
RICE BLAST DISEASE

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22 Understanding and Modeling Leaf Blast Effects on Crop Physiology and Yield

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INTRODUCTION

Blast disease, caused by the Ascomycete *Magnaporthe grisea* (anamorph *Pyricularia grisea*) (Rossman *et al.*, 1990), is generally considered the principal fungal disease of rice (*Oryza sativa*), because of its wide distribution and its destructiveness under favorable conditions (Ou, 1985). Rice is most susceptible to *P. grisea* in the seedbed, and during the tillering and heading stages of the crop (Anderson *et al.*, 1947). During early growth stages lesions are mainly formed on leaves, whereas after heading the pathogen infects the panicle or the neck node. Accordingly, the rice blast pathosystem is divided into two major subsystems: the leaf and the panicle blast pathosystems (Teng *et al.*, 1991). Lesion formation on leaves is followed by premature leaf senescence of infected leaf tissue, especially in case of heavy infections. The highest fraction of leaf area covered by lesions is usually reached around maximum tillering, followed by a gradual decline in disease severity. This gradual decline has been attributed to adult plant resistance (Yeh and Bonman, 1986; Koh *et al.*, 1987; Roumen, 1993). The resistance of newly formed leaf tissue increases with time, and leaves appearing on physiologically older plants obtain this property faster. Consequently, leaf blast is mainly present before flowering.

After heading, *P. grisea* may infect the panicle or the neck node. Panicle blast causes direct yield losses, since filling of the grains on infected panicles is poor at best. For this reason, and because panicle blast occurs late in the season when the farmer has invested all of his production inputs for the crop, panicle blast is the more serious phase of the blast disease. Previous studies to estimate yield

loss due to panicle blast have shown that panicle blast incidence may be linearly related to yield loss, using simple empirical damage functions (Kuribayashi and Ichikawa, 1952; Goto, 1965; Padmanabhan, 1965; Katsube and Koshimizu, 1970; Tsai, 1988; Torres and Teng, 1993). Comparison of the various studies show that the estimated yield loss ranged from 0.4 to 1.0% per percent infected panicles. Ou (1985) ascribed this variation to differences in the time of infection: the earlier the infection, the larger the loss.

Estimation of yield loss due to leaf blast by means of correlation studies has proven more difficult (Ou, 1985). Leaf blast is mainly present before flowering. This period consists of the vegetative and the reproductive phase and is characterized by the formation of source and sink capacity for yield formation. It is only after flowering that the source is used to fill the grains. Leaf blast thus mainly affects grain growth indirectly, through a long-term effect of the disease on crop production. It was the aim of the present study to quantitatively explain the effect of leaf blast on growth and production of a rice crop based on insight into the physiological processes underlying damage (Bastiaans, 1993a).

METHODOLOGY

In the early 1970s Zadoks (1973) reviewed attempts to relate yield loss to disease and categorized them as critical point, multiple point and area under the disease progress curve (AUDPC) models. The models differ in the epidemic characteristics that are used to predict crop loss. Critical point models use one measurement of disease severity, multiple point models use several measurements, and AUDPC models use the integrated level of disease for the entire epidemic. All models are used to derive empirical damage functions by applying regression analysis to field data. The models directly relate a measure of disease intensity to yield or yield loss, without considering the causes of yield reduction (Fig. 22.1, method a). For this reason, the question remains whether empirical damage functions are specific for the conditions (time, location, and cultivar) in which they were derived, or whether they have a more general applicability.

In the 1980s awareness grew that a complete understanding of crop loss would not be possible without considering the physiological response of crops to disease (Gaunt, 1978; Madden, 1983). Therefore the crop, rather than the disease, was used as the basis for the determination of crop loss (Fig. 22.1, method b). Several papers appeared in which yield of infected crops was directly related to the green leaf area at a single growth stage (Lim and Gaunt, 1986), to green leaf area duration (Rotem *et al.*, 1983) or to the cumulative amount of radiation intercepted by the green leaf area of the crop (Haverkort and Bicomumpaka, 1986; Waggoner and Berger, 1987). Implicitly this type of relationship assumes that the effect of a disease on crop production is limited to a reduction in photosynthetic leaf area. For some pathosystems, like *Phytophthora infestans* in potato, this assumption has proven valid (van Oijen, 1990). However, apart from a reduction in the amount of intercepted radiation, diseases may also alter the utilization efficiency of intercepted radiation for crop growth (Johnson, 1987). In these situations the relation between yield and intercepted radiation becomes more complex.

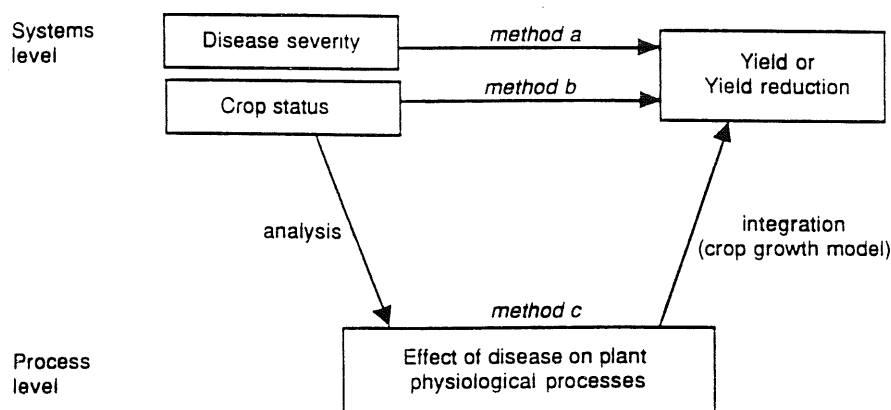


Fig. 22.1. Schematic representation of three methods for determining yield loss due to a foliar pathogen. With the third method research is conducted at two levels of integration: the process and the systems level. Mechanistic crop growth models are required to bridge the gap between both integration levels.

Another methodology in line with a more crop-oriented approach was developed by Rabbinge and Rijdsdijk (1981). In their approach, attention is first concentrated on the whole plant level, being the next lower level of integration (Fig. 22.1, method c). At this level the various ways through which a disease interferes with basic plant growth processes (photosynthesis, respiration) or existing biomass (leaf senescence) are identified (Boote *et al.*, 1983). Research is conducted to determine dose-response relationships between the amount of disease and the extent to which a process is affected. Subsequently, the relationships are introduced in a mechanistic crop growth model to determine the consequences of the disease effects for crop growth and production. The model enables the determination of yield reduction due to various epidemics under variable environmental conditions, therewith meeting the limitations of empirical damage functions. It is this approach that was used in the present study on yield reduction in rice due to leaf blast.

EFFECT OF LEAF BLAST ON THE PHYSIOLOGY OF INDIVIDUAL LEAVES

The main function of leaves is the absorption of light and the conversion of light energy into carbohydrates through photosynthesis. Foliar diseases reduce the photosynthetic rate of leaves, since lesion formation reduces the amount of photosynthetically active leaf tissue. For some pathosystems this is the only mechanism through which the pathogen reduces the leaf photosynthetic rate of the host (*Puccinia recondita* in wheat, Spitters *et al.*, 1990; and *Phytophthora infestans* on potato, van Oijen, 1990). For other pathosystems the leaf photosynthetic rate is further reduced through an effect of the pathogen on photosynthesis of the green leaf tissue surrounding the lesions (*Erysiphe graminis* on wheat, Rabbinge *et al.*, 1985; and *Alternaria alternata* on cotton, Ephrath *et al.*,

1989). As far as the effect of *P. grisea* on leaf photosynthetic rate of rice is concerned, no direct observations have been reported. However, an indirect observation of Goto (1965), who reported that yield loss due to leaf blast exceeded yield loss caused by cutting off of a percentage of leaf area equal to the percentage leaf covered by blast, indicated that leaf blast influences the host plant more than just through a loss in leaf area.

A second effect on the physiology of leaves after infection by a pathogen is an enhanced rate of respiration. This increase can be attributed to the combination of fungal respiration and an increased respiration of the host. Toyoda and Suzuki (1957) reported an increase in the respiration of rice leaves after infection with *P. grisea*. The increase was connected with a shift from the glycolytic to the pentose phosphate pathway, a phenomenon generally observed in plants infected by biotrophic pathogens (Shaw and Samborski, 1957; Smedegaard-Petersen, 1984). In contrast, Burrell and Rees (1974) did not detect an increased respiration of rice leaves after infection by *P. grisea*.

A first step in the present analysis was the quantification of the effect of *P. grisea* on photosynthesis and respiration, by measuring the CO₂ exchange rate of individual rice leaves. The experimental data were used to derive relations between leaf blast severity and photosynthesis and respiration.

Leaf photosynthetic rate

Photosynthesis is the use of energy from light for the production of glucose from water and carbon dioxide, and is generally measured as the rate of CO₂ uptake. In Fig. 22.2 the dependence of leaf CO₂ assimilation on absorbed photosynthetically active radiation (PAR) is given. This photosynthesis light response curve is characterized by the assimilation rate at light saturation (P_{\max} ; $\mu\text{g CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and the initial slope or efficiency at low light intensity (ϵ ; $\mu\text{g CO}_2 \text{ J}^{-1}$).

The effect of leaf blast on leaf photosynthetic rate at high light intensities (P_{\max}) was measured and related to disease severity (the fraction of leaf area covered by lesions). Measurements were conducted in a field and a greenhouse experiment. The results indicated that the working hypothesis (leaf blast reduces leaf photosynthetic rate through a reduction in green leaf area only) was not valid (Fig. 22.3). The reduction in leaf photosynthetic rate of infected leaves, expressed as a fraction of leaf photosynthetic rate of healthy leaves, surpassed disease severity. The disease thus not only reduced the amount of green leaf area, it also reduced the photosynthetic activity of green leaf tissue surrounding the lesions. This observation resulted in the virtual lesion concept (Bastiaans, 1991). A virtual lesion consists of a visual lesion and a surrounding halo, in which the photosynthetic activity is zero (Fig. 22.3). The size of the halo is chosen such that the reduction in leaf photosynthetic rate is fully accounted for. Parameter β expresses the ratio between virtual and visual lesion area and characterizes the effect of the disease on leaf photosynthetic rate. The parameter can be used to relate the photosynthetic rate of diseased leaf tissue (P_x) to disease severity (x):

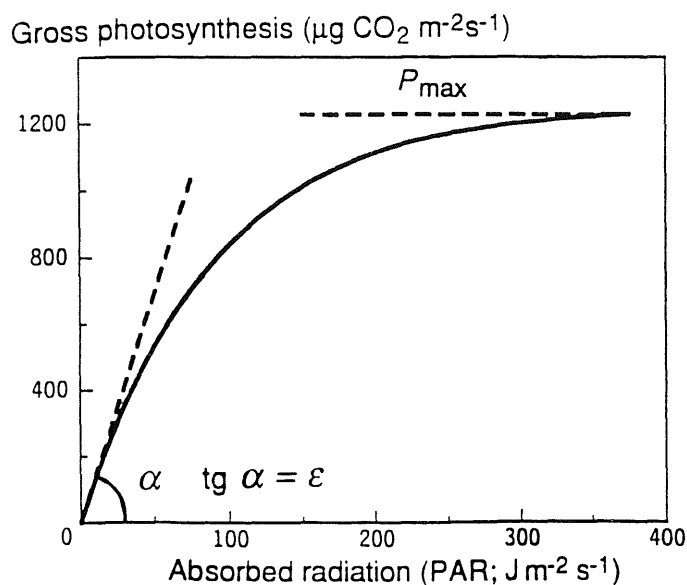


Fig. 22.2. A typical CO_2 assimilation–light response curve for an individual leaf. The response curve is characterized by the initial light use efficiency (ϵ ; $\mu\text{g CO}_2 \text{ J}^{-1}$) and the assimilation rate at light saturation (P_{max} ; $\mu\text{g CO}_2 \text{ m}^{-2} \text{ s}^{-1}$).

$$P_x = P_0(1 - x)^\beta \quad (1)$$

in which P_0 is the photosynthetic rate of comparable healthy leaf tissue. The reduction in P_{max} and ϵ were characterized by β -values of 3.7 ± 0.6 and 3.0 ± 0.7 , respectively (Bastiaans, 1991, 1993b). This demonstrates that the effect of leaf blast on photosynthetic rate of rice leaves is three to four times as high as expected on the basis of visible lesion size.

Differences in β among rice cultivars would imply genotypic differences in tolerance, which can be defined as the ability of the host to endure the presence of the pathogen with reduced disease symptoms and/or damage (Parlevliet, 1979). To investigate the presence of genetic variation in β , three cultivars with a susceptible infection type were selected. The cultivars differed in relative infection efficiency (RIE), a major component of partial resistance to leaf blast in rice (Toriyama, 1975; Ahn and Ou, 1982; Yeh and Bonman, 1986; Roumen, 1993). Photosynthesis measurements did not indicate the presence of genetic variation in β (Bastiaans and Roumen, 1993). Therefore it was concluded that β is not a suitable selection criterion in breeding rice for tolerance to leaf blast. This conclusion is emphasized in Fig. 22.4, where the impact of the observed genetic variation in β and the impact of the genetic variation in RIE on leaf photosynthetic rate are compared.

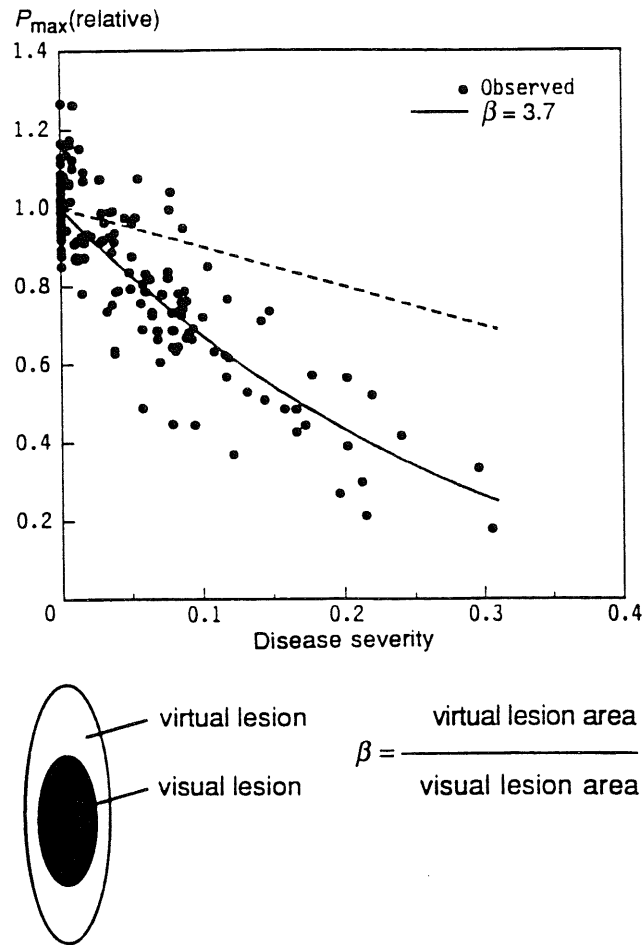


Fig. 22.3. The assimilation rate at light saturation (P_{max} ; on a relative scale) of leaves infected by *Pyricularia grisea* in relation to disease severity as measured in a greenhouse experiment. The dotted line represents the working hypothesis: the effect of leaf blast is limited to a reduction in green leaf tissue. The solid line gives the best fit using equation 1. This equation is derived from the virtual lesion concept (see text). Parameter β expresses the ratio between virtual and visual lesion areas.

Leaf dark respiration

The effect of the disease on leaf dark respiration (R_d ; $\mu\text{g CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) was measured in two greenhouse experiments. Dark respiration was defined as the CO_2 production measured after a dark period of 25 min. Both experiments indicated clearly that the rate of dark respiration increased with increasing disease severity (Fig. 22.5). Dark respiration was related to disease severity by:

$$R_x = R_0(1 - x) + \rho R_0 x \quad (2)$$

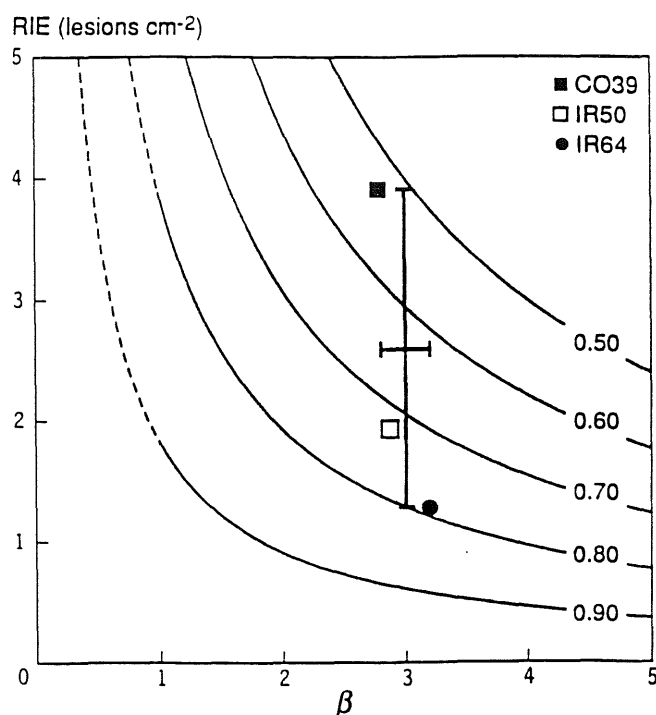


Fig. 22.4. Relative infection efficiency (RIE) and parameter β as measured for three rice cultivars after inoculation with *Pyricularia grisea*, and the implications for relative leaf photosynthetic rate (P_x/P_0). Curves are isolines referring to combinations of RIE and β with an equal relative net leaf photosynthetic rate (Bastiaans and Roumen, 1993; reprinted by permission of Kluwer Academic Publishers).

in which R_0 and R_x are the rate of dark respiration of healthy and diseased leaf tissue, respectively. This function is based on the observation that in general a respiratory increase is restricted to the area of the lesion and its near surrounding area (Samborski and Shaw, 1956; Bushnell and Allen, 1962). Here it is assumed that an increase is restricted to the visible lesion area. The parameter ρ expresses the ratio between the respiration of a lesion and that of an identical area of healthy leaf tissue. The increase in dark respiration was characterized by a ρ -value of 4.5 ± 1.3 (Bastiaans, 1993b).

INTEGRATION STEP 1: FROM INDIVIDUAL LEAVES TO A RICE CANOPY

The importance of the measured effects of leaf blast on leaf physiology, as determined by their consequences for crop production and yield, is difficult to assess. Effects on leaf physiology and effects on grain yield represent two different levels of aggregation, and are therefore difficult to relate. Mechanistic crop growth models can help to bridge the gap between these two aggregation levels. The effects of the disease on basic plant growth processes are introduced in a crop

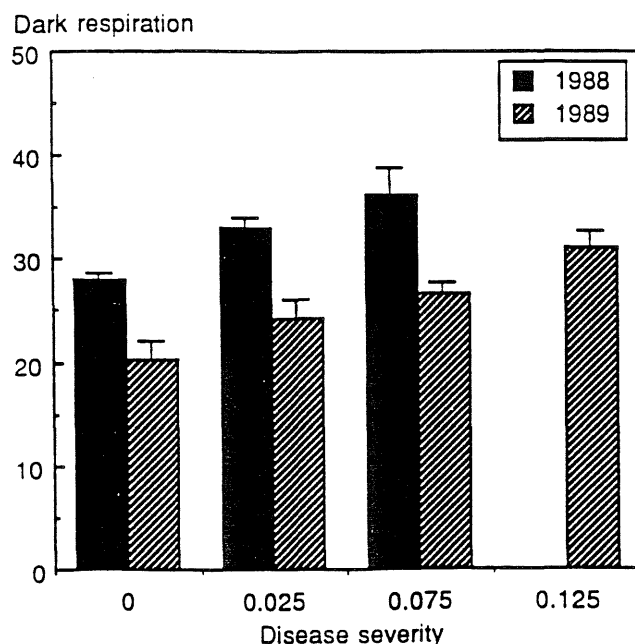


Fig. 22.5. Dark respiration (R_d ; $\mu\text{g CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) of rice leaves infected by *Pyricularia grisea* in relation to disease severity, as measured in two greenhouse experiments. Vertical bars represent standard errors of the mean.

growth model, in order to estimate the effect on yield (Rabbinge and Rijsdijk, 1981; Boote *et al.*, 1983; Rabbinge and Bastiaans, 1989). Kropff (1989), in a study on the effects of SO_2 on production of a broad bean crop (*Vicia faba*), refined the described approach. In between the quantification of effects of SO_2 on leaf physiology and the use of the crop growth model for the estimation of effects on yield, he introduced a validation of the assimilation and respiration routines of the model. Canopy photosynthesis of control and fumigated crops was measured in the field and used to evaluate the performance of the specified routines. The validated routines were introduced later into a crop growth model to analyze and predict effects on crop yield.

A similar procedure was used in the present study. The experimentally obtained relations between leaf blast severity and the assimilation rate at light saturation (P_{max}), the initial light use efficiency (ϵ) and the rate of dark respiration (R_d) of rice leaves were introduced into a model to simulate the effects of leaf blast on canopy photosynthesis. Photosynthetic rate of rice canopies infected with *P. grisea* was determined in a field experiment, to evaluate the performance of this model. In this way the first step in the integration from effects of leaf blast on individual leaves to effects of the disease on grain yield was made.

Table 22.1. Characteristics of rice canopies at the time of photosynthesis measurement and measured canopy CO₂ exchange rate (CER) in a control plot (plot A) and in two plots inoculated with *P. grisea* at mid and early tillering (plots B and C, respectively).

	Plot A	Plot B	Plot C
Leaf area index	4.49a ^a	4.80a	4.66a
Disease severity ^b	0.003a	0.046b	0.044b
Fraction dead leaf area	0.01a	0.03b	0.15c
CER ($\mu\text{g CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	1432.00a	1219.00b	953.00c

^a Means in the same row followed by the same letter are not significantly different according to *t*-test ($P < 0.05$).

^b Fraction of green (healthy + diseased) leaf area covered by lesions.

Experimental determination of canopy photosynthesis

Canopy CO₂ exchange rate (CER; $\mu\text{g CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) was measured for a rice crop at maximum tillering in three different plots. The control crop (plot A) was slightly infected with *P. grisea*, due to influx of spores from neighboring plots. A small amount of dead leaf tissue, found in the lower part of the canopy, consisted of naturally senescing leaves (Table 22.1). The other two plots were inoculated with *P. grisea* at mid (plot B) and early tillering (plot C), resulting in a higher disease severity and a higher fraction of dead leaf area at the time of measurement. The amount of dead leaf area was moderate in plot B and high in plot C, reflecting the differences in time of inoculation. Significant differences between the CER of the three plots were observed. Compared to the control plot the CERs of plot B and C were reduced by 15% and 33%, respectively.

Modeling the effect of leaf blast on canopy photosynthesis

More interesting than the observed differences in CER was whether the reduction in canopy photosynthesis could be explained by the adverse effects of leaf blast on photosynthesis and respiration of individual leaves and by the presence of dead leaf tissue. For that purpose a model for the calculation of instantaneous rates of canopy photosynthesis was constructed. The model comprised routines for the calculation of photosynthesis and respiration of an elementary model for crop growth (MACROS-L1D; Penning de Vries *et al.*, 1989), and routines to generate diurnal trends of radiation and temperature on the basis of daily weather data. The model was run with a time interval of 0.25 h. A schematic representation of the model is given in Fig. 22.6. A detailed description of the model is given by Bastiaans and Kropff (1993).

To account for the effect of leaf blast on photosynthesis and respiration, disease severity and the fraction of dead leaf area were introduced into the model. Photosynthesis–light response characteristics of green leaf tissue (healthy + diseased leaves) were related to observed disease severity, using parameter β .

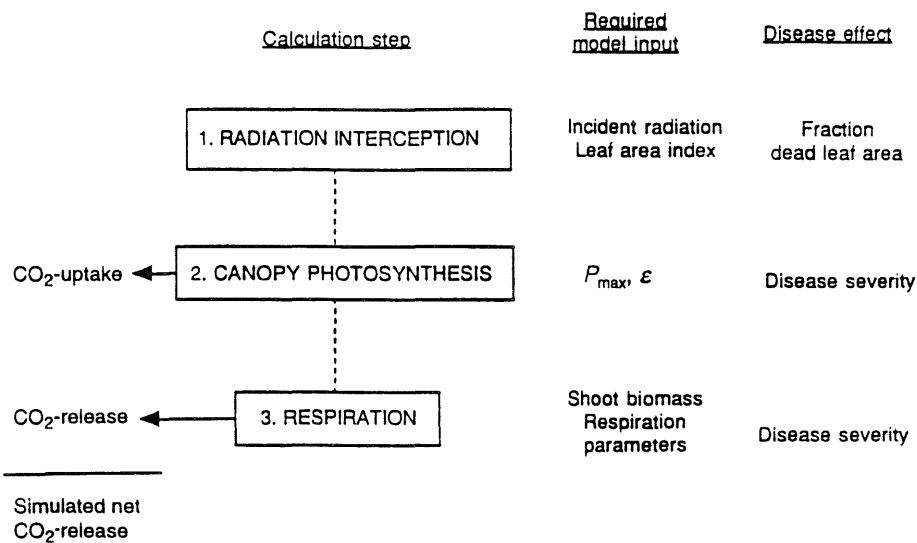


Fig. 22.6. Simplified representation of the most important calculation steps and typical input data for a model on canopy CO₂ exchange rate (CER). Special attention is given to the effect of leaf blast on CER.

Dead leaves do not contribute to photosynthesis, but light interception by this part of the canopy was accounted for. Optical characteristics of diseased and dead leaf tissue were assumed to be identical to the characteristics of healthy leaf tissue.

The effect of leaf blast on respiration was introduced as an increased rate of leaf maintenance respiration. Implicitly, this assumes that assimilate requirement of processes related to the presence of the disease have priority over growth. The increase in respiration was related to disease severity and characterized by parameter ρ . Maintenance requirement of dead leaf tissue is nil and was therefore not considered.

Canopy CO₂ exchange rate for control and inoculated canopies was accurately simulated with the model (Fig. 22.7). The observed reduction in CER can thus be explained by the adverse effect of blast lesions on leaf photosynthesis and respiration and by the existence of dead leaf tissue, resulting from disease-induced senescence. In Table 22.2 a more detailed analysis of the reduction in CER is given. The effects of blast lesions and dead leaf tissue were separated, and further dissected. Lesions cause a decrease in green leaf tissue, a reduction in photosynthetic rate of the remaining green leaf tissue, and an increased respiration. In successive runs these damage mechanisms were removed one after the other, and the subsequent increase in CER was defined as the reduction due to the newly removed damage mechanism. Clearly, the reduction in photosynthetic rate of the remaining green leaf tissue was the most important effect of blast lesions, whereas the increased respiration contributed only marginally to the overall effect.

Dead leaf tissue causes a reduction in photosynthetically active leaf tissue and reduces light intensity in lower leaf layers by light interception (shading). The

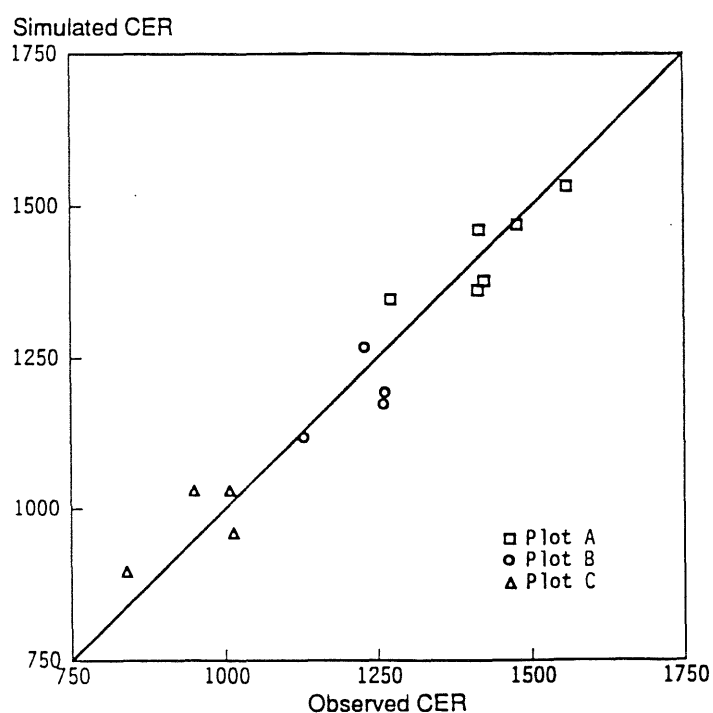


Fig. 22.7. Comparison of observed and simulated canopy CO_2 exchange rate (CER; $\mu\text{g CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) (Bastiaans and Kropff, 1993).

Table 22.2. Contribution of blast lesions and dead leaf tissue to the overall reduction in canopy CO_2 exchange rate (CER; $\mu\text{g CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) of rice crops inoculated with *Pyricularia grisea*. The contribution of the identified damage mechanisms related to blast lesions and dead leaf tissue are specified and expressed as a fraction of the total reduction due to blast lesions and dead leaf tissue, respectively.

	Plot B ^a	Plot C ^a
Total reduction in CER	213 (100%)	479 (100%)
Reduction related to blast lesions	173 (81%)	163 (34%)
Contribution of identified damage mechanisms		
Decrease in green leaf tissue	54 (0.31)	49 (0.30)
Reduction in leaf photosynthetic rate	109 (0.63)	104 (0.64)
Increase in respiration	10 (0.06)	10 (0.06)
Reduction related to dead leaf tissue	40 (19%)	316 (66%)
Contribution of identified damage mechanisms		
Decrease in green leaf tissue	13 (0.32)	95 (0.30)
Shading	27 (0.68)	221 (0.70)

^a Plot B inoculated at mid tillering and plot C inoculated at early tillering stage.

increase in simulated CER after removal of dead leaf tissue corresponds to the reduction due to shading. The further increase in simulated CER after replacing dead leaf tissue by an identical area of healthy leaf tissue, equals the reduction due to the reduction in photosynthetically active leaf tissue. The analysis showed that shading accounted for two-thirds of the overall reduction due to dead leaf tissue. The importance of this mechanism is determined by the position of dead leaf tissue in the canopy. In the case of natural leaf senescence dead leaf tissue is mainly found in lower leaf layers, and then shading is not an important mechanism.

The three plots in the experiment represent rice crops at various stages of infection, offering the opportunity to theorize about the way a reduction in CER evolves after establishment of lesions of *P. grisea*. The most prominent effect of the lesions is an inhibitory effect on photosynthesis of the surrounding green leaf tissue, which causes a reduced utilization efficiency of intercepted radiation. Newly emerging leaves become infected, whereas earlier infected leaves are subject to an accelerated senescence. As a result, the fraction of diseased leaf area remains more or less constant, whereas the fraction of dead leaf area increases. Consequently, the reduction in CER will increase as a result of an increased reduction in the amount of radiation intercepted by green foliage. The difference in CER of plots B and C is thus mainly due to a difference in intercepted radiation, and reflects the difference in fraction of dead leaf area that existed due to a difference in onset of the epidemic. This analysis suggests that in the long run crop production suffers more from the accelerated senescence of infected leaf tissue than from the initial disturbances in leaf physiology.

INTEGRATION STEP 2: FROM A SINGLE DEVELOPMENT STAGE TO A GROWING SEASON

Determining the effect of leaf blast on canopy photosynthesis represents just an intermediate step in the extrapolation of the effects of leaf blast on leaf physiology to effects of the disease on crop production. Since the effect of the disease on canopy photosynthesis is well understood, a second integration step can be made. The effect of the disease on the performance of a canopy is integrated over an entire growing season, to determine the effect on yield. Similar to the previous integration step from individual leaves to a rice canopy, this second integration step was realized by combining experimental research and modeling.

A special feature of leaf blast is that the disease is mainly present before flowering. In the development of a rice crop, flowering marks an important transition. The period prior to flowering is characterized by the construction of a canopy, and the formation of storage organs (grains). It is in this development phase that leaf blast severity is highest, and will have a direct effect on crop growth rate. After flowering, when leaf blast severity has generally dropped to a low level, the canopy is used to fill the grains and grain yield is determined. Leaf blast thus mainly affects grain yield indirectly, through a long-term effect of the disease on crop production. Experimental data were used to determine whether the long-term effect of the disease on crop production is passed on through an effect on the source (carbon or nitrogen economy) or through an effect on the sink.

Identifying the mechanism of yield reduction

The effect of leaf blast on crop production was studied in an experimental field at the lowland research site of the International Rice Research Institute (IRRI), Los Baños, The Philippines. A randomized complete block design with three treatments in five replicates was used (plot size: 12 × 3.6 m). One treatment was used as the control (treatment A), while the other two treatments were inoculated with *P. grisea* during mid (treatment B) and early tillering (treatment C), respectively. From maximum tillering on, fungicides were used to stop the development of the disease, since an undisturbed further development would have destroyed the crop. Neck blast infections were prevented in all treatments by applying fungicides at booting and heading. Disease development and the effect of the disease on crop growth was studied through periodic harvesting (Fig. 22.8). Further experimental details are given by Bastiaans (1993c).

The first aim of this experiment was to identify the mechanism through which the initial reduction in crop growth rate during the presence of the disease affects the formation of grain yield later on. The observations on leaf and canopy photosynthesis demonstrated that leaf blast primarily reduces carbohydrate production. Associated with this reduction is a reduction in crop growth and leaf area formation. The positive feedback between crop growth, leaf area formation and radiation interception further enhances the negative effect of the disease on crop growth (Blackman, 1919). In the case of heavy infestations of leaf blast, the feedback mechanism is further enhanced by an accelerated senescence of infested leaf tissue. Ultimately, all processes result in a reduced amount of green leaf area during ripening, and accordingly carbohydrate supply during grain filling is reduced. This is the most obvious mechanism through which leaf blast, present before flowering, reduces grain yield formation. Lim and Gaunt (1986) reported such a mechanism of yield reduction in the pathosystem barley-mildew in case of early epidemics. The observations on leaf area index (LAI) confirm that during ripening the LAI of the inoculated crops was clearly smaller than the LAI of the control crop (Fig. 22.8A).

The utilization efficiency of intercepted radiation during grain filling is another important determinant of carbohydrate supply in this period. In rice, as in other crop species, this efficiency is largely determined by the N content of the leaves, since the maximum rate of leaf photosynthesis is almost proportional to the fraction of N in leaves (Cook and Evans, 1983). Uptake of N after flowering is generally low and N content of leaf tissue during grain filling is therefore mainly determined by N uptake before flowering. Moreover, N redistribution from leaf blades contributes considerably to N supply during grain filling. A reduced amount of accumulated N at flowering may thus eventually limit yield. This is the second mechanism through which leaf blast may have a long-term effect on yield.

The results of the experiment demonstrate that leaf blast reduces the N uptake of the crop (Table 22.3). This reduction resulted from differences in N uptake before flowering, since total shoot N during ripening was fairly constant in both healthy and inoculated crops. Despite the reduction in N uptake in the inoculated crops, the shoot N content at flowering and maturity was identical or

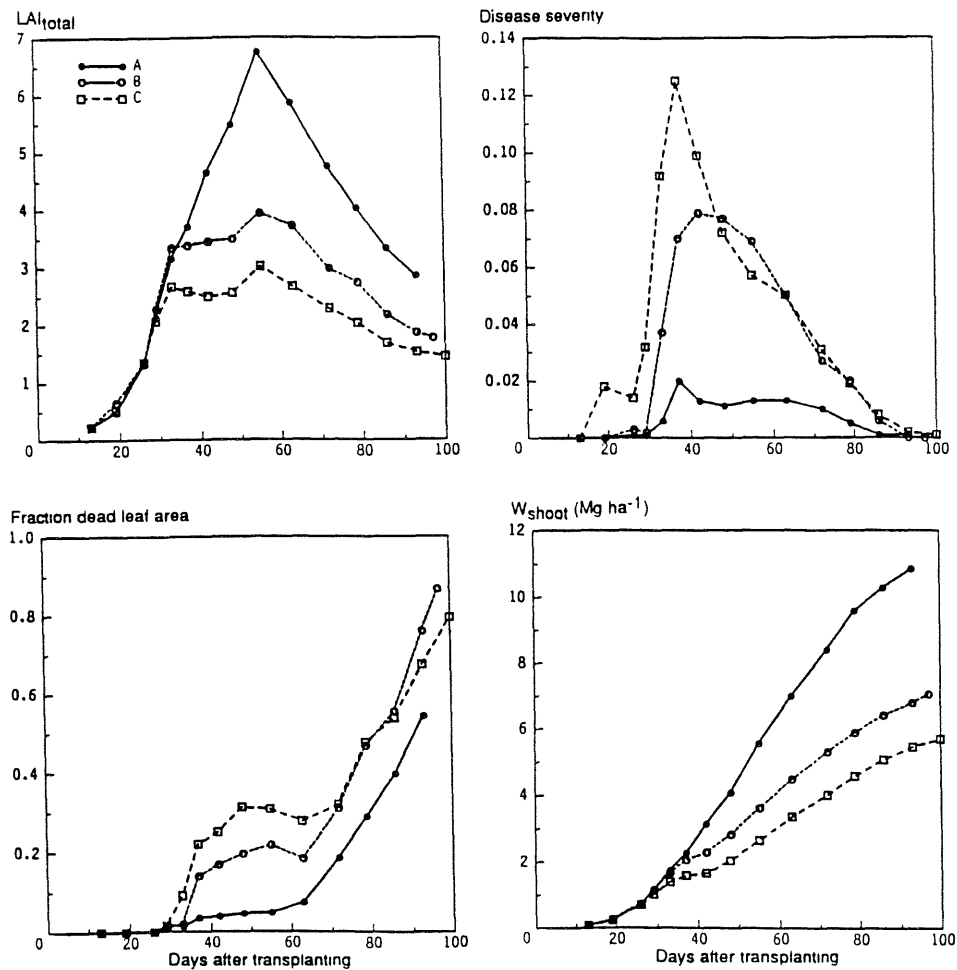


Fig. 22.8. Time course of total leaf area ($\text{LAI}_{\text{total}}$; ha ha^{-1}), disease severity, fraction of dead leaf area and shoot dry weight (W_{shoot} ; Mg ha^{-1}) of rice in a control crop (treatment A) and in crops inoculated with *Pyricularia grisea* (treatments B and C) (Bastiaans, 1993c).

higher and the same was found for the N content of individual shoot organs. This indicates that the reduced N uptake in the inoculated crops before flowering was not responsible for the yield reduction observed.

A reduced sink formation is the third mechanism through which leaf blast may eventually reduce grain yield. Tiller number, floret number and spikelet number are all determined before flowering. Their numbers are regulated through the carbohydrate supply of the canopy in specific initiation periods (Penning de Vries *et al.*, 1989). Moreover, 1000 grain weight of rice is also determined before flowering, since this characteristic is primarily controlled by the size of the hulls. The product of spikelet number and 1000 grain weight of rice is referred to as maximum eventual yield (Matsushima, 1970). If leaf blast reduces

Table 22.3. Nitrogen (N) uptake and nitrogen content of the shoot and relevant shoot organs of rice at flowering and maturity, as observed in a control crop (treatment A) and in crops inoculated with *Pyricularia grisea* at mid and early tillering (treatments B and C, respectively).

	Treatment A	Treatment B	Treatment C
Total N uptake (kg N ha ⁻¹)	122.0a	88.0b	70.0b
N content (mg g ⁻¹) at flowering			
Total shoot	17.5a ^a	18.7a	18.9a
Green leaf tissue	33.4a	36.4b	38.5c
Stem tissue	11.2a	13.7b	14.4b
N content (mg g ⁻¹) at maturity			
Total shoot	11.2a	12.1b	12.2b
Panicle	12.9a	13.7b	13.6b

^a Means in the same row followed by the same letter are not significantly different according to *t*-test ($P < 0.05$).

Table 22.4. Grain yield and yield components of rice cultivar IR50 as observed in a control crop (treatment A) and in crops inoculated with *Pyricularia grisea* at mid and early tillering (treatments B and C, respectively).

	Treatment A	Treatment B	Treatment C
Panicle number (m ⁻²)	581.0a ^a	605.0b	623.0c
Spikelets per panicle	65.0a	45.0b	37.0c
1000 grain weight (g) ^b	21.1a	20.1b	19.7b
Maximum eventual yield (Mg ha ⁻¹) ^b	7.9a	5.4b	4.5c
Fraction filled grains	0.85a	0.80b	0.78b
Actual grain yield (Mg ha ⁻¹) ^b	6.7a	4.3b	3.5c

^a Means in the same row followed by the same letter are not significantly different according to *t*-test ($P < 0.05$).

^b Rough rice at 140 g moisture kg⁻¹.

maximum eventual yield more than proportionally the reduction in grain yield may be sink determined.

Yield component analysis demonstrated that leaf blast reduced maximum eventual yield through a reduction in spikelet number and a reduction in 1000 grain weight (Table 22.4). More important, however, was the observation that in the inoculated treatments the relative reduction in actual yield surpassed the relative reduction in maximum eventual yield. This is reflected in a reduced fraction of filled grains of the inoculated crops and demonstrates that the reduction in grain yield is exclusively source determined. The observations are in line with data on yield reduction reported by Goto (1965), who also observed reductions in spikelet number, 1000 grain weight and fraction filled grains due to leaf blast. Based on this analysis it is concluded that the long-term effect of leaf blast on crop production is solely passed on through an effect on carbon economy. Therefore the model analysis will be restricted to this aspect of yield formation.

Table 22.5. Cumulative radiation interception (PARCUM), radiation use efficiency (RUE) and harvest index (HI) of rice in a control crop (treatment A) and crops inoculated with *Pyricularia grisea* at mid and early tillering (treatments B and C, respectively).

	Treatment A	Treatment B	Treatment C
PARCUM ((MJ PAR)m ⁻²)	403.0a	315.0b	260.0c
RUE (g dry matter (MJ PAR) ⁻¹)	2.69a	2.16b	2.10b
Total shoot dry weight (g m ⁻²)	1090.0a	710.0b	570.0c
HI	0.53a	0.52a	0.53a
Grain yield (g m ⁻²) ^b	670.0a	430.0b	350.0c

^a Means in the same row followed by the same letter are not significantly different according to *t*-test ($P < 0.05$).

^b Rough rice at 140 g moisture kg⁻¹.

Modeling the effect of leaf blast on crop production

A simple model

Crop productivity can be analyzed in terms of solar radiation interception by green leaf area (PARCUM; MJ m⁻²) and radiation use efficiency (RUE; g dry matter MJ⁻¹) (Monteith, 1977). Accordingly, Johnson (1987) distinguished two broad categories of effects of pests and diseases on crop growth: effects on radiation interception and effects on radiation use efficiency. Multiplication of total shoot dry matter and harvest index (HI) yields grain yield. This simple model was used to make a first analysis of the effects of leaf blast on crop production (Bastiaans, 1993d):

$$\begin{aligned} \text{Yield} &= \text{Radiation Interception} \times \text{Radiation Use Efficiency} \times \text{Harvest Index} \\ &= \text{PARCUM} \quad \times \quad \text{RUE} \quad \times \quad \text{HI} \\ [\text{g m}^{-2}] &= [(\text{MJ PAR}) \text{ m}^{-2}] \quad \times \quad [\text{g} (\text{MJ PAR})^{-1}] \quad \times \quad [-] \end{aligned}$$

Radiation interception of photosynthetically active radiation by green leaf foliage was calculated on a daily basis for every plot (RI; MJ m⁻² d⁻¹), using a model that consisted of the radiation routines of an elementary model of crop growth. Leaf area index, disease severity and the fraction of dead leaf area were input to this model. Summation of intercepted radiation over the growing season resulted in the cumulative radiation interception (PARCUM; MJ m⁻²). Radiation use efficiency was calculated by dividing the observed total shoot dry matter by PARCUM. Harvest index was determined at maturity.

The analysis with the RI × RUE model demonstrates that leaf blast in rice is a pathosystem in which the pathogen reduces the dry matter production of the crop through a reduction in cumulative radiation interception and a reduction in radiation use efficiency (Table 22.5). No significant difference was present between the RUE of the inoculated crops (treatments B and C). Therefore, the difference in dry matter production between B and C resulted mainly from a

difference in cumulative radiation interception. After initiation of the disease, lesion coverage and disease induced senescence caused a direct reduction of RI. An indirect reduction of RI as a result of leaf blast was caused by a decline in new leaf area formation. This decline resulted from a reduced crop growth rate, which was caused by previous reductions of leaf blast in RI and RUE. The importance of this mechanism depends strongly on the development stage of the crop, since the underlying positive feedback between crop growth, leaf area formation and radiation interception is strongest during early growth stages (Blackman, 1919). Previously, Lim and Gaunt (1986) and van Oijen (1991) pointed at the importance of the available leaf area at initiation of a disease for leaf area duration and cumulative radiation interception. It can be concluded that the difference in disease severity together with the difference in LAI at the initiation of leaf blast, caused by the difference in inoculation date, are the most prominent factors responsible for the observed differences in total dry matter production of the inoculated treatments in this experiment.

Harvest index was not affected in this experiment. This is probably related to the timing of the inoculations. The crop was only inoculated during early development stages. A simulation study demonstrated that leaf blast epidemics late in the reproductive phase are expected to cause a clear reduction in harvest index (Bastiaans and Teng, 1994).

A mechanistic crop growth model

A mechanistic model of crop growth (MACROS-L1D; Penning de Vries *et al.*, 1989) was used to analyze the causes of the reduction in the utilization efficiency of intercepted radiation (Fig. 22.9). The effects of leaf blast on photosynthesis and respiration were introduced into this model in an identical way as in the model on canopy photosynthesis. To account for the effect of leaf blast on photosynthesis and respiration, disease severity and the fraction of dead leaf area were introduced in the model. Similarly, the measured LAI was input to the model. The model was initialized with dry weights of leaves and stems of the first harvest and run until final harvest. Model performance was evaluated by comparing the simulated and observed shoot dry weight over time (Bastiaans, 1993d).

Simulation of dry matter production of the control crop resulted in a good agreement with the observed dry matter production (Fig. 22.10). This demonstrates the thoroughness of the basic crop growth model and indicates that any dissimilarity between simulated and observed shoot dry weight of the inoculated crops is likely to be due to an error in the simulation of leaf blast effects.

Total dry matter production of the inoculated crops was overestimated (Fig. 22.10). The overestimation appeared during the first weeks after the onset of the disease. After that time the difference between simulated and observed dry weight stabilized at approximately 550 kg ha^{-1} , in both treatments. The overestimation indicates that during the establishment of the disease the effects of leaf blast on leaf photosynthetic rate and respiration were inadequate to explain fully the reduction in crop growth rate. The stabilization of the overestimation in the consecutive period till maturity indicates that later on the two effects gave a sufficient explanation of the reduction in RUE.

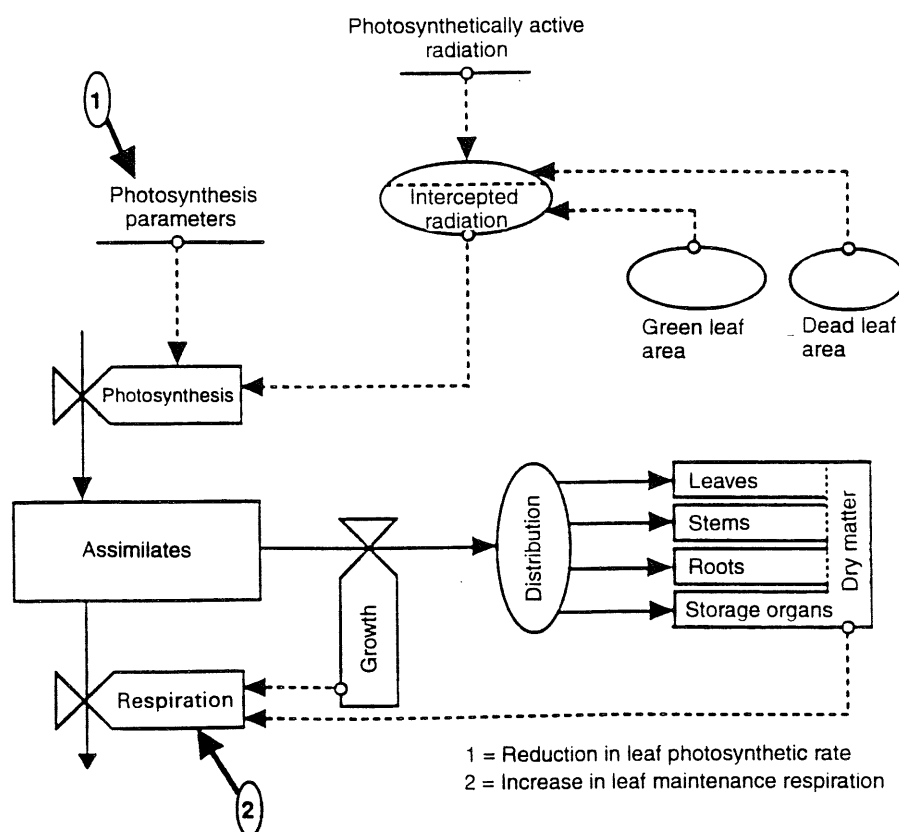


Fig. 22.9. Diagram illustrating schematically the calculation procedure of daily crop growth rate in model MACROS-L1D, and the various ways through which leaf blast affects crop growth rate. Leaf area (green + dead) is introduced as a forcing function. Quantities are shown in boxes, processes in valve symbols, flow of material by lines and flow of information by dotted lines.

The utilization of intercepted radiation for dry matter production can be subdivided into three processes: CO_2 assimilation, allocation of assimilates and utilization of assimilates for dry matter production. The canopy photosynthesis measurements demonstrated that the effects of leaf blast on leaf photosynthetic rate and respiration satisfactorily explained the effect of leaf blast on CO_2 assimilation. The overestimation of shoot dry weight after the onset of the disease observed in this study therefore most likely results from an effect of leaf blast on one of the last two processes.

An increased allocation of assimilates to the roots would be an appropriate explanation for the observed dissimilarity between observed and simulated shoot dry weight. Since root biomass was not determined in the field experiment, this hypothesis could not be validated. However, according to the functional balance theory of Brouwer (1962), an attack by a foliar disease and the succeeding reduction in crop photosynthesis is more likely to be followed by an increased

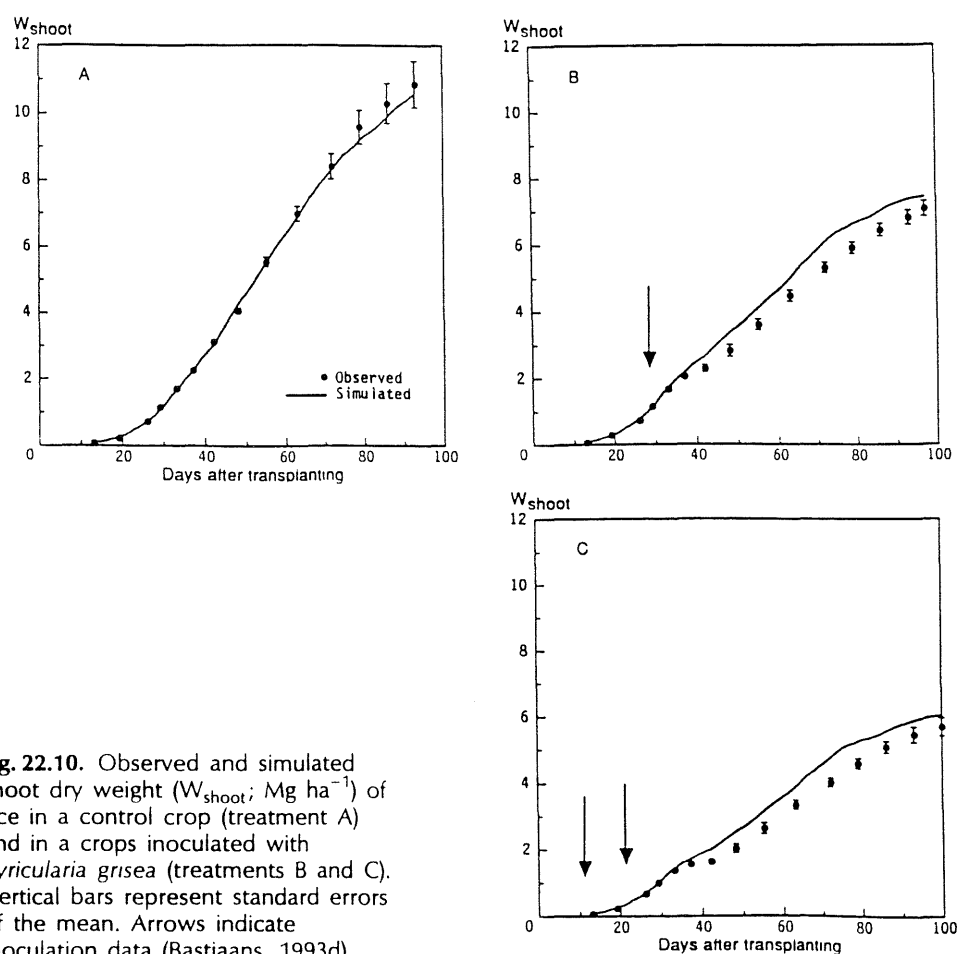


Fig. 22.10. Observed and simulated shoot dry weight (W_{shoot} ; Mg ha^{-1}) of rice in a control crop (treatment A) and in a crops inoculated with *Pyricularia grisea* (treatments B and C). Vertical bars represent standard errors of the mean. Arrows indicate inoculation data (Bastiaans, 1993d).

allocation of assimilates to the shoot. Such a shift in the allocation pattern of assimilates was for instance observed in wheat after infection with *Puccinia striiformis* (Siddiqui and Manners, 1971). An increased allocation of assimilates to the roots after infection of rice with leaf blast is therefore considered to be unlikely.

Consequently, the overestimation of shoot dry weight is probably caused by a less efficient utilization of produced carbohydrates for crop growth. In a study on the effect of leaf rust on crop production of winter wheat, van Roermund and Spitters (1990) introduced the uptake of assimilates by the fungus for spore production as a potential damage mechanism. They estimated that the pathogen used 230–570 $\text{kg CH}_2\text{O ha}^{-1}$ for spore production and related processes. Data on the rate of sporulation of blast lesions are diverse, but data on the production pattern of lesions are rather uniform (Kato *et al.*, 1970; Kato and Kozaka, 1974; Ou, 1985; Kim *et al.*, 1987). Lesions start to produce spores immediately after their appearance, and spore production may last for 20–30 days. Spore production

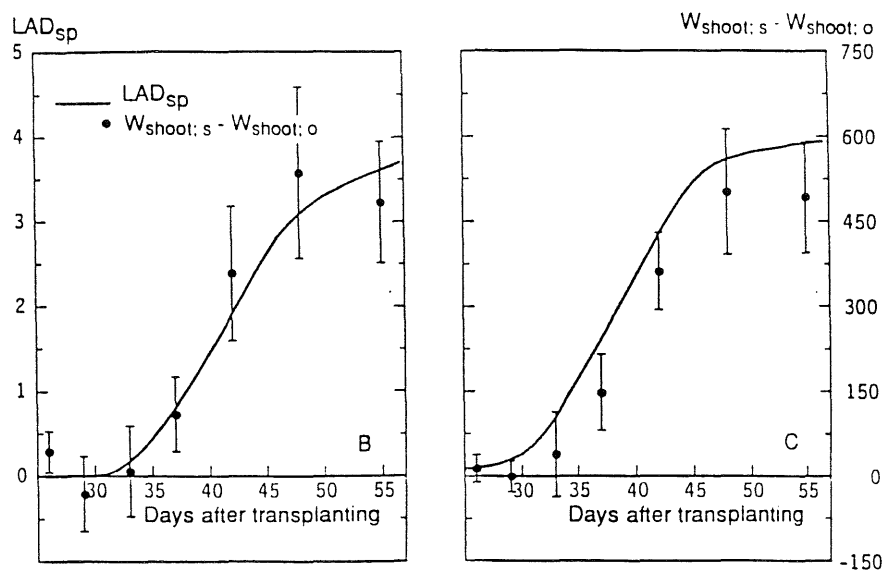


Fig. 22.11. Simulated leaf area duration of sporulating blast lesions (LAD_{sp} ; days) and the difference between simulated and observed total shoot dry weight ($W_{shoot:s} - W_{shoot:o}$; $kg\ ha^{-1}$) for rice crops inoculated with *Pyricularia grisea* (treatments B and C). Vertical bars represent standard errors of the mean (Bastiaans, 1993d).

reaches its peak between 3 and 8 days after lesion appearance, and 90% or more of the spores are produced during the first 14 days. These last observations were used to simulate the amount of actively sporulating leaf area in the various plots of the experiment. For each day the leaf area occupied with lesions (Diseased Area Index, DAI; Zadoks, 1961) was calculated through multiplication of the green leaf area index and disease severity. The newly colonized leaf area was calculated daily and derived from the increase in DAI. Next, the amount of actively sporulating leaf area for any particular day was estimated through summation of the amount of leaf tissue that was colonized during the last 14 days. Integration of the daily amount of actively sporulating leaf area over time yields the leaf area duration of sporulating leaf tissue (LAD_{sp} in days). The time course of this integral shows a striking similarity with the time course of the difference between simulated and observed shoot dry weight (Fig. 22.11). If the overestimation of shoot dry weight was completely caused by the use of carbohydrates by the pathogen for spore production, the growth reduction per ha of sporulating leaf tissue would amount to approximately $150\ kg\ dry\ matter\ d^{-1}$. This corresponds to a carbohydrate withdrawal of around $200\ kg\ CH_2O\ (ha\ sporulating\ lesions)^{-1}\ d^{-1}$.

The present result illustrates the necessity of model validation. Comparison of observed and simulated shoot dry weight in the course of time indicated the absence of an important damage mechanism. Combined with the results of the independent validation of the subroutines on canopy photosynthesis, the missing damage mechanism could be identified. A direct measurement of the costs involved in the production of spores would further strengthen the

model. However, detailed information would then be required on the rate of spore production, the weight of individual spores and, most important, the energy efficiency of the spore production process. For the moment, the indirect estimation of the carbohydrate requirement for spore production and related processes seems a usable alternative.

CONCLUSION

The interaction between experimental research and model development resulted in a better understanding of yield reduction in rice due to leaf blast. This demonstrates the usefulness of the ecophysiological approach to yield loss assessment. Leaf blast was shown to reduce the yield of a rice crop through a reduction in cumulative radiation interception and a reduction in radiation use efficiency. The reduced radiation interception was caused by lesion coverage, premature leaf senescence and a reduced leaf area formation. The reduction in photosynthetic efficiency of the remaining green leaf tissue and the uptake of assimilates by the pathogen for spore production were the main factors responsible for the reduced utilization efficiency of intercepted radiation.

The study resulted in a model that can be used to estimate yield reduction in rice due to leaf blast for various epidemics under variable environmental conditions. Therefore, the model is an appropriate tool in constructing damage functions, which are of primary importance for applying the concept of integrated pest management in blast control.

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