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The relationship of leaf wetness duration and disease progress of glume blotch, caused by *Stagonospora nodorum*, in winter wheat to standard weather data

A. Djurle[1], B. Ekbom[2] and J. E. Yuen[1,3]
[1]*Department of Plant Pathology and* [2]*Department of Entomology, Swedish University of Agricultural Sciences, P.O. Box 7044, S-750 07 Uppsala Sweden (Fax: 18 672890);* [3]*Department of Cancer Epidemiology, Uppsala University, University Hospital, S-751 85 Uppsala, Sweden*

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Abstract

Almost 50% of the variation in leaf wetness duration can be explained by maximum and minimum temperatures, rainfall and hours with relative humidity above 90% on a daily basis. All of these parameters can be estimated from a standard weather station. If variables related to wind are added the level of explanation increases to 69–76%. Leaf wetness duration explained up to 42% of the rate of disease increase (RDI) for *S. nodorum*. Leaf wetness duration was accumulated over a 5-day 'window' period and correlated with rate of disease increase after a 7-day 'lag' period. Standard weather variables could explain 20–34% of the disease increase. The relevance of these statistical models to disease prediction is discussed.

Introduction

The development of fungal diseases in a crop depends on climatic conditions, especially factors relating to moisture [Huber and Gillespie, 1992]. Predicting the course of disease development is therefore contingent on substantial knowledge about the conditions relating to moisture in the canopy. While it is possible to measure leaf wetness using special instruments this is not a realistic alternative for forecasting disease development. A method for relating macroclimatic weather measurements, such as those available from standard weather stations, to the microclimate in the crop is a necessary step in developing disease forecasts.

The relationship between macro- and microclimate, particularly for leaf wetness, has been addressed in different ways [Smith, 1962; Wallin, 1963; Lomas and Shashoura, 1970; Crowe *et al.*, 1978; Gillespie and Sutton, 1979; Häckel, 1980, 1984; Pedro and Gillespie, 1982a, 1982b; Royle and Butler, 1986; Huber, 1988; 1992] and with different results and conclusions. A 'general rule' states that the canopy will be wet when relative humidity at screen height is $\geq$90% [Smith, 1956; Thompson, 1981; Sutton *et al.*, 1984; Friesland and Schrödter, 1988; Campbell and Madden, 1990], although its limitations are not denied.

For infection and development of *Stagonospora nodorum* (Berk.) Castellani and Germano (Syn: *Septoria nodorum* Berk.) in a wheat crop, leaf wetness is a crucial factor [Shearer and Zadoks, 1972, 1974; Eyal *et al.*, 1977; Jeger *et al.*, 1981]. Free water on the leaves is required for release of spores from pycnidia and for dispersed spores to complete the infection process. The leaf wetness duration necessary for infection of *S. nodorum* varies with other conditions, such as temperature, relative humidity and varietal susceptibility [Holmes and Colhoun, 1974; Rapilly and Skajennikoff, 1974; Eyal *et al.*, 1977] and it is therefore not possible to state a fixed number of hours for the infection process.

The intent of this study is threefold: 1) to relate easily obtainable weather data to leaf wetness durations measured by special instruments in the crop canopy, 2) to relate the rate of disease progress, caused by *S. nodorum* epidemics in wheat crops, to leaf wetness duration and other weather data and 3) to estimate the

accuracy of using only easily obtainable weather data for describing disease progress.

Materials and methods

The experiments were carried out in winter wheat (cv. Folke) in 1986–1988 in the county of Uppland, Sweden. In 1986 and 1988 one field with two plots (each 11×32 m) in 1987 two fields (plot size 30×30 m) about 10 kilometers apart were monitored. Conidial suspensions (2.5–4 × 10^5 conidia per ml) were produced from mixtures of several field isolates of *Stagonospora nodorum*. The crops were spray inoculated by means of spraying equipment with a 4 m wide boom at DC 30–32 [Zadoks *et al.*, 1974] in 1986 and 1987, but otherwise treated according to normal agricultural practice. No inoculation or disease assessment was made in 1988.

During the growing season repeated measurements of the number of living leaves and the size of leaves at different leaf layers on the main tillers were made. After heading (DC 73–83) the number of ears per square meter was counted. From these measurements leaf area index (LAI) was calculated. The statistical analysis used PC–SAS (SAS Institute Inc., Box 8000, Cary, North Carolina, USA).

Collection and treatment of weather data

We have chosen to include the following moisture or wetness related variables: rainfall, relative humidity, partial vapour pressure, temperature, windspeed, dewpoint temperature and number of dry and wet periods per day plus daylength and leaf area index. For all plots two sets of measurements were made: conventional weather data and measurements in the canopy. The variables measured are listed in Table 1.

In all plots in 1986 and 1988 and for one of the plots in 1987 (located at the same site as the 1986 and 1988 plots) temperature, windspeed and rainfall were measured at a weather station (run by the University) less than 200 m from the plots. In the second experiment in 1987 temperature and rainfall were recorded by a data-logger (Delta-T Devices Ltd, Burwell, Cambridge CB5 0EJ, England) placed in a Stevenson screen in the field. A thermohygrograph in the screen, calibrated repeatedly with an Assman psychrometer, was used to measure relative humidity. No windspeed was measured in this experiment and therefore windspeed data from the other field was used in the analysis. All measurements were made hourly except for rainfall which was recorded daily. Figure 1 shows daily maximum and minimum temperature, rainfall and crop development stage (DC) for each of the three years.

In each plot three De Wit leaf wetness recorders [Post, 1959; Sutton *et al.*, 1984] were placed close to each other at 17, 40 and 75 cm above ground. This corresponded to the positions of the 3–4 uppermost leaves of the wheat plant and were to account for vertical variation in the canopy's microclimate. The leaf wetness recorders were calibrated by comparing the instruments with occurrence of visible moisture on the wheat leaves during dew formation and subsequent drying periods after dew and rain.

Relative humidity, saturation vapour pressure, partial vapour pressure and dewpoint temperature were calculated from weather station or data-logger temperature data. All data was then transformed into daily values (Table 1). When a variable represented number of hours per day, it was recalculated into proportions and then arcsine-square root transformed in order to give the variable a uniform variance [Bartlett, 1947]. The daily weather data was based on 'bio-time', that ran from 8 a.m. to 8 a.m. the following day, allowing the previous night's dew to dry up before a new day began. All weather data was classified as either screen weather (S)(=macroclimate) or field weather (F)(=microclimate)(see Table 1) depending on its source. Daylengths during the experimental period were calculated from latitude and Julian day and ran from 18.8 h (June 1) to 17.34 h (Aug. 1). Daily changes in leaf area index were calculated by linear regression on available data.

Leaf wetness duration and weather

The time period covered in the analysis of screen and field weather was June 30–July 22. During this 23 day period a full set of weather data could be obtained from each field. The analysis was generally done by plot, by year and for all plots and years together.

When two weather variables were highly correlated with each other, because of common origin, only one of them was included at any one time in the following analysis. Stepwise and multiple regression procedures in SAS were then used in order to identify important variables and find equations that could describe microclimate as a function of macroclimate variables.

All field variables were tried in turn in the analysis, but most attention was paid to leaf wetness duration at different heights (HLWT/HLWM/HLWB)(Table 1).

Table 1. Weather variables; measured hourly, calculated from hourly measurements into daily values and compiled into 5-days wide 'windows'. (F = measurements taken in the field, S = measurements taken from a standard weather station)

Measured variable (–/hour)	Calculated variable (–/day)	Abbreviation	Window variable (–/5 days)	Abbreviation
Temperature (S)	1. Maximum (°C)	TMAX	1. Mean maximum temperature 2. Max. maximum temperature	TMAX MAXMAX
	2. Minimum (°C)	TMIN	1. Mean minimum temperature 2. Min. minimum temperature	XTMIN MINMIN
	3. Mean (°C)	TMEAN	Mean mean temperature	XTMEAN
	Dewpoint temperature: hours when dewpoint temperature is ≤ 1 °C below drybulb temperature (h)	HTDIFF	Mean number of hours when dewpoint temperature is ≤ 1 °C below drybulb temperature	XHTDIFF
	Mean partial vapour pressure (Pa)	PVMEAN	Mean, max. and min. of mean partial vapour pressure	XPVMEAN PVMAX PVMIN
	Relative humidity: hours with RH >90% (h)	HRH	Total hours with RH >90%	HRHS
Relative humidity (screen)(S)[a]	Hours with RH >90% (h)	HRH	Total hours with RH >90%	HRHS
Leaf wetness (Top/Middle/Bottom level)(F)	1. Hours with leaf wetness (h)	HLWT/HLWM/HLWB	1a. Sum of hours with leaf wetness, measured 1b. Sum of hours with leaf wetness, calculated	HLWTS/HLWMS/HLWBS HLWTC/HLWMC/HLWBC
	2. Number of periods with leaf wetness (–)	WETT/WETM/WETB	2. Mean number of periods with leaf wetness	XWETT/XWETM/XWETB
	3. Number of dry periods (–)	DRYT/DRYM/DRYB	3. Mean number of dry periods	XDRYT/XDRYM/XDRYB
Rainfall (F,S)	1. Sum (mm) 2. Incidence (–)	MM RAINF	1. Sum 2. number of days with rainfall	MMS RAINS
Windspeed (S)	1. Mean (m/sec) 2. Hours with ≤ 1 m/s (h) 3. Hours with $\leq$ m/s (h)	WINDX HWIND1 HWIND2	1. Mean 2. Sum of hours with ≤ 1 m/s 3. Sum of hours with ≤ 2 m/s	XWINDX HWIND1S HWIND2S

[a]) in one field in 1987

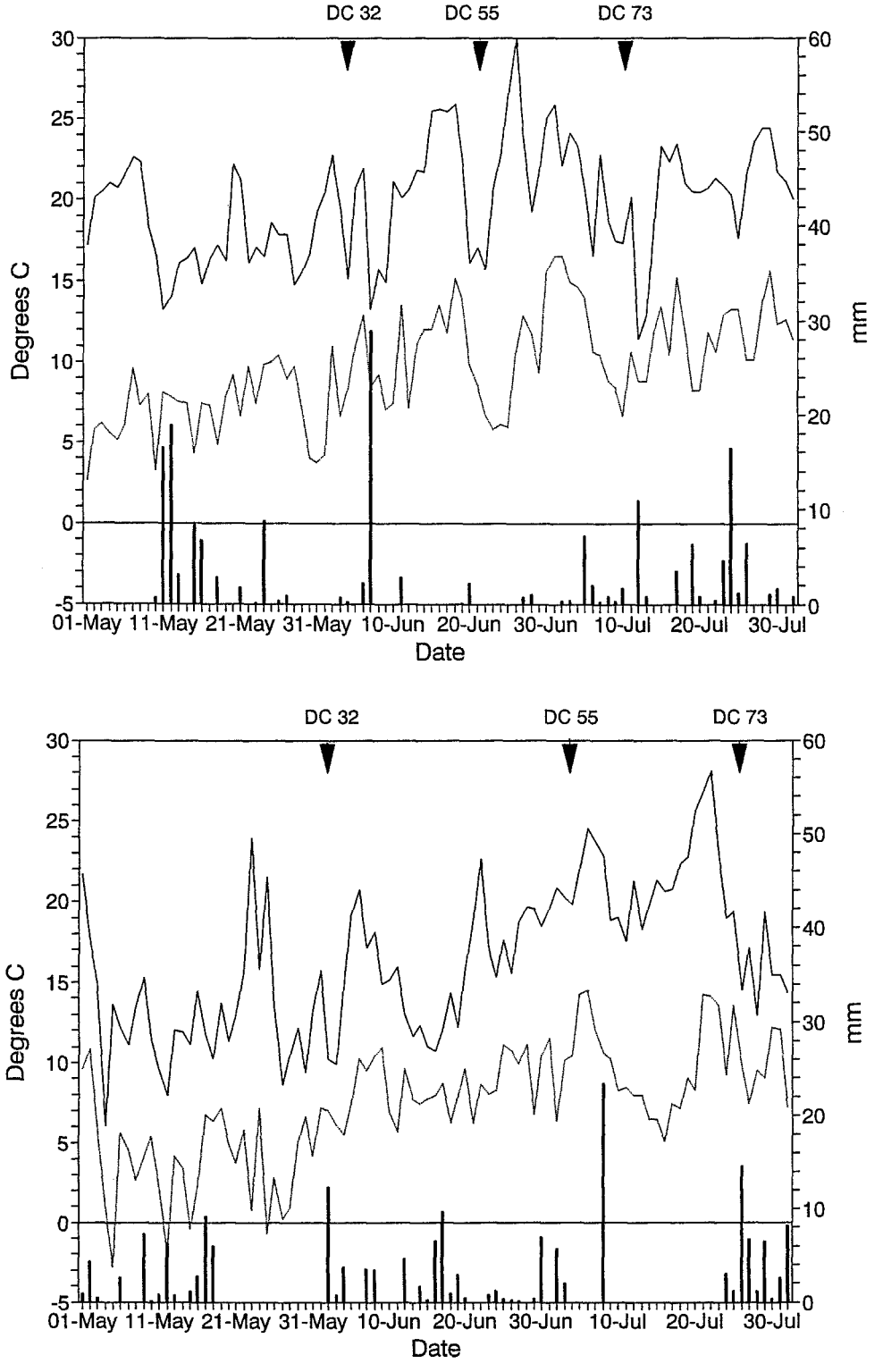

Fig. 1. Temperature (max. —— and min. - - - - -), rainfall | and crop development stages (DC) for Uppsala May–July 1986–1988.

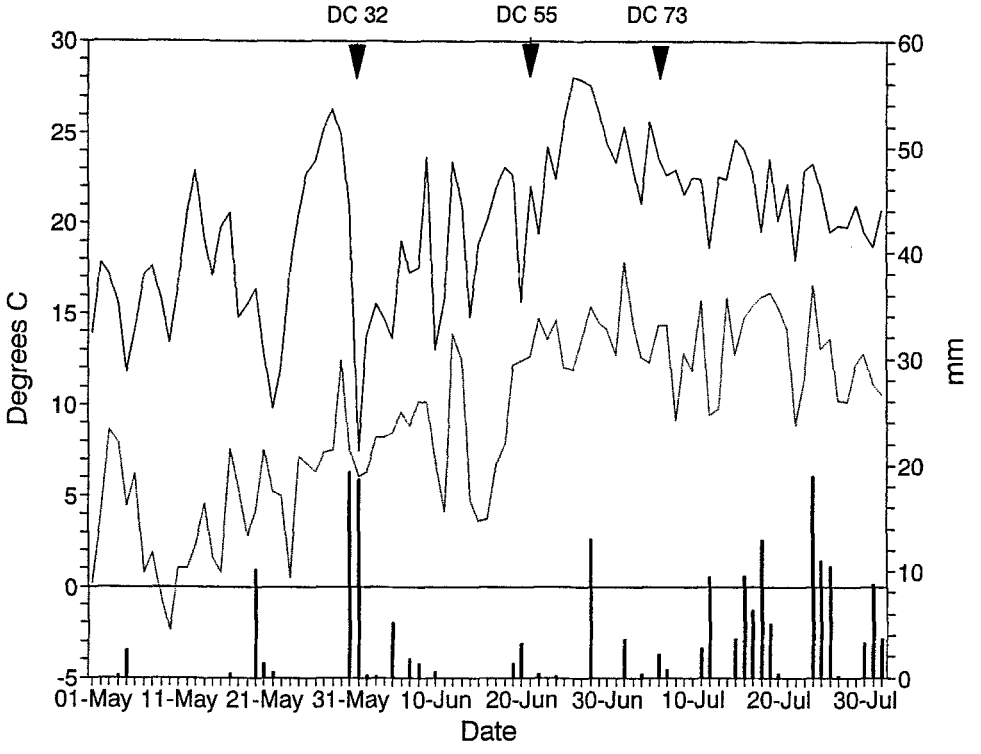

Fig. 1. Continued.

The best models resulting from the whole data set were tested on data for individual years in order to see how well a general model would fit in a specific year.

Rate of disease increase and leaf wetness

Disease assessments were made at regular intervals in the plots. Disease severity, in % leaf area diseased, was recorded on each of the 4–6 uppermost leaves and the ear on each of 25 marked plants once a week in 1986 and twice per week in 1987. The daily rate of disease increase on each leaf was obtained by calculating the slope of a line between two observations (arcsine-square root transformed). It was then assumed that the increase was equally large every day during that period. In the analysis of disease increase and weather all available data were used; 39 days in 1986, 60 and 46 days respectively in 1987. In the ears disease occurred late and the severity did not exceed 2% before harvest. They were therefore not treated further in the analysis.

The rate of disease increase on each leaf level (the slope) and its relationship with the transformed weather data, especially leaf wetness and rainfall, was tested using Proc Corr, Stepwise linear regression and Proc GLM in SAS. 'Weather windows' were created by summing (variables expressing hours and rainfall) or taking the mean (temperatures, vapour pressure and number of wet and dry periods) of the values of each weather variable over 1-, 3-, 4-, 5- and 7-day periods respectively. The 'windows' were introduced since the disease observation on one day is more likely to result from weather conditions over a period of time some time in the past – although there are exceptions [Royle *et al.*, 1986]. The new variables thus created are listed in the last two columns of Table 1. The 'window' data was used instead of the daily weather data in the continued analysis.

Due to the time lag between weather and its visible effect on disease, weather data was pushed forward in time between 0 and 18 days in the analysis ('lag'). This means that disease increase could be compared with weather that occurred during a 1–7 day period 0–18 days previously. When there was missing data in the 'windows', the 'window' values represented a minimum that occurred during the period in question. If data for the whole 'window' was missing, it was not included in the analysis.

Two kinds of stepwise regression models were fitted: The slope for one leaf level vs.; 1) the number of hours of leaf wetness at a particular height in the

crop and/or the mean number of leaf wetness periods per day and 2) all weather variables. All models were run for the whole data set. As with the examination of micro- and macroclimate relationships in the canopy, only one of two highly correlated variables expressing related factors were included in the analysis.

Rate of disease increase and weather

When models for rate of disease increase as a function of leaf wetness and weather were selected for all three leaf levels, an attempt was made to substitute the leaf wetness component (HLWTS/HLWMS/HLWBS) with corresponding leaf wetness values derived from weather station data (see above).

Results

Correlation analysis

Correlation analysis showed that no single macroclimate variable was sufficiently correlated with canopy leaf wetness to allow it to be used alone as a leaf wetness predictor. A combination of several variables was necessary.

Many of the macroclimate variables were highly intercorrelated. High correlations ($r > 0.8$) were found for HRH – HTDIFF, TMAX – TMEAN, WINDX – HWIND2 and LAI – DAYLEN in all individual years and additionally TMIN – TMEAN, WINDX – HWIND1 and HWIND1 – HWIND2 when the analysis was run with all years together. Either one in each pair was therefore excluded in the continued analysis. The variable that made the best contribution to the model was finally retained. Leaf wetness durations measured by adjacent instruments were highly correlated ($r > 0.8$). Neither of these were therefore used together in the same model.

Leaf wetness duration and weather

Leaf wetness could be predicted with several different sets of variables. We used the following criteria to determine which variables to include in the models:

- the models should have a maximum of four variables,
- the same variables should be used for each instrument level,
- the variables used in the models should be relatively easy to measure and
- these criteria should be applied without great loss of accuracy in the model.

Table 2. R^2-values when the models for leaf wetness duration a, b and c respectively were 'forced' on individual years

	Model	All Years	1986	1987	1988
Top: HLWT	a	0.437	0.880	0.739	0.626
Middle: HLWM	b	0.499	0.886	0.605	0.680
Bottom: HLWB	c	0.492	0.727	0.551	0.512

This selection process resulted in the following models common to all years and fields:

In the top of the canopy:

$$HLWT = 0.977 + 0.0295 \times MM - 0.0162 \times TMAX^{a} - 0.0221 \times TMIN + 0.263 \times HRH \qquad r^2 = 0.437 \quad N=122 \qquad (a)$$

In the middle of the canopy:

$$HLWM = 1.38 + 0.0343 \times MM - 0.0430 \times TMAX - 0.00611 \times TMIN^{a} + 0.257 \times HRH \qquad r^2 = 0.499 \quad N=123 \qquad (b)$$

In the bottom of the canopy:

$$HLWB = 1.37 + 0.0416 \times MM - 0.0778 \times TMAX + 0.0457 \times TMIN + 0.174 \times HRH^{a} \qquad r^2 = 0.492 \quad N=109 \qquad (c)$$

Each model was significant at $p < 0.001$ and the individual independent variables, except one, were significant ($p < 0.05$–0.001). Higher coefficients of determination could be obtained by fitting the above models to individual years, but the number of non-significant variables increased (Table 2). Other models that were obtained, but rejected according to the criteria above, are listed in Appendix 1.

Disease increase and leaf wetness

For all models tested a 'window' width of 5 days resulted in higher r^2-values than the narrower or wider ones. The optimum length of the 'lag' period varied with leaf level and with variables included in the analysis. Generally it was 8–9 days for leaf 1, 6–7 days for leaf 2 and 6 days for leaf 3. The results presented below are based on a 'lag' period of 7 days since our aim has been to use the same width of 'windows', the same length of 'lag' periods and the same variables for all leaf levels.

[a]) Not significant at $p < 0.05$

Table 3. General models for the rate of disease increase (RDI) on the three uppermost leaf levels as a function of leaf wetness. Data from Uppsala 1986–1987. 'Window' = 5 days and 'lag' = 7 days

	INTERC	HLWTS	XWETT	r^2	N
Leaf 1:	−0.0136	0.0115		0.298	159
	−0.0317	0.00425	0.0271	0.378	159
Leaf 2:	−0.00146[a]	0.0139		0.418	133
	−0.0128	0.00948	0.0171	0.446	133
Leaf 3:	+0.0222	0.0188		0.225	100
	−0.00335[a]	0.0118	0.0335	0.302	100

[a]) Not significant at $p < 0.05$

The rate of disease increase (RDI) could be predicted by leaf wetness duration (HLWTS/HLWMS/HLWBS) or by leaf wetness duration and mean daily number of leaf wetness periods (XWETT/XWETM/XWETB) during a 'window' period. Data from the uppermost leaf wetness recorder were the best predictor of RDI at all leaf levels (Table 3). All models were significant ($p < 0.001$) and individual variables were also significant ($p < 0.05$–0.001) with the exception of footnoted parameters in Table 3.

A better prediction of RDI could be obtained by using models containing HLWTS/HLWMS, RAINS, XTMAX and XTMIN.

Leaf 1:

$$RDI = -0.0289^a + 0.00893 \times HLWTS + 0.00551 \times RAINS + 0.00127 \times XTMAX - 0.00160 \times XTMIN \qquad r^2 = 0.336 \quad N=159 \qquad (d)$$

Leaf 2:

$$RDI = -0.143 + 0.0120 \times HLWMS + 0.00767 \times RAINS + 0.0114 \times XTMAX - 0.0104 \times XTMIN \qquad r^2 = 0.474 \quad N=159 \qquad (e)$$

Leaf 3:

$$RDI = -0.0866 + 0.0119 \times HLWMS - 0.00135 \times RAINS^a + 0.0113 \times XTMAX - 0.0111 \times XTMIN \qquad r^2 = 0.474 \quad N=126 \qquad (f)$$

For the lowest leaf level the best models were obtained when data from the middle leaf wetness recorder was used. All models were significant ($p < 0.001$) and individual parameters were also significant ($p < 0.05$–0.001) unless footnoted otherwise.

[a]) Not significant at $p < 0.05$

Disease increase and weather

When the leaf wetness duration parameters in equations d), e) and f) were substituted with values calculated from equations a) and b), the following models for the rate of disease increase were the results.

Leaf 1:

$$RDI = -0.0707 + 0.00828 \times RAINS + 0.00338 \times XTMAX - 0.00208 \times XTMIN^a + 0.00718 \times HLWTC \qquad r^2 = 0.196 \quad N=195 \qquad (g)$$

Leaf 2:

$$RDI = -0.138 + 0.0121 \times RAINS + 0.0120 \times XTMAX - 0.0118 \times XTMIN + 0.00651 \times HLWMC \qquad r^2 = 0.274 \quad N=169 \qquad (h)$$

Leaf 3:

$$RDI = -0.0825^a + 0.0009 \times RAINS^a + 0.0117 \times XTMAX - 0.0121 \times XTMIN + 0.00621 \times HLWMC^a \qquad r^2 = 0.341 \quad N=136 \qquad (i)$$

The last variable HLWTC and HLWMC in equation g) and h) and i), respectively, is the calculated leaf wetness duration during the 'window' period. The models are statistically significant ($p < 0.001$) and individual variables are also significant ($p < 0.05$–0.001) unless mentioned otherwise in the footnote.

Discussion

It is possible to estimate daily leaf wetness duration in the field with easily obtainable data from a nearby weather station. Almost 50% of the variation in leaf wetness duration can be explained by maximum and minimum temperature, rainfall and hours with relative humidity above 90%. More complicated equations could be used to further improve accuracy. Adding wind as a variable may contribute to explaining how quickly the leaf dries. With wind (HWIND2) included the level of explanation increases to 69–76% (Appendix 1).

The rate of disease increase was used instead of disease severity to partially correct for autocorrelation [Zadoks, 1961; Butt and Royle, 1974]. The use of rates also provides a good picture of disease development and its variation in relation to other factors [Vanderplank, 1963]. General models were found for the relationship between rate of disease increase (RDI)

[a]) Not significant at $p < 0.05$

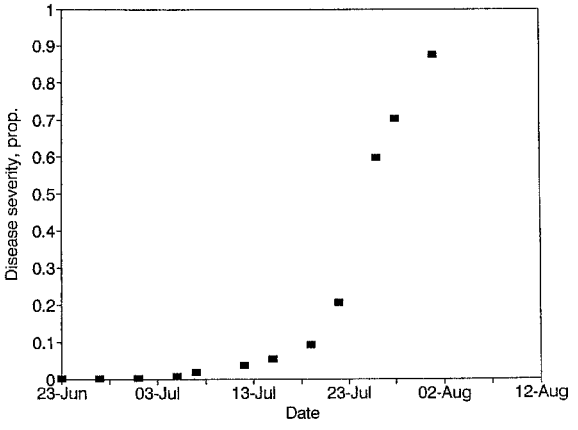

Fig. 2. Disease progress on leaf no. 2 in field no. 3 (1987).

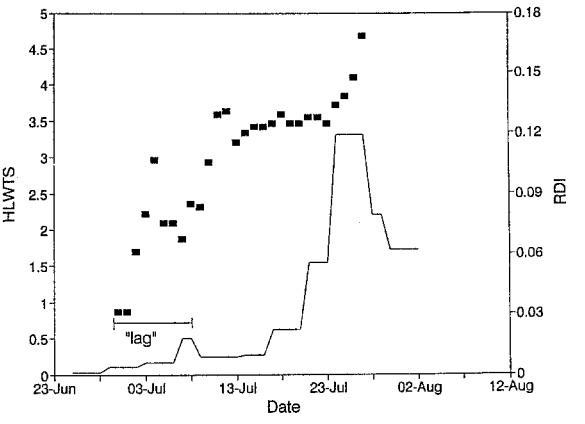

Fig. 3. Field no. 3 (1987). ■ Leaf wetness duration during a 5-day 'window' (HLWTS) measured by the uppermost leaf wetness recorder and — Rate of disease increase (RDI) on leaf no. 2. The dependent variables originate from arcsine-square root transformed data.

and weather observations over a three year period. Leaf wetness duration in itself explains 22–42% of the RDI, depending on leaf level (Table 3). Since symptom expression and latency periods are related to wetness interruptions in addition to wetness duration [Shearer and Zadoks, 1972, 1974] the addition of the variable that represents these interruptions (XWETT) increases the explanatory power to 30–45%.

To illustrate the relationships between previous leaf wetness events and the rate of disease increase, we have used an example from the data. Figure 2 shows disease progress on the second leaf from the top in one field from 1987. In Fig. 3 RDI is plotted as a function of time. Leaf wetness duration (HLWTS), representing a 5-day 'window' is simultaneously plotted. Long durations of leaf wetness are correlated with high rates of disease increase 7 days later (=the 'lag'). After July 27 high disease severity in combination with beginning of senescence kept RDI low despite favourable leaf wetness conditions. Figure 4 shows the RDI as a function of HLWTS for the same leaf level but in all fields. The shape of the curve would suggest that a threshold of 28 hours of leaf wetness during a 5 day period is necessary for a substantial increase in disease development. The validity of this statement needs further investigation.

Better models for prediction of RDI could be obtained by adding rain days and maximum and minimum temperature (as in equations d–f), increasing the r^2 to 34–47%.

The number of rain days (RAINS) within a 'window' had a negative relationship to RDI for the third leaf level (eq. f), whereas the relationship is positive for the first and second leaf. A plausible explanation would be that this variable represents splash dispersal events, and that the splash initiating rain drops not reach this leaf level, with two well developed leaf levels above it. With no spore splash, fewer new infections follow and disease progress will consist mainly of lesion growth. In this study, the effect of rain on disease increase on leaf 3 could be retention of moisture, which mainly is included in the leaf wetness variable. On the other hand, if the splashing raindrops reach the third leaf the resulting disease increase would be more pronounced on the two upper leaves than on the third leaf [Shaw and Royle, 1993]. The effects of rainfall and splash cannot be separated in this study.

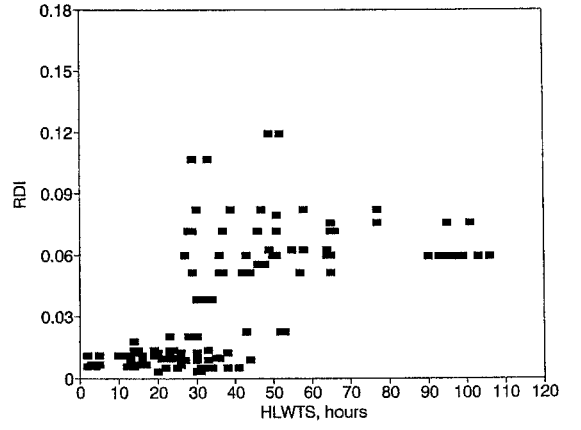

Fig. 4. Rate of disease increase (RDI) on leaf no. 2 in relation to leaf wetness duration during a 5-day 'window' with 7 days 'lag' in all fields (HLWTS). The dependent variable originates from arcsine-square root ransformed data.

The 'lag' periods that produced the best models were not the same for all 3 leaf levels. While one explanation could be in experimental errors or the particular statistics used, another reason could be that younger leaves are less susceptible to disease and are at the top of the plant and may dry faster. Therefore the disease progress rate is slower on these leaves than on older, lower leaves [Aust and Hau, 1983; Jönsson, 1985]. Assuming that new infections have occurred in a 'window', the 'window' width and the 'lag' period together would represent an incubation period of 6–14 days, depending on leaf level.

The attempt to explain the rate of disease increase with a combination of weather variables and replacing leaf wetness duration with a function of screen weather variables (eq. g–i) was less successful, although 20–34% of RDI could be explained by this method. This was to be expected, since not all the information regarding leaf wetness duration is contained in the screen weather data.

Several other investigations have addressed dew duration (only one cause of leaf wetness) instead of leaf wetness [Wallin, 1963; Crowe *et al.*, 1978; Pedro and Gillespie, 1982a,b]. In a temperate climate where both rain and dew occur during the growing season, there is no reason to separate different causes of leaf wetness. The difficulty to separate between dry and wet periods with the instruments used, as pointed out by Jones [1986], was overcome by doing several visual comparisons of wetness on the leaves with position of the ink pen on the instrument. When a leaf changes from wet to dry, or the opposite, is a subjective decision. With electronic sensors [Huband and Butler, 1984; Sutton *et al.*, 1984], the same problem exists, though then it is a question of deciding at which resistance the real leaf changes from dry to wet and vice versa.

Usually the attempts to forecast further disease increase (often to guide fungicide application) is based on the amount of disease on the 3–4 uppermost leaves. The estimates we obtained can be compared to the wetness requirements for the fungus in connection with spore release, germination and infection, and if the pathogen is actually present appropriate forecasts for the risk for further disease increase can be made. In a *S. nodorum* model [Djurle and Yuen, 1991] disease development is stimulated on each of 10 individual leaf levels plus the ear. The three equations for leaf wetness duration can be used at their corresponding leaf levels in this model and replace earlier empirical estimates.

The number of hours when relative humidity is above 90% is the most important variable in the suggested models, but by itself it is not sufficient as a leaf wetness predictor. The 'general rule' that leaves are wet when RH at screen height is >90% could not be applied in this study. Lomas and Shashoura [1970] and Thompson [1981] have had similar experiences with 85% and 90% criteria, respectively. We can agree with the former authors, that accurate measurements are best taken within the crop, but where appropriate instruments are lacking an estimate of leaf wetness duration from standard weather station data is an alternative. The canopy structure or the density of the crop expressed as LAI has an effect on leaf wetness duration [Scott *et al.*, 1985], although the variable LAI was not significantly related to leaf wetness duration in this study.

Similar approaches with 'windows', 'lags' and linear regression have been taken by Bahat *et al.* [1980], Coakley *et al.* [1985, 1988] and Chuang and Jeger [1987]. In the studies with *Septoria tritici* leaf blotch of wheat [Coakley *et al.*, 1985], the WINDOW was wider and the 'lags' longer than ours. Their predictions were based on minimum temperature and days with no precipitation during 'window' periods 1–2 months before heading. Those studies encompassed several disease cycles between the observed environmental 'windows' and the final disease severity. Our study, on the other hand, examined environmental 'windows' and their effect on subsequent disease development within a single disease cycle. Long term disease predictions were not attempted in this study, since our experience with *S. nodorum* in Sweden is that when conducive weather is followed by unfavourable conditions, disease development will be retarded and damaging levels may not be reached.

There are few studies on the incubation period of *S. nodorum*. According to Eyal *et al.* [1987] it is 7–14 days and from the results reported by Rapilly *et al.* [1981] similar figures can be calculated. Scharen [1964] and Royle *et al.* [1986] report 2 weeks and 2–4 weeks respectively. Our estimate of 6–14 days is, by comparison, on the low side, but has been confirmed by visual observations in the field.

Conclusions

Earlier studies conclude that the actual weather is the crucial factor for a *S. nodorum* epidemic to develop or not [King *et al.*, 1983; Djurle and Yuen, 1991].

This study has quantified the weather factor to account for almost 50% of the variation in the rate of disease increase. Of the remaining 50%, some of it could still be found in the weather (in part due to our criteria when selecting the models) but the main source for further explanation is related to biological factors. One factor that complicates these studies is the confounding of calendar time, level of disease and plant age, and their true effects cannot be completely disentangled. Separate treatment of lesion growth and new infections would probably improve the models. Leaf age and susceptibility are other factors that influence disease increase.

The relationships between leaf wetness duration and screen weather and RDI and weather presented in this paper, can be used to determine whether the microclimate in the crop is conducive for disease development and to assess the influence of current weather on future disease.

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Appendix 1. Models for leaf wetness duration at three heights in the crop as a function of screen weather variables.

Eq.	INTERC	MM	TMAX	TMIN	HWIND2	PVMEAN	HRH	RAINF	r^2
HLWT									
1	0.776	0.0243	−0.0457	−0.0325	0.435	0.0547	0	0	0.691
2	0.735	0.0280	−0.0301	−0.000453[a]	0.537	0	0.152	0	0.636
3	0.970	0.0235	−0.0436	−0.0639	0	0.0821	0	0	0.577
4=c	0.977	0.0295	−0.0162[a]	−0.0221	0	0	0.263	0	0.437
HLWM									
5	1.11	0.0254	−0.0755	−0.0215	0.439	0.0673	0	0	0.763
6	1.09	0.0312	−0.0574	0.0178	0.582	0	0.147	0	0.690
7	1.31	0.0250	−0.0739	−0.0540	0	0.0961	0	0	0.669
8=b	1.38	0.0343	−0.0430	−0.00611[a]	0	0	0.257	0	0.499
HLWB									
9	0.813	0	−0.0910	0	0.265	0.0818	0	0.376	0.689
10	1.06	0.0303	−0.108	0.0323	0.382	0.0660	0	0	0.651
11	1.09	0.0378	−0.0907	0.0692	0.536	0	0.0804[a]	0	0.599
12	1.24	0.0305	−0.108	0.00368[a]	0	0.0917	0	0	0.604
13=c	1.37	0.0416	−0.0778	0.0457	0	0	0.174[a]	0	0.492

[a]) Not significant at $p < 0.05$