimate of light leaf spot incidence. Whatever the sampling strategy, current disease assessment based forecasting methods are time-consuming; the prospect of using immuno-diagnostic methods to obtain rapid, accurate diagnoses (Foster et al., 1999) is to be welcomed.

There are prospects for using assessments of *P. brassicae* apothecial development and ascospore release to develop new, more accurate systems for providing growers with advance warning of onset of light leaf spot epidemics, but the expertise and time required to make the assessments will mean that they can only be used on a regional basis. However, recent improvements in diagnostic (Foster et al., 1999) and information technology (Evans et al., 1999a) offer real potential for development of continuous, interactive, crop-specific forecasts based on the spore biology of *P. brassicae.* Understanding and modelling of factors such as local primary inoculum sources, dispersal processes (primary and secondary) and how weather factors influence disease progress through the season will allow new forecasts to be much more crop-specific and 'real time' in nature. Furthermore, the delivery of such forecasts via the Internet will allow them to be interactive and updated continuously. Thus, a detailed understanding of the epidemiology of light leaf spot can be used to develop forecasts that are robust, accurate and easily delivered to growers to guide decisions about strategies for control of light leaf spot on winter oilseed rape.

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