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A simulation model for the development of brown rust epidemics in winter wheat

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Abstract

A model simulating the progress of *Puccinia recondita* severity, expressed as a percentage of rusted leaf area (both as average and its 95% confidence interval) on individual wheat leaves over the course of a growing season, with a time step of one day, was elaborated using laboratory and field data from literature. Data on the stages of each infection cycle (uredospore germination, penetration, latency, uredium eruption and infectiousness) were transformed into model parameters by curve fitting, Montecarlo stochastic procedures, corrections and empirical assumptions. Data on host growth, like the timing of all phenological stages, the dynamic of the green area of each leaf from appearance to complete senescence, and tillering were obtained from a specific sub-model. Model validation was performed on actual data not used in model building and representing a wide range of conditions (several winter wheat cultivars grown at eight locations in northern Italy between 1990 and 1994) by using subjective, non-parametric and parametric tests: it revealed a satisfactory agreement between the data simulated by the model and actual data.

Introduction

Brown rust, caused by *Puccinia recondita* Rob. and Desm. f. sp. *tritici* Eriks. and Henn., is the most important disease of wheat world-wide. In northern Italy it appears every year (Rossi et al., 1990), when the growth stage of the wheat is between 55 and 73 of the decimal code (Zadoks et al., 1974). To control rust, the farmers usually apply fungicides at heading (Pancaldi and Brunelli, 1988). Even though it is an effective strategy (because the inoculum is still low and the period left for rust development after the time when the fungicide loses efficacy is short, Daamen, 1991; Hims and Cook, 1991) calendar spraying is not reasonable, because 1) epidemics vary from light to severe according to weather conditions, and 2) fungicide application is profitable only when rust causes severe epidemics (Milus, 1994; Sutherland et al., 1993).

Therefore, in addition to a model able to simulate disease appearance (Rossi et al., 1996), a reliable forecast for leaf rust progress is essential for the organization of an advisory system.

Two different approaches have been used to forecast rust development. Some forecasting systems consider the effect of weather on the disease by means of empirical rules (Chester, 1943; Minkevich and Zakharova, 1987), or flow charts (Statler and Helgeson, 1988), or disease indices (De La Rocque, 1988; Paveley, 1993), or regression equations (Eversmeyer and Burleigh, 1970; Burleigh et al., 1972). Other models forecast rust severity on the basis of the dynamic of the epidemic, using a fixed relative growth rate of the disease (Shaner and Hess, 1978; Fleming, 1983; Daamen, 1991).

In this work we present a simulation model for the development of leaf rust epidemics which blends the two earlier approaches. In fact it is based on the effect of meteorological conditions on the uredospore cycles.

A similar approach has been used for other rust diseases, like *Phakopsora pachyrhizi*/soybean (Yang et al., 1991b), *Hemileia vastatrix*/coffee (Kushalappa et al., 1983), *Uromyces appendiculatus*/bean (Berger et al., 1995), *Puccinia striiformis*/wheat (Luo and Zeng, 1995), and for wheat brown rust, too, by Benizri and Projetti (1992): this model has not been published in a complete version and it is available in a commercial computerized version only (De La Rocque, 1992).

Materials and methods

RUSTDEP (RUST Development of EPidemics) model description

The model simulates the progress of disease severity, expressed as a percentage of rusted leaf area (both as average and its 95% confidence interval), on individual leaves, over the course of a growing season, with a time step of one day, as a result of the increase in the diseased area caused by each infection cycle (Figure 1).

Information about the interactions between stages of disease cycles, weather conditions and host characteristics are incorporated into a system dynamic model, as shown in Figure 2.

The infection process begins when uredospores germinate on wheat leaves and the resulting germ tubes produce infection structures which penetrate into leaf tissue and cause latent infections. At the end of the latent period a part of the infections established erupt uredia on leaves: infection becomes visible as a rusted leaf area. Urediospores produced from uredia are dispersed and some part of these can cause new infections on viable and healthy leaf tissues. Infectious uredia actively contribute to the epidemic during their infectious period: later they become old and sterile and their contribution ends.

Weather and the host's variables influence the rates of change from one disease stage to another and from one disease cycle to another: therefore they determine the progress of epidemic.

This model uses the basic structure of the logistic model (Van der Plank, 1963), which best describes the disease progress under field conditions (Yang et al., 1991a).

Variables and constants used in the model are listed in Table 1, following DeWit and Goudriaan (1978).

On day j, disease severity on each L^{th} leaf is calculated as follows:

$$RLA_{Lj} = RLA_{L(j-1)} + DRLA_{Lj} \cdot CV$$

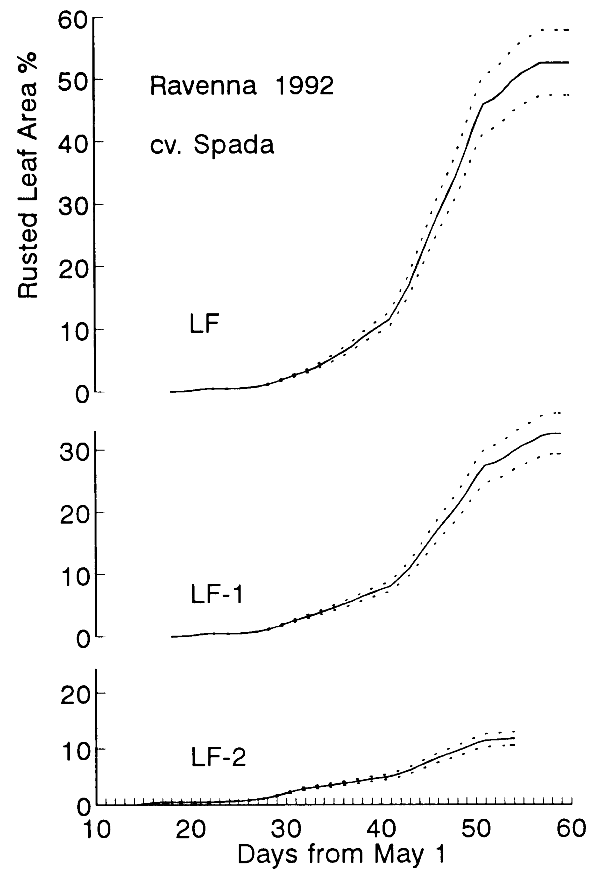

Figure 1. Output of the RUSTDEP model: simulation of brown rust severity on the leaves from the flag leaf (LF) to the antepenultimate leaf (LF-2), respectively (— average and . . . 95% confidence interval) (cv. Spada, Ravenna 1992).

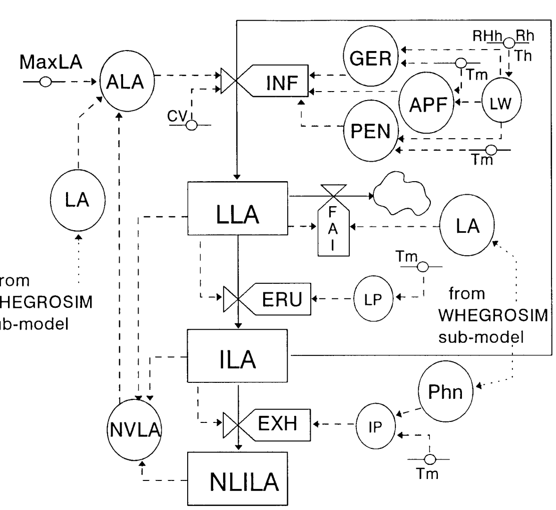

Figure 2. Relational diagram of RUSTDEP drawn according to Leffelaar and Ferrari (1989) (see Table 1 for abbreviations).

Table 1. Variables and constants used in the RUSTDEP model

State variables	
LLA	leaf area with latent infections ($cm^2 \cdot cm^{-2}$)
ILA	infectious leaf area ($cm^2 \cdot cm^{-2}$)
NLILA	no longer infectious leaf area ($cm^2 \cdot cm^{-2}$)
RLA*	total rusted leaf area (= ILA + NLILA) ($cm^2 \cdot cm^{-2}$)
DRLA*	daily increase of RLA (= ILA·INF·ALA·FAI) ($cm^2 \cdot cm^{-2}$)
Rate variables	
INF	infection efficiency of uredospores (0–1)
FAI	failure rate of latent infections (0–1)
ERU	eruption rate of uredia (0–1)
EXH	exhaustion rate of uredia (0–1)
Auxiliary and intermediate variables	
GER	germination of uredospores on leaves (0–1)
APF	appresssorium formation (0–1)
PEN	penetration into leaves (0–1)
LA	leaf area (green leaf area) ($cm^2 \cdot leaf^{-1}$)
ALA	affectable leaf area ($cm^2 \cdot cm^{-2}$)
NVLA	leaf area no longer vulnerable to infection ($cm^2 \cdot leaf^{-1}$)
LP	latent period (days)
IP	infectious period (days)
LW	leaf wetness ($hours \cdot day^{-1}$)
Phn	wheat growth phase (Ph1 to Ph6)
Constants and parameters	
MaxLA	maximum leaf area ($cm^2 \cdot leaf^{-1}$)
CV	host effect on DRLA (number < 1)
Tm	daily mean temperature ($°C \cdot day^{-1}$)
Th	hourly temperature ($°C \cdot h^{-1}$)
RHh	hourly relative humidity ($\% \cdot h^{-1}$)
Rh	hourly amount of rainfall ($mm \cdot h^{-1}$)

* Variables used in the model but not shown in the relational diagram of Figure 2 because they are the sum or the product of other variables.

where: RLA_L = total rusted leaf area (or disease severity) on the L^{th} leaf; $DRLA_L$ = daily increase of RLA_L; CV = host effect on DRLA.

The leaf positions (L1, L2, ..., LF-1, LF, where LF is the flag leaf) are considered separately because the contributions to potential grain yield and the disease progress curves for individual leaves are different from each other (Seck et al., 1991; Rao et al., 1992). Likewise the main stem and tillers are considered separately.

For each L^{th} leaf, the increase of the rusted leaf area on each j^{th} day is:

$$DRLA'_{Lj} = ILA_i \cdot INF_i \cdot ALA_{Li} \cdot FAI_{Lj}$$

where: i = j-LP, where LP is the latent period; ILA = infectious leaf area; INF = infection efficiency of uredospores; ALA = affectable leaf area; FAI = failure rate of latent infections.

Since the pustules produced by infections established on the i^{th} day do not all open simultaneously (Metha and Zadoks, 1970), a delay function for DRLA is considered according to the data from Shaner et al. (1978). For each k^{th} day around j (j–2 to j+2):

$$DRLA_{Lk} = DRLA'_{Lj} \cdot ERU_k$$

where: ERU_k = eruption rate of uredia on each k^{th} day: $ERU_{j-2} = 0.06$; $ERU_{j-1} = 0.26$; $ERU_j = 0.38$; $ERU_{j+1} = 0.26$; $ERU_{j+2} = 0.04$.

Latent period (LP). LP is the time, expressed in days, that elapses between the arrival of uredospores on the leaf surface and the eruption of uredia (Zadoks and Schein, 1979). LP depends on temperature (Johnson, 1980; Rao et al., 1990; Jasvir-Singh et al., 1989). To calculate LP, data from Johnson (1980) on the length of latency (expressed as the number of days from inoculation until 50% of the uredia erupt) are regressed on Tm:

$$LP = 61.023 \cdot Tm^{-0.7019}$$

Infectious Leaf Area (ILA). ILA_i is the amount of leaf area that is occupied by infectious uredia, at day i: it represents the amount of secondary inoculum well, because it is proportional to the number of available uredospores (Burleigh et al., 1969). ILA is calculated as a part of RLA: the area having old sterile uredia is subtracted from the total rusted leaf area:

$$ILA_i = \sum_{L=1}^{9} (RLA_{Li} - RLA_{L(i-IP)})$$

where: L = leaf number (from 1 to 9); IP = infectious period.

IP is the period of uredospore production by a uredium; due to the fact that rusted tissues are no longer infectious when this period is over, they do not partecipate in the epidemic any more and are removed. To calculate IP, data from Tomerlin et al. (1983) were preferred to the equation from Jasvir-Singh et al. (1989) ($IP = 10.94–0.26 \cdot Tm$), because they agreed better with the data observed at field level in the Po Valley or given by both Mehta and Zadoks (1970) and Wang and Casulli (1995). Data on the length of the infectious period (in days) observed on the wheat ‘Thatcher’ arti-

Table 2. Infectious period (days) of *P.recondita* f.sp. *tritici* on cv. Thatcher at three growth stages and at different temperatures (from Tomerlin et al., 1983)

Tm (°C)	Growth stages		
	Seedling	Heading	Anthesis
21.1	19	63	32
23.9	21	48	29
26.7	19	25	20
29.4	14	20	15

ficially inoculated at three growth stages were used in the Tm range 21–30 °C (Table 2). Values of IP for Tm and wheat growth stages between the tabulated values were calculated using a linear interpolation; to make interpolation between the growth stages the number of days between stages was derived from the WHEGROSIM sub-model. IP was considered unaffected by growth stages after anthesis, and by Tm in the 10–20 °C range (Teng et al., 1978).

Infection efficiency of uredospores (INF). INF is the proportion of available uredospores which cause new infections. Infection involves germination of uredospores on leaves (GER), appressorium formation (APF), and penetration into leaves (PEN).

Germination of uredospores on the leaf surface depends on temperature and free water in the form of leaf wetness (Clifford and Harris, 1981; Eversmeyer et al., 1988). Germination can be inhibited by light because hydration initiates a series of reactions that temporarily render spores light-sensitive (Chang et al., 1973), but this effect can be left out because under field conditions it is negligible (Eversmeyer et al., 1988). Formation of appressoria depends on temperature and leaf wetness too, whereas free water is not necessary for the other infection structures (substomatal vesicles, infection hyphae and haustorium mother cells): appressoria remain able to produce penetrating hyphae even after the leaf surface has dried (Eversmeyer et al., 1988).

To calculate GER, APF and PEN, data from Clifford and Harris (1981) on the percentage of uredospores germinated on wheat leaves, on the percentage of germ tubes able to produce appressoria, and on the percentage of penetration through stomata were expressed as a proportion of a maximum value and interpolated by polynomial regressions, considering Tm and LW as independent variables. For each day i:

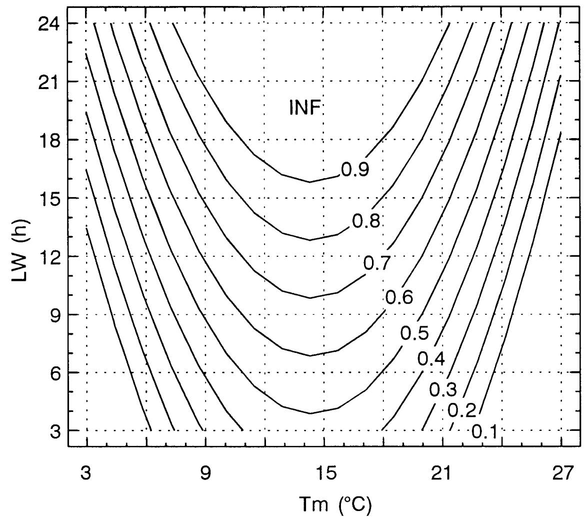

Figure 3. Relationship between mean air temperature (Tm), leaf wetness (LW) and infection efficiency of brown rust uredospores (INF) drawn as contour plot (see text for the polynomial function).

- $GER_i = (-14.035 + 15.217 \cdot Tm_i - 0.586 \cdot Tm_i^2 + 0.852 \cdot LW_i)/100$
- $APF_i = (-60.125 + 15.339 \cdot Tm_i - 0.544 \cdot Tm_i^2 + 3.401 \cdot LW_i)/100$
- $PEN_i = (-159.867 + 17.423 \cdot Tm_i - 0.527 \cdot Tm_i^2 + 5.787 \cdot LW_i)/100$
- if $LW_i < 3$, GER_i and $APF_i = 0$
- if GER_i, or APF_i, or $PEN_i < 0$, GER_i, or APF_i, or $PEN_i = 0$
- if GER_i, or APF_i, or $PEN_i > 1$, GER_i, or APF_i, or $PEN_i = 1$.

Fitted data were obtained for each variable, from 0 to 30 °C of Tm, and from 3 to 24 h of LW. Then a common regression was calculated for the three variables (Figure 3), on the assumption that all these monocyclic components are present in the field each time during the epidemics:

- $INF_i = (-78.011 + 15.995 \cdot Tm_i - 0.556 \cdot Tm_i^2 + 3.346 \cdot LW_i)/100$
- if $LW_i < 3$, $INF_i = 0$
- if $INF_i < 0$, $INF_i = 0$
- if $INF_i > 1$, $INF_i = 1$.

Affectable leaf area (ALA). ALA is the total amount of a leaf area that can be infected. It is a part of the total leaf area.

For each i^{th} day and each L^{th} leaf, ALA is calculated as follows:

$$ALA_{Li} = (LA_{Li} - NVLA_{Li})/MaxLA_L$$

where: LA = leaf area (green leaf area); NVLA = leaf area no longer vulnerable to infection; MaxLA= maximum leaf area.

LA ($cm^2 \cdot leaf^{-1}$), on each i^{th} day is simulated by the specific sub-model WHEGROSIM, as well as MaxLA ($cm^2 \cdot leaf^{-1}$).

NVLA ($cm^2 \cdot leaf^{-1}$) is computed as follows:

$$NVLA_{Li} = (RLA_{L(i-1)} + LLA_{Li}) \cdot MaxLA_L$$

where: LLA = leaf area with latent infections.

LLA_{Li} is the total amount of the area of the L^{th} leaf that is in the latent phase of infection. It is an infected area without any visible disease symptoms. It is calculed as follows:

$$LLA_{Li} = RLA_{Lj} - RLA_{Li}$$

Failure rate (FAI). The failure rate of latent infections is based on the consideration that a part of the latent infections cannot go on till the eruption of uredia. FAI depends on the leaf area that is physiologically dead; it is calculated by assuming that the leaf tissue occupied by a latent infection and the healthy tissue have the same probability to die:

– when $LA_{Lj} \geq LA_{Li}$, $FAI_{Lj} = 1$
– when $LA_{Lj} < LA_{Li}$, $FAI_{Lj} = LA_{Lj} / LA_{Li}$.

Host resistance (CV). In many wheat cultivars (the slow-rusting cultivars) resistance towards *P.recondita* is a rate-reducing resistance (*sensu* Nelson, 1978). In epidemiological terms, resistance reduces the apparent infection rate of epidemics as an effect of changes in the basic infection rate, due to reduced effectiveness of the uredospores in causing new infections (Shaner and Hess, 1978; Knott and Mundt, 1991) and less abundant sporulation, due to a reduction in both the size of the uredia (Shaner, 1983) and in the uredospore yield (Wang and Casulli, 1995), in the latent period (Shaner et al., 1978; Johnson, 1980), and in the infectious period (Zhang et al., 1993). Lacking precise data on the effect of each wheat cultivar in changing ILA, LP, INF, and FAI, the rate-reducing effect of any cultivar is included in the CV variable, which is < 1.

Stochastic procedures. Stochastic elements were incorporated into the model to reflect unknown variability in: i) the number of days from inoculation until 50% of the uredia erupt (LP); ii) the proportion of available uredospores which cause new infections (INF).

As described by Giosuè et al. (1995), following the Monte-Carlo method a probability distribution was assigned to LP and INF, which were assumed to be normally distributed. Parameters of normal distributions were derived from the regression equations used to compute LP and INF: $\mu = 10$ and $\sigma = 0.5$ for LP; $\mu = 0.5$ and $\sigma = 0.025$ for INF. Ten days is the average of LP in the range 6–14 days, which corresponds to the possible Tm range during rust epidemics (about 9 to 25 °C); 0.5 days is the standard deviation of LP values estimated by the regression analysis. In the case of INF, 0.5 is the intermediate value of INF range (from 0 to 1) and 0.025 is the standard deviation from regression analysis. Using the standardized normal distribution, the probability associated with each value of the two variables was determined in the intervals: 6–14 days (step 0.5) for LP; 0–1 (step 0.02) for INF. A set of random numbers was then associated with each variable value, in such a way that the set width was proportional to the probability of each variable value. To obtain a set of output values of RLA on each j^{th} day and for each L^{th} leaf, the model ran 50 times using, each time, a different LP and INF value from the probability distribution, as determined by a random number generator (the Rnd function of Visual Basic version 3, Microsoft Corporation, 1993); the result is then a set of 50 disease progress curves. To evaluate the set of RLA values generated by the 50 stochastic runs, the mean value and its 95% confidence interval were calculated each day. Using 50 iterations, the mean value of RLA_j obtained with the stochastic procedure is similar to the value obtained deterministically (Giosuè et al., 1995).

WHEGROSIM (WHEat GROwth SIMulation) sub-model description

The model represents a re-elaboration of the models from Porter (1984) and Weir et al. (1984), limited to the timing of all phenological stages, leaf-by-leaf development and tillering. The basic concepts are reported in the previously cited papers, whereas the mathematical formulation of the model is described here; it was performed using data from literature (Reyneri and Grignani, 1989; Tuttobene et al., 1993), sometimes adapted to the environmental conditions of the Po Valley on the basis of the results obtained by validation (not shown here). The model allows simulation of both the phenology of wheat growth and the dynamic of the green area of each leaf from its appearance to complete senescence (Figure 4).

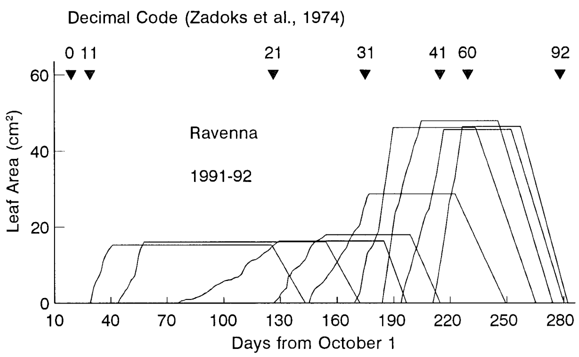

Figure 4. Output of the WHEGROSIM: simulation of the phenology of wheat growth and the dynamic of the green area of each leaf on main stems (Ravenna, 1991/92).

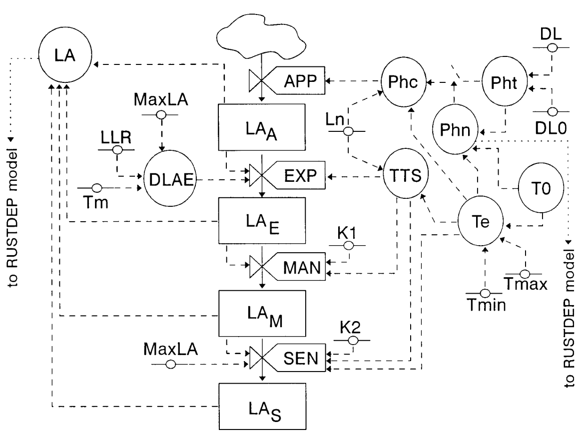

Figure 5. Relational diagram of WHEGROSIM drawn according to Leffelaar and Ferrari (1989) (see Table 3 for abbreviations).

The relational diagram for the leaf growth of winter wheat is shown in Figure 5. Variables and constants used in the model are listed in Table 3.

Phenological development. Phenological development predicts the beginning and ending dates for 6 phases (Phn): Ph1, sowing to emergence (Decimal Code 11 of Zadoks et al., 1974); Ph2, emergence to tillering (DC 21); Ph3, tillering to stem elongation (DC 31); Ph4, stem elongation to booting (DC 41); Ph5, booting to anthesis (DC 60); Ph6, anthesis to ripening (DC 92).

The duration of each period is measured as thermal time, using the following summation:

$$TTS = \sum_{d=1}^{n} Te_d \, Pht_d$$

where:

– TTS = thermal time summation: 167, 132, 156, 240, 117 and 500 for Ph1 to Ph6, respectively;

Table 3. Variables and constants used in the WHEGROSIM submodel

State variables	
LA_A	leaf area at leaf appearance ($cm^2 \cdot leaf^{-1}$)
LA_E	leaf area during leaf expansion ($cm^2 \cdot leaf^{-1}$)
LA_M	leaf area during leaf maximum size maintenance ($cm^2 \cdot leaf^{-1}$)
LA_S	leaf area during leaf senescence ($cm^2 \cdot leaf^{-1}$)
Rate variables	
APP	rate of leaf appearance
EXP	rate of leaf expansion
MAN	rate of leaf maintenance
SEN	rate of leaf senescence
Auxiliary and intermediate variables	
Phc	phyllochrone (°C)
Pht	photoperiodic factor ($h \cdot day^{-1}$)
Phn	wheat growth phase (Ph1 to Ph6)
LA	leaf area (green leaf area) ($cm^2 \cdot leaf^{-1}$)
DLAE	daily increase of LA during expansion ($cm^2 \cdot leaf^{-1}$)
TTS	thermal time summation (°C)
Te	daily effective temperature ($°C \cdot day^{-1}$)
T0	basal temperature (°C)
Constants and parameters	
MaxLA	maximum leaf area ($cm^2 \cdot leaf^{-1}$)
LLR	lamina and leaf ratio ($cm^2 \cdot cm^{-2}$)
DL	daylength ($h \cdot day^{-1}$)
DL0	photoperiodic effective hours ($h \cdot day^{-1}$)
Tm	daily mean temperature ($°C \cdot day^{-1}$)
Tmin	minimum daily temperature ($°C \cdot day^{-1}$)
Tmax	maximum daily temperature ($°C \cdot day^{-1}$)
Ln	leaf position (L1 to L9 = LF flag leaf)
K1	constant for leaf maintenance (= 2.345)
K2	constant for leaf senescence (= 1.115)

– d = day counter, from beginning (d = 1) to ending (d = n) of each phase;

– Te = daily effective temperature (in $°C \cdot day^{-1}$):

$$Te_d = [(Tmax_d + Tmin_d)/2]–T0$$

where: T0 (basal temperature) = 2 during Ph1; T0 = –2 during Ph2 and Ph3; T0 = 0 during Ph4 and Ph5; T0 = 9 during Ph6; Tmax and Tmin = maximum and minimum daily temperature;

– Pht = photoperiodic factor (only from Ph2 to Ph5):

$$Pht_d = (DL_d\text{-}DL0)/(24\text{-}DL0)$$

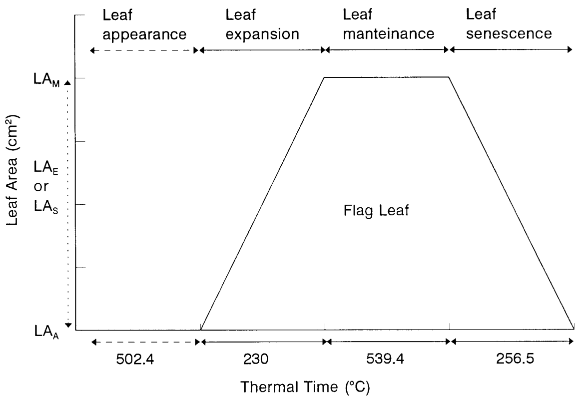

Figure 6. Phases of leaf growth (flag leaf) from appearance to senescence as a function of thermal time (°C) and correspondent leaf area (cm^2) (see Table 3 for abbreviations).

where: DL_d = daylength, DL0 = photoperiod-effective hours (equal to 6) (in hd^{-1}).

Leaf growth. The leaf growth is divided into 4 phases; for each L^{th} leaf: 1) appearance, from the sowing to the appearance of the L^{th} leaf; 2) expansion, from appearance to final leaf size; 3) full photosynthetic activity, in which the leaf maintains its maximum size; 4) senescence, in which leaf tissue dies rapidly (Figure 6).

Leaf appearance. The length of the leaf appearance period depends on the phyllochrone (Phc), which is the thermal time required to produce successive leaves; the day on which the L^{th} leaf appears is determined as follows:

$$\sum_{z=1}^{n_L} (Te_z \cdot Pht_z) = Phc_L$$

where:

- z = day counter, from emergence (z = 1) to appearance (z = n) of the L^{th} leaf;
- Phc is equal to 38, 79.2, 131.8, 190.6, 261.9, 336.7, 409.1, 502.4 for L ranking from 2 to 9, respectively.

Leaf expansion till the final size. Following leaf appearance, the model assumes that each leaf expands during a fixed period at a rate determined by effective air temperature, till a final size.

The day in which the L^{th} leaf reaches its final size is determined as follows:

$$\sum_{z=1}^{n_L} Te_z = TTS_L$$

where:

- z = day counter, from appearance of the L^{th} leaf (z = 1) to reaching of final size (z = n);
- TTS_L is equal to 120, 130, 171, 198, 264, 270, 280, 280, 230 for L ranking from 1 to 9, respectively.

During leaf expansion, the leaf area (LA_L) on each z^{th} day is calculated as follows, up to a maximum value ($MaxLA_L$) from Gallagher (1979):

$$LA_{Lz} = LA_{Lz-1} + (DLAE_{Lz} \cdot LLR)$$

where: DLAE = daily increase of leaf (sheat and lamina) area ($cm^2 \cdot d^{-1}$) during expansion; LLR = ratio between lamina and leaf (Gallagher, 1979).

DLAE is a function of mean air temperature. It is calculated by a polynomial regression:

$$DLAE_{Lz} = -0.2623 + 0.4140 \cdot Tm_z - 0.0948 \cdot Tm_z^2 + 0.0101 \cdot Tm_z^3 - 0.0003 \cdot Tm_z^4$$

Leaf maintenance at maximum size. When each leaf has reached its final size, it remains at maximum size before its green area starts to decline. Therefore on day z: $LA_{Lz} = MaxLA_L$. The length of leaf maintenance is calculated as: $TTS_L \cdot 2.345$.

Leaf senescence. The length of the period in which the leaf completes senescence is calculated as: $TTS_L \cdot 1.115$. On day z, the leaf area of the senescent leaf is calculated as follows:

$$LA_{Lz} = MaxLA_L - \{[MaxLA_L / (TTS_L \cdot 1.115)] \cdot \sum_{v=1}^{z} Te_v\}$$

where: v = number of days between the beginning of senescence and z. When $LA_L \leq 0$, the leaf is dead and $LA_L = 0$.

Tillering. Tillers appear at the same time as the 4^{th} leaf. Leaf growth on tillers is calculated like that on the main stem.

Model validation

Following Anderson (1974), a set of historical data collected previously and not used for model building were used for model validation.

The data consisted of disease severity values, assessed weekly on five 100-culm samples as a percentage of the rusted leaf area on each leaf from LF to LF-2, on several winter wheat cultivars (*Triticum aestivum* L. and *T. durum* Desf.) grown in big plots at eight locations in the Emilia-Romagna region (lying in the districts of Piacenza, Parma, Reggio, Modena, Bologna, Ferrara, Ravenna, and Forlì), over five years (from 1989/90 to 1993/94).

Simulations were made using a computerized version of the model programmed with Visual Basic Version 3.0 (Microsoft Corporation, 1993).

To run both models, hourly data of air temperature, relative humidity and rainfall were obtained from meteorological stations placed in the neighbourhood of the experimental fields by both the Meteorological Service of Emilia-Romagna and the Agrometeorological Network of Piacenza; they were used to calculate Tm, Tmax, Tmin. Leaf wetness duration (LW) was estimated from hourly data of temperature, relative humidity and rainfall (Th, RHh, Rh) using a numerical model (Galliani et al., 1993). The daylength (DL) was calculated according to Keisling (1982).

RUSTDEP was initialized on the day of the first record of rust in the field, using the correspondent value of assessed disease severity. The model started to run four days in advance, considering that the assessed disease severity results from the first infection cycle and that the appearance of these uredia is distributed during a period of five days at the rate of 0.06, 0.32, 0.7, 0.96, and 1, respectively (Shaner et al., 1978). For instance, if rust was observed on May 20 with disease severity equal to 0.002 on any leaf, the model ran starting from May 16 setting RLA according to the cited rates ($RLA_{May16} = 0.002 \cdot 0.06$; $RLA_{May17} = 0.002 \cdot 0.32$; $RLA_{May18} = 0.002 \cdot 0.7$; $RLA_{May19} = 0.002 \cdot 0.96$; $RLA_{May20} = 0.002 \cdot 1$).

WHEGROSIM was initialized on October 20, that is the central day of the prevalent sowing period in the considered wheat-growing area (Lega et al., 1993).

The coefficient CV was defined empirically for each cultivar by running the model using a set of values (CV = 1 to 0.6, step 0.05) and choosing the best fit of actual data by means of a visual comparison.

In this work only a few representative examples are shown: the bread wheat ‘Spada’ grown at Piacenza, from 1990/91 to 1993/94; the bread wheats ‘Eridano’, ‘Centauro’, ‘Recital’, and the durum wheats ‘Duilio’, ‘Neodur’ grown at Piacenza, Ferrara, and Ravenna in 1993/94; the bread wheats ‘Mirtos’ and ‘Oderzo’ grown at Ferrara and Ravenna in 1993/94, respectively, where rust epidemics were very severe.

Three validation methods were performed (Teng, 1981).

Subjective validation. Disease severity data assessed in the field and simulated by the model were visually compared. Agreement was considered acceptable if the simulated data fell into the 95% confidence interval for the mean of field data (Zadoks, 1979) for the greater part of the time of disease progress.

Statistical validation using non-parametric tests. Simulated and field data were considered as two independent random samples with unknown distribution functions represented by F(x) and G(x). The null hypothesis that F(x) and G(x) were the same for all x from $-\infty$ to $+\infty$ was tested using the Kolmogorov-Smirnov two-sample test (Sidney, 1978): maximum absolute distance (D) between the cumulative distribution functions of the two samples was computed and compared with tabulate values (T). If D was lower than T, then the null hypothesis was accepted and model output was considered statistically similar to field observation.

Statistical validation using regression analysis. Model outputs (dependent variable) were regressed against field data (independent variable) and the properties of the linear model were examined: for each set of results, representing pairs of simulated and field data, the null hypotheses that a (intercept of regression line) is equal to 0 and b (slope of regression line) is equal to 1 were tested using the Student t-test: $t_a = (a-0)/S.E._a$; $t_b = (b-1)/S.E._b$.

If the t-test for a and b was not significant, then both null hypotheses were accepted and the model was considered a statistically accurate simulator of the field data.

If the t-test for a or b was significant, then both null hypotheses were simultaneously tested using the F-test. F-statistic was computed as:

$$F = \{(n-2) \cdot [n \cdot a^2 + 2n \cdot Y \cdot a \cdot (b-1)] + [\Sigma\, Y_i^2 \cdot (b-1)^2]\}/(2n \cdot S^2)$$

where n is the number of observations, a and b are the regression parameters, Y is the mean of model simulations, Y_i are individual model simulations and S is the standard error of the dependent variable (Teng, 1981).

Results and discussion

Epidemics considered for validation covered a wide range of disease severity, from light epidemics, like that which developed at Piacenza in 1994 (maximum of about 1% of rusted area on the flag leaves of ‘Centauro’ and ‘Neodur’), to severe epidemics, like that which

Table 4. Results of validation of RUSTDEP using visual comparison, Kolmogorov-Smirnov test and regression analysis, for the epidemics which occurred on the flag leaf of winter wheat 'Spada' (CV=1) at Gariga (Piacenza), from 1991 to 1994

Year	Visual	D^2	a [3]	$S.E._a$	t_a	b^4	$S.E._b$	t_b	F	R^2
1991	agr[1]	ns[5]	–0.004	0.091	ns	0.95	0.035	ns	–[6]	0.999
1992	agr	ns	–0.03	0.289	ns	0.98	0.174	ns	–	0.941
1993	agr	ns	–0.45	0.401	ns	1.01	0.101	ns	–	0.981
1994	agr	ns	0.44	0.432	ns	0.93	0.079	ns	–	0.986

[1] agr = agreement; [2] D = statistic of the Kolmogorov-Smirnov test; [3] a = intercept; [4] b = slope; [5] ns = not significant; [6] – = test not performed.

Table 5. Results of validation of RUSTDEP using visual comparison, Kolmogorov-Smirnov test and regression analysis, for the epidemics which occurred on the flag leaf of five winter wheat cultivars (Eridano, CV=0.75; Centauro, CV=0.85; Recital and Duilio, CV=0.80; Neodur, CV=0.90) at three locations in 1994

Location and Cultivar	Visual	D^2	a^3	$S.E._a$	t_a	b^4	$S.E._b$	t_b	F	R^2
Gariga (Piacenza)										
Eridano	agr[1]	ns[5]	2.37	1.113	ns	0.73	0.132	ns	–[6]	0.886
Centauro	agr	ns	–0.04	0.042	ns	0.82	0.051	*[7]	**[8]	0.992
Recital	agr	ns	0.33	0.353	ns	1.02	0.162	ns	–	0.930
Duilio	agr	ns	0.05	0.212	ns	1.19	0.172	ns	–	0.960
Neodur	agr	ns	–0.12	0.015	ns	1.15	0.022	*	**	0.999
Guarda Ferrarese (Ferrara)										
Eridano	agr	ns	–1.07	0.401	ns	1.29	0.065	*	ns	0.998
Centauro	agr	ns	0.34	0.655	ns	1.03	0.030	ns	–	0.999
Recital	agr	ns	2.40	2.294	ns	1.06	0.134	ns	–	0.969
Duilio	agr	ns	0.37	0.028	*	1.51	0.021	**	–	0.999
Neodur	agr	ns	–1.73	0.916	ns	1.21	0.132	ns	–	0.988
Ravenna										
Eridano	agr	=[9]	=	=	=	=	=	=	=	=
Centauro	agr	ns	1.07	1.756	ns	1.25	0.157	–	ns	0.984
Recital	agr	ns	–0.22	0.315	ns	0.96	0.021	ns	–	0.999
Duilio	agr	ns	–0.26	0.007	*	0.92	0.002	**	–	0.999
Neodur	agr	ns	–0.12	0.068	ns	1.26	0.062	*	*	0.995

[1] agr = agreement; [2] D = statistic of the Kolmogorov-Smirnov test; [3] a = intercept; [4] b = slope; [5] ns = not significant; [6] – = test not performed; [7] * = significant at $P \leq 0.05$; [8] ** = significant at $P \leq 0.01$; [9] = = statistical analysis not performed because only two actual values were available.

occurred at Ferrara in 1994 (maximum of about 60% on 'Mirtos').

Visual comparison between actual and simulated data shows a constant acceptable agreement (Table 4 to Table 6): in the greater part (80%) of the cases considered, the simulated disease severity constantly fell into the 95% confidence interval for the mean of actual data (Figures 7 and 8). In the remaining cases (20%) simulations went out of the confidence limits in one or two points, usually at a low level of disease severity (Figure 9). This could be due to the fact that disease severity is difficult to assess during the first part of an epidemic because of the effect of foci (Rao et al., 1990) and the high variability in disease incidence point to point in the field (James and Shih, 1973); therefore a number of samples greater than that used to collect the data available for validation should be used to assess rust severity better.

The Kolmogorov-Smirnov test showed that simulations were statistically similar to field observations. In all cases, the maximum distance between the distribution of field data was lower than the critical values, at both 99% and 95% probability levels (Table 4 to Table 6).

Table 6. Results of validation of RUSTDEP using visual comparison, Kolmogorov-Smirnov test and regression analysis, for the epidemics which occurred on the three top leaves of winter wheat 'Mirtos' and 'Oderzo' (CV=0.85) at two locations in 1994

Location and Cultivar	Visual	D^2	a^3	$S.E._a$	t_a	b^4	$S.E._b$	t_b	F	R^2
Ferrara cv. Mirtos										
Flag leaf (LF)	agr[1]	ns[5]	–0.62	0.537	ns	1.26	0.141	ns	–[6]	0.967
LF-1	agr	ns	0.28	0.328	ns	0.92	0.078	ns	–	0.982
LF-2	agr	ns	0.40	1.020	ns	0.98	0.037	ns	–	0.956
Ravenna cv. Oderzo										
Flag leaf (LF)	agr	ns	–0.45	0.368	ns	0.928	0.028	*[7]	ns	0.997
LF-1	agr	ns	0.04	0.041	ns	1.12	0.060	ns	–	0.999
LF-2	agr	=[8]	=	=	=	=	=	=	=	=

[1] agr = agreement; [2] D = statistic of the Kolmogorov-Smirnov test; [3] a = intercept; [4] b = slope; [5] ns = not significant; [6] – = test not performed; [7] * = significant at $P \leq 0.05$; [8] = statistical analysis not performed because only two actual values were available.

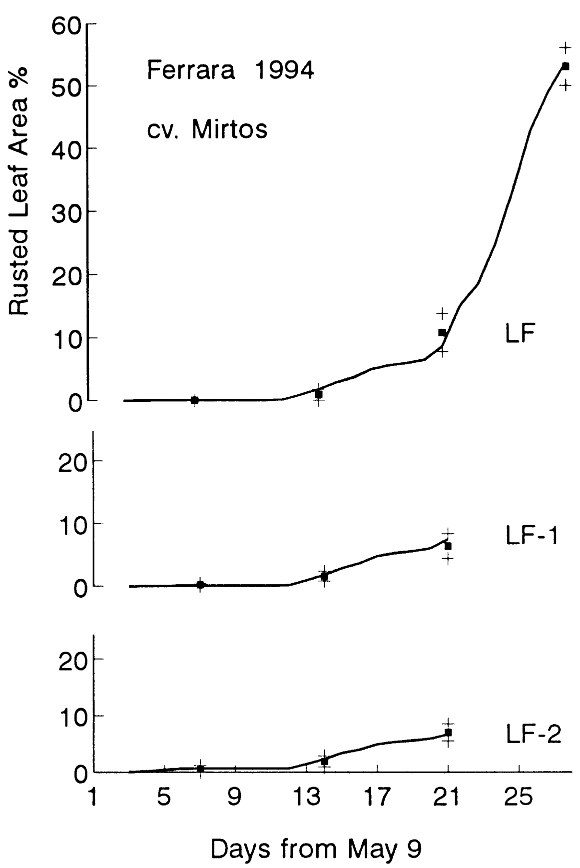

Figure 7. Comparison between brown rust severity on wheat leaves assessed in the field and simulated by RUSTDEP (cv. Mirtos, Ferrara 1994). ■ average of field data; + 95% confidence interval for the average of field data; — average of simulated data.

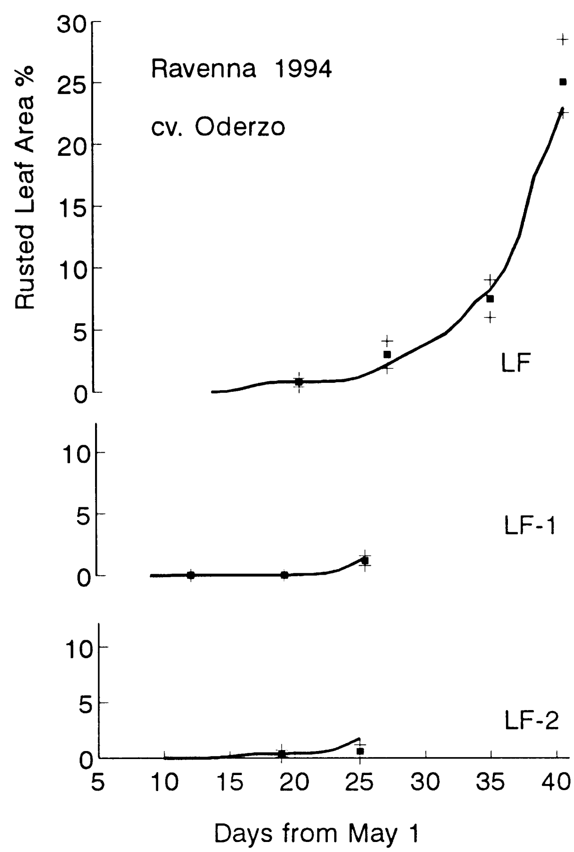

Figure 8. Comparison between brown rust severity on wheat leaves assessed in the field and simulated by RUSTDEP (cv. Oderzo, Ravenna 1994). ■ average of field data; + 95% confidence interval for the average of field data; — average of simulated data.

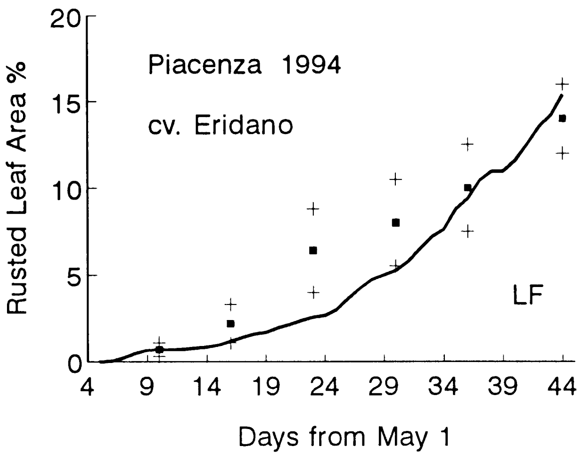

Figure 9. Comparison between brown rust severity on the flag leaf assessed in the field and simulated by RUSTDEP (cv. Eridano, Piacenza 1994). ■ average of field data; + 95% confidence interval for the average of field data; — average of simulated data.

The t-test showed that in fifteen out of twenty-five cases, neither a or b were significantly different from the hypotheses tested: a = 0 and b = 1, which is a perfect accordance between actual and simulated rust severity. The slope was significant in seven cases (five at the 95% probability level and two at the 99%), while the intercept was significantly different from 0 only in two cases (at the 95%). The F-test was significant for 'Centauro' at Piacenza and for 'Neodur' at Piacenza and Ravenna. This result could induce us to reject the hypothesis of concordance between actual and simulated data even though differences between the two sets of values are negligible in practice (Figure 10). Then the statistical test leads to misinterpret results. This is a limit of the test which computes the t-statistic on the basis of standard error for the regression coefficients: when simulated values are very similar to the actual values, the error is low and even a small shifting of the regression line from the line of perfect agreement leads to computation of high and significant t values.

On the basis of results, the model can be considered accurate and robust (Knudsen et al., 1987): it allows to simulate the progress of rust severity well in a wide range of conditions.

Conclusions

The simulation model for leaf rust epidemics considers the relationships between pathogen, host and weather, based on laboratory and field data from literature. The

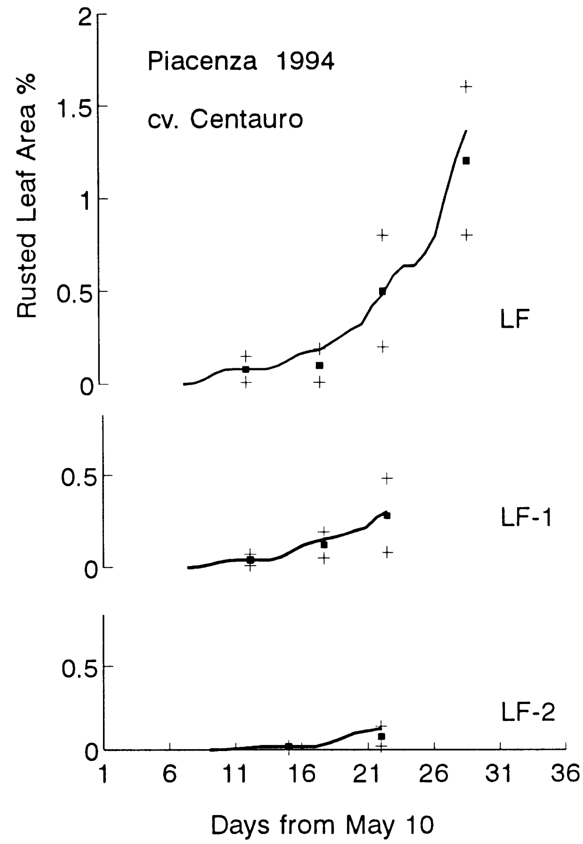

Figure 10. Comparison between brown rust severity on wheat leaves assessed in the field and simulated by RUSTDEP (cv. Centauro, Piacenza 1994). ■ average of field data; + 95% confidence interval for the average of field data; — average of simulated data.

data were transformed into model parameters using curve fitting, stochastic procedures, corrections and empirical assumptions when quantitative data were not available. Because the model makes accurate simulations based on input data not used in model building and representing a wide range of conditions, this approach can be considered successful.

In future works the model could be used to better understand relationships between host, pathogen and weather or to improve the strategies for rust control.

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