Understanding yield reduction in rice due to leaf blast

Promotoren: dr. ir. R. Rabbinge
                 hoogleraar in de produktie-ecologie, met bijzondere aandacht
                 voor de plantaardige produktie

                 dr. J.C. Zadoks
                 hoogleraar in de ecologische fytopathologie

Lammert Bastiaans

Understanding yield reduction in rice due to leaf blast

Proefschrift
ter verkrijging van de graad van doctor
in de landbouw-en milieuwetenschappen
op gezag van de rector magnificus,
dr. C.M. Karssen,
in het openbaar te verdedigen
op dinsdag 21 september 1993
des namiddags te twee uur in de Aula
van de Landbouwuniversiteit te Wageningen

Stellingen

1. De ene lesie is de andere niet.
   Dit proefschrift

2. De verlaagde produktie van een rijstgewas na een aantasting door de brand-vlekkenziekte kan worden verklaard uit een verminderde onderschepping van licht en een verminderde benutting van het onderschepte licht.
   Dit proefschrift

3. De verhoogde respiratie van rijstbladeren na infektie door *Pyricularia oryzae* beïnvloedt nauwelijks de opbrengst.
   Dit proefschrift

4. De asymmetrische verdeling van de ademhaling over de dag draagt bij aan de namiddag-depressie in het dagelijks verloop van de netto CO_2-uitwisse-lingssnelheid van een gewas.
   Dit proefschrift

5. De stelling "niet simuleren zonder experimenteren" is onvoldoende terug te vinden in trainingscursussen in de systeemanalyse.

6. De ruime keuzevrijheid van de studenten aan de Landbouwuniversiteit bij het samenstellen van hun vakkenpakket en de hoge kwaliteit van de Wageningse afgestudeerde staan niet los van elkaar.
   Onderwijsvisitatie landbouwwetenschappen, VSNU, 1993.

7. Bij het terugdringen van het bestrijdingsmiddelengebruik in de landbouw ligt de nadruk te eenzijdig op een verlaging van de hoeveelheid aktieve stof.

8. De vurigste pleidooien voor het werken op contractbasis worden gehouden door mensen met een vaste aanstelling.

9. Eén van de grootste verdiensten van de biotechnologie is dat zij de hooggespannen verwachtingen weet te consolideren.

10. De veronderstelling dat het wereldrecord op de marathon vanaf 1998 bij de vrouwen scherper zal staan dan bij de mannen is onjuist.
    Whipp, B.J. & Ward, S.A., 1992. Will women soon outrun men? Nature, 355: 25

11. De in de westerse cultuur veelvuldig gehanteerde directe benadering heeft er toe geleid dat minder belang wordt gehecht aan non-verbale communicatie.

12. De grote hoeveelheid naslagwerken over het tekstverwerkingsprogramma Word Perfect is illustratief voor het gebruikersonvriendelijke karakter van dit pakket.

13. Basketbal in Nederland is als korfbal in Papua New-Guinea.

14. Twee AIO's op één kussen, daar past geen kleintje tussen.

Lammert Bastiaans
Understanding yield reduction in rice due to leaf blast
Wageningen, 21 september 1993

Abstract

The study described in this thesis focuses on a quantitative understanding of the effect of leaf blast on growth and production of a rice crop, based on insight in the physiological processes underlying damage. For this purpose, experimental research was conducted at two levels of integration: plant and crop. Research was first conducted at the plant level and focused on the effects of the disease on photosynthesis and respiration. To determine the consequences of these physiological disturbances for crop growth and production, submodels for the effects of leaf blast on photosynthesis and respiration were constructed and introduced in a mechanistic model for crop growth. Experimental research at the crop level was used to validate and improve the extended crop growth model. At the same time the model was used to analyse the results of the field experiments. This interaction resulted in a better understanding of yield reduction in rice due to leaf blast and in a model that can be used to estimate yield reduction due to leaf blast for various epidemics under variable environmental conditions.

additional index words: model, *Oryza sativa*, photosynthesis, *Pyricularia oryzae*, respiration, simulation, systems analysis

Voorwoord

Gedurende het onderzoek en het schrijven van dit proefschrift heb ik de hulp en steun gehad van vele mensen. Graag wil ik van de gelegenheid gebruik maken om hen hiervoor te bedanken. Mijn promotoren, prof.dr.ir. R. Rabbinge en prof.dr. J.C. Zadoks, wil ik bedanken voor de inspirerende wijze waarop zij mij hebben begeleid. Rudy, jij was altijd in staat in zeer korte tijd tot de kern van de zaak door te dringen. Je waakte over de grote lijnen van het onderzoek en liet me de vrijheid daarbinnen mijn eigen keuzes te maken. Je optimistische instelling en het in mij gestelde vertrouwen heb ik als zeer stimulerend ervaren. Professor Zadoks, ik wil u bedanken voor de gedegen wijze waarop u de concept artikelen van commentaar hebt voorzien en de ruime tijd die u steeds nam voor onze besprekingen. Tijdens onze eerste bijeenkomst omschreef u uw functie als die van een luis in de pels. De negatieve associatie die deze vergelijking met zich meebrengt werd evenwel niet bewaarheid. Onze besprekingen verliepen in een plezierige sfeer en uw kritiek was opbouwend van karakter. Daarnaast kwam u met talloze ideeën en suggesties voor het vervolg van het onderzoek. Het was mede hierdoor dat ik steeds weer volledig opgeladen en vol goede moed de Binnenhaven verliet.

Naast mijn promotoren heeft Martin Kropff een belangrijke rol gespeeld bij de totstandkoming van dit proefschrift. In eerste instantie als collega op de vakgroep Theoretische Produktie-ecologie en later als projectleider op het IRRI. Martin, met je goede kennis van zaken en je inspirerende persoonlijkheid, ben je in staat een sfeer te creëren waarin het zeer goed werken is. Ik heb daar dankbaar gebruik van gemaakt.

Het onderzoek werd uitgevoerd binnen het SARP-project. In Wageningen vormden Henriette Drenth en Hein ten Berge de harde kern van dit project. Het was zeer plezierig om met jullie samen te werken. Op de Filippijnse basis waren het Frits Penning de Vries en Don Jansen die de weg plaveiden. Ik heb veel profijt gehad van het voorwerk dat jullie hebben verricht. Gon van Laar pendelde tussen beide locaties en ik heb daardoor, zowel op de Born-Zuid als tussen de rijst, nuttig gebruik kunnen maken van haar adviezen op velerlei gebied.

Over the years the size of the SARP-group at IRRI increased. I would like to thank all members for the pleasant time I shared with them at IRRI. Jacque Alagos and Teng Reyes were always available for discussions on various topics, like crop physiology, software problems and personal affairs. Francis Wagan and Susan Telosa were responsible for a smooth settlement of administrative affairs and enabled me to fully concentrate on research.

Part of the research was conducted at the International Rice Research Institute. I would like to thank the board of IRRI for the opportunity they offered me to make use of their facilities. Paul Teng and Mike Bonman of the Department of Plant Pathology are kindly acknowledged for their support and interest in my work. Claro Q. Torres, former postdoctoral scientist at IRRI, helped me to become familiar with the pathosystem leaf blast-rice. Leonardo Licardo, Lamberto Almario, Mario Ilagan, Ignacio Medallon and Roberto Tagaro are kindly acknowledged for their contribution to the experimental part of the work. I will never forget our true team spirit. Ellen Silab took care of the production of the spores for inoculation. The support of Rico Pamplona to the measurements of canopy photosynthesis was essential.

Edna Galinato, John Gaunt, Olivier Panaud, Ian Simpson and Marco Wopereis, you were perfect housemates and responsible for the necessary distraction after working hours.

Op het IRRI ontmoette ik bovendien een andere Nederlander, Ed Roumen, werkzaam aan hetzelfde pathosysteem. Ed, ik denk met veel plezier terug aan onze voorspoedige samenwerking, die resulteerde in het tweede hoofdstuk van dit proefschrift.

A couple of times I visited the Central Rice Research Institute in Cuttack (India). I would like to thank the board of CRRI for these opportunities. I have very good memories of the time I spent with the members of the simulation team. Dr. P. Ranga Reddy, Dr. R.N. Dash, Dr. M.V.R. Murthy, Dr. S.K. Nayak and Dr. K.S. Rao thank you all for your kind hospitality and the valuable discussions we had.

In Nederland werd het werk uitgevoerd op de vakgroep Theoretische Produktie-ecologie. De vakgroepsleden wil ik bedanken voor de gezellige werksfeer. Yvonne Rombout, Lien Uithol en Hennie de Ruiter droegen zorg voor het afhandelen van velerlei zaken. Rob Dierkx was verantwoordelijk voor de goede hard- en software voorzieningen. Daniël van Kraalingen en Kees Rappoldt hebben vele vrije uurtjes gestopt in het ontwikkelen van een tekenprogramma en andere gebruikersvriendelijke programmatuur. Ik heb dankbaar gebruik gemaakt van de resultaten van hun nimmer aflatende ijver.

Contents

The rice blast disease

Blast disease is generally considered as the principal disease of rice (*Oryza sativa* L.), because of its wide distribution and its destructiveness under favourable conditions (Ou, 1985). The disease is caused by a fungus belonging to the ascomycetes that is known under various names. Currently, the most commonly used names are *Magnaporthe grisea* (Hebert) Barr, used to describe the teleomorph, and *Pyricularia oryzae* Cavara and *Pyricularia grisea* Sacc., used to describe the anamorph (Rossman et al., 1990).

The life cycle of the fungus starts when conidia are deposited on a rice plant. Infection is soon followed by the colonization of host tissue, and after four to five days the first symptoms are visible to the naked eye. In susceptible host genotypes, rapidly enlarging whitish or grey lesions emerge that often develop a brown margin and a yellow halo in a later stage. The lesions are elliptical or spindle-shaped. Sporulation occurs in the central grey area of the lesion. Conidia are formed on conidiophores and dispersed by wind or by rain splash.

Rice is most susceptible to *P. oryzae* in the seedbed, and during 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. The resistance of newly formed leaf tissue increases with time (Yeh and Bonman, 1986; Koh et al., 1987; Roumen, 1993). Leaves that appear on physiologically older plants obtain this property faster. Consequently, leaf blast is mainly present before flowering.

After heading, *P. oryzae* may infect the panicle or the neck node. Panicle blast causes direct yield losses, since filling of the grains on infected panicles is

1

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 most serious phase of the blast disease. Several studies were made to estimate yield loss due to panicle blast. In most studies panicle blast incidence was linearly related to yield loss (Kuribayashi and Ichikawa, 1952; Goto, 1965; Padmanabhan, 1965; Katsube and Koshimizu, 1970; Tsai, 1988a), resulting in simple empirical damage functions. Comparison of the various studies showed that the estimated yield loss ranged from 0.4-1.0% 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. After flowering, the source is used to fill the grains. Leaf blast thus mainly affects grain growth indirectly, through a delayed effect on crop production. Consequently, a thorough understanding of the yield physiology is a prerequisite for the construction of a reliable damage model.

Disease-loss appraisal

During the late 1960's a growing concern evolved about the consequences of environmental pollution. Accordingly, a need arose for more sophisticated disease management schemes that could justify and rationalize the use of fungicides. Implementation of disease management schemes aiming at economic control requires the estimation of economic loss due to different amounts of disease. Therefore, disease-loss appraisal received much interest during this period.

In the early 70's, Zadoks (1973) reviewed the 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. For this reason, the question remains whether empirical damage functions are specific for the conditions (time, location and cultivar) in which

2

they were derived, or whether they have a more general applicability.

In the 80's, the 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. 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 Bicamumpaka, 1986; Waggoner and Berger, 1987). Implicitly, this type of relation 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.

Another methodology in line with a more crop oriented approach was developed by Rabbinge and Rijsdijk (1981). In their approach disease intensity or a host characteristic is not directly related to yield or yield reduction. Attention is first concentrated on the whole plant level, being the next lower level of integration. 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 relations between the amount of disease and the extent to which a process is affected. Subsequently, the relations 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. Examples of crop loss studies that were based on a study of the effects of the harmful agent on physiological processes are given by Rabbinge and Rijsdijk (1981), Boote et al. (1983), Rabbinge et al. (1985), van der Werf (1988), Kropff (1989), van Roermund and Spitters (1990), Rossing (1991) and Schans (1993).

Objective and approach

The main objective of the present study was to quantitatively explain the effect of leaf blast on growth and production of a rice crop based on insight in the effects of the pathogen on physiological plant processes. For this purpose, experimental research was conducted at two levels of integration: plant and crop, conform the methodology developed by Rabbinge and Rijsdijk (1981). Research started at the plant level and focused on the effects of the disease on photosynthesis and respiration. To determine the consequences of these physiological disturbances for crop growth and production, submodels for the effects of leaf blast on photosynthesis and respiration were constructed and introduced in a mechanistic model for crop growth. Experimental research at the crop level was used to validate and improve the extended crop growth model. At the same time the model was used to analyse the results of the field experiments. This interaction resulted in a better understanding of yield reduction in rice due to leaf blast and in a model that can be used to estimate yield reduction due to leaf blast for various epidemics under variable environmental conditions.

The experiments were conducted with rice cultivar IR50, a blast susceptible cultivar which is still grown in large parts of south east Asia. Isolate Po6-6 was used for inoculation. The rice crop was grown under irrigated conditions, with ample nitrogen. Similarly, rice plants grown in pots were raised with an ample supply of water and nutrients. In this way yield limitation due to a shortage of water and nutrients was avoided, and full attention could be given to the yield reducing effect of the fungal pathogen.

Outline of the thesis

Experimental work on effects of leaf blast on leaf photosynthetic rate and respiration is presented in Chapters 1 to 3. The effect of leaf blast on leaf photosynthetic rate at light saturation is discussed in Chapter 1. Data from CO_2 exchange measurements were used to develop a simple model that relates the reduction in leaf photosynthetic rate to the fraction of leaf area covered by lesions (disease severity). To investigate the presence of genotypic differences in tolerance, the reduction in leaf photosynthetic rate due to leaf blast was determined for various rice cultivars (Chapter 2). In Chapter 3 the study on effects of leaf blast on physiological processes was extended with observations on the effect of the disease on initial light use efficiency and respiration.

4

The observations described in Chapters 1 to 3 were used to develop submodels for the effect of leaf blast on photosynthesis and respiration. These submodels were introduced in a model for canopy photosynthesis in order to determine effects of leaf blast on photosynthesis of rice canopies (Chapter 4). Model performance was validated with experimental data from CO_2 exchange measurements of healthy and inoculated rice canopies in the field.

An experimental analysis of leaf blast effects on crop growth and production is presented in Chapter 5. The same experimental data were used to validate a crop growth model that contained the submodels for leaf blast effects on photosynthesis and respiration (Chapter 6). Based on this comparison, the model was extended with a submodel that accounts for carbohydrate uptake by the pathogen for spore-production. In Chapter 7, the extended crop growth model is described and used to study yield reduction in rice due to leaf blast by means of simulation.

Ratio between virtual and visual lesion size as a measure to describe reduction in leaf photosynthesis of rice due to leaf blast

L. BASTIAANS

Department of Theoretical Production Ecology, Wageningen Agricultural University, P.O. Box 430, 6700 AK Wageningen, The Netherlands

Abstract. The effect of *Pyricularia oryzae,* the causal organism of blast in rice, on net photosynthetic rate of rice leaves was measured in the field and in a greenhouse experiment. Leaf blast reduced photosynthesis not only through a reduction in green leaf area, but also through an effect on photosynthesis of the remaining green leaf tissue. A function was derived to relate the net photosynthetic rate of diseased leaf area (P_x) to the photosynthesis of comparable healthy leaf area (P_0) and disease severity (x): $P_x = P_0(1-x)^\beta$. This function is based on the assumption that the visual lesion is part of a virtual lesion in which photosynthesis is negligible. The parameter β expresses the ratio between virtual and visual lesion size, and characterizes the effect of the pathogen on leaf photosynthesis for the entire range of measured disease severities. A value of β between three and four gave a good description of the effect of leaf blast on net photosynthetic rate of rice leaves, indicating a much stronger effect of leaf blast on leaf photosynthesis than expected on the basis of visible lesion size.

1.1 Introduction

After infection of rice leaves with *Pyricularia oryzae* Cavara, the causal organism of blast in rice *(Oryza sativa* L.), elliptical shaped lesions appear on leaves of susceptible cultivars. Goto (1965) 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. This extra reduction meant that leaf blast influenced the host plant more than just the loss in leaf area. For various pathosystems, an effect of the pathogen on photosynthesis of the remaining green leaf area has been reported (for example, *Erysiphe graminis* on wheat [Rabbinge et al., 1985] and *Alternaria alternata* on cotton [Ephrath et al., 1989]). Pathosystems in which the pathogen did not impair photosynthesis of healthy leaf tissue have also been reported (for example, *Puccinia recondita* on wheat [Spitters et al., 1990] and *Phytophthora infestans* on potato [van Oijen, 1990]). Obviously, the effect of a pathogen on host photosynthesis varies according to the pathosystem under consideration.

As far as the effect of *P. oryzae* on photosynthesis of rice is concerned, only observations on canopy photosynthesis of seedlings have been reported. Both Burrell and Rees (1974) and Padhi et al. (1978) observed a marked reduction in canopy photosynthesis of inoculated seedlings, when compared with the performance of healthy plants. Whether the reduction was solely attributable to a reduction in green leaf area was not determined.

In this study, the effect of *P. oryzae* on leaf photosynthesis was measured, and a function was derived to describe the dependence of leaf photosynthetic

8

rate on the fraction of leaf area with blast lesions.

1.2 Materials and methods

In an experimental field at the International Rice Research Institute, Los Baños, the Philippines, net rates of leaf photosynthesis were measured to determine the effect of leaf blast on photosynthesis of rice leaves. Similar observations were made in Wageningen, the Netherlands, at the Centre for Agrobiological Research, using rice plants grown in a greenhouse.

Plant material in the field experiment

In the spring of 1988, a field experiment was conducted to assess yield loss due to rice blast. Part of the plant material in this experiment was used for measurements of leaf photosynthesis. In the experiment, 11-day-old seedlings of *O. sativa* (cultivar IR50) were transplanted in a large plot (2500 m^2), at a planting distance of 0.2×0.2 m. Fertilizer (N-P-K : 60-50-50 kgha^{-1}) was applied 2 days before transplanting. Plants were grown under irrigated conditions. Three days after transplanting, different densities of blast diseased seedlings were planted between rows of the rice seedlings. In this way, different levels of blast epidemics were generated in the field. A disease rating at maximum tillering revealed that diseased leaf area per hill, affected by blast, ranged from 0 to 50%. At the same growth stage, rates of leaf photosynthesis were measured, using plants in randomly selected healthy and diseased parts of the experimental field. Fully developed leaves in the top layers of the canopy were selected for the determination of leaf photosynthesis. Due to the natural disease development, measured leaves contained lesions in different developmental stages.

Plant material in the greenhouse experiment

Rice plants (cultivar IR50) were grown in 21-cm diameter closed pots filled with sand. Before sowing, seeds were kept in moist petri dishes for 5 days. Germinated seeds were selected and five seeds were sown per pot. Plants were grown in a greenhouse during the summer of 1988. Measurements revealed that radiation inside was 70% of the radiation outside the greenhouse. Temperature ranged between 18 °C during the night and 30 °C in day-time and relative

humidity (RH) varied between 60% (day) and 95% (night). Nitrogen fertilizer was added to the pot soils at a rate of 500 mg NH_4NO_3 per pot at 12 and 22 days after sowing. The pots were inundated by maintaining the water level at 0-1 cm above the soil surface.

Plants were inoculated with *P. oryzae* at 27 days after sowing. The fungus was grown on prune agar at a temperature of 28 °C. Inoculum was prepared as described by Mackill and Bonman (1986) and the spore density was adjusted to 5×10^4 conidia ml^{-1}. Gelatine was added to the inoculum in a concentration of 2.5 gL^{-1}. Plants were sprayed with inoculum until run-off using a portable air compressor. Control plants were sprayed with a gelatine solution. All plants were incubated in a moist chamber for 36 hours at 23 °C.

Symptoms appeared on leaves 3-4 days after inoculation and new spores were produced after further lesion development. Since conditions in the greenhouse were favorable for infection, newly infected leaves with lesions in different developmental stages appeared. This closely resembled a situation of natural disease development in the field. At maximum tillering, 2.5 weeks after inoculation, photosynthesis on leaves of healthy and diseased plants was measured.

Photosynthesis measurements

In both experiments, net rates of photosynthesis were measured with a portable leaf chamber analyzer (Analytical Development Co., UK). The rate of photosynthesis was calculated following the procedure described by von Caemmerer and Farquhar (1981). In the field experiment photosynthesis was measured at light saturation. Average conditions within the chamber were: 330 $Jm^{-2}s^{-1}$ of photosynthetically active radiation (400-700 nm; PAR), temperature of 34 °C, and RH of 63%. In the greenhouse experiment, an incandescent lamp was used to reach a high incident radiation at a stable level. Average conditions within the chamber were: 230 $Jm^{-2}s^{-1}$ of PAR, temperature of 31 °C and a RH of 43%.

In both experiments, fully developed leaves in the top layers of the canopy were selected. After photosynthesis was measured, the enclosed part of the measured leaf was harvested, and leaf width was determined. Total leaf surface was calculated by multiplying leaf width with the length of the leaf chamber (5.6 cm). The lesions on this part of the leaf were traced on a plastic sheet with a fine black overhead marker. Total area of traced lesions was determined with a digital video image analyzer (Area Meter System 3439; DELTA-T Devices Ltd., England). Lesions of both chronic and acute lesion type (Ou, 1985) were

10

observed. Chronic lesions are brown, whereas acute lesions have a grayish center, a brown margin and are sometimes surrounded by a yellow halo. For this study, a visible lesion was defined to consist of brown (chronic) or grayish, brown and yellow (acute) leaf area. Small differences in intensity of the green color were sometimes observed around lesions of the acute type. However, leaf area of any green color was defined as not being part of a visible lesion.

Accordingly, disease severity was defined as the fraction of leaf area covered by visible lesions. In both experiments, disease severity on measured leaves ranged from 0 to 0.3.

Model to relate disease severity and leaf photosynthetic rate

Justesen and Tammes (1960) described a formula to estimate the fraction of leaf area remaining visibly healthy $(1-x)$ when both the number of lesions and the fraction of leaf area occupied by a single lesion are known. This formula takes into account the possible overlap of individual lesions:

$$(1-x) = (1-\alpha)^n \tag{1.1}$$

in which x = visibly diseased fraction of the leaf area; n = number of lesions (spots) per leaf; α = fraction leaf area occupied by a single lesion, that can be calculated as A/M, with A = the area of a single lesion (spot) and M = the area of a leaf.

An implicit assumption made in equation 1.1 is that the probability of infection on any part of the leaf is proportional to the area of this part, regardless of its position on the leaf and the presence of former infections. An identical formula is valid if the influence of a pathogen is not restricted to the visual lesion with area A, but to a larger area AA, which is called the virtual lesion. In that case the fraction of leaf area remaining virtually healthy $(1-y)$ can be estimated as:

$$(1-y) = (1-\beta\alpha)^n \tag{1.2}$$

in which y = virtually diseased fraction of leaf area, and $\beta = AA/A$, the ratio between the leaf area occupied by the virtual lesion and the leaf area occupied by the visual lesion. After rewriting equation 1.1:

$$n = \ln(1-x)/\ln(1-\alpha)$$

and substituting into equation 1.2, a relation between x and $(1-y)$ is obtained:

$$(1-y) = (1-\beta\alpha)^{\ln(1-x)/\ln(1-\alpha)} \qquad (1.3)$$

A more convenient representation of this function is:

$$(1-y) = C^{\ln(1-x)} \qquad (1.4)$$

in which

$$C = (1-\beta\alpha)^{1/\ln(1-\alpha)} \qquad (1.5)$$

a factor only depending on the relative area occupied by a single lesion (α) and the ratio between areas occupied by a virtual and a visual lesion (β). When the logarithm of the left-hand term of equation 1.4 is taken, and plotted against $\ln(1-x)$ a straight line with slope $\ln(C)$ is obtained:

$$\ln(1-y) = \ln(C)\ln(1-x) \qquad (1.6)$$

Using equation 1.5 gives:

$$\ln(C) = \ln(1-\beta\alpha)/\ln(1-\alpha) \qquad (1.7)$$

Since $\ln(1-z)$ is almost equal to $-z$, when $0 < z < 0.2$ (if z is any variable),

$$\ln(C) \approx -\beta\alpha/-\alpha = \beta \qquad (1.8)$$

when $\beta\alpha < 0.2$. Equation 1.6 then reduces to

$$\ln(1-y) = \beta\ln(1-x) \qquad (1.9)$$

This result implies that as long as a virtual lesion does not occupy more than 20% of the area of a leaf, the relation between visibly diseased leaf area and affected leaf area is only determined by β. This also holds for a disease with variable lesion size, as long as β is independent of lesion size. Combining equation 1.4 and equation 1.8 results in:

$$y = 1 - (e^{\beta})^{\ln(1-x)} = 1-(1-x)^{\beta} \qquad (1.10)$$
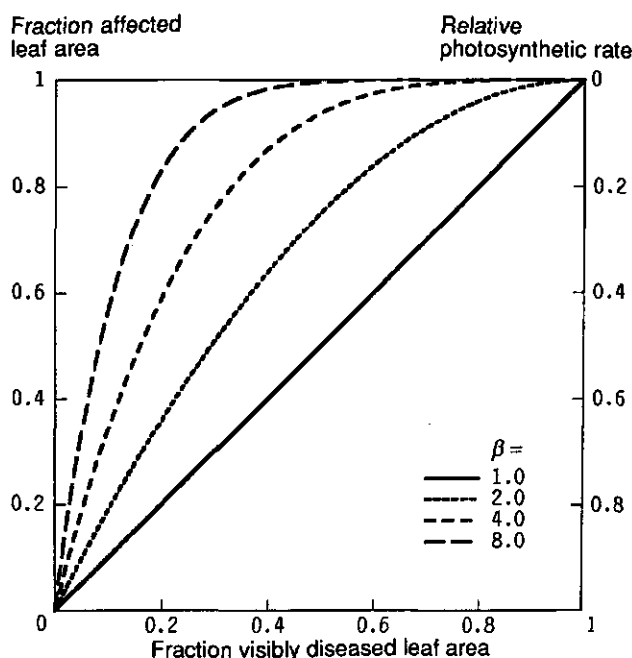
Figure 1.1 The fraction affected leaf area (y) and the relative photosynthetic rate (P_x/P_0) of infected leaves in relation to the fraction visibly diseased leaf area (x) for a leaf spot disease. A lesion is assumed to be part of a virtual lesion in which photosynthesis is negligible. The parameter β expresses the ratio between virtual and visual lesion area.

In Figure 1.1 this equation is used to obtain the relation between the fraction visibly diseased leaf area (x) and the fraction affected leaf area (y), for various values of β. If leaf photosynthesis in the affected part of the leaf is impaired, the fraction of leaf area remaining virtually healthy will be expressed in the ratio of photosynthesis of the infected leaf and photosynthesis of a comparable healthy leaf:

$$(1-y) = P_x/P_0 \tag{1.11}$$

in which P_x = photosynthesis of a leaf with disease severity x, and P_0 = photosynthesis of a healthy leaf. Combining equation 1.10 with equation 1.11 results in:

$$P_x/P_0 = (1-x)^\beta \tag{1.12}$$

in which the relative photosynthesis of an infected leaf is given in dependence of disease severity (Fig. 1.1). After the measured rates of photosynthesis of both healthy and diseased leaves were expressed as a fraction of the average leaf

13

photosynthetic rate of healthy leaves, the parameter β was determined by using nonlinear regression analysis. This analysis was performed by using the Genstat statistical package (Genstat 5 Reference Manual, 1987).

Independent sets of data used to explore utility of the model with other pathosystems

Two data sets on reduction of leaf photosynthesis in winter wheat due to leaf rust (Spitters et al., 1990) and powdery mildew (Rabbinge et al., 1985) were used to explore the utility of the model for other pathosystems. Spitters et al. (1990) measured leaf photosynthesis of the flag leaf on wheat cultivar Cappelle Desprez. The measurements were taken in the field, using a portable leaf chamber gas analyser similar to the one described previously. All measurements were made at light saturation provided by an incandescent lamp cooled by a fan. The percentage of remaining green leaf area on the infected leaf was determined. Measurements were taken in the whole range from 100 to 0% green leaf area. The results of individual measurements were presented in a graph, and were used for this analysis.

Rabbinge et al. (1985) measured leaf photosynthesis on wheat cultivar Okapi at development stage DC 32 (decimal code; Zadoks et al., 1974). Plants were grown in pots, in a greenhouse, and inoculated 2.5 weeks before measurement of photosynthesis. Equipment for routine measurements of photosynthesis as described by Louwerse and van Oorschot (1969) was used to measure rates of leaf photosynthesis at different light intensities. The percentage of leaf area

Table 1.1 Net photosynthetic rate (± standard error of the mean) of rice leaves infected by *Pyricularia oryzae*, measured at high radiation levels, in field and greenhouse experiments.

		Field experiment			Greenhouse experiment	
		Net photosynthesis			Net photosynthesis	
Severity[a]	No.	(kg CO_2 ha^{-1}h^{-1})	P_x/P_0	No.	(kg CO_2 ha^{-1}h^{-1})	P_x/P_0
0.00	38	44.1 ± 0.5	1.00	43	40.4 ± 0.5	1.00
0.00-0.05	36	39.6 ± 0.7	0.90	48	38.5 ± 0.9	0.95
0.05-0.10	19	33.7 ± 1.3	0.76	40	30.5 ± 1.0	0.75
0.10-0.15	11	28.3 ± 1.6	0.64	12	25.7 ± 1.6	0.64
0.15-0.20	3	24.1 ± 1.5	0.55	6	18.1 ± 1.7	0.45
> 0.20	9	20.9 ± 1.9	0.47	8	14.8 ± 2.0	0.37

[a] Leaves were grouped according to fraction of leaf area covered by blast lesions (disease severity).

14

covered with mildew lesions was determined, and ranged from 0 to 10%. Average values of measured rates of photosynthesis, based on at least nine measurements, were presented in a table. The rate of photosynthesis at light saturation was used for this analysis.

1.3 Results and discussion

In both the field and greenhouse experiments, the reduction in leaf photosynthesis of infected leaves, expressed as a fraction of leaf photosynthetic rate of healthy leaves, surpassed disease severity (Table 1.1). The disease not only reduced the amount of green leaf area, but also affected the photosynthesis of the remaining green leaf tissue. The measurements of leaf photosynthesis from the field and greenhouse experiments are shown in Figures 1.2 and 1.3, respectively. Net rate of photosynthesis was expressed relative to the average measured photosynthesis of healthy leaves. Equation 1.12 was used to describe the relation between disease severity and leaf photosynthesis. In both experiments, a β value between three and four gave the best description of leaf photosynthetic rate in dependence of severity. The percentage variance accounted for by these curves was 71% in Figure 1.2 and 74% in Figure 1.3. Based on these percentages, together with the homogeneous distribution of residual variance around the fitted curves, equation 1.12 gave an adequate quantitative description of the effect of leaf blast on photosynthesis of rice leaves. This demonstrates that the effect of leaf blast on leaf photosynthetic rate of rice leaves, for the measured range of severities, can be expressed with a single parameter.

The same equation gave a good description of the relation between leaf photosynthetic rate and disease severity reported for other pathosystems (Table 1.2). The reduction in leaf photosynthetic rate due to leaf rust in wheat was characterized with a β value that did not differ significantly from one. This is in accordance with the conclusion drawn by Spitters et al. (1990) that after leaf rust infection the photosynthetic capacity of the remaining green surface is not affected. The β value for powdery mildew in wheat expressed clearly that the pathogen's effect on leaf photosynthetic rate of the host is much stronger than in the case of leaf blast in rice.

Although the measurements of leaf photosynthesis demonstrate that leaf blast of rice reduced the photosynthesis of the remaining green leaf tissue, the measurements neither clarify the mechanism responsible for this reduction nor the location of this effect. The strongest reduction in leaf photosynthesis would be expected in the surroundings of the visual lesion. This situation could result
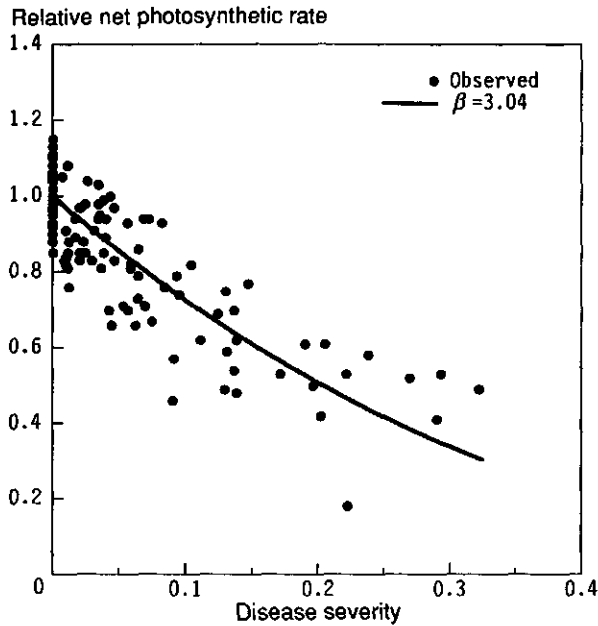
Figure 1.2 Relative net photosynthetic rate of leaves infected by *Pyricularia oryzae* in relation to disease severity as measured in a field experiment. Equation 1.12 was used to describe the relative photosynthetic rate of an infected leaf in dependence of disease severity, using the best-fitting β value.
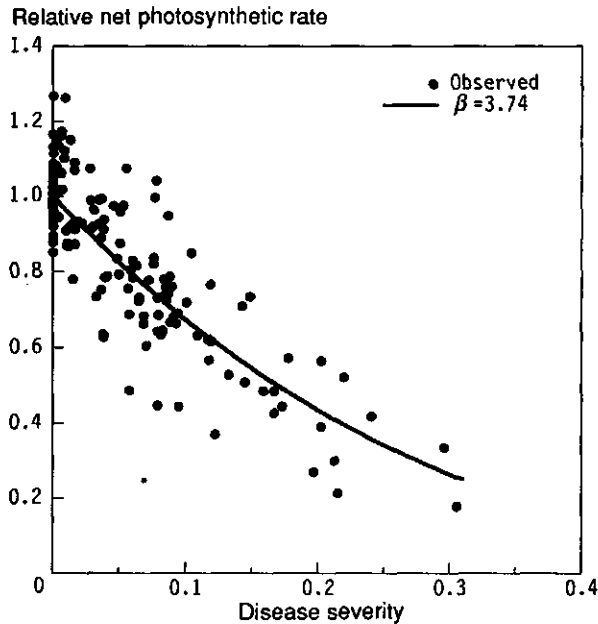
Figure 1.3 Relative net photosynthetic rate of leaves infected by *Pyricularia oryzae* in relation to disease severity as measured in a greenhouse experiment. Equation 1.12 was used to describe the relative photosynthetic rate of an infected leaf in dependence of disease severity, using the best-fitting β value.

from production and secretion of a toxic compound, which then diffuses to the surrounding area of the lesion. Toxins produced by *P. oryzae* have been isolated from diseased plant tissues (Tamari and Kaji, 1954), but effects of the isolated toxins on leaf photosynthesis have not been reported. Yoshii (1937) reported that cell walls and cell inclusions in the central part of the lesion of *P. oryzae* disintegrate. As a result of this disintegration, the transport of either water or assimilates or both may be impaired, and consequently the leaf tissue situated near the lesion may be affected. A reduced relative water content may affect photosynthetic rate either indirectly by closure of the stomata, or directly through an inhibition at the chloroplast level (Kaiser, 1987). Reduced translocation of assimilates may result in accumulation of carbohydrates (Neales and Incoll, 1968). For various plant species a strong negative relation between carbohydrate accumulation and net uptake of CO_2 was observed, indicating feedback inhibition of photosynthesis (e.g. Chatterton, 1973; Upmeyer and Koller, 1973; Ku et al., 1978; Azcón-Bieto, 1983).

Waggoner and Berger (1987) argued that radiation absorbed by healthy leaf area is adequate to explain yield in most pathosystems. Following their reasoning, one may wonder whether leaf photosynthesis measurements contribute to a quantitative understanding of disease-induced yield loss. Johnson (1987) however, distinguished two major effects of diseases on crop growth: a reduction in the solar radiation interception by green leaf area (RI), and a reduction in the radiation use efficiency (RUE). The present study indicates that leaf blast in rice is an example of a host-pathogen combination in which both effects occur. For an analysis of crop growth in terms of RI and RUE, only the time course of green leaf area is needed. Determination of disease severity and its effect on photosynthesis is not a prerequisite. However, for purposes of crop

Table 1.2 Characterization of the reduction in leaf photosynthetic rate of the host due to the presence of a pathogen, for various pathosystems, using the estimated parameter β.

Pathosystem [a]	β	r^2	Source
Puccinia recondita- winter wheat	1.26 ± 0.17 [b]	0.77	Spitters et al. (1990)
Pyricularia oryzae- rice	3.04 ± 0.18 3.74 ± 0.19	0.71 0.74	Field experiment Greenhouse experiment
Erisyphe graminis- winter wheat	8.74 ± 1.70	0.84	Rabbinge et al. (1985)

[a] The presented data refer to measurements at high light intensities.

[b] Standard error of estimated β.

protection rather than analyzing in retrospect, the construction of damage relations is the ultimate aim. This requires the relation between RUE of green leaf tissue and disease severity. Next to the level of disease, other factors will have their impact on an aggregated parameter as RUE, preventing the existence of a general relationship between disease severity and RUE. Experimental determination of this relation for all possible combinations of crop status and environmental factors will take a lot of effort. Introduction of the measured leaf photosynthesis damage relationship into a process-level crop growth simulator, as proposed by Boote et al. (1983), provides quantitative insight into the consequences for crop growth and grain yield. A well-documented growth model for rice, in which the calculation of canopy photosynthesis is based on leaf photosynthetic rate of various leaf layers, has been developed recently (MACROS; Penning de Vries et al., 1989). Such a model enables the establishment of the relation between RUE of green leaf tissue and disease severity for various conditions. Summarizing the outcomes in graphs or simple regression equations will be very useful for the application of the type of model discussed by Johnson (1987). In my opinion, using simple models, and parameterizing them with the results from more detailed models, will enhance the impact of both model types on the construction of damage relations.

Effect on leaf photosynthetic rate by leaf blast for rice cultivars with different types and levels of resistance

L. BASTIAANS[1] & E.C. ROUMEN[2]

[1] Department of Theoretical Production Ecology, Wageningen Agricultural University, P.O. Box 430, 6700 AK Wageningen, The Netherlands

[2] Department of Plant Breeding, Wageningen Agricultural University, P.O. Box 386, 6700 AJ Wageningen, The Netherlands

Abstract. The effect of an inoculation with *Pyricularia oryzae* (isolate Po6-6) on net leaf photosynthetic rate of rice *(Oryza sativa)* was studied with four cultivars. Measurements were taken on the sixth leaf of the main culm of plants in the early tillering stage. On cultivars CO39, IR50 and IR64 a susceptible infection type developed, but a clear difference in relative infection efficiency of the cultivars was observed. The highest number of lesions developed on leaves of CO39, whereas the lowest number was found on leaves of IR64. For all three cultivars the effect of a single lesion on the reduction in net leaf photosynthetic rate was found to be equal to a reduction in leaf area of three times the area occupied by the visible lesion. On IR68, a cultivar with complete resistance, brown specks of pinpoint size appeared without any effect on net leaf photosynthetic rate.

2.1   Introduction

Leaf blast (causal organism: *Pyricularia oryzae* Cavara) reduces leaf photosynthetic rate of rice *(Oryza sativa* L.) not only through a reduction in green leaf area, but also through an effect on photosynthesis of green leaf tissue surrounding the lesion (Bastiaans, 1991). To quantify the reduction in leaf photosynthetic rate, the concept of the virtual lesion, consisting of a visual lesion and a halo, was introduced. Photosynthetic rate inside a virtual lesion is considered to be zero, and the area of the halo is chosen such that the reduction in leaf photosynthetic rate is fully accounted for. Measurements indicated that the ratio between virtual and visual lesion size (β) was independent of disease severity. Parameter β is therefore a suitable measure for the effect of the pathogen on leaf photosynthetic rate. Differences in β among 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). The objective of the present study was to investigate the presence of genetic variation in β. For this purpose three cultivars with a susceptible infection type, but with a different relative infection efficiency (RIE) were used. RIE is a major component of partial resistance to leaf blast in rice (Toriyama, 1975; Ahn and Ou, 1982; Yeh and Bonman, 1986).

The effect of inoculation with *P. oryzae* on net leaf photosynthetic rate of a cultivar with complete resistance was also determined. Smedegaard-Petersen and Tolstrup (1985) suggested that complete resistance to a disease may have a limiting effect on yield. They referred to the energy expenses of defense reactions that inhibit or prevent pathogen growth. With incompatible powdery mildew-barley combinations they observed a temporary increase in respiration

after inoculation. The second objective of this study was therefore to determine whether an inoculation with *P. oryzae* would lead to a substantial increase in respiration of a cultivar with complete resistance. Such an increase will manifest itself as a marked reduction in net leaf photosynthetic rate.

2.2 Materials and methods

Plant cultivation and inoculation

Two pot experiments were conducted in the spring of 1989, at the International Rice Research Institute (IRRI), Los Baños, the Philippines. Plants of *O. sativa* were grown in 12 cm diameter plastic cups. Cultivar IR50 was used as a reference. Before sowing, seeds were kept in moist Petri dishes for 5 days. Seven germinated seeds were sown per cup. Cups were randomly distributed over mobile benches of 1.5 m². Plants were raised without standing water. Soil moisture content in the cups was monitored twice a day and water was supplied if necessary. Nitrogen fertilizer $((NH_4)_2SO_4)$ was applied in three dressings, equivalent to 5 g N m^{-2} (0.057 g N/pot) each. The first dressing was applied just after emergence, the second after unfolding of the fourth leaf, and the third after unfolding of the sixth leaf.

Leaf developmental stage is known to influence both RIE and leaf photosynthetic rate, and therefore measurement of RIE and leaf photosynthetic rate were restricted to those plants on which the sixth leaf appeared three days before inoculation. Isolate Po6-6 of *P. oryzae* was used for inoculation. The fungus was grown on prune agar at a temperature of 28 °C. Inoculum was prepared as described by Mackill and Bonman (1986) and the spore density was adjusted to circa 50000 conidia ml^{-1}. Per bench 200 ml of inoculum was sprayed. After inoculation, the plants were incubated in a humid cage for 14 hours, at a temperature of about 25 °C.

Photosynthesis measurements

Measurements of leaf photosynthetic rate were conducted in a conditioned room with a temperature between 24 and 28 °C. Light for photosynthesis measurements was obtained by 4 HPLIT lamps (Philips, the Netherlands) of 400 W each, mounted in a wooden frame. A waterbath, constructed of glass and filled with a water layer of 7 cm, was installed just below the lamps to intercept

heat radiation. Previous to the measurement, plants were put on a table top below the waterbath for an adaptation period of 30 min. Leaf photosynthetic rate was determined with a portable leaf chamber analyzer (Analytical Development Co., UK). Average conditions within the leaf chamber were: 1460 $\mu Em^{-2}s^{-1}$ of photosynthetically active radiation (400-700 nm; PAR), temperature of 32 °C, and a relative humidity of 65%. The rate of photosynthesis was calculated following the procedure described by von Caemmerer and Farquhar (1981). Leaves of the same cultivar were grouped, and specific leaf weight and nitrogen content (Kjeldahl) were determined.

Experiment 1

Plants of cultivars CO39, IR50 and IR64 were grown and inoculated. From earlier studies it was known that these cultivars develop a susceptible infection type after inoculation with isolate PO6-6, but differ in RIE (Roumen, 1992). RIE was considered as the number of sporulating lesions that developed per
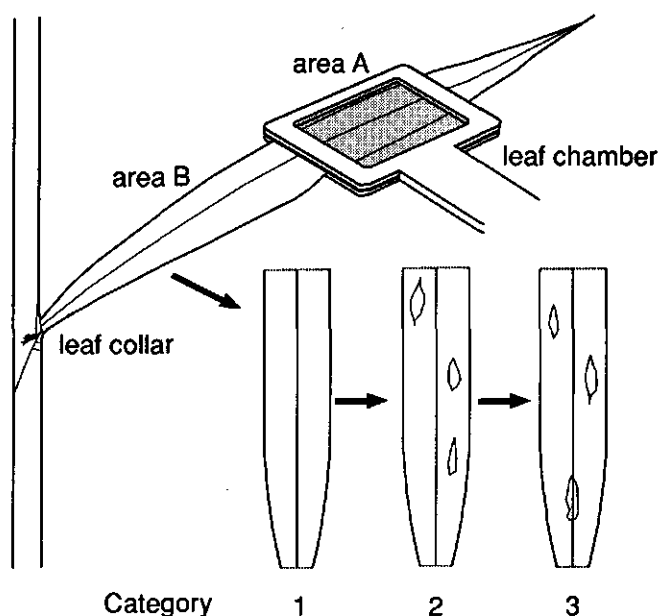
Figure 2.1 Schematic representation of the measurement of net leaf photosynthetic rate. Disease severity was determined on the leaf part enclosed by the leaf chamber (area A). The presence and position of lesions between the leaf collar and the nearest edge of the leaf chamber (area B) was used to categorize measured leaves (category 1: no lesions; category 2: lesions on the laminae, but not on the central vein ; category 3: lesions also on the central vein).

unit area of leaf tissue after inoculation. The presence of a gray center was used as a criterion to distinguish sporulating from non-sporulating lesions (Jeanguyot, 1983). The number of lesions was recorded six days after inoculation (DAI).

Net leaf photosynthetic rate was determined at 7 to 10 DAI. The fraction of leaf area covered with lesions (disease severity) was estimated according to the procedure described by Bastiaans (1991). Disease severity was determined for the area of leaf tissue enclosed by the leaf chamber (area A; Fig. 2.1). Measured leaves were classified in three categories, based on the presence and position of lesions on the leaf part between the leaf collar and the basal edge of the leaf chamber (area B; Fig. 2.1). Results within the first two categories were used to relate net photosynthetic rate of inoculated leaves (P_x) to disease severity (x), using an extended version of the model derived by Bastiaans (1991):

$$P_x = \gamma P_0 (1-x)^\beta \qquad (2.1)$$

In this model, P_0 is the average leaf photosynthetic rate of comparable noninoculated leaf area. Parameters γ and β are proportionality factors which characterize the effect of an inoculation on leaf photosynthetic rate. For each cultivar, γ and β were determined by using the nonlinear least squares regression algorithm DUD (Ralston and Jennrich, 1979) of the SAS statistical package.

Experiment 2

Plants of cultivars IR50 and IR68, a cultivar with complete resistance against isolate PO6-6, were grown and inoculated. Three DAI small brown specks of pinpoint size appeared on both cultivars. From that day onwards net leaf photosynthetic rate was determined on three consecutive days for both noninoculated and inoculated plants of IR50 and IR68. After photosynthesis measurement, total leaf area inside the leaf chamber was determined, and both the number of sporulating and non-sporulating lesions were counted.

2.3   Results

A clear difference in RIE was observed between cultivars CO39, IR50 and IR64 (Table 2.1). As expected, IR64 had the lowest infection frequency,
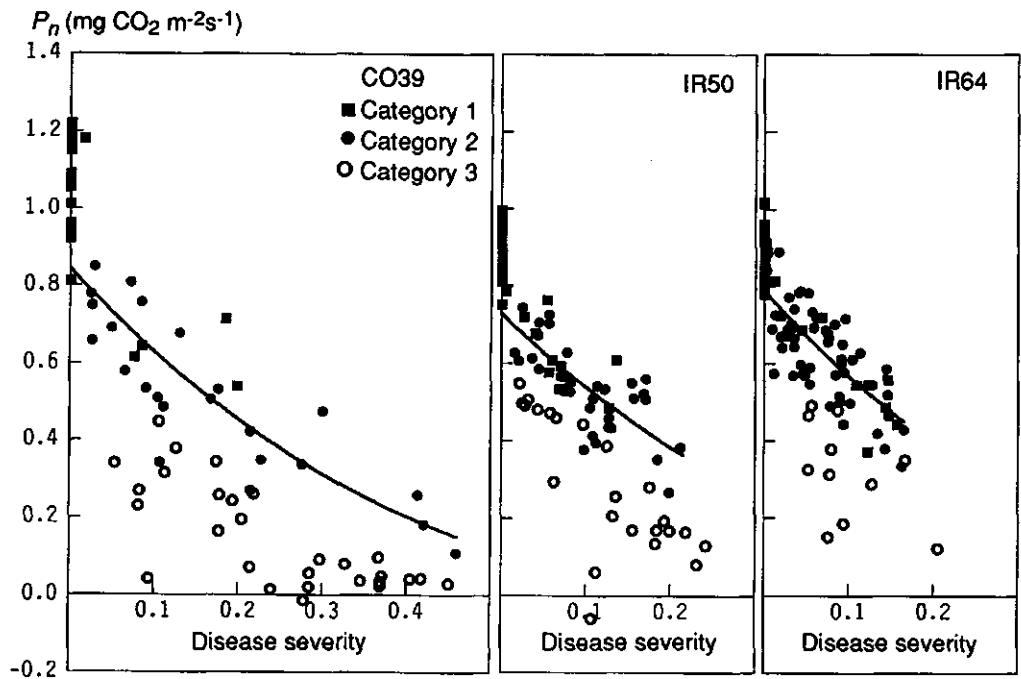
Figure 2.2 Net leaf photosynthetic rate (P_n) of three rice cultivars inoculated with *Pyricularia oryzae*, in relation to disease severity. Lesions were classified in three categories; see Figure 2.1.

whereas the infection frequency of CO39 was clearly the highest. Leaf nitrogen content of the three cultivars was identical.

Table 2.1 Relative infection efficiency (RIE) and parameters characterizing the leaf photosynthetic rate (P_0, γ and β; equation 2.1) of three rice cultivars after inoculation with *Pyricularia oryzae*. Means (RIE, P_0) and estimated parameters (γ, β) are given with their standard error. Results were obtained from leaves classified in category 1 and 2 (Fig. 2.1). Relevant leaf characteristics are given.

| | Cultivar | | | | | |
	CO39		IR50		IR64	
No.[a]	17 + 28		20 + 44		26 + 67	
RIE (lesions cm^{-2})	3.91 ± 0.33	(a)[b]	1.94 ± 0.17	(b)	1.29 ± 0.09	(c)
P_0 (mg CO_2 m^{-2}s^{-1})	1.07 ± 0.03	(a)	0.90 ± 0.02	(b)	0.89 ± 0.02	(b)
γ	0.79 ± 0.05	(a)	0.81 ± 0.03	(a)	0.89 ± 0.03	(b)
β	2.8 ± 0.5	(a)	2.9 ± 0.4	(a)	3.2 ± 0.4	(a)
N-content (gm^{-2})	1.08		1.08		1.06	
Specific leaf weight (gm^{-2})	26.3		23.9		24.6	

[a] Number of observations on noninoculated + inoculated leaves.

[b] Means in the same row, followed by the same letter are not significantly different according to t-test (P<0.05).

Measurements on noninoculated plants indicated that leaf photosynthetic rate of CO39 was higher than that of IR50 and IR64, despite the similarity in leaf nitrogen content. In Figure 2.2 the measured leaf photosynthetic rate is plotted against disease severity. Equation 2.1 described the effect of leaf blast on leaf photosynthetic rate of inoculated leaves reasonably well. Residual variance was homogeneously distributed around the fitted curves. The coefficient of variation of individual measurements of leaf photosynthetic rate (CV), calculated as the square root of the error mean square divided by the overall mean, varied between 13% (IR64) and 23% (CO39) for inoculated leaves, and between 8% (IR64) and 13% (CO39) for noninoculated leaves. This increase in CV after inoculation can partly be explained by the experimental error in the determination of disease severity and the variation in the effect of the pathogen. Another part of the increase will be due to the imperfections of the model. Leaves of category 3 were not included in the regression. The presence of lesions on the central vein had a negative effect on the photosynthetic rate of the distal part of the leaf. On average, leaf photosynthetic rate was reduced with an extra 0.25 mg CO_2 $m^{-2}s^{-1}$. Such an effect was absent if lesions were only present on the laminae alongside the central vein.

The overall effect of an inoculation with *P. oryzae* on leaf photosynthetic rate is reflected in γ and β (Table 2.1). No significant differences were found between the β-value of the three cultivars. A value of three indicates that the effect of a single lesion on leaf photosynthetic rate corresponds to a reduction

Table 2.2 Net leaf photosynthetic rate (P_n; mg CO_2 $m^{-2}s^{-1}$) of a susceptible (IR50) and a resistant (IR68) rice cultivar at different days after inoculation (DAI) with *Pyricularia oryzae*. Lesion density on inoculated leaves (lesions cm^{-2}) is given for both nonsporulating (LD_{non-sp}) and sporulating (LD_{sp}) lesions. Values are means ± standard error.

DAI	Noninoculated			Inoculated			LD_{non-sp}	LD_{sp}
	No.	P_n		No.	P_n			
IR50								
3	11	1.03 ± 0.03	(a)[a]	15	0.93 ± 0.03	(b)	0.9 ± 0.2	0.0
4	16	1.01 ± 0.02	(a)	16	0.85 ± 0.04	(b)	1.0 ± 0.2	1.1 ± 0.2
5	14	1.02 ± 0.03	(a)	18	0.79 ± 0.04	(b)	1.2 ± 0.2	1.6 ± 0.3
IR68								
3	13	1.02 ± 0.03	(a)	15	1.04 ± 0.03	(a)	1.8 ± 0.3	0.0
4	12	1.01 ± 0.03	(a)	13	0.99 ± 0.04	(a)	1.8 ± 0.5	0.0
5	15	1.04 ± 0.03	(a)	16	1.01 ± 0.02	(a)	2.2 ± 0.5	0.0

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

in leaf area of three times the area occupied by the visible lesion. This value corresponds to earlier observations on IR50 (Bastiaans, 1991). Parameter γ represents the part of the effect that is not related to disease severity. It expresses the ratio between the average photosynthetic rate of inoculated but symptomless leaf area, and the photosynthetic rate of noninoculated leaf area. For all cultivars this parameter was found to be significantly smaller than one. With naturally infected leaves γ was found to be equal to one, and therefore neglected (Bastiaans, 1991).

On cultivar IR68 small brown specks of pinpoint size were first observed on the third day after inoculation. After appearance the specks did not develop any further. This reaction is typical for incompatibility between host and pathogen. In the next days only few new specks appeared (Table 2.2). Simultaneously, no significant differences in photosynthetic rate were observed between leaves of noninoculated and inoculated plants of IR68.

On IR50, as on IR68, small brown specks were first observed at the third day after inoculation. The number of specks was lower than on IR68. On the fourth day after inoculation the first symptoms were observed of what later on appeared to be sporulating lesions. The number of lesions of sporulating type increased during the following days. On the day of appearance the lesions were characterized by a whitish centre surrounded by a small dark green zone. The following day the size of the whitish centre was 1.5 by 1 mm with a narrow brown zone around it. A significant reduction in leaf photosynthetic rate of inoculated plants of IR50 was already observed at three DAI, before the first symptoms of sporulating lesions were detected. This reduction further increased after appearance and enlargement of the lesions.

2.4 Discussion

Two parameters (γ and β) were needed to characterize the effect of an inoculation with *P. oryzae* on leaf photosynthetic rate. With naturally infected leaves γ was found to be equal to one and could therefore be neglected (Bastiaans, 1991). It is not unlikely that γ-values smaller than one are typical for artificially inoculated plants. This may be due to the development of lesions of the second generation. The first of such lesions are only expected to appear at 9 DAI (incubation period first lesion + latent period second lesion; 5+4 days). By that time their area hardly contributes to disease severity, but, as was demonstrated in the second experiment, leaf photosynthetic rate will already be reduced. Such a reduction is independent of disease severity, since lesions of the

26
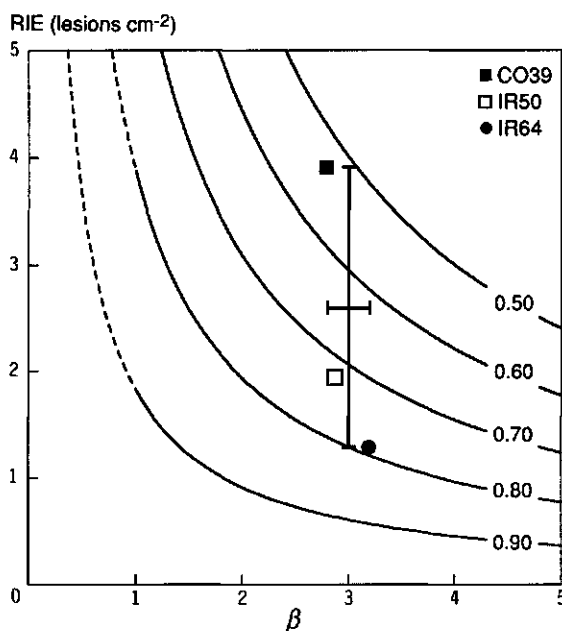
Figure 2.3 Relative infection efficiency (RIE) and parameter β as measured for three rice cultivars after inoculation with *Pyricularia oryzae*, and the implications for relative net leaf photosynthetic rate (P_x/P_0). Curves are isolines referring to combinations of RIE and β with an equal relative net leaf photosynthetic rate (equation 2.4).

second generation may also originate from spores that developed on neighbouring plants. Noninoculated plants however will not be affected, since they were kept separately from the inoculated plants. The significantly higher γ of IR64 would in this case be explained by its lower RIE.

For all cultivars a β of three was measured. This value is similar to previous results (Bastiaans, 1991). As the results do not indicate the presence of genetic variation in β, it is concluded that β is not a suitable selection criterion in breeding rice for tolerance to leaf blast. This conclusion is emphasized in Figure 2.3, where the impact of the genetic variation in β and the impact of the genetic variation in RIE are compared. Isolines for relative leaf photosynthetic rate (P_x/P_0) were constructed for combinations of β and RIE. A function derived by Justesen and Tammes (1960) was used to relate RIE (n; lesions cm^{-2}) and disease severity (x) :

$$(1-x) = (1-\alpha)^n \tag{2.2}$$

In this formula α is the area occupied by a single lesion. In the present

27

experiment α was measured between 7 and 10 DAI and found to be 0.056 cm^2, regardless of cultivar. This value was used in the present analysis. Substitution in equation 2.1, and assuming $\gamma=1$, results in:

$$P_x/P_0 = (1-\alpha)^{n\beta} \tag{2.3}$$

which after transformation yields the equation for the isolines:

$$n\beta = \ln(P_x/P_0)/\ln(1-\alpha) \tag{2.4}$$

In Figure 2.3 the three cultivars are characterized by the values for β and RIE measured in this experiment. It is shown that the differences in RIE fully account for the calculated differences in relative leaf photosynthetic rate among cultivars.

Lesions on the central vein caused a marked reduction in the photosynthetic rate of the distal part of the leaf. Disintegration of leaf-tissue in the central part of the blast lesion, as reported by Yoshii (1937), most likely resulted in a disturbed transportation of water and assimilates. Consequently, the relative water content of the leaf may be reduced, and the level of carbohydrates may be enhanced. Both effects may result in a reduction in leaf photosynthetic rate (Kaiser, 1987; Azcón-Bieto, 1983; Ku et al., 1978). Their position on the central vein enhances the impact of the referred lesions. Furthermore, these lesions were mainly found close to the leaf base were leaf width is small. This limited the possibilities of compensation through cross veinal transport. With lesions on either side of the central vein effects were localised. This observation confirms the statement of Zadoks and Schein (1979), that lesions of equal size but in different positions do not necessarily have an equal effect on plant growth.

Incompatibility in *O. sativa - P. oryzae* interactions resulted in the formation of small brown specks of pinpoint size, most of which appeared at three DAI. An effect on net leaf photosynthetic rate was not observed. Also in the next two days, when only few new specks appeared, net leaf photosynthetic rate was not affected. The specks did not develop any further, and therefore an effect on three or more days after their appearance is considered to be unlikely. A highly localized reduced net photosynthetic rate during the first days after inoculation cannot be excluded. However, the absence of a lasting effect makes the existence of a measurable effect on rice grain yield due to complete resistance against leaf blast unlikely.

28

Effect of leaf blast on photosynthesis-light response characteristics of rice leaves

L. BASTIAANS

Department of Theoretical Production Ecology, Wageningen Agricultural University, P.O. Box 430, 6700 AK Wageningen, The Netherlands

Abstract. The effect of *Pyricularia oryzae*, the causal organism of leaf blast in rice, on photosynthesis characteristics of rice leaves was measured in two greenhouse experiments. Leaf blast reduced photosynthesis not only through a reduction in green leaf area, but also through an effect on photosynthesis of green leaf tissue surrounding the lesions. The assimilation rate at light saturation (P_{max}) was more affected than the initial light use efficiency (ε). Dark respiration (R_d) increased as a result of infection. The experimental data were used to derive relations between leaf blast severity and P_{max}, ε and R_d.

3.1 Introduction

Infection of rice leaves by *Pyricularia oryzae* Cavara, the causal organism of leaf blast in rice (*Oryza sativa* L.), leads to formation of typical spindle-shaped lesions. After infection, the physiology of rice leaves is affected. Toyoda and Suzuki (1957) have observed an increased respiration in the green tissue surrounding blast lesions. This increase was connected with a shift from the glycolytic to the pentose phosphate pathway, a phenomenon generally observed in plants infected by biotrofic 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. oryzae*. Bastiaans (1991) measured photosynthetic rate of healthy and infected leaves at light saturation. The measurements showed that leaf blast reduced leaf photosynthetic rate not only through a reduction in green leaf area, but also through an effect on photosynthesis of the remaining green leaf tissue.

Knowledge of plant physiological processes and the way they are affected by a disease can be used to analyse and predict the effect of the disease on crop growth and production. Rabbinge and Rijsdijk (1981) introduced an eco-physiological approach in which effects of diseases on plant physiological processes are introduced in a mechanistic crop growth model to estimate their effect on yield. The present study deals with the first step of this approach; the quantification of the effect of the disease on relevant plant physiological processes. After inoculation with *P. oryzae*, the effect of leaf blast on photosynthesis-light response characteristics of rice leaves was determined. The experimental data were used to derive 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). In a further study, these relations will be introduced in a model for canopy photosynthesis, to compute and explain effects of leaf blast on photosynthesis of rice canopies (Bastiaans and Kropff, 1993).

30

3.2 Materials and methods

Plant material and inoculation

During the summers of 1988 and 1989 plants of *O. sativa* were cultivated in a greenhouse, at the Centre for Agrobiological Research (CABO-DLO), Wageningen, the Netherlands. Rice plants of cultivar IR50 were grown in 21 cm diameter closed pots. Before sowing, seeds were kept in moist petri dishes for 5 days. Five germinated seeds were sown per pot. In 1988, pots were filled with sand. Nitrogen fertilizer was added at a rate of 500 mg NH_4NO_3 per pot at 12 and 22 days after sowing (DAS). In 1989, pots were filled with clay. Fertilizer was added at a rate of 350 mg N (urea), 321 mg K (K_2SO_4), and 78 mg P (KH_2PO_4) prior to sowing. From 24 DAS till 30 DAS, additional fertilizer was applied as Hoagland solution at a rate of 100 ml per pot per day (in total: 105 mg N, 118 mg K, and 16 mg P). All pots were inundated. Plants were raised without supplementary radiation. Average global radiation inside the greenhouse was 10.7 MJd^{-1} in 1988 and 7.2 MJd^{-1} in 1989. Average daylength in both years was 16 h. Temperature ranged between 30 $^{\circ}$C and 18 $^{\circ}$C (day/night) and relative humidity varied between 60% and 95% (day/night).

Plants were inoculated with *P. oryzae* (isolate Po6-6) at 27 (1988), 30 and 32 DAS (1989). The fungus was grown on prune agar at a temperature of 28 $^{\circ}$C. Inoculum was prepared as described by Mackill and Bonman (1986) and the spore density was adjusted to 50000 (1988) and 250000 (1989) conidia ml^{-1}. Gelatin was added to the inoculum in a concentration of 2.5 gL^{-1}. Plants were sprayed until runoff, using a portable air compressor, and incubated in a moist chamber for 36 h at 23 $^{\circ}$C. In each experiment the inoculations were restricted to one inoculum-density, since inoculations with *P. oryzae* generally lead to a large variation in lesion density (E.C. Roumen; pers. comm., 1988). Control plants were sprayed with a gelatin solution.

Leaf photosynthesis measurements

Equipment comparable to the type described by Louwerse and van Oorschot (1969) was used to analyse the effect of *P. oryzae* on photosynthesis-light response characteristics of leaves. Light response curves of youngest, completely unfolded leaves were measured 7-11 days after inoculation (DC 27-29; Decimal Code, Zadoks et al., 1974). Five to six leaves were fixed in a leaf

chamber. In 1988, irradiance was decreased in 5 steps from 300 to 0 $Jm^{-2}s^{-1}$ of photosynthetically active radiation (PAR; 400-700 nm). Radiation intensity was modified after stabilization of the reading of CO_2-uptake, after approximately 30 minutes. In 1989, irradiance was increased in 5 steps from 0 to 180 $Jm^{-2}s^{-1}$ PAR. Average conditions within the leaf chamber were as follows: 340 ppm CO_2, temperature of 23 °C, and RH between 45-60%. After photosynthesis was measured, disease severity, specific leaf weight and N-content were determined. Disease severity was defined as the fraction of leaf area covered with lesions and determined according to the procedure described by Bastiaans (1991). Disease severity ranged from 0.00 to 0.08 in 1988, and from 0.00 to 0.15 in 1989.

Data-analysis

The CO_2 assimilation-light response curve for individual leaves can be described by a negative exponential function, which is characterized by the photosynthesis parameters P_{max} (net CO_2 assimilation rate at light saturation) and ε (initial light use efficiency), and the respiration parameter R_d (dark respiration) (Goudriaan, 1982). Dark respiration was defined as the CO_2-production measured after a dark period of 25 minutes. P_{max} and ε were determined by fitting the negative exponential function to the measured data of net photosynthetic rate, using the non linear regression option of the Genstat statistical package (Genstat 5 Reference Manual, 1987).

To analyse the effect of leaf blast, all three parameters were related to disease severity (x). For the photosynthesis parameters (P_{max}, ε) the concept of the virtual lesion was used (Bastiaans, 1991) :

$$P_x = P_0(1-x)^\beta \tag{3.1}$$

in which P_0 and P_x are the photosynthesis parameters for healthy and diseased leaf area, respectively. Parameter β is a proportionality constant, which expresses the ratio between the measured reduction in photosynthetic rate due to a single lesion and the expected reduction assuming that only the lesion is photosynthetically inactive. Dark respiration was related to disease severity by:

$$R_x = R_0(1-x)+\rho R_0 x \tag{3.2}$$

in which R_0 and R_x are the rate of dark respiration of healthy and diseased

32

Table 3.1 Estimated parameter values (± standard error) of net CO_2 assimilation rate at light saturation (P_{max}), initial light use efficiency (ε), and dark repiration (R_d) of healthy leaves.

	1988 (No.=4)		1989 (No.=6)	
P_{max} (mg CO_2 m^{-2}s^{-1})	1406. ± 27	(a)[a]	820. ± 38	(b)
ε (mg CO_2 J^{-1})	13.7 ± 0.5	(a)	15.8 ± 0.4	(b)
R_d (mg CO_2 m^{-2}s^{-1})	28.2 ± 1.1	(a)	20.2 ± 1.9	(b)
Leaf N-content (g N m^{-2})	1.77 ± 0.03	(a)	1.11 ± 0.03	(b)
Specific leaf weight (g m^{-2})	29.1 ± 0.7	(a)	28.8 ± 0.8	(a)

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

leaf area, 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 Genstat statistical package was used to determine $\beta_{P_{max}}$, β_ε and ρ.

3.3 Results

The negative exponential function gave an accurate description of the net CO_2 assimilation-light response for both healthy and diseased leaves. Estimated values for P_{max}, ε and R_d of healthy leaves are given in Table 3.1. Significant differences between both years were found for all three parameters.

Leaf blast was found to have a clear effect on the parameters which characterize the net CO_2 assimilation-light response curve (Fig. 3.1). The disease decreased both P_{max} and ε. The values of $\beta_{P_{max}}$ and β_ε differed

Table 3.2 Estimated values (± standard error) of parameters which characterize the effect of leaf blast on net CO_2 assimilation rate at light saturation ($\beta_{P_{max}}$), initial light use efficiency (β_ε) and dark respiration (ρ) of rice leaves. For an explanation of the parameters see text.

	1988 (No.=20)		1989 (No.=28)	
$\beta_{P_{max}}$	3.67 ± 0.83	(a)[a]	4.45 ± 0.59	(a)
β_ε	3.18 ± 0.81	(a)	2.97 ± 0.31	(a)
ρ	4.41 ± 1.45	(a)	4.67 ± 0.99	(a)

[a] Means in the same row, followed by the same letter, are not significantly different according to t-test (P<0.05).
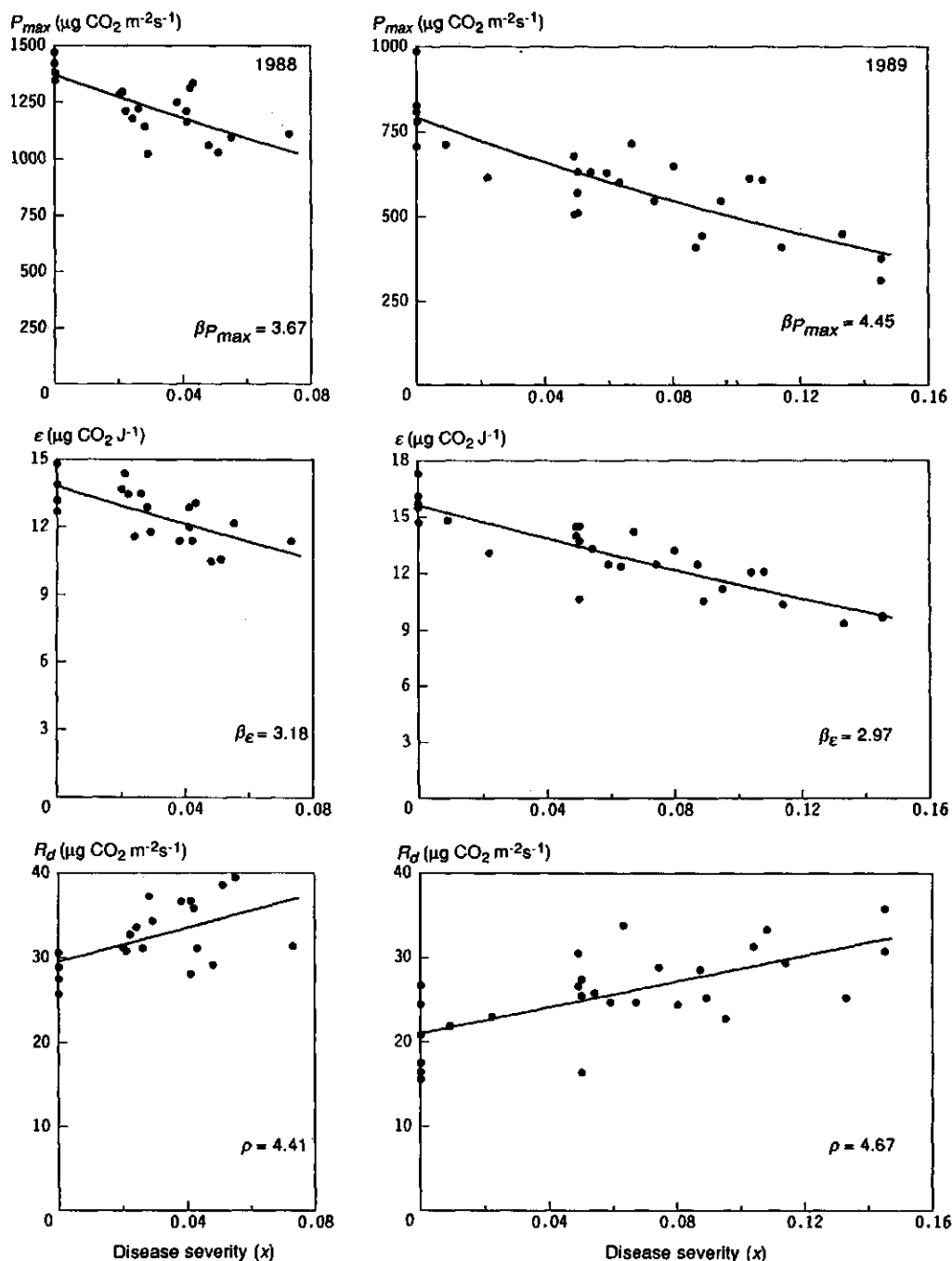
Figure 3.1 Photosynthesis and respiration parameters of rice leaves infected by *Pyricularia oryzae* in relation to disease severity, as measured in two greenhouse experiments (●, observed; P_{max} is assimilation rate at light saturation; ε is initial light use efficiency; R_d is dark respiration). Equations 3.1 and 3.2 were used to describe the relation between disease severity and photosynthesis and respiration parameters, respectively (————).

34

significantly from one, indicating that the reduction was larger than could be explained through the reduction in green leaf area (Table 3.2). In both years the effect on P_{max} was larger than the effect on ε, but only in 1989 this difference was significant.

Dark respiration increased with increasing disease levels. Although there was a large variation between individual observations, the value of ρ was almost identical in both years and differed significantly from one (Table 3.2).

3.4 Discussion

The CO_2 assimilation-light response curve of healthy leaves of plants grown in 1988 differed significantly from the response curve of plants grown in 1989. Apart from the differences in P_{max}, ε and R_d, light saturation in 1989 was reached at a relatively low radiation intensity. During measurement, radiation was increased to a maximum of 180 $Jm^{-2}s^{-1}$ PAR, since at higher light intensities photoinhibition occurred. This phenomenon may be explained by the lower level of radiation during the nursing of the plants grown in 1989. Plants grown under a low radiation regime tend to react as shade plants, with light saturation reached at low light intensities (Björkman, 1981). Apart from the lower radiation during the nursing of the plants, leaf N-content in 1989 was lower. Cook and Evans (1983) found a consistent and linear relation between photosynthetic rate at light saturation and leaf N-content of several *Oryza* species. Comparison with their data demonstrates that the difference in P_{max} can be attributed to the difference in leaf N-content.

The sequence of light intensities during measurement of photosynthetic rate may have contributed to the higher R_d in 1988. In 1988 light intensity was gradually decreased and dark respiration was determined at the end of the measurement period. As a result, dark respiration may have been enhanced by the production of carbohydrates during the preceding measurement of photosynthetic rate at high light intensities. A direct relation between photosynthesis in the preceding light period and the rate of dark respiration was for instance demonstrated in wheat (Azcón-Bieto and Osmond, 1983). In 1989 the measurements started with the determination of dark respiration, after which the light intensity was gradually increased.

The observed difference in ε between both years is surprising, since ε is a conservative value (Björkman, 1981). An analysis with the model of Marshall and Biscoe (1980) revealed that the leaf photosynthesis-light response in 1989 tended towards a Blackman-curve. Fitting a Blackman-type of response with a

negative exponential function leads to an overestimation of ε, as was most likely the case in 1989. Nevertheless, the negative exponential was used, since the model of Marshall and Biscoe did not give a significantly better fit, even though it consists of one extra parameter.

Although the photosynthesis-light response curve of plants grown in 1988 differed from the response curve of plants grown in 1989, a similar effect of the pathogen was measured in both years. The reduction in P_{max} and ε surpassed the reduction in green leaf area, indicating that the effect of the disease is not limited to the visibly affected part of the leaf, but exceeds the limits of the lesion. Previous measurements showed that the effect of a single blast lesion on leaf photosynthetic rate at light saturation corresponds to a reduction in leaf area of three-four times the area occupied by the visible lesion (Bastiaans, 1991). The present observations confirm this finding.

The different β values for the effects on P_{max} and ε allow some speculations to be made on the physiological basis of the effect of leaf blast on photosynthesis of rice leaves. Effects of pathogens on CO_2 assimilation can be divided into effects on photosynthetic events *per se* and effects on photosynthesis related processes (Buchanan et al., 1981). The first category of effects will lead to an increased carboxylation resistance, whereas an increased stomatal resistance is an example of the second category (Rabbinge et al., 1985). A reduced ε as a result of a direct effect on stomatal behaviour is unlikely. Even if diffusion of CO_2 into the leaf is impaired, it is doubtful whether CO_2 will become a limiting factor at low light intensities. Therefore, the reduction in ε is more likely to result from a hindered photosynthetic event *per se*. The same mechanism will be partly responsible for the reduction in P_{max}. However, the larger β value for the effect of leaf blast on P_{max} indicates that another mechanism is contributing to the overall effect at light saturation. This extra reduction may be due to either a reduced photosynthetic event *per se*, or a reduced diffusion of CO_2. Detailed physiological research is required if a better insight in the mechanisms responsible for the reduction in leaf photosynthetic rate is desired.

Toyoda and Suzuki (1957) observed an increase in the respiration of rice leaves after infection with *P. oryzae*. The present observations confirm this finding. If the increased respiration was solely attributed to an increased respiration in the visible lesion area, respiration of this part of the leaf would be 4.5 times as high as respiration of green leaf tissue. In a further study the measured effect of leaf blast on both photosynthesis and respiration will be introduced in a mechanistic model for canopy photosynthesis (Bastiaans and Kropff, 1993). This will enable a comparison of the relative importance of both damage mechanisms to the reduction in crop growth rate.

Effect of leaf blast on photosynthesis of rice canopies

L. BASTIAANS[1] & M.J. KROPFF[2]

[1] Department of Theoretical Production Ecology, Wageningen Agricultural University, P.O. Box 430, 6700 AK Wageningen, The Netherlands

[2] International Rice Research Institute, P.O. Box 933, 1099 Manila, The Philippines

Abstract. The effect of *Pyricularia oryzae*, the causal organism of leaf blast in rice, on photosynthetic rate of a rice crop was determined with mobile equipment in the field. Canopy CO_2 exchange rate (CER) was significantly reduced in plots inoculated with *P. oryzae*. The experimentally obtained data were used to evaluate the performance of a model for the effects of leaf blast on canopy photosynthesis. The model comprised photosynthesis and respiration routines of a mechanistic crop growth model, extended with submodels for effects of leaf blast on both processes. Canopy photosynthesis and the effect of leaf blast on CER were accurately simulated with the model. Analysis showed that the reduction in canopy photosynthesis was mainly due to an adverse effect of lesions on leaf photosynthetic rate and to shading by dead leaf area resulting from disease induced senescence. A sensitivity analysis demonstrated the importance of the vertical distribution of the disease in the canopy. This implies that disease monitoring for crop loss assessment should consider vertical disease distribution.

4.1 Introduction

Leaf blast (causal organism: *Pyricularia oryzae* Cavara) is an important constraint for the production of rice (*Oryza sativa* L.). Infection by the fungus in the vegetative growth phase of rice leads to formation of typical spindle-shape lesions on leaves. Heavily infected leaves die completely. Goto (1965) tried to mimic leaf blast injury in experiments by progressive artificial defoliation of a disease-free canopy. However, grain yield of the artificially defoliated plants was greater than that of diseased rice plants, indicating that leaf blast influenced the host plant more than just through a loss in leaf area. This conclusion is supported by Toyoda and Suzuki (1957), who observed an increased respiration in the surrounding green tissue of blast lesions. Moreover, Bastiaans (1991) measured that leaf blast reduced photosynthetic rate of the remaining green part of infected leaves.

The importance of the observed effects of leaf blast on leaf physiology, as determined by their effect on grain 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. This approach starts with the quantification of the effect of the disease on basic plant growth processes. Submodels simulating these effects are then coupled to models simulating growth and production of the crop, 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

38

of a broad bean crop (*Vicia faba* L.), 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 model at an intermediate aggregation level. Canopy photosynthesis was measured in the field and used to evaluate the performance of a model for the effects of SO_2 on canopy photosynthesis. The thus validated model was later on introduced in a crop growth model to analyse and predict effects on crop yield.

In the present study the effect of leaf blast on canopy photosynthesis was explained from the effect leaf blast has on photosynthesis characteristics of individual leaves. 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 determined in a previous study (Bastiaans, 1993a). These relations were used to construct a model for effects of leaf blast on canopy photosynthesis. Photosynthetic rate of rice canopies infected with *P. oryzae* was determined in a field experiment, to evaluate the performance of the model. In addition, the model was used to quantify the contribution of the various damage mechanisms to the reduction in canopy photosynthesis. Moreover, the importance of the vertical disease distribution was determined.

4.2 Materials and methods

Plant material and inoculation

In the 1990 wet season, a field experiment was conducted at the lowland research site of the International Rice Research Institute (IRRI), Los Baños, Philippines. On 6 November, 13-day-old rice seedlings of cultivar IR50 were transplanted in a plot of 750 m². Plants were grown under irrigated conditions. Fertilizer was applied one day before transplanting (N-P-K: 60-50-50 kg ha⁻¹). Additional nitrogen was applied at a rate of 30 kg N ha⁻¹ at 29 days after transplanting (DAT). Insecticides (triazophos at 8 and 27 DAT, carbofuran at 17 DAT) were applied to control insects. Three plots of 12 m x 3.6 m were pegged out, of which one (plot A), was used as control. The other two plots were inoculated with *P. oryzae* (isolate Po6-6). Plot B was inoculated at 27 and 34 DAT, whereas plot C was inoculated at 20 and 34 DAT. Timing of the first inoculation varied, to establish two different levels of leaf blast. Inoculum was prepared as described by Mackill and Bonman (1986) and the spore density

was adjusted to 75000 conidia ml^{-1}. Gelatine was added to the inoculum in a concentration of 2.5 gL^{-1}. Per inoculation 5 L of inoculum was sprayed per plot. The night after inoculation, plots were covered with plastic to increase leaf wetness duration. Covering was repeated during the following three nights, after spraying of 5 L distilled water per plot.

Canopy photosynthesis measurements

Canopy CO_2 exchange rate (CER; mg CO_2 m^{-2}s^{-1}) was measured on 19 December (43 DAT) between 1115 and 1215 h using a mobile gas exchange system (Walz, Effeltrich, Germany) according to the procedure described by Dingkuhn et al. (1990). A transparent mylar-covered chamber with an aluminum frame (0.4 x 0.4 x 0.75 m) was placed over the canopy (2 x 2 hills) for less than 90 s while a continuously flowing air sample was collected through a 20 m teflon tubing. The CO_2 concentration of the gas sample was determined with a BINOS-1 infrared gas analyzer (Heraeus, Hanau, Germany). Gas mixing and wind generation inside the chamber were achieved using a fan located just above the canopy. The CO_2 exchange rate of the canopy was calculated from the rate of linear decrease in sample CO_2 concentration. Net canopy photosynthesis was computed by subtracting the separately determined floodwater CO_2 release (175 mg CO_2 m^{-2}s^{-1}) from canopy CO_2 exchange. Average conditions at the time of measurement were: 360 Jm^{-2}s^{-1} of photosynthetically active radiation (PAR; 400-700 nm) and a temperature of 30 ^{o}C. Absorption of light by the mylar-covered chamber was about 10 %.

Measurements were followed by destructive plant sampling for a layerwise determination of canopy characteristics and disease intensity. Leaves were classified according to the distance from stem base to leaf collar (<0.10 m, 0.10 to 0.15 m, 0.15 to 0.20 m, and > 0.20 m). Within each height category, leaves of healthy (with no lesions), diseased (with at least one blast lesion) and dead type were distinguished. Leaf area was determined for each type separately. Disease severity, defined as the fraction of green leaf area covered by lesions, was estimated by scoring the number and size of lesions on a randomly selected leaf sample. Dry weight of green (healthy and diseased) leaf blades, of dead leaf blades, and of stems + leaf sheaths was determined, as was N concentration of green leaf tissue (Kjeldahl).

Based on the distribution of leaf area over height categories and the average leaf blade length, a reconstruction of the canopy was made, assuming an average leaf angle of 65 degrees. The reconstructed canopy was divided in five layers of equal height. Leaf characteristics (specific leaf weight and N-content),

disease severity and the fraction dead leaf area were calculated per layer. These data, and the dry weight of the various shoot organs, were used as model inputs.

Modelling instantaneous canopy photosynthesis (CER)

In order to compare simulated effects of leaf blast with measurements, a model for calculation of the diurnal course of instantaneous canopy photosynthesis was developed. The model comprised routines for calculation of photosynthesis and respiration of an elementary model for crop growth (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.

The procedure for calculation of gross canopy photosynthesis was basically identical to the procedure described by Spitters (1986). Daily global irradiance was input to the model, and used to generate diurnal trends of total, direct and diffuse radiation reaching the top of the canopy (Spitters et al., 1986). After accounting for reflection, the light profile within the canopy was determined by calculating the decrease in radiation flux with canopy depth for both diffuse and direct radiation (Goudriaan, 1988). On the basis of both light profiles, absorption can be derived for any depth within the canopy. Substitution into the photosynthesis-light response of single leaves then gives the assimilation rate per unit leaf area at the concerning depth in the canopy. In this model, five canopy layers were distinguished and the instantaneous photosynthesis per canopy layer was calculated using a three-point Gaussian integration (Goudriaan, 1986). Instantaneous canopy photosynthesis was obtained by adding up the photosynthesis of the five layers. A negative exponential function, comprising the gross assimilation rate at light saturation ($P_{g,max}$) and the initial light use efficiency (ε), was used to describe the CO_2 assimilation-light response of individual leaves (Goudriaan, 1982). $P_{g,max}$ was related to leaf N-content (g N m^{-2}), according to the relationship derived by Penning de Vries et al. (1990).

Respiration was modelled according to the principles of McCree (1970) and Thornley (1970), who assumed that the produced assimilates were used for either maintenance or growth. In the model maintenance was assumed to take precedence over growth. Maintenance respiration was calculated per organ and proportional to the organ dry weight. To account for an effect of temperature ($Q_{10}=2$.; Penning de Vries, 1975), daily minimum and maximum temperature

41
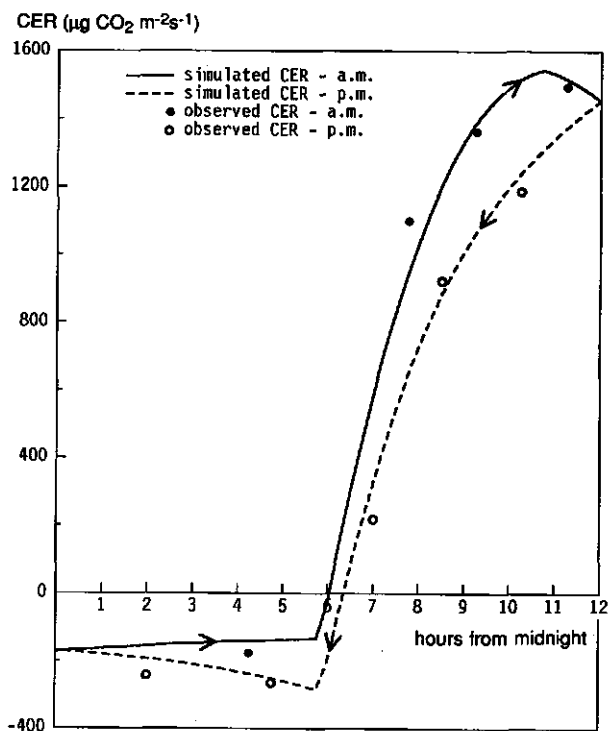
Figure 4.1 Simulated and measured diurnal course of canopy CO_2 exchange rate (CER; $\mu g\ CO_2\ m^{-2}s^{-1}$) of a direct seeded rice crop of IR64 at 69 days after seeding. Model inputs and measured CER are derived from Dingkuhn et al. (1990).

were inputs to the model. The diurnal trend of temperature was generated according to Parton and Logan (1981). To express the dependence of maintenance respiration on metabolic activity (Penning de Vries, 1975), maintenance was further related to gross photosynthesis. This part of maintenance respiration was estimated to be equal to ten percent of gross canopy photosynthesis (Penning de Vries et al., 1989).

The assimilates remaining after provision of maintenance respiration, were used as substrate for growth. Substrate utilization for growth was assumed to proceed according to a first order rate of decay, and the half-life of this process was related to temperature according to observations of McCree (1974; for white clover and sorghum) and Ryle et al. (1976; for barley). Growth respiration reflects the metabolic costs of converting assimilates into structural dry matter. Growth respiration and growth were calculated per organ and based on the production values of biochemical components calculated by Penning de Vries (1972).

CER was calculated as gross photosynthesis minus maintenance and growth respiration. Comparison of model results with measurements of Dingkuhn et al.

Gross photosynthesis (μg CO_2 m^{-2}s^{-1})
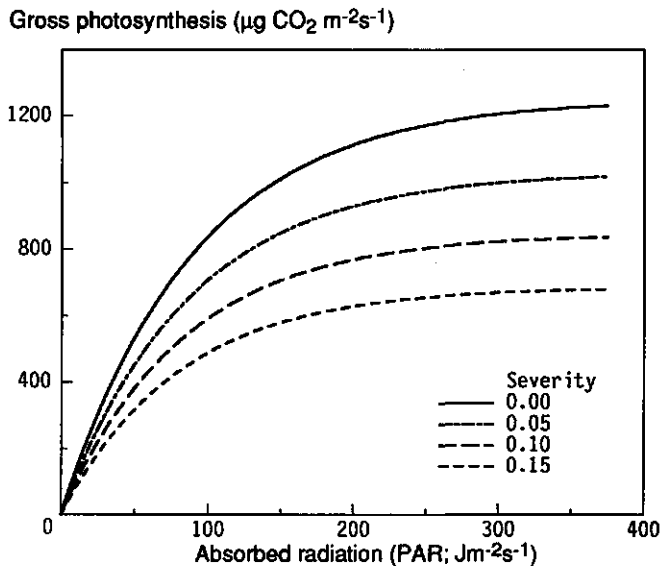
Figure 4.2 Photosynthesis-light response curves of standardized rice leaves (leaf N-content 1.5 g N m^{-2}; specific leaf weight 30 gm^{-2}), demonstrating the effect of leaf blast on gross photosynthetic rate. Curves summarize the results of earlier observations (Bastiaans, 1991 & 1993a).

(1990), who measured CER at various times during the day, demonstrates that the model gives a realistic simulation of the diurnal course of canopy photosynthesis (Fig. 4.1). Instantaneous crop growth rate was obtained through summation of organ growth rates. This rate was integrated over the day to obtain the daily crop growth rate (CGR; g dry matter m^{-2}d^{-1}).

Modelling the effects of leaf blast

To account for the effect of leaf blast on photosynthesis, disease severity and the fraction dead leaf area were specified per layer. Photosynthesis-light response characteristics of green leaf tissue (healthy + diseased leaves) were related to observed disease severity, using parameter β (Bastiaans, 1993a). This proportionality constant expresses the ratio between the reduction in photosynthetic rate due to the presence of a single lesion and the expected reduction according to visible lesion size. The reduction in $P_{g,max}$ and ε were characterized by β-values of 3.7 and 3.0, respectively (Bastiaans, 1991 & 1993a). Typical photosynthesis-light response curves of diseased leaf tissue are given in Fig. 4.2. Dead leaves did 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

43

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 (Bastiaans, 1993a). This parameter expresses the ratio between the respiration related to the presence of a single lesion and the respiration of an identical area of green leaf tissue. Following Bastiaans (1993a), a value of 4.5 was used. Maintenance requirement of dead leaf tissue is nil and was therefore not considered.

Model validation and application

CER observed in the present experiment was compared with the simulated CER at the time of actual measurement, to validate model performance. After validation, the model was used to analyse the importance of the various damage mechanisms. For this analysis the effect on CGR was studied, since this value contains the influence of the disease integrated over the day. In addition, a sensitivity analysis was carried out for parameters characterizing the effect of leaf blast on photosynthesis and respiration ($\beta_{P_{max}}$, β_ε, ρ). Finally, the model was used to examine the importance of the vertical disease distribution.

4.3   Results

Measured effect of leaf blast on CER

Table 4.1 gives relevant characteristics of the canopies in the various plots at the time of photosynthesis measurement. The control plot was slightly infected, due to influx of spores from neighbouring plots. A small amount of dead leaf area, found in the lower part of the canopy, consisted of naturally senescing leaves. In plot B and C disease severity and the fraction dead leaf area were higher than in plot A. The fraction dead leaf area was moderate in plot B and high in plot C. In Fig. 4.3 more details are given on the vertical distribution of healthy, diseased and dead leaf tissue. Plant height was clearly affected by the disease. Leaf area index was not affected, but leaves in the noninoculated plot had a higher specific leaf weight. Leaf nitrogen contents of the three plots were

44
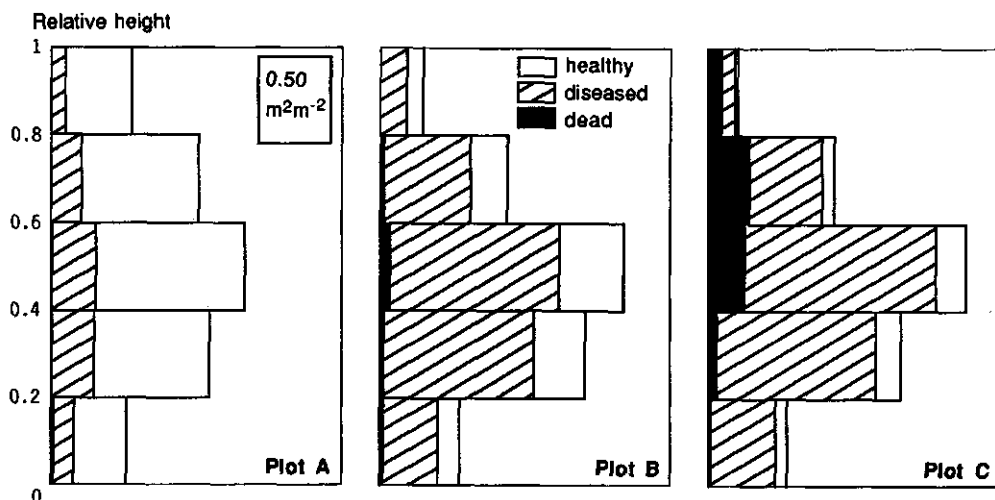
Relative height

Figure 4.3 Vertical distribution of healthy, diseased and dead leaf area of the rice crop in the three experimental plots. Height is expressed on a relative scale. The rectangle in A represents 0.5 unit of leaf area.

identical. In all plots a N-profile was found, with leaf N-content in the top layer about 30% higher than in the bottom layer. Significant differences between in CER of the three plots were observed. Compared to the control plot the CER's plot B and C were reduced by 15% and 33%, respectively.

Table 4.1 Characteristics of rice canopies at the time of photosynthesis measurement and measured canopy CO_2 exchange rate (CER).

	Plot A	Plot B	Plot C	S.E.D.[a]
Number of observations	6	4	4	
Plant height (m)	0.68 (a)[b]	0.60 (b)	0.54 (c)	0.02 (0.02)
Shoot dry weight (gm^{-2})	291. (a)	274. (a)	298. (a)	20. (22.)
Leaf area index	4.49 (a)	4.80 (a)	4.66 (a)	0.39 (0.43)
Leaf N-content (g N m^{-2})	1.21 (a)	1.14 (a)	1.18 (a)	0.04 (0.04)
Specific leaf weight (gm^{-2})	34.3 (a)	30.7 (b)	31.2 (b)	0.9 (1.0)
Disease severity[c]	0.003 (a)	0.046 (b)	0.044 (b)	0.9 (1.0)[d]
Fraction dead leaf area	0.01 (a)	0.03 (b)	0.15 (c)	1.5 (1.6)[d]
CER (μg CO_2 m^{-2}s^{-1})	1432. (a)	1219. (b)	953. (c)	57. (62.)

[a] Standard error of difference of means applied to comparison of plot A with plot B or C, and plot B with plot C (values between brackets).

[b] Means in the same row followed by the same letter are not significantly different according to t-test (P<0.05).

[c] Fraction of green (healthy + diseased) leaf area covered by lesions.

[d] Data were analysed after arc sine transformation. S.E.D.-values of transformed data are given.

45
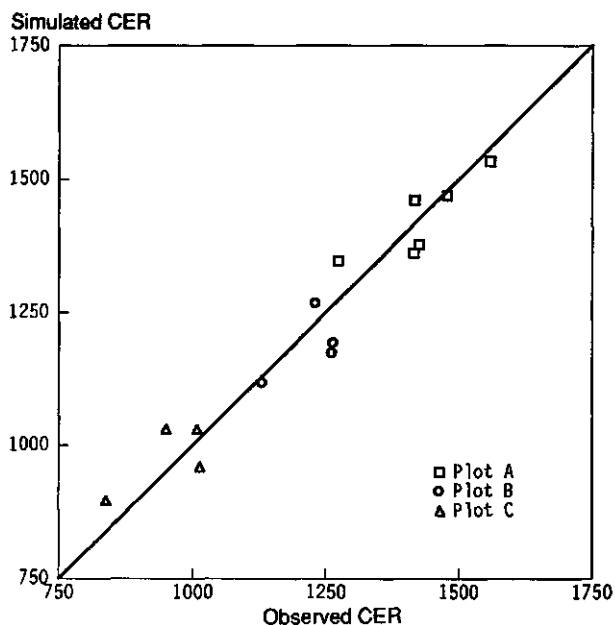
Figure 4.4 Comparison of observed and simulated canopy CO_2 exchange rate (CER; $\mu g\ CO_2\ m^{-2}s^{-1}$).

Table 4.2 Contribution of blast lesions and dead leaf tissue to the overall reduction in growth rate of rice crops with different levels of leaf blast (Table 4.1), as simulated with the model. The contribution of the identified damage mechanisms related to blast lesions and dead leaf tissue are specified and expressed as a percentage of the total reduction due to blast lesions and dead leaf tissue, respectively. CGR is crop growth rate in g dry matter $m^{-2}d^{-1}$.

	Plot A		Plot B		Plot C	
CGR of a healthy canopy[a]	21.3		21.2		21.5	
Total reduction in CGR due to leaf blast	0.3	(1.00)	4.0	(1.00)	8.0	(1.00)
Reduction in CGR due to blast lesions	0.2	(0.66)	3.2	(0.81)	2.7	(0.34)
Contribution of identified damage mechanisms:						
- decrease in green leaf tissue		29%		31%		30%
- reduction in leaf photosynthetic rate		65%		63%		64%
- increase in respiration		6%		6%		6%
Reduction in CGR due to dead leaf tissue	0.1	(0.34)	0.8	(0.19)	5.3	(0.66)
Contribution of identified damage mechanisms:						
- decrease in green leaf tissue		52%		32%		30%
- shading		48%		68%		70%

[a] A healthy canopy is defined as a canopy in which disease severity is nil and dead leaf tissue is replaced by an identical area of healthy leaf tissue.

46

Canopy CO_2 exchange rate for control and inoculated canopies was accurately simulated with the model (Fig. 4.4). The observed reduction in CER can thus be explained by the adverse effect of blast lesions on leaf photosynthetic rate and respiration and by the existence of dead leaf tissue, resulting from disease induced senescence. In Table 4.2 a detailed analysis of the reduction in CGR 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 CGR 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 increase in simulated CGR after removal of dead leaf tissue corresponds to the reduction due to shading. The further increase in simulated CGR 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, in canopies where dead leaf tissue was present in the upper part, shading accounted for two thirds of the overall reduction due to dead leaf tissue (plot B and C). Shading was relatively less important when dead leaf tissue was present in the lower part of the canopy (plot A).

Summarizing the effects of the disease on CGR in an effect on radiation interception by green leaf area (RI) and an effect on radiation use efficiency (RUE), as proposed by Johnson (1987), demonstrated that leaf blast reduced both (Table 4.3). The reduction in RUE in plots B and C was almost identical. This reduction is mainly a result of the inhibitory effects of lesions on

Table 4.3 Simulated crop growth rate (CGR) analysed in terms of radiation interception by green leaf area (RI) and radiation use efficiency (RUE), of canopies with a different level of leaf blast (Table 4.1).

	plot A	plot B	plot C
Simulated CGR (g dry matter $m^{-2}d^{-1}$)	21.0 (1.00)	17.2 (0.82)	13.5 (0.64)
- RI ($MJm^{-2}d^{-1}$)	8.1 (1.00)	7.6 (0.94)	5.9 (0.73)
- RUE (g dry matter MJ^{-1})	2.59 (1.00)	2.27 (0.88)	2.30 (0.89)

photosynthesis of the surrounding green leaf tissue, and therefore related to disease severity. Disease severity of both plots was nearly the same (Table 4.1). The difference in CGR of plot B and C was therefore mainly due to the difference in RI, and reflected the difference in fraction dead leaf area that existed due to a difference in onset of the epidemic.

Sensitivity analysis

A sensitivity analysis was carried out with a canopy identical to the average canopy observed in plot B. The analysis was focused on model parameters which characterize the effect of leaf blast on photosynthesis and respiration ($\beta_{P_{max}}$, β_{ε} and ρ). The standard values of these parameters were reduced and increased with their standard error, and the model was run after every parameter change. The resulting reduction or increase in the simulated reduction in CGR was determined and expressed as a percentage of the simulated reduction in CGR due to blast lesions (Table 4.4). In addition, the relative sensitivity of the parameters with respect to the reduction in CGR was calculated. Relative sensitivity was defined as the ratio of percentage change in simulated reduction and percentage change in parameter input value. Typical weather data for a clear and a cloudy day were obtained from IRRI's meteorological station, and used to compare sensitivity under various weather conditions.

Calculation of the ratio between the standard error and the mean of the

Table 4.4 Sensitivity of the simulated reduction in crop growth rate of rice to changes in model parameters that characterize the effect of leaf blast on CO_2 assimilation rate at light saturation ($\beta_{P_{max}}$), initial light use efficiency (β_{ε}) and dark respiration (ρ). The simulated percentage change in the reduction in crop growth rate due to a change in input value equal to the standard error (σ) of the respective parameter is given. Relative sensitivity (RS) was calculated as the ratio of percentage change in the reduction in crop growth rate and percentage change in input parameter. The analysis was performed for a clear and a cloudy day, using the rice crop in plot B. Only the reduction in crop growth rate due to blast lesions was considered.

| | Standard values[a] | σ | Clear day | | | Cloudy day | | |
| | | | Reduction | | | Reduction | | |
			$-\sigma$	$+\sigma$	RS	$-\sigma$	$+\sigma$	RS
$\beta_{P_{max}}$	3.7	0.6	−6%	+6%	+0.39	−2%	+2%	+0.15
β_{ε}	3.0	0.7	−10%	+10%	+0.44	−15%	+15%	+0.64
ρ	4.5	1.3	−2%	+2%	+0.08	−4%	+4%	+0.12

[a] Parameter values and their standard error were derived from Bastiaans (1991 & 1993a).

various parameters gave values of 0.16, 0.23 and 0.29 for $\beta_{P_{max}}$, β_ε and ρ, respectively. This demonstrates that the estimated value of respiration parameter ρ is less reliable than the estimated values of the photosynthesis parameters. On the other hand, comparison of relative sensitivities demonstrates that the simulated CGR is more affected by changes in one of the photosynthesis parameters than by changes in ρ (Table 4.4). On a clear day $\beta_{P_{max}}$ and β_ε were found equally important. On a cloudy day the simulated reduction in CGR was more sensitive to changes in β_ε than to changes in $\beta_{P_{max}}$, as large fractions of leaf area received low light intensities during a large fraction of the day. The reliability of the estimated parameter value and the relative sensitivity of the parameter in the model both influenced the percentage change of the simulated reduction in CGR given in Table 4.4. The result clearly indicates that, with respect to the simulation of the reduction in CGR due to leaf blast, the estimation of β_ε is the weakest link.

Vertical disease distribution

Daamen (1989) described vertical distribution of mildew in wheat by a simple power function:

$$CA_{lesion} = (CA_{leaf})^b \tag{4.1}$$

in which CA_{lesion} is the cumulative lesion area divided by the total lesion area, and CA_{leaf} is the same quotient for green leaf area. Both variates were calculated from top to bottom of the canopy. Parameter b describes the steepness of the gradient. A value of 1.29 gave a good description of the vertical distribution of leaf blast observed in plot B. The model was used to determine values of b resulting in a 5% deviation of the simulated reduction in CGR due to blast lesions. Small changes in the steepness of the disease gradient already caused such a deviation, indicating that simulated CGR is sensitive to vertical disease distribution (Fig. 4.5B). In a further analysis the canopy was dissected in five layers of equal leaf area. For each layer the severity which resulted in a 5% deviation of the reduction in CGR due to blast lesions was determined (Fig. 4.5C). The analysis demonstrated that the model is more sensitive to changes in disease severity in the top of the canopy, than to changes in severity in lower canopy layers. Lesions in the top layers of the canopy thus contribute more to the reduction in CGR.
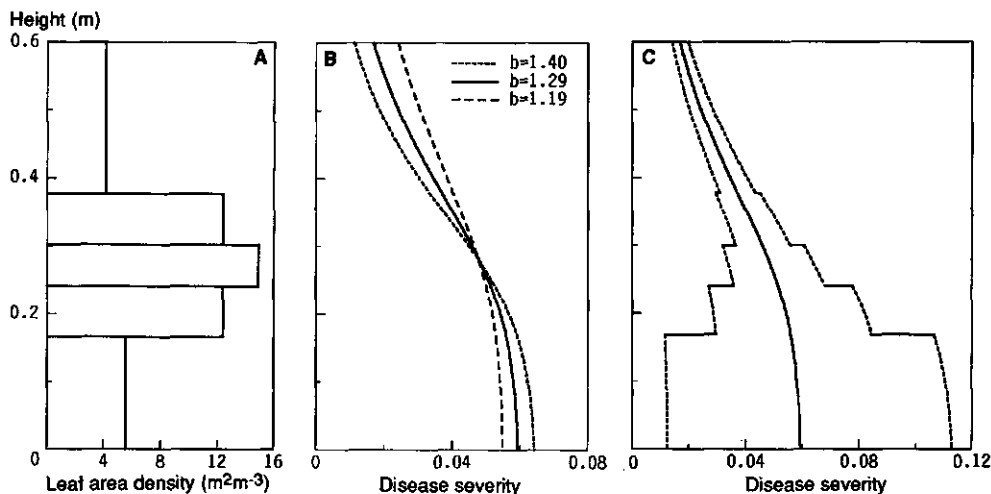
Figure 4.5 Vertical distribution of leaf area (A) and disease severity (B, C) as observed in plot B. The rectangles in A represent five layers of equal leaf area. A power function was used to describe actual disease distribution (b=1.29) and distributions leading to a 5% deviation in the simulated reduction in crop growth rate due to blast lesions (B). The higher sensitivity for disease present in the top of the canopy is illustrated by indicating, layerwise, the change in severity required for a 5% deviation in the simulated reduction in crop growth rate due to blast lesions (C).

4.4 Discussion

Photosynthesis of rice canopies in the noninoculated plots was accurately simulated with the model. This emphasizes the soundness of the well documented photosynthesis and respiration routines, as was previously demonstrated by Kropff and Goudriaan (1989). Likewise the reduction in CER due to leaf blast was properly simulated. This illustrates that the identified damage mechanisms adequately explain the observed reduction in canopy photosynthesis. CGR's of canopies suffering from leaf blast are reduced through a reduction in both radiation use efficiency (RUE) and radiation interception by green leaf area (RI). Although Waggoner and Berger (1987) claimed that yield loss in most pathosystems can be explained through a reduction in RI, several other diseases are reported to affect RUE as well as RI (e.g. *Cercospora* sp. leafspot in peanuts (Boote et al., 1980) and *Verticillium dahliae* in potato (Bowden and Rouse, 1991)). The contribution of both components to the overall reduction varies and is related to the relative extent of diseased and dead leaf area.

The three plots in the experiment represent rice crops at various stages of infection, offering the opportunity to theorize about the way the reduction in

50

CGR evolves. After infection with *P. oryzae* lesions develop. The most prominent effect of these lesions is an inhibitory effect on photosynthesis of the surrounding green leaf tissue, which causes a reduced RUE. Simultaneously the lesions decrease the amount of green leaf area, herewith reducing RI. Newly emerging leaves become infected, whereas earlier infected leaves are subject to an accelerated senescence. As a result, the fraction diseased leaf area remains more or less constant, whereas the fraction dead leaf area increases. Consequently, the reduction in CGR will increase as a result of an increased reduction in RI (Fig. 4.6). 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.

The reduction in leaf photosynthetic rate in dependence of leaf blast severity is represented by a curvilinear relation. Non-linearity means that use of averages should be avoided, since their use may lead to serious over- or underestimations (de Wit & van Keulen, 1987; Nonhebel, 1992). In the present
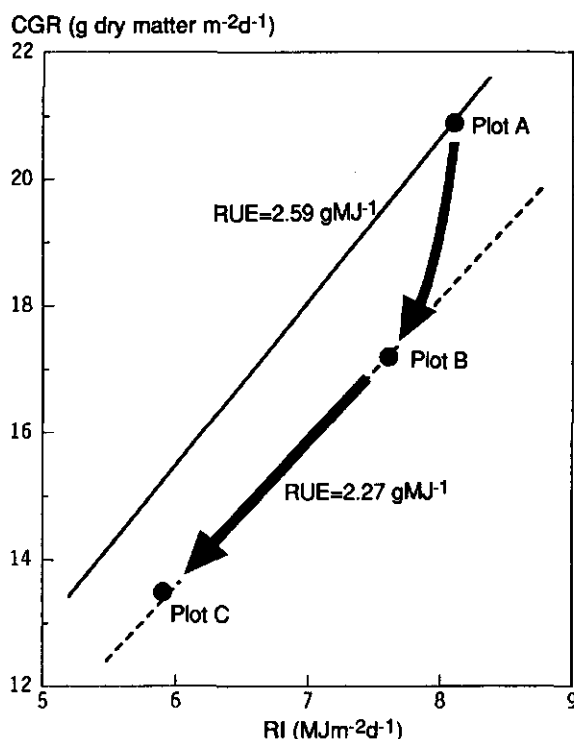
Figure 4.6 Simulated crop growth rate (CGR; g dry matter $m^{-2}d^{-1}$), radiation interception by green leaf area (RI; $MJm^{-2}d^{-1}$) and radiation use efficiency (RUE; g dry matter MJ^{-1}) of the rice crop in the three experimental plots. The arrows illustrate the hypothesis on the time course of the reduction in CGR due to leaf blast.

case this implies that instead of an average disease severity for green leaf tissue, the leaves should be classified according to disease severity. Photosynthesis parameters ($P_{g,max}$, ε) and the corresponding rate of photosynthesis should be calculated for each category and their contributions should be added to obtain the rate of crop photosynthesis. A more detailed examination demonstrated that in the present case the error caused by the use of an average severity is relatively small compared to the error caused by uncertainty in $\beta_{P_{max}}$ and β_{ε}. This is mainly due to the fact that leaves with a disease severity exceeding 0.30 are hardly found, since these leaves generally die. Moreover, the function that is used to describe the relation between disease severity and $P_{g,max}$ and ε is fairly linear up to a disease severity of 0.30 (Bastiaans, 1991). Saturation would only appear at higher disease severities. This justifies the use of an average disease severity in case of the simulation of the reduction in CGR of rice due to leaf blast.

Vertical disease distribution was recognized as an important determinant of the reduction in CGR. The analysis revealed that lesions in the top layers of the canopy contribute more to the reduction in CGR than lesions on leaves in lower layers. Since the effect of the lesions on $P_{g,max}$ and ε differs only slightly, this difference is mainly a reflection of the photosynthesis profile of the canopy, which depends to a great extent on light distribution. The observation implies that recognition of a vertical disease profile becomes particularly important in crops with higher LAI's, since in these situations a considerable difference exists between the contribution of upper and lower layers to the overall photosynthetic rate of the canopy. In general, disease monitoring for crop loss assessment should account for vertical disease distribution, or concentrate on the upper layers. In EPIPRE, a disease and pest warning system for wheat, this principle is already applied for powdery mildew and *Septoria* sp., as disease monitoring is restricted to the upper three leaves (Zadoks, 1989). The presently developed model for effects of leaf blast on canopy photosynthesis of rice may contribute to the determination of an optimal sampling procedure for leaf blast in rice.

Identification of the mechanism responsible for yield reduction in case of leaf blast in rice

L. BASTIAANS

Department of Theoretical Production Ecology, Wageningen Agricultural University, P.O. Box 430, 6700 AK Wageningen, The Netherlands

Abstract. Rice crops grown under irrigated conditions were inoculated with *Pyricularia oryzae* during early growth stages to study the effect of leaf blast on yield formation. The inoculations led to severe epidemics of leaf blast around maximum tillering, characterized by the presence of typical blast lesions and an accelerated senescence of heavily infested leaf tissue. Leaf blast led to a prolonged tillering and a delay in flowering and maturity.

Crop growth and leaf area formation declined sharply during establishment of the disease and continued to be reduced till maturity. This resulted in a marked reduction of total dry matter production and grain yield. Dry matter distribution was not affected. Leaf blast reduced spikelet number, 1000 grain weight, and the number of filled grains. From this last observation it was concluded that the reduction in grain yield was exclusively source determined.

Nitrogen uptake of the inoculated crops before flowering was reduced compared to the N uptake of the control crop, but shoot N content of the inoculated crops at flowering was higher. Uptake of nitrogen after flowering was negligible in both healthy and inoculated crops. Redistribution from vegetative tissue was therefore the main source of N for grain growth. The higher N content of the shoot organs in the inoculated crops during ripening led to the conclusion that the reduced N supply was not a limiting factor during grain growth. Consequently, the reduction in grain yield was solely determined by a reduced carbohydrate supply.

5.1 Introduction

Rice blast caused by *Pyricularia oryzae* Cavara is an important constraint in the production of rice (*Oryza sativa* L.). Rice plants are most susceptible to *P. oryzae* in the seedling, early tillering and heading stages of the crop (Anderson et al., 1947). During early growth stages symptoms are mainly found on leaves, and referred to as leaf blast (Ou, 1985). Leaf blast severity usually reaches its peak around maximum tillering, followed by a gradual disappearance of the disease. This gradual decline has been attributed to adult plant resistance (Torres, 1986; Yeh and Bonman, 1986; Koh et al., 1987). Consequently, leaf blast is mainly present before flowering. This period is characterized by the formation of source and sink capacity for yield formation, whereas sink filling only occurs after flowering (Evans, 1975). Leaf blast thus mainly affects grain yield indirectly. Identification of the mechanism of yield reduction was the aim of the present study.

Leaf blast primarily reduces carbohydrate production. This reduction is caused by an effect of blast lesions on leaf photosynthetic rate and respiration (Bastiaans, 1991 & 1993a). Associated with the reduction in carbohydrate

production is a reduction in crop growth and leaf area formation. The positive feedback between radiation interception, crop growth and leaf area formation during early growth stages (Blackman, 1919) further enhances the negative effect of the disease on crop growth. The existence of this feedback mechanism enables the growth reducing effect of the disease to continue even after disappearance of the disease, as was previously demonstrated for the powdery mildew-spring barley pathosystem (Lim and Gaunt, 1986). In case of heavy infestations of leaf blast, the feedback mechanism is further enhanced by an accelerated senescence of infested leaf tissue (Bastiaans and Kropff, 1993). 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, may reduce grain yield formation.

The utilization efficiency of intercepted radiation during grain filling is another important determinant of carbohydrate supply in this period. In rice, just as in other crop species, the maximum rate of leaf photosynthesis is almost proportional to the fraction N in leaves (Cook and Evans, 1983). Uptake of N after flowering is low (Akita et al., 1987) 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 in the crop at flowering may thus eventually limit yield. A reduced N uptake before flowering is therefore a second mechanism through which leaf blast may indirectly reduce grain yield formation.

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 is referred to as maximum eventual yield (Matsushima, 1970). If leaf blast reduces maximum eventual yield more than proportionally the reduction in grain yield may be sink determined. A reduced sink formation is therefore a third mechanism through which leaf blast may reduce grain yield formation.

The aim of the present study was to identify the mechanism(s) through which the initial reduction in crop growth rate before flowering eventually limits grain yield in case of leaf blast in rice. For this purpose a field experiment was conducted in which the effect of the disease on various processes was studied through periodic harvesting. Analysis of the experimental

data was used to determine whether the reduction in grain yield was source (carbohydrate or nitrogen) or sink determined.

5.2 Material and methods

Plant material and inoculation

From December 1990 till April 1991 a field experiment was conducted at the lowland research site of the International Rice Research Institute (IRRI), Los Baños, Philippines. A randomized complete block design with five replicates was used. Plot size was 43.2 m^2 (12 x 3.6 m). On 5 December 1990 12-day-old rice seedlings of cultivar IR50 were transplanted at three plants hill^{-1} and hill spacing of 0.20 x 0.20 m. Frequency and timing of inoculations and fungicide applications varied per treatment to establish three levels of leaf blast (Table 5.1). Inoculum (*P. oryzae*; isolate Po6-6) was prepared as described by Mackill and Bonman (1986) and the spore density was adjusted to 75000 conidia ml^{-1}. Gelatine was added to the inoculum in a concentration of 2.5 gL^{-1}. Per inoculation 5 L of inoculum was sprayed per plot. The night after inoculation plots were covered by plastic, to increase leaf wetness duration. Covering was repeated during the following three nights, after spraying of 5 L distilled water per plot. After a period of uncontrolled development edifenphos (Hinosan) and pyroquilon (Coratop 2.7G) were used to repress the leaf blast

Table 5.1 Time schedule of inoculations (– = no inoculation, + = inoculation with *Pyricularia oryzae*) and fungicide applications (– = no application, H = spraying of Hinosan, C = application of Coratop 2.7G), used to regulate leaf blast severity in various treatments of a field experiment with rice.

|	Days after transplanting	Treatment A	B	C
Inoculation				
17 December	12	–	–	+
27 December	22	–	–	+
2 January	28	–	+	–
Fungicide application				
27 December	22	H	–	–
8 January	34	H	–	H
11 January	37	H	H	H
14 January	40	C	C	C
18 January	44	H	H	H

epidemic.

Fertilizer inputs consisted of a basal N-P-K application (60-50-50 kg ha^{-1}) one day before transplanting. Additional nitrogen was applied at 22, 49 and 56 days after transplanting (DAT) at rates of 30, 20 and 20 kg N ha^{-1}. All N was applied as ammonium-sulphate. Floodwater was introduced immediately after transplanting and kept at 5-10 cm depth. Previous to an inoculation the entire field was drained for one day to obtain plants with a slight water stress. Floodwater was reintroduced at the afternoon following inoculation. Fortnightly application of triazophos (Hostathion) was used to control insects. Neck blast infections were prevented by applying pyroquilon at booting (50 DAT) and three sprayings of edifenphos starting at first heading (60, 68 and 76 DAT). Weeds were controlled by handweeding.

Plant sampling

From 13 DAT till maturity plant samples were collected for the determination of disease severity; tiller number; leaf area index (LAI); leaf blade, stem and panicle dry weight; and N content of green leaf tissue. Plant samples were collected with intervals varying from 3 till 9 days, depending on disease progress. Sampling intervals were smallest from 26 till 48 DAT, when disease developed most rapidly. Sample size was 18 hills (0.72 m^2) before flowering (63 DAT) and 24 hills (0.96 m^2) from flowering till maturity. Six hills were used for detailed observations. The remaining hills were cut to pieces, ovendried and weighed, for a more accurate determination of accumulated dry matter.

Disease severity, defined as the fraction of green leaf area covered by lesions, was estimated by scoring the number and size of lesions on a randomly selected leaf sample. Leaf area was measured using a leaf area meter (LI-COR, USA), and determined for green and dead leaf tissue separately. Tissue dry matter was determined separately for green leaf blades, dead leaf blades, stems and leaf sheaths, and emerged panicles after oven-drying at 70 $^{\circ}$C. Total N in green leaf tissue was analysed using the Kjeldahl method. From 48 DAT total N in all shoot components was determined with the same method, and used to study N translocation during ripening.

At maturity, a grain sample collected from a 5 m^2 harvest area per plot was oven-dried and weighed. Grain yield (rough rice) was expressed at 140 g moisture kg^{-1}. Six rice hills were processed separately and used for yield component analysis.
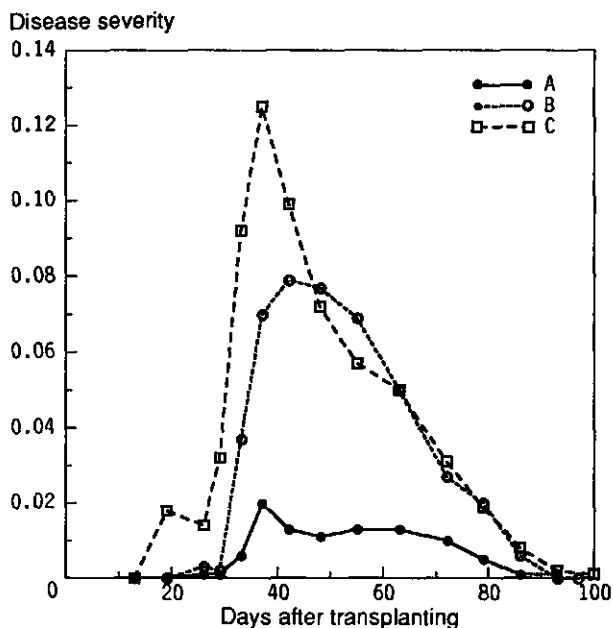
Figure 5.1 Time course of severity of rice leaf blast in a control crop (A) and in crops inoculated with *Pyricularia oryzae* (B, C).

5.3 Results

Disease development

In treatment C the earliest blast lesions appeared five days after the first inoculation with *P. oryzae*. Disease severity remained low and therefore a second inoculation was carried out at 22 DAT. This inoculation was more successful, and a rapid increase in disease severity was observed (Fig. 5.1). Starting from 34 DAT, fungicides were applied to hamper a further development of the disease (Table 5.1), since at that stage the first tillers died as a result of infection. Disease severity arrived at its peak a couple of days after the first fungicide application. From then onwards a gradual decline in disease severity was observed, resulting from the dying of heavily infested leaf tissue and the formation of new green leaf tissue. During ripening most of the remaining blast lesions were observed in the lower part of the canopy.

In treatment B the first inoculation at 28 DAT was succesfull, and disease severity increased rapidly. A gradual decline in disease severity began shortly after the first fungicide application at 37 DAT.

Despite the regular application of fungicides, the control crop (treatment A)

58
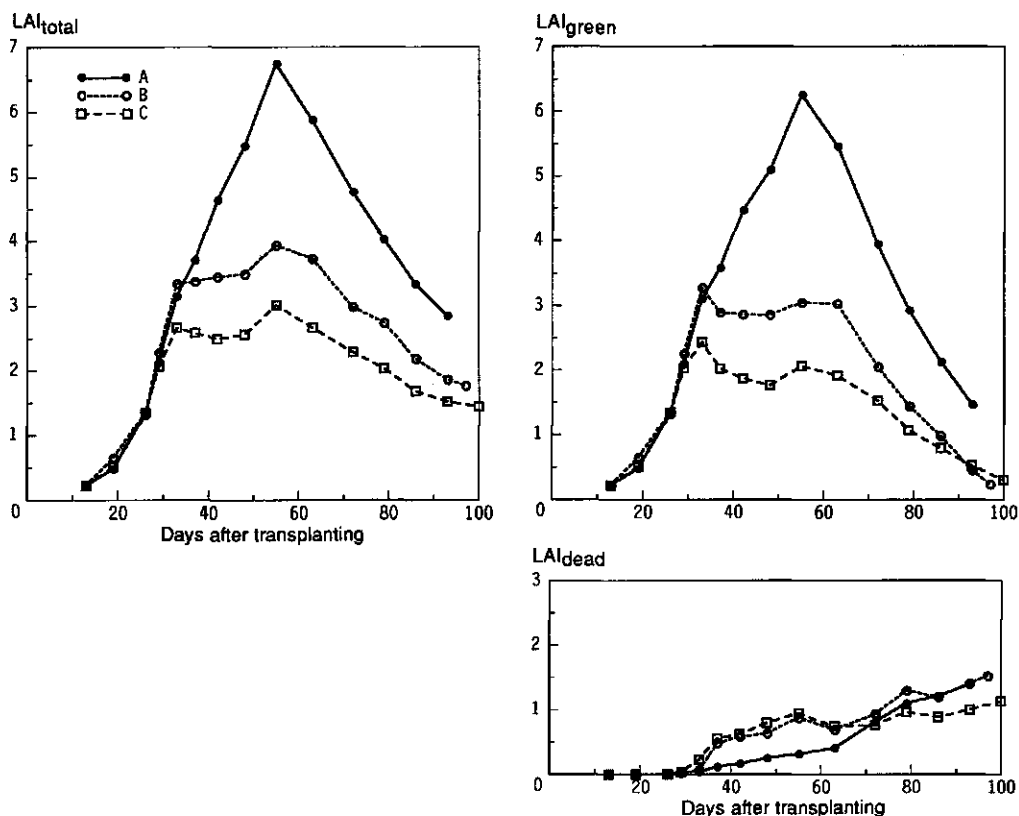
Figure 5.2 Time course of total (LAI$_{total}$), green (LAI$_{green}$) and dead (LAI$_{dead}$) leaf area (ha ha^{-1}) of rice in a control crop (A) and in crops inoculated with *Pyricularia oryzae* (B, C).

was not entirely free of leaf blast. Disease severity was, however, kept at a low level. The application of fungicides used to prevent blast infections on neck node and panicle were effective in all treatments. Symptoms were rare and not scored. No significant injury due to insect pests was observed.

Leaf area

The rapid increase in disease severity in the inoculated crops was followed by an accelerated senescence of heavily infested leaf tissue, beginning at 30-35 DAT (Fig. 5.2). Then the amount of green leaf area was slightly reduced for about 15-20 days. Apparently, the rate of production of new green leaf tissue could not keep pace with the rate of senescence. Total leaf area in the inoculated crops remained constant during this period, and a clear difference developed with the LAI of the control crop. An increase in total and green leaf area of the

59
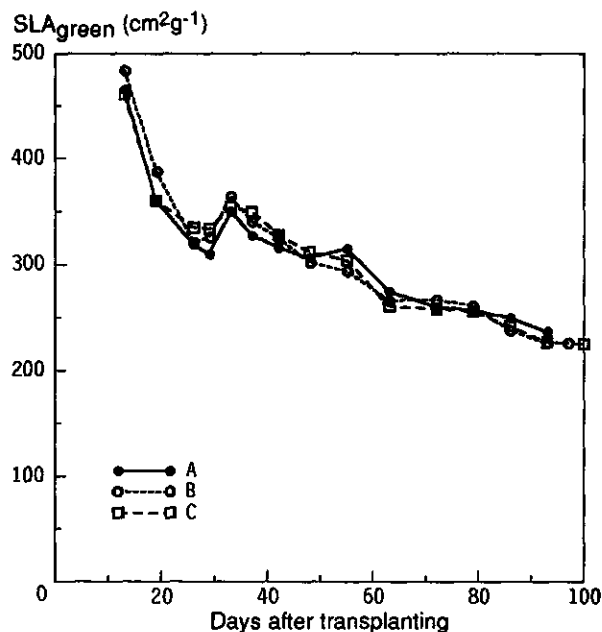
Figure 5.3 Time course of specific leaf area of green tissue (SLA$_{green}$; cm^2 g^{-1}) of rice in a control crop (A) and in crops inoculated with *Pyricularia oryzae* (B, C).

inoculated crops was observed after 48 DAT, and coincided with a recovery in dry matter production.

A sharp decline in total and green leaf area began at 55 DAT, shortly before flowering. This reduction was observed in all plots and continued till maturity. The reduction in green leaf tissue (on a weight basis) followed an exponential decline. The relative death rate (RDR) of the control crop (0.05 d^{-1}) was identical to the RDR of treatment C, whereas the RDR of treatment B was slightly higher (0.06 d^{-1}).

Specific leaf area (SLA) of green leaf tissue was not affected by blast (Fig. 5.3).

Dry matter production and distribution

The time course of dry matter production is given in Figure 5.4. A significant reduction in dry matter growth was observed in the inoculated crops. Reduction became noticeable at the transition from the exponential to the lineair growth phase (25-35 DAT). This transition coincided with the rapid increase in disease severity in the inoculated crops. Growth rate in the inoculated crops remained

60
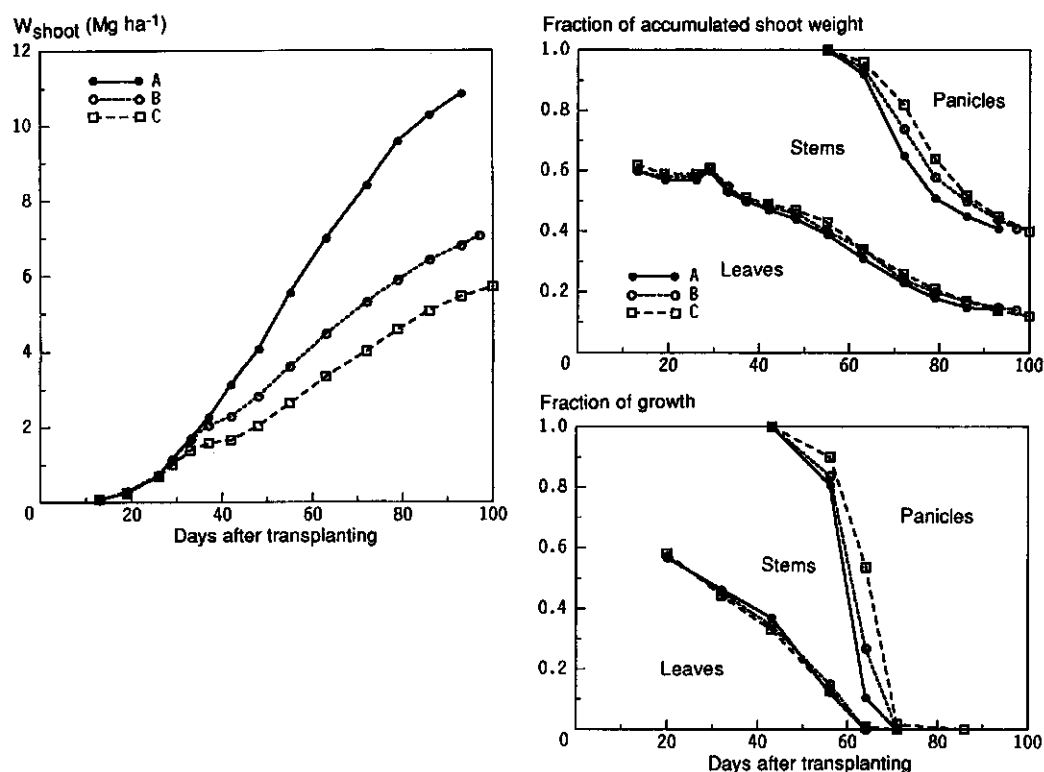
Figure 5.4 Time course of total above ground dry matter (W_{shoot}; Mg ha^{-1}) of rice in a control crop (A) and in crops inoculated with *Pyricularia oryzae* (B, C). Distribution of the accumulated dry matter over the various shoot organs and the ditribution pattern of newly produced dry matter are also presented as a function of time.

low for about 10 to 14 days. The inoculated crops gradually recovered, and a linear increase in accumulated dry matter was observed, starting from 48 DAT. Growth rate in the inoculated crops (99 and 82 kg dry matter ha^{-1}d^{-1} for treatment B and C, respectively) remained significantly lower than in the control crop (175 kg dry matter ha^{-1}d^{-1}). A decline in crop growth rate at the end of the ripening phase was apparent in all crops. The inoculated crops matured later than the healthy crop (4 and 7 days for treatment B and C, respectively). Duration of the ripening phase was not affected, since flowering was delayed to a similar extent.

In Figure 5.4 the distribution of accumulated dry weight over the various shoot organs is given. The observed distribution was used to derive the allocation pattern of newly produced dry matter, which is also presented in Figure 5.4. A distinction was made between leaf blades, stems (including leaf sheaths) and panicles. Distribution of dry weight over leaf and stem was not

61

affected. Panicle growth in the inoculated crops was delayed compared to the control crop. This delay corresponded with the delay in flowering. At maturity no significant differences between the dry matter distribution of inoculated and control crops were observed.

The amount of stem reserves allocated to the grains was estimated as the difference in weight of the stems at flowering and maturity. The contribution of stem reserves to the overall grain production was 30% in healthy and inoculated crops.

Yield and yield components

Grain yield was markedly reduced in the inoculated crops and this reduction reflected the reduction in dry matter production (Table 5.2). Yield component analysis demonstrated a small increase in panicle number, and small decreases in 1000-grain weight and fraction filled spikelets. The main effect of leaf blast on yield components however, was a reduction in the number of spikelets per panicle. This component alone explained about 85% of the reduction in grain yield.

The observed increase in panicle number was associated with a prolonged tillering (Fig. 5.5). Consequently, heading and maturity were delayed, and an increased variability in the development of individual tillers was observed. At maturity tiller number was still more than 10% higher than in the control crop. Differences in panicle number were much smaller, due to a higher fraction non-productive tillers in the inoculated crops. Unripe panicles, non-panicle bearing tillers and dead tillers contributed to the high number of non-

Table 5.2 Dry matter production, grain yield and yield components of rice cultivar IR50 as observed in the control crop (A) and in crops inoculated with *Pyricularia oryzae* (B, C).

| | Treatment | | | | | | | | |
	A			B			C		
Total dry matter (Mg ha⁻¹)	10.9	(100)	(a)[a]	7.1	(65)	(b)	5.7	(52)	(c)
Grain yield (Mg ha⁻¹)[b]	6.7	(100)	(a)	4.3	(64)	(b)	3.5	(52)	(c)
panicle number (m⁻²)	581	(100)	(a)	605	(104)	(b)	623	(107)	(c)
spikelets panicle⁻¹	64.8	(100)	(a)	44.6	(69)	(b)	37.1	(57)	(c)
filled spikelets	0.85	(100)	(a)	0.80	(94)	(b)	0.78	(92)	(b)
1000-grain weight (g)[b]	21.1	(100)	(a)	20.1	(95)	(b)	19.7	(93)	(b)

[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
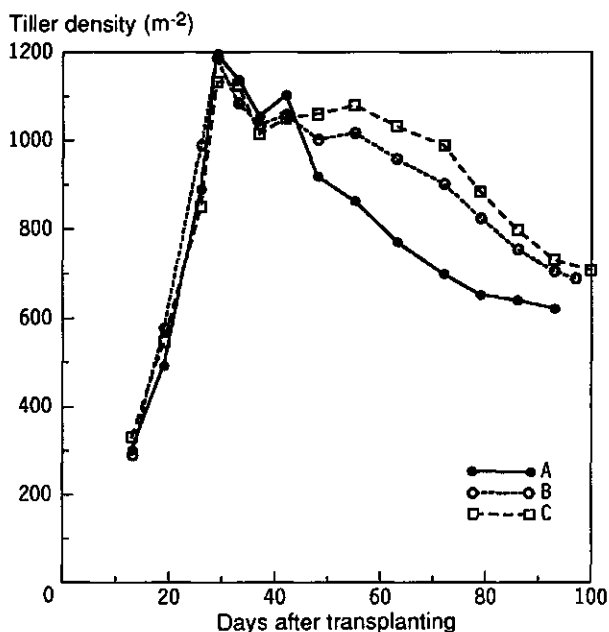
Figure 5.5 Time course of total tiller number (m^{-2}) of rice in a control crop (A) and in crops inoculated with *Pyricularia oryzae* (B, C).

productive tillers.

N-crop status and translocation

N content of green leaf tissue was determined throughout the season (Fig. 5.6). In the noninoculated crop N content was stable till 26 DAT. A sharp decline in N content till 37 DAT was then followed by a more gradual decline towards maturity. N content of green leaf tissue in the inoculated crops was identical to the N content of the control crop till 37 DAT. Later the N content was on average 0.4 and 0.8 mg g^{-1} higher in treatments B and C, respectively. Redistribution of N from dead leaf tissue may have contributed to this increased N content in green leaf tissue.

Total shoot N and its distribution over the various organs was determined starting from 48 DAT. There was a considerable N uptake between 48 and 63 DAT, but N uptake after flowering was negligible (data not shown). A clear difference in total shoot N during ripening was present between the control and the inoculated crops (on average 122, 88, and 70 kg N ha^{-1} for treatments A, B, and C, respectively). Although N uptake in the inoculated crops was
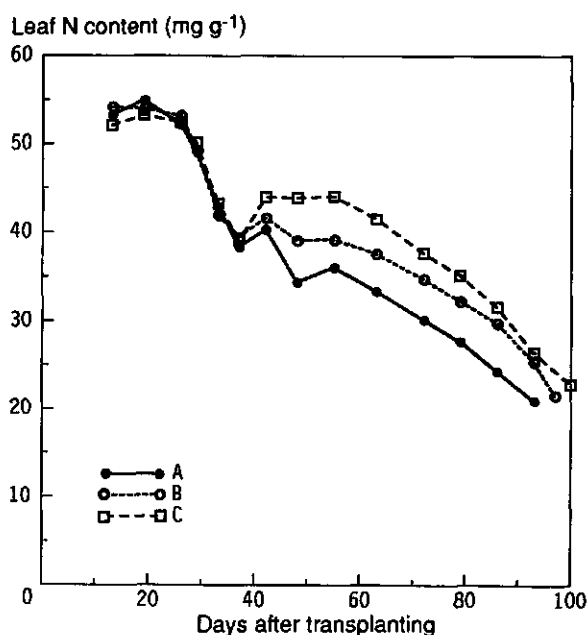
Figure 5.6 Time course of N content of green leaf tissue (mg g^{-1}) of rice in a control crop (A) and in crops inoculated with *Pyricularia oryzae* (B, C).

Table 5.3 Nitrogen content (N; mg g^{-1} dry weight) and the distribution of dry matter over the various shoot organs (F_{dm}), at flowering and maturity, of a control crop (A) and of crops inoculated with *Pyricularia oryzae* (B, C). Both observations were used to calculate the distribution of nitrogen over the various shoot organs (F_N).

	N			F_{dm}			F_N		
	A	B	C	A	B	C	A	B	C
Flowering									
Leaf									
- green	33.4	36.4	38.5	0.28	0.21	0.17	0.53	0.41	0.35
- dead	15.2	15.3	15.8	0.03	0.09	0.11	0.03	0.07	0.09
- total	31.6	30.1	29.6	0.31	0.30	0.28	0.56	0.48	0.44
Stem	11.2	13.7	14.4	0.61	0.58	0.59	0.39	0.42	0.45
Panicle	11.2	14.9	15.4	0.08	0.12	0.13	0.05	0.09	0.11
Total	17.5	18.7	18.9	1.00	1.00	1.00	1.00	1.00	1.00
Maturity									
Leaf									
- green	21.0	21.6	22.8	0.05	0.02	0.02	0.10	0.03	0.05
- dead	8.7	12.6	12.3	0.09	0.12	0.10	0.07	0.12	0.10
- total	13.2	13.1	14.8	0.14	0.14	0.12	0.17	0.15	0.15
Stem	6.3	7.9	8.0	0.27	0.27	0.28	0.15	0.18	0.18
Panicle	12.9	13.7	13.6	0.59	0.59	0.60	0.68	0.67	0.67
Total	11.2	12.1	12.2	1.00	1.00	1.00	1.00	1.00	1.00

Table 5.4 Nitrogen accumulation in the rice panicle during ripening and the estimated contribution of reallocation from leaf and stem in a control crop (A) and in crops inoculated with *Pyricularia oryzae* (B, C). Nitrogen reallocation from root to panicle was considered as nitrogen uptake.

| | Treatment | | |
	A	B	C
N accumulation in the panicle during ripening (kg ha^{-1})	77	50	40
Estimated N reallocation from leaf tissue (kg ha^{-1})	43	26	17
Estimated N reallocation from stem tissue (kg ha^{-1})	29	22	19
Estimated N uptake during ripening (kg ha^{-1})	5	2	4
Ratio between N reallocation from leaf and stem tissue	1.5	1.2	0.9

reduced, shoot N content was higher. The same was true for the N content of green leaf tissue, dead leaf tissue, stem material, and the panicle (Table 5.3). Contrary to the distribution of dry matter, the distribution of N over the various shoot organs at flowering was affected as a result of the disease. The fraction of total N present in the leaves varied from 0.56 in the control crop, to 0.44 in the most heavily infested crop. This difference was related to the higher fraction dead leaf tissue of the inoculated crop. At maturity, the distribution of N over leaf, stem and panicle in healthy and inoculated crops was almost identical. About two thirds of total shoot N was present in the panicle. The remaining part was about equally distributed over leaf and stem.

The data in Table 5.3 were used to calculate the translocatable N in the vegetative tissue at flowering and maturity. Non-remobilizable N concentrations of 7.5 and 3.0 mg N g^{-1} in leaf and stem tissue respectively were used in these calculations (Penning de Vries et al., 1990). Translocation from dead leaf tissue was excluded, and the fraction non-structural stem material at flowering was assumed to be 0.30 (Yoshida, 1981). The difference in translocatable N at flowering and maturity is a reasonable estimate of N reallocation from vegetative tissue to the panicle (Spiertz & van Keulen, 1980). In the inoculated crops a clear increase in the relative contribution of the stem to the overal N reallocation was observed (Table 5.4).

5.4 Discussion

Total above ground dry weight of crops inoculated with *P. oryzae* was markedly reduced. The reduction in crop growth rate became noticeable shortly after the onset of the disease. The initial reduction in crop growth rate can be attributed to the direct effect of blast lesions on photosynthesis and

respiration of infected leaf tissue (Bastiaans, 1991 & 1993a). The succeeding increase in dead leaf area, resulting from accelerated senescence of heavily infested leaf tissue, further enhanced the reduction in crop growth rate (Bastiaans and Kropff, 1993). Associated with the reduction of crop growth was a reduction in leaf area formation. As a result radiation interception was affected, which in turn contributed to the reduction in dry matter production. A more detailed analysis of the reduction in dry matter production will be given in a next paper (Bastiaans, 1993c).

The reduction in grain yield reflected the decrease in total shoot dry weight, since leaf blast did not affect the distribution of dry matter over the various shoot organs. Harvest index for both healthy and inoculated crops was about 0.53, a common value for modern rice varieties (Yoshida, 1981). Reduction in grain yield and total dry matter production in the earliest inoculated crop (treatment C) was 48%, compared to 36% in the crop that was inoculated one to two weeks later (treatment B). These reductions lie within the broad range of yield losses due to leaf blast reported in other studies (0-80%: Goto, 1965; Tsai, 1988b). The effect of leaf blast on shoot/root-ratio was not investigated.

Leaf blast reduced the number of spikelets per m^2 and the 1000 grain weight. Both components are mainly determined before heading, and their product is defined as maximum eventual yield (Matsushima, 1970). Slight modifications in 1000 grain weight after heading are possible. However, 1000 grain weight of rice is primarily controlled by the size of the hulls, which is determined before heading. During ripening the fraction of filled grains governs the ratio between actual and maximum eventual yield. In the control plot this ratio was 0.85, a common value for rice grown under normal conditions (Yoshida, 1981). Leaf blast significantly reduced the fraction of filled grains, indicating that the extent of the reduction in grain yield was predominantly 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 of filled grains due to leaf blast.

The reduction in spikelet number in this experiment resulted from a slight increase in panicle number and a strong reduction in number of spikelets per panicle. The early inoculations led to low LAI's, and the absence of dominating tillers. Consequently, tillering was prolonged. During spikelet formation the combination of a low LAI and a high tiller number led to a low growth rate per tiller, and accordingly to the formation of a low number of spikelets per tiller. This observation endorses the ability of the rice crop to tune sink capacity to source capacity throughout its development, as was extensively demonstrated by Matsushima (1970). Goto (1965) did not report the time of inoculation, but in

his experiment the reduction in spikelet number resulted from a strong reduction in panicle number and a slight increase in spikelets per panicle. Such a combination would be expected with infections in the late tillering or early reproductive phase, when compensation through tillering is excluded.

Nitrogen uptake in the inoculated crops was markedly reduced. 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 was increased. This indicates that N uptake before flowering was less reduced than dry matter production. A limited uptake of N after flowering is a common observation in rice (Akita et al., 1987). Consequently, redistribution from vegetative tissue was the main source of N for grain growth. In the inoculated crops the high fraction dead leaf tissue reduced the relative contribution of N reallocation from leaf tissue. Accordingly, the relative contribution of reallocotion from stem tissue increased. As the N content of the shoot organs in the inoculated crops during ripening was higher than in the control crop, N supply was not a limiting factor during grain growth.

The analysis demonstrates that the reduction in grain yield formation is exclusively caused by a reduced carbohydrate supply during grain filling. The carbohydrate supply during grain filling consists of two components: allocated stem reserves, which have been produced before flowering, and newly produced assimilates. Since the contribution of stem reserves to the overall grain production was 30% in healthy and inoculated crops, the reduction in both components was identical. The reduction in newly produced assimilates is caused by a reduced rate of carbohydrate production, since leaf blast did not affect the duration of the grain filling period. The reduction reflects the lower amount of green leaf area that was present in the inoculated crops during ripening. Obviously, the effects of leaf blast on leaf area formation and leaf senescence are responsible for the effect of the disease on yield formation.

Analysis of the reduction in dry matter production of rice due to leaf blast, using two models with different complexity

L. BASTIAANS

Department of Theoretical Production Ecology, Wageningen Agricultural University, P.O. Box 430, 6700 AK Wageningen, The Netherlands

Abstract. Effects of leaf blast on dry matter production of rice observed in a field experiment were analysed in terms of cumulative radiation interception by green foliage (PARCUM; MJm^{-2}) and radiation use efficiency (RUE; g dry matter MJ^{-1}). Leaf blast caused significant reductions in total dry matter production as a result of a decrease in PARCUM and a decrease in RUE. Reductions in intercepted radiation (RI; $MJm^{-2}d^{-1}$) and RUE were first observed shortly after the introduction of the disease. RI was significantly reduced till maturity. The reduction in RUE disappeared towards maturity, simultaneous with a gradual decline in disease severity.

Analysis with a mechanistic model of crop growth showed that previously determined effects of leaf blast on leaf photosynthetic rate and respiration could explain the reduction in RUE during a large part of the growing season. During the first weeks after the onset of the disease the two effects were insufficient to fully explain the observed reduction in RUE. It was hypothesized that the unexplained part of the reduction in RUE in that period was a result of carbohydrate withdrawal by the pathogen for spore production.

6.1 Introduction

Rice crops (*Oryza sativa* L.) inoculated with *Pyricularia oryzae* Cavara during early growth stages showed a reduced N-uptake, leaf area and sink formation (Bastiaans, 1993b). Analysis showed that the reduction in grain yield was solely source determined. The reduction reflected the reduction in total dry matter production, since the disease did not affect harvest index. In this paper the observed reduction in dry matter production is subjected to a more detailed analysis, using two crop growth models with different complexity.

Crop productivity can be analyzed in terms of solar radiation interception by green leaf area ($MJm^{-2}d^{-1}$) 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 RI and effects on RUE. Interpretation of leaf blast effects on canopy CO_2 exchange rate with a model for canopy photosynthesis, demonstrated that leaf blast reduced RI as well as RUE (Bastiaans and Kropff, 1993). The analysis was limited to one development stage of the crop (maximum tillering), at two to three weeks after inoculation. The first objective of the present study was to determine the time course of leaf blast effects on RI and RUE throughout the growing season.

A second model was used to analyse the causes of the reduction in the utilization efficiency of intercepted radiation. Previous studies indicated some

of the mechanisms through which leaf blast reduces RUE. It was found that blast lesions, apart from a reduction in photosynthetically active leaf tissue, reduced the photosynthetic rate of the remaining green leaf tissue (Bastiaans, 1991). Additionally, dark respiration was increased as a result of infection (Bastiaans, 1993a). The second objective of this study was to determine whether the effects of leaf blast on leaf photosynthetic rate and repiration could sufficiently explain the reduction in RUE throughout the growing season. For this purpose the two effects were introduced in a mechanistic model of crop growth. Shoot dry weights simulated with the crop growth model were compared with those obtained experimentally.

6.2 Materials and methods

Field experiment

The effect of leaf blast on a rice crop was studied in an experimental field at the lowland research site of the International Rice Research Institute (IRRI), Los Baños, Philippines. A randomized complete block design with three treatments in five replicates was used. One treatment was used as the control (treatment A), while the other two treatments were inoculated with *P. oryzae* during early (treatment C) and mid tillering (treatment B), 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. Disease development and the effect of the disease on crop growth were studied through frequent harvesting (Fig. 6.1). Further experimental details were given by Bastiaans (1993b).

Separating effects of leaf blast on crop growth in effects on RI and effects on RUE

Radiation interception of photosynthetically active radiation by green foliage (RI; $MJm^{-2}d^{-1}$) was calculated on a daily basis for every plot, using a model that consisted of the radiation routines of an elementary model of crop growth (Penning de Vries et al, 1989). Field observations on total leaf area, disease severity (fraction green leaf area covered by lesions) and fraction dead leaf area were used as model inputs. Values between observation dates were obtained by linear interpolation. Optical characteristics of diseased and dead

71
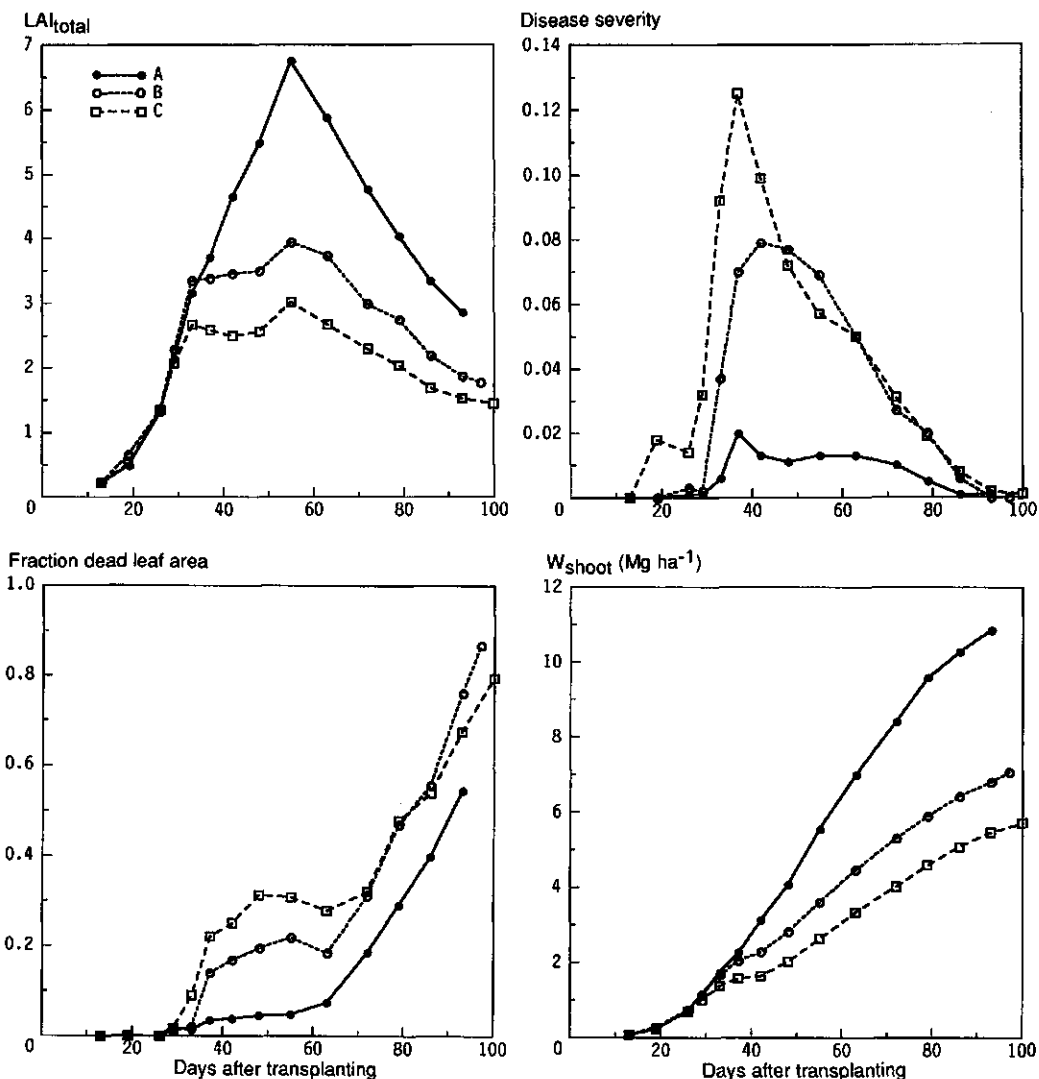
Figure 6.1 Time course of total leaf area (LAI_{total}; $ha ha^{-1}$), disease severity, fraction dead leaf area and shoot dry weight (W_{shoot}; $Mg ha^{-1}$) of rice in a control crop (A) and in crops inoculated with *Pyricularia oryzae* (B, C). Graphs summarize the results of a previously described field experiment (Bastiaans, 1993b).

leaf tissue were assumed to be identical to the characteristics of healthy leaf tissue. Data of daily total global radiation were obtained from IRRI's meteorological station. Photosynthetically active radiation (PAR; 400-700 nm) was assumed to be 50% of the total global radiation.

The model was used to calculate the daily amount of PAR that penetrated the canopy, and the daily amount of PAR that was transmitted by the canopy. Their difference equals the intercepted amount of PAR, which was multiplied

by the fraction green leaf area to obtain RI. The fraction green leaf area ($F_{LA_{green}}$) was calculated as:

$$F_{LA_{green}} = (1 - F_{LA_{dead}}) \times (1 - x) \qquad (6.1)$$

in which $F_{LA_{dead}}$ = fraction dead leaf area, and x = disease severity. The fraction intercepted radiation (RI_f) was defined as the ratio between RI and incident PAR.

Till flowering only one canopy layer was distinguished, and RI was calculated under the assumption that lesions and dead leaf tissue were homogeneously distributed in the canopy. After flowering natural senescence occurred, starting at the bottom of the canopy. To account for the uneven distribution of dead leaf tissue, four canopy layers were distinguished. Radiation interception was calculated per layer, starting at the top of the canopy. RI of the canopy was obtained by adding up the RI of the four layers.

Cumulative radiation interception (PARCUM; MJm^{-2}) was calculated for five successive periods of approximately two to three weeks. Radiation use efficiency (RUE; g dry matter MJ^{-1}) for each period was calculated by dividing the observed increase in total dry matter by PARCUM.

A further analysis of leaf blast effects on RUE

An extended version of the MACROS-L1D model, of which a comprehensive description is given by Penning de Vries et al. (1989), was used to simulate the growth of the rice crop in every plot. MACROS-L1D is an elementary crop growth model, which simulates the time course of dry matter production. The model simulates crop growth in production situations with an ample supply of water and nutrients, where growth is only determined by the incoming radiation, temperature and some physiological plant characteristics. The model operates with time steps of one day. The basis for the calculation of the daily dry matter production is the rate of gross CO_2 assimilation of the canopy. This rate is calculated from the radiation profile in the canopy and the assimilation response of individual leaves. Part of the carbon fixed by the assimilation process is respired to provide energy for the biological functioning of the crop (maintenance). The remainder is incorporated into structural dry matter (growth). This daily dry matter increase is distributed over the various plant organs, in dependence of the phenological development stage of the crop. Numerical integration in time gives the time course of dry matter.

73

Effects of leaf blast on photosynthesis and respiration were introduced in the original version of the model, in an identical way as described by Bastiaans and Kropff (1993). The aim of the extended model was to determine whether the effects on respiration and photosynthesis fully explain the reduction in the utilization efficiency of intercepted radiation. Since the model was used for an analysis of the backgrounds of leaf blast effects on RUE, the LAI was not simulated in the model, but the measured LAI was input to the model. This enables a restriction of the analysis of leaf blast effects on crop production to direct effects of the disease on physiological processes. Various model parameters were derived from the field experiment (Table 6.1). This further reduces the potential number of causes in case of a dissimilarity between simulated and observed dry matter production.

The relative death rate of leaves (RDR; d^{-1}) after flowering was calculated from the observed decrease in green leaf weight. Such a standard derivation of the RDR before flowering is not possible, since changes in leaf weight before flowering are the net result of senescence of existing leaf tissue and formation of new leaf tissue. Therefore, the RDR of green leaf tissue before flowering was calculated from the increase in dead leaf tissue in that period:

$$RDR = (WLVD_{t_2} - WLVD_{t_1})/(0.5 \times (WLVG_{t_1} + WLVG_{t_2}) \times (t_2 - t_1)) \qquad (6.2)$$

where WLVD = dry weight of dead leaf tissue ($kgha^{-1}$), WLVG = dry weight of green leaf tissue ($kgha^{-1}$) and t_1 and t_2 refer to the dates of two successive harvests, expressed as days after transplanting. The thus calculated RDR was related to the average of the disease severities observed at t_1 and t_2. The results obtained with the data from the individual plots were grouped in four severity classes. This led to a relation between disease severity and leaf senescence from which the rate of weight loss of green leaf tissue before flowering was derived (Fig. 6.2).

Table 6.1 Experiment-specific crop variables, that were used as inputs to the crop growth model.

Date of first and final harvest	(-)
Dry weight of leaves and stems at first harvest	($kgha^{-1}$)
Leaf Area Index as a function of time	(-)
Nitrogen content of green leaf tissue as a function of time	(gm^{-2})
Disease severity as a function of time	(-)
Fraction dead leaf area as a function of time	(-)
Dry matter distribution over the shoot organs as a function of time	(-)
Fraction remobilizable stem dry weight at flowering	(-)
Relative death rate of green leaf tissue	(d^{-1})

74
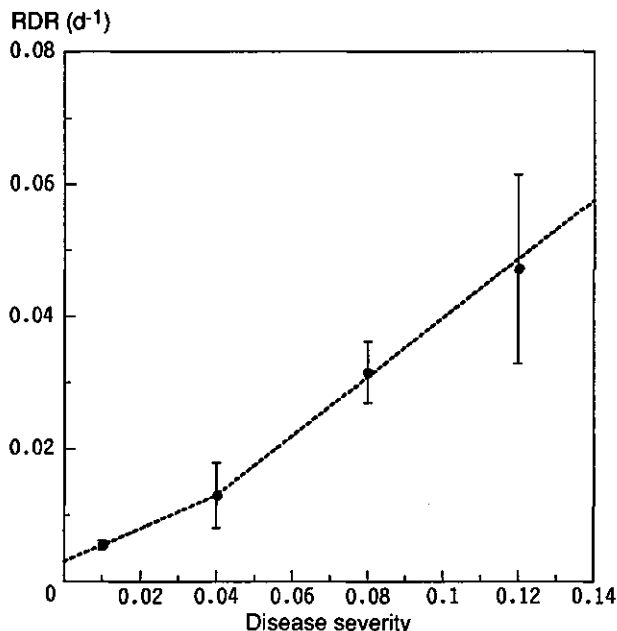
Figure 6.2 Relation between disease severity of leaf blast and relative death rate of green leaf weight (RDR; d^{-1}) of rice crops, as derived from field observations according to the procedure described in the text. The dotted line represents the relation used in the crop growth model to calculate the loss rate of green leaf weight before flowering. Vertical bars represent the standard errors of the mean.

After initialization of the model with dry weights of leaves and stems of the first harvest, the model was run until final harvest. Model performance was evaluated by comparing the simulated and observed shoot dry weight in course of time.

6.3 Results

Radiation interception and radiation use efficiency

Three distinguished phases are observed in the curve that describes the fraction intercepted radiation of the control crop (Fig. 6.3). Till 38 DAT the fraction intercepted radiation increased rapidly (construction phase). Between 38 and 67 DAT more than 80% of the incident radiation was intercepted by the green leaf area of the crop. Saturation of light interception at LAI's over 4 was responsible for the flattening of the curve in this period (saturation phase).

75
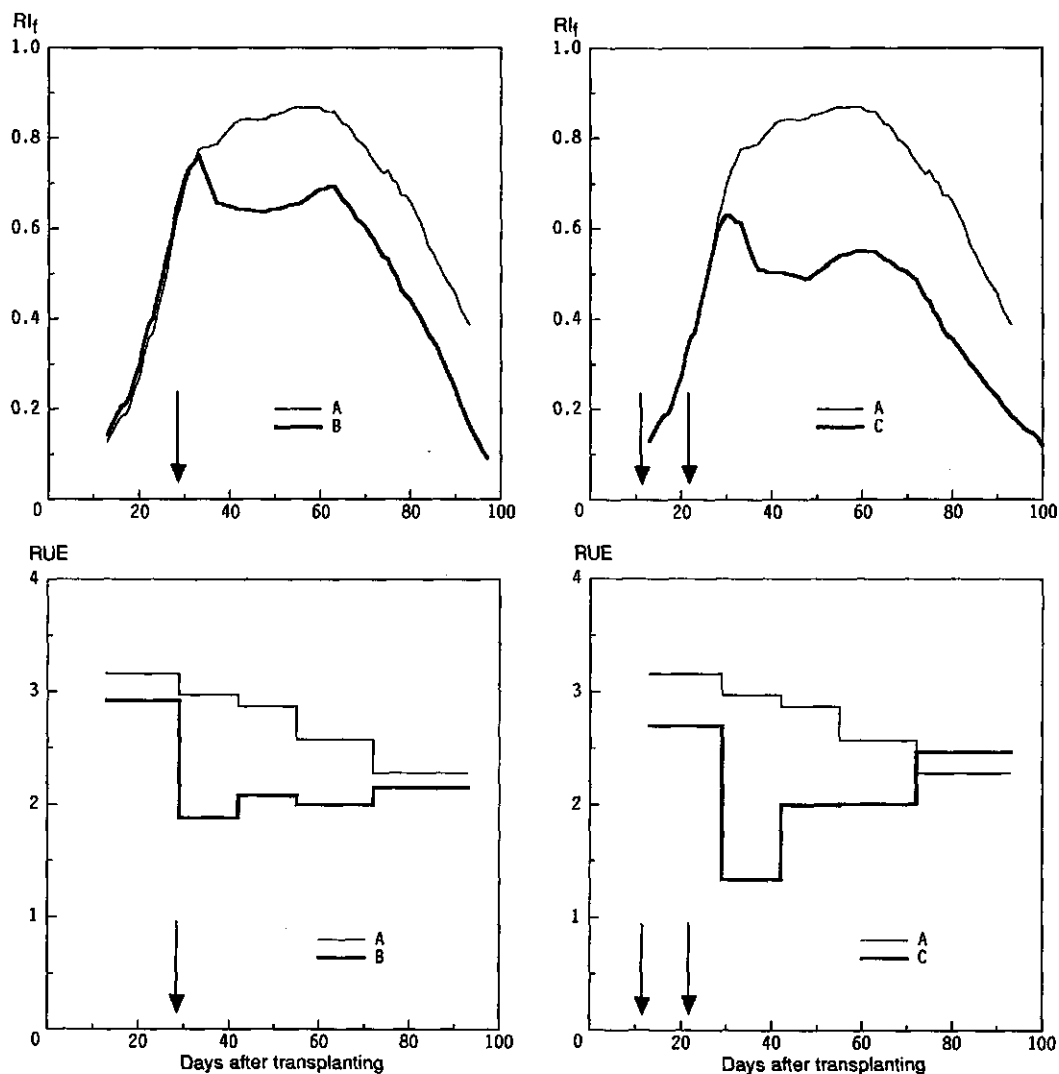
Figure 6.3 Time course of the fraction of intercepted radiation (RI$_f$) and the radiation use efficiency (RUE; g dry matter (MJ PAR)$^{-1}$) of crops inoculated with *Pyricularia oryzae* (treatment B and C). Thin lines are used to represent RI$_f$ and RUE of the control crop (treatment A). Arrows indicate inoculation data.

From 67 DAT on, light interception by green leaf area decreased rapidly as a result of leaf senescence (decline phase). The average radiation use efficiency (RUE) of the control crop was 2.69 g dry matter (MJ PAR)$^{-1}$ (Table 6.2). RUE decreased gradually towards maturity (Fig. 6.3).

Leaf blast caused significant reductions in both RI$_f$ and RUE (Fig. 6.3, Table 6.2). Radiation interception was already hampered in the construction phase, and remained low during the saturation phase of the control crop. The

76

fraction of radiation intercepted in this period varied between 0.6 and 0.7 for treatment B, and between 0.5 and 0.6 for treatment C. Reduction of radiation interception began at the same time in healthy and inoculated crops, with almost equal rates of decline. Therefore, the differences in fraction intercepted radiation between control and diseased crops were maintained.

The reduction in RUE in the diseased crops showed a clear relation with disease severity. The strongest reduction in RUE was observed during the establishment of the disease, between 29 and 42 DAT (Fig. 6.3, Table 6.2). From then on RUE gradually recovered. Between 72 and 93 DAT, when disease severity had dropped to a low level, significant differences between RUE of the various treatments resolved.

Simulation of dry matter production

Simulation of dry matter production of the control crop resulted in a good agreement with the observed dry matter production (Fig. 6.4). This demonstrates the thoroughness of the assimilation and respiration routines of

Table 6.2 Cumulative radiation interception (PARCUM; MJm^{-2}) and radiation use efficiency (RUE; g dry matter $(MJ\ PAR)^{-1}$) of rice in a control crop (A) and in crops inoculated with *Pyricularia oryzae* (B, C), calculated for five consecutive periods.

Period	treatment A			treatment B			treatment C		
PARCUM									
13-29 DAT[a]	34.4	(1.00)	a[b]	37.2	(1.08)	a	34.4	(1.00)	a
29-42 DAT	66.6	(1.00)	a	60.4	(0.91)	b	49.0	(0.74)	c
42-55 DAT	84.4	(1.00)	a	62.6	(0.74)	b	48.8	(0.58)	c
55-72 DAT	110.2	(1.00)	a	84.8	(0.77)	b	68.4	(0.62)	c
72-93 DAT	107.2	(1.00)	a	70.4	(0.66)	b	59.6	(0.56)	b
13-93 DAT	402.8	(1.00)	a	315.4	(0.78)	b	260.2	(0.65)	c
RUE									
13-29 DAT	3.16	(1.00)	a	2.92	(0.92)	a	2.70	(0.85)	a
29-42 DAT	2.97	(1.00)	a	1.88	(0.63)	b	1.34	(0.45)	b
42-55 DAT	2.87	(1.00)	a	2.08	(0.72)	b	2.00	(0.70)	b
55-72 DAT	2.57	(1.00)	a	2.00	(0.78)	b	2.01	(0.78)	b
72-93 DAT	2.28	(1.00)	a	2.15	(0.94)	a	2.47	(1.08)	a
13-93 DAT	2.69	(1.00)	a	2.16	(0.80)	b	2.10	(0.78)	b

[a] Days after transplanting

[b] Means in the same row followed by the same letter are significantly different according to t-test (P<0.05).
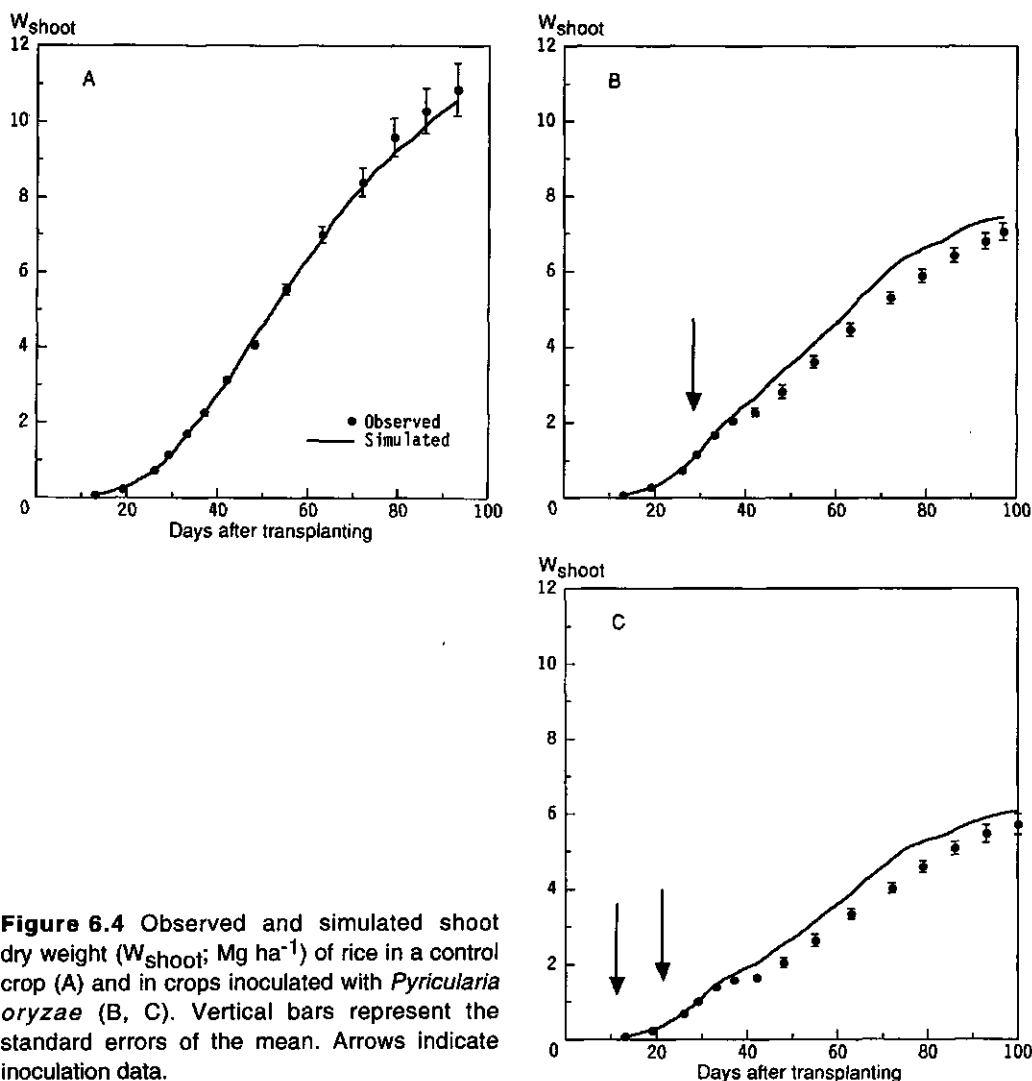
Figure 6.4 Observed and simulated shoot dry weight (W_{shoot}; Mg ha^{-1}) of rice in a control crop (A) and in crops inoculated with *Pyricularia oryzae* (B, C). Vertical bars represent the standard errors of the mean. Arrows indicate inoculation data.

the 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. 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 kgha^{-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 fully explain 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.

6.4 Discussion

The analysis with the RI/RUE model confirms 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 (Bastiaans and Kropff, 1993). The difference in reduction of RUE between the inoculated crops (treatments B and C) was not significant (Table 6.2). Therefore, the difference in dry matter production between B and C resulted completely 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 on 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 (1991a) 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 LAI at the initiation of leaf blast, caused by the difference in inoculation date, was the most prominent factor responsible for the observed differences in total dry matter production of the inoculated treatments in this experiment.

During the establishment of the disease the effects of leaf blast on leaf photosynthetic rate and respiration were inadequate to fully explain the observed reduction in RUE. 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. In an earlier study, it was demonstrated that the effects of leaf blast on leaf photosynthetic rate and respiration satisfactory explained the effect of leaf blast on CO_2 assimilation (Bastiaans and Kropff, 1993). 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 either 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
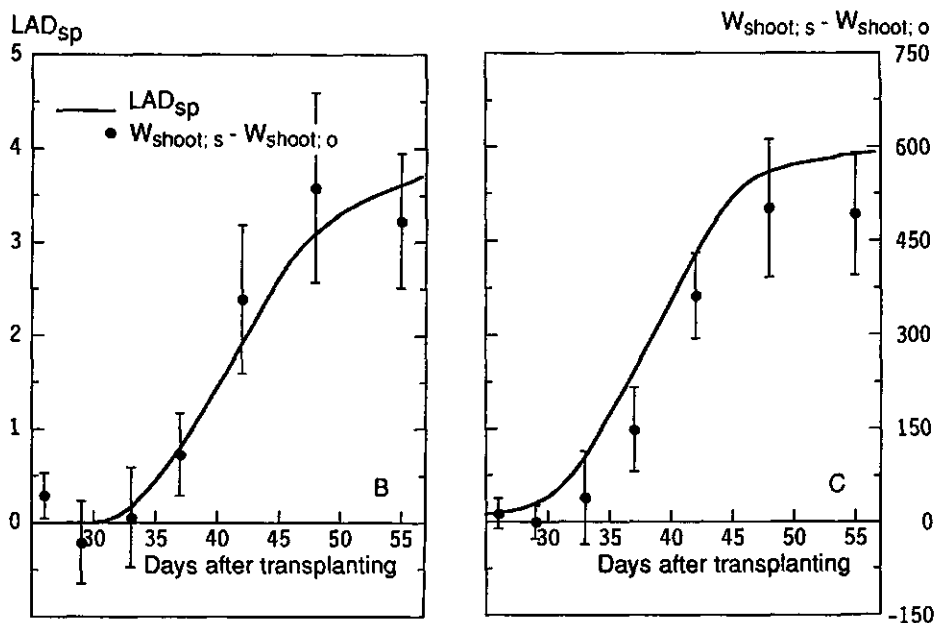
Figure 6.5 Simulated leaf area duration of sporulating blast lesions (LAD_{sp}; d) and the difference between simulated and observed total shoot dry weight ($W_{shoot,s} - W_{shoot,o}$; $kgha^{-1}$) for rice crops inoculated with *Pyricularia oryzae* (treatment B and C). Vertical bars represent the standard errors of the mean.

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 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 to 570 kg CH_2O ha^{-1} for spore production and related processes. Data on the rate of sporulation of blast lesions are diverging, but data on the production pattern of the lesions are rather uniform (Kato et

80

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 to 30 days. Spore production reaches its peak between 3 to 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 d). 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. 6.5). 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 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)$^{-1}d^{-1}$.

Use of crop growth models in studies on crop loss reflects the growing awareness among plant pathologists that the remaining healthy leaf area, rather than the severity of the disease, forms a solid basis for crop loss assessment (Waggoner and Berger, 1987). In this study two different types of crop growth models were used to analyse the reduction in dry matter production in rice due to leaf blast. Recently, Rossing et al. (1992) discussed the merits and limitations of each approach. They concluded that the RI/RUE approach is a good starting point for analysis, because of the conceptual simplicity and the ease of empirical parameter estimation. This approach allows two broad categories of disease effects to be distinguished: effects on RI and effects on RUE. For more detailed analysis, especially of disease effects on RUE, the use of mechanistic crop growth models is required. The present study illustrates these conclusions.

Simulation of yield reduction in rice due to leaf blast

L. BASTIAANS[1] & P.S. TENG[2]

[1] Department of Theoretical Production Ecology, Wageningen Agricultural University, P.O. Box 430, 6700 AK Wageningen, The Netherlands

[2] International Rice Research Institute, P.O. Box 933, 1099 Manila, The Philippines

Abstract. Yield reduction in rice due to epidemics of leaf blast starting before flowering was studied by means of simulation. Leaf blast is able to cause considerable reductions in grain yield of rice for a wide range of onset times. Epidemics starting in the vegetative phase of the crop led to a reduced formation of leaf area, thereby causing a clear reduction in dry matter production and yield. Epidemics starting in the reproductive phase led to a low growth rate during the ripening phase of the crop, resulting in a poor kernel filling and a low harvest index. Least damage was caused by epidemics starting early in the vegetative or late in the reproductive phase of the crop.

The simulation study demonstrated that lesion coverage and leaf senescence, being the disease effects that directly affect radiation interception, were responsible for 50 to 70% of the yield reduction due to leaf blast. The direct effects on radiation use efficiency were responsible for the remaining part of yield reduction. From the effects that reduce the radiation use efficiency of the crop, the reduction in leaf photosynthetic rate and the assimilate uptake by the pathogen for spore production were equally important. The contribution of the increased respiration of infected leaf tissue to the overall yield reduction was negligible.

7.1 Introduction

Blast disease of rice (*Oryza sativa* L.) caused by *Pyricularia oryzae* Cavara is one of the most serious diseases of rice worldwide. The pathogen can infect nearly all parts of the shoot and is commonly found on the leaf blade (early infections) and the panicle (late infections). Accordingly, two phases of the disease are distinguished: leaf blast and panicle blast (Ou, 1985; Teng et al., 1991). Infection of panicles usually is economically more important, as panicle infections can directly cause severe yield losses. Yield reduction due to panicle blast is often linearly related to the fraction infected panicles, and estimates of the reduction in yield vary from 0.4 to 1% per percentage of infected panicles (Kuribayashi and Ichikawa, 1952; Goto, 1965; Padmanabhan, 1965; Katsube and Koshimizu, 1970). The observed variation is attributed to differences in time of infection; the earlier the infection the greater the loss in yield (Ou, 1985).

Attempts to relate yield reduction in rice by leaf blast to disease severity have proven more difficult (Ou, 1985). A first problem is that leaf blast affects grain yield only indirectly, through its effect on crop growth before flowering. Secondly, it is almost impossible to characterize epidemics of leaf blast by a few parameters relevant for yield loss. For correlative studies, the availability of such parameters is of primary importance. A third problem is the difficulty of

excluding panicle blast in field experiments designed to study the effect of leaf blast. Finally, the generalization value of empirical damage functions across years, locations and varieties is generally low, and this suggests that for any possible combination of the major components of the agroecosystem a separate forecasting formula would have to be developed (Teng et al., 1991).

For these reasons, systems analysis was used to quantify yield loss in rice due to leaf blast. This approach tries to understand the causes of yield reduction by combining experimental research with the development of explanatory simulation models (Rabbinge and Rijsdijk, 1981; Boote et al., 1983; Rabbinge and Bastiaans, 1989). The experimental research is conducted at two levels of integration; plant and crop. A mechanistic simulation model for crop growth is used to link the observations at the two levels. At the plant level the effect of the disease on basic plant growth processes was studied. Leaf blast reduced the leaf photosynthetic rate at high and at low light intensities and increased the respiration rate of infected leaf tissue (Bastiaans, 1991 & 1993a). The size of the disease effects on photosynthesis and respiration were related to disease severity, and these relations were introduced in a mechanistic crop growth model. Field experimentation demonstrated that observed reductions in canopy photosynthesis of infected crops could be adequately explained by the adverse effects of leaf blast on photosynthesis and respiration, and by the presence of dead leaf tissue (Bastiaans and Kropff, 1993). The effect of the disease on crop production could not be explained without accounting for assimilate uptake by the pathogen for spore production (Bastiaans, 1993c). For this reason the crop growth model was extended with a submodel that simulates carbohydrate uptake by the pathogen for spore production.

In the present study the crop growth model was used to study yield reduction in rice due to leaf blast. The main objectives of the present study were 1). to determine to what extent yield reduction depends on the development stage of the crop during which the disease is present, and 2). to determine the contribution of the various damage mechanisms to the overall reduction in crop growth and production.

7.2 Materials and methods

Simulation of crop growth

To simulate growth and production of rice, the MACROS-L1D model

described by Penning de Vries et al. (1989) was used. MACROS-L1D simulates the time course of dry matter production in production situations with an ample supply of water and nutrients, where growth is only determined by the incoming radiation, temperature and some physiological plant characteristics. Dry matter production is obtained by integrating the crop growth rate over time, using a time step of one day. The daily rate of crop growth (dW/dt; kg dry matter $ha^{-1}d^{-1}$) is calculated from the gross photosynthetic rate of the canopy (A_g; kg CH_2O $ha^{-1}d^{-1}$), maintenance respiration (R_m; kg CH_2O $ha^{-1}d^{-1}$) and the carbohydrate requirement for the formation of structural plant material (C_r; kg CH_2O (kg dry matter)$^{-1}$):

$$dW/dt = (A_g - R_m) / C_r$$

The daily rate of canopy photosynthesis is obtained by integrating instantaneous rates of leaf photosynthesis over the leaf area index of the canopy and over the day. Leaf photosynthetic rate is computed from the incident amount of photosynthetically active radiation (PAR) above the canopy, the distribution of light over the leaves and the photosynthesis-light response of individual leaves. This response is characterized by the maximum rate of gross photosynthesis ($P_{g,max}$) and the light use efficiency at low light intensities (ε). Maintenance respiration represents the carbohydrates that are respired to provide energy for the biological functioning of the crop. Its rate depends on the composition and amount of biomass and is affected by temperature. The assimilates remaining after provision of maintenance respiration are used as substrate for growth. The carbohydrate requirement for the formation of structural plant material depends on the chemical composition of the dry matter formed.

The daily dry matter increase is allocated to the various growing plant organs; leaves, stems, roots and panicles. The allocation pattern depends on the phenological development stage of the crop, which is linearly scaled from emergence to flowering and from flowering to maturity. Development rate is calculated as a function of daily mean temperature.

Effect of leaf blast on crop growth

Leaf blast affects the rate of crop growth by a reduction in leaf photosynthetic rate, an increase in leaf maintenance respiration, uptake of assimilates by the pathogen and premature leaf senescence (Fig. 7.1).

Leaf photosynthetic rate. Leaf blast reduces the photosynthetic rate of infected leaves not only through a reduction in green leaf area, but also through

86
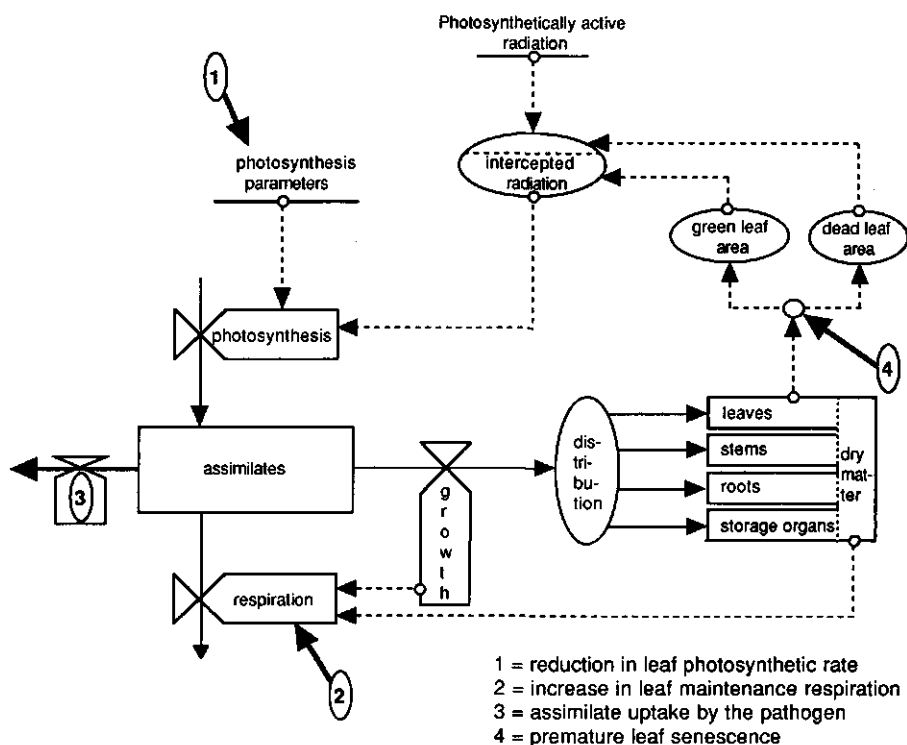
Figure 7.1 Diagram illustrating schematically the calculation procedure of daily crop growth rate in model MACROS-L1D, and the various ways through which leaf blast affects crop growth rate. Quantities are shown in boxes, processes in valve symbols, flow of material by lines and flow of information by dotted lines.

a reduction in the photosynthetic activity of the remaining green leaf tissue. The assimilation rate at light saturation ($P_{g,max}$) was more affected than the initial light use efficiency (ε) (Bastiaans, 1993a). Multiplication factors for both parameters in dependence of disease severity are given in Fig. 7.2A.

Leaf maintenance respiration. Leaf dark respiration increases with increasing disease level. This effect can be attributed to the combination of fungal respiration and an enhanced respiration of the host. Measurements indicated that the respiration related to a lesion was 4.5 times as high as the respiration of an identical area of healthy leaf tissue (Bastiaans, 1993a). This value was used to determine the multiplication factor for leaf maintenance respiration in dependence of disease severity (Fig. 7.2B).

Assimilate uptake by the pathogen. Data on the production pattern of blast lesions indicate that the lesions start to produce spores immediately after their appearance (Kato et al., 1970; Kato and Kozaka, 1974; Ou, 1983; Kim et

87
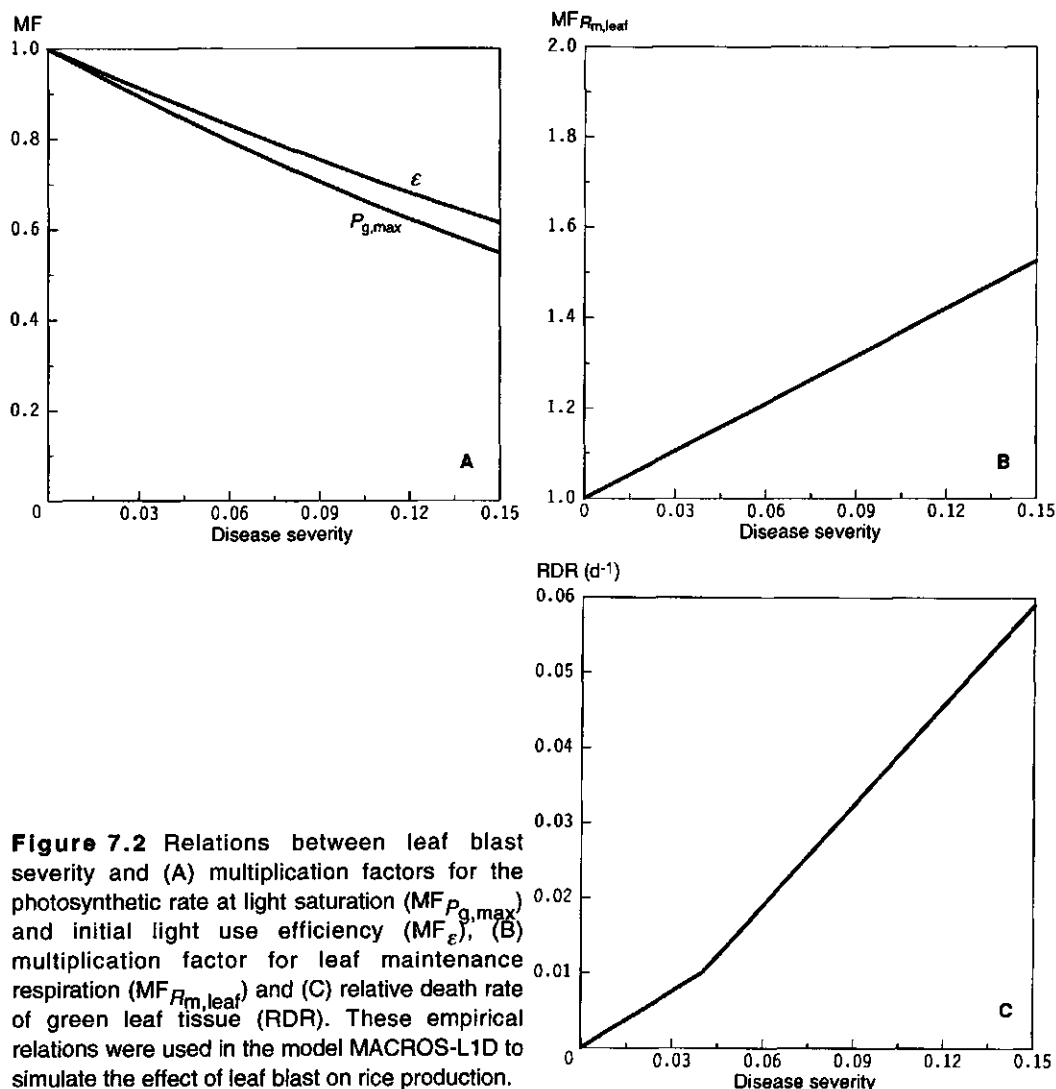
Figure 7.2 Relations between leaf blast severity and (A) multiplication factors for the photosynthetic rate at light saturation ($MF_{P_{g,max}}$) and initial light use efficiency (MF_ε), (B) multiplication factor for leaf maintenance respiration ($MF_{R_{m,leaf}}$) and (C) relative death rate of green leaf tissue (RDR). These empirical relations were used in the model MACROS-L1D to simulate the effect of leaf blast on rice production.

al., 1987). Spore production may last for 20 to 30 days, but 90% or more of the spores are produced during the first 14 days. In the present simulation, spore production of lesions was described by a block function with constant rate during the first 14 days, and zero rate there after. Carbohydrate withdrawal for spore production was estimated at 200 kg CH_2O (ha sporulating lesions)$^{-1}$d^{-1} (Bastiaans, 1993c).

Premature leaf senescence. Disease induced leaf senescence increased with increasing disease severity (Bastiaans, 1993c). The relative death rate of green leaf tissue (RDR; d^{-1}) in dependence of disease severity is given in Figure 7.2C.

Effect of leaf blast on crop development

Stress during early growth stages of rice leads to a prolonged tillering, and accordingly flowering and maturity are delayed. This general response to early stress was also observed after infection by leaf blast (Bastiaans, 1993b). During the specific stress period a reduced crop growth rate is accompanied by a reduced development rate of the crop. In the model the reduction in development rate was directly related to the reduction in crop growth rate. The ratio between the assimilates available for growth and the actual production of assimilates (F_{cgr}) was used as a measure for the reduction in crop growth rate and calculated as:

$$F_{cgr} = (A_g - R_m - U_p) / A_g$$

in which U_p = rate of assimilate uptake by the pathogen (kg CH_2O ha^{-1}d^{-1}). In a healthy crop about 70% of the assimilates is available for growth. Since maintenance respiration (R_m) and the uptake of assimilates by the pathogen (U_p) are assumed to have priority over growth, a reduced production of assimilates will result in values of F_{cgr} smaller than 0.7. A low F_{cgr} corresponds to a low crop growth rate, and accordingly the development rate of the crop is reduced. Data of a previously described field experiment (Bastiaans, 1993b) were used to determine a relation between F_{cgr} and a multiplication factor for the development rate, MF_{dvr} (Fig. 7.3). The influence of the disease on the development rate of the crop was limited to the tillering phase of the crop.

Disease progress

The crop growth model was extended with a submodel that described a logistic increase in disease severity in time. The onset time of the epidemic, the maximum disease severity and the time required to reach this maximum severity were inputs to the model. With these input data the model calculates the corresponding logistic rate of increase r, which is used to simulate the increase in disease severity. Disease development is thus introduced as a forcing function, independent of the crop and prevailing weather conditions.

In this study the time required to arrive at the maximum disease severity was set to 14 days, whereas the onset time and the maximum disease severity were varied. After arriving at the maximum disease severity a further
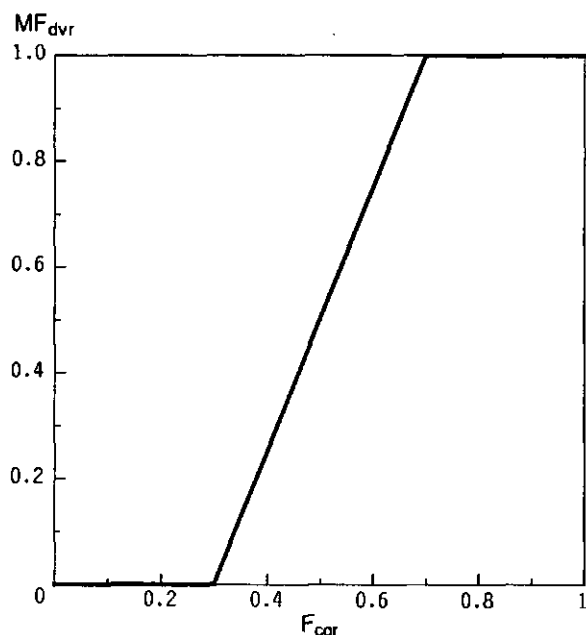
Figure 7.3 Relation between F_{cgr} (the ratio between the daily amount of assimilates used for crop growth and the daily assimilate production) and a multiplication factor for the phenological development rate of the crop (MF_{dvr}).

development of the disease was suspended. From then on disease severity gradually declined, by assuming that leaves subjected to disease induced senescence have a disease severity of 0.25. This last value was estimated from field observations. Leaves with a disease severity exceeding 0.25 are hardly found, since leaves with a high lesion density generally die.

Lesions and dead leaf tissue, resulting from premature leaf senescence, were assumed to be homogeneously distributed over the canopy in horizontal and vertical direction.

Determining the importance of the onset time of the disease

In consecutive simulation runs the onset time of the epidemic was increased from 13 to 63 days after transplanting (DAT), with intervals of one day. Epidemics starting before 13 DAT were not considered, since it usually takes 10 to 14 days for a crop to recover from the transplanting shock. During this period an open canopy structure is observed, preventing the development of a serious epidemic. Leaf blast epidemics starting after flowering (63 DAT) are also rare, due to adult plant resistance.

90

Maximum leaf blast severity was successively set to 0.05, 0.10 and 0.15, where disease severity was defined as the fraction green leaf area covered by lesions. A disease severity of 0.15 represents a severe infection, since dead leaf area is not included in this measure of disease severity.

Yield formation was studied in more detail with three epidemics, starting during early tillering (15 DAT), tillering (29 DAT) and stem elongation (43 DAT), respectively. Since rice is most susceptible to *P. oryzae* during early development stages, the onset times were chosen during these early stages.

Determining the importance of the various damage mechanisms.

Leaf blast reduces crop production through effects that primarily cause a reduced radiation interception and effects that primarily cause a reduced radiation use efficiency. The reduction in radiation interception is caused by lesion coverage and premature leaf senescence, whereas radiation use efficiency is reduced by means of a reduced leaf photosynthetic rate, an increased rate of leaf dark respiration and the uptake of assimilates by the pathogen for spore production. In successive simulation runs one of the damage mechanisms was removed, and the subsequent increase in simulated rice production was defined as the reduction due to the damage mechanism removed. In this way the contribution of the various damage mechanisms to yield reduction was estimated.

Definition of development phases in rice

The terminology used to describe the main development phases of rice is slightly different from the terminology used for other food grains, like wheat. In rice, three development phases are distinguished; the vegetative, the reproductive and the ripening phase (Yoshida, 1981). The vegetative phase refers to the period from germination to the initiation of panicle primordia; the reproductive phase to the period from panicle primordia initiation to heading or flowering; and the ripening phase to the period from flowering to maturity. In this paper, the terminology of Yoshida (1981) will be used. Vegetative and reproductive phase together will be referred to as the pre-flowering phase.

7.3 Results

Onset time of the epidemic.

In Figure 7.4 grain yield is given in dependence of the onset time of the epidemic, for maximum disease severities of 0.05, 0.10 and 0.15, respectively. The time span before 63 DAT covers the development phase before flowering. Yield loss is greatest due to epidemics with an onset time in the middle of the
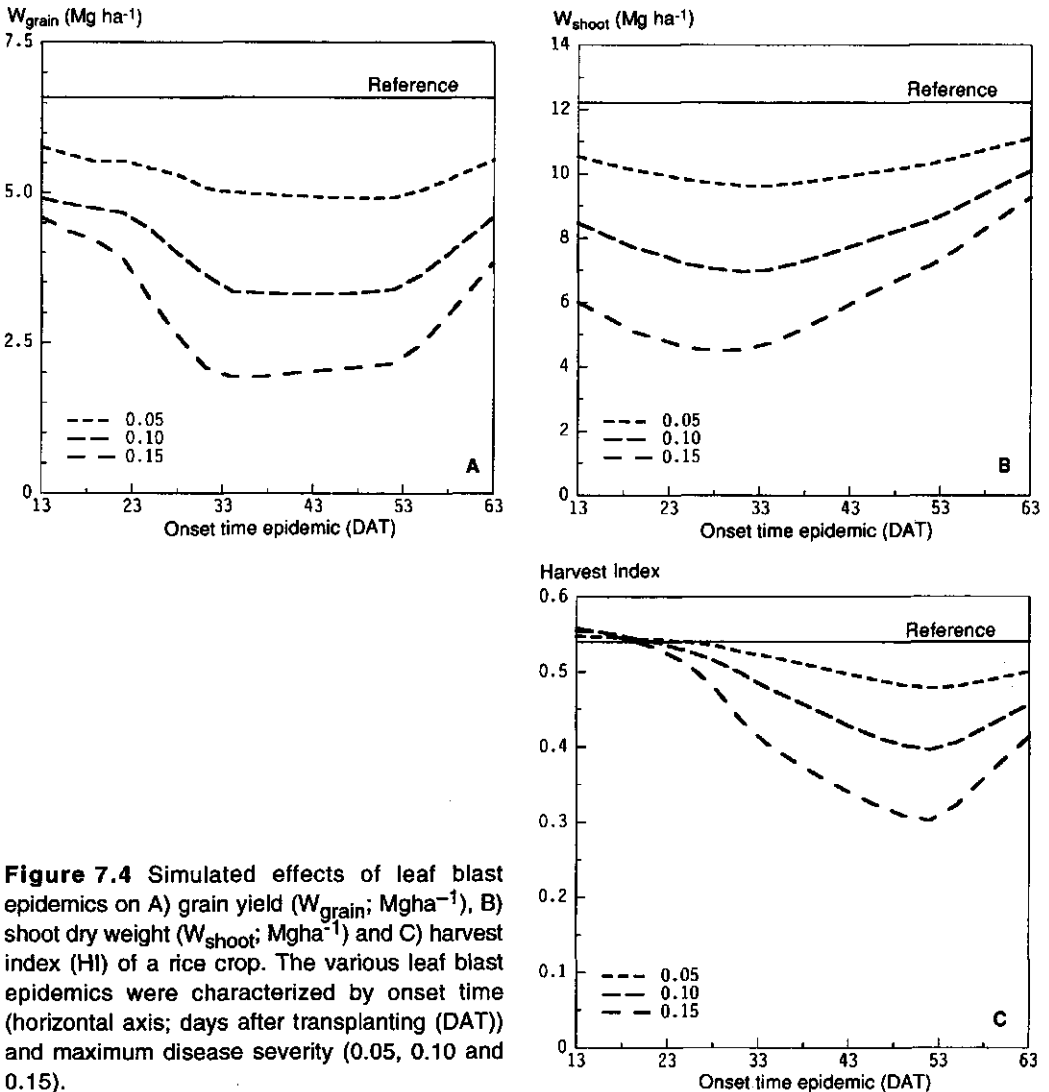
Figure 7.4 Simulated effects of leaf blast epidemics on A) grain yield (W_{grain}; Mgha^{-1}), B) shoot dry weight (W_{shoot}; Mgha^{-1}) and C) harvest index (HI) of a rice crop. The various leaf blast epidemics were characterized by onset time (horizontal axis; days after transplanting (DAT)) and maximum disease severity (0.05, 0.10 and 0.15).

92

pre-flowering phase, and less with earlier and later epidemics (Fig. 7.4A). Dry matter production was most severely reduced with epidemics that started around 30 DAT (Fig 7.4B). Later onset times of the epidemic gave a lower reduction in dry matter production. The higher dry matter production in case of epidemics with a later onset time was counterbalanced by a reduced harvest index (Fig. 7.4C).

A more detailed study of yield reduction due to leaf blast was made for epidemics starting during early tillering (15 DAT), tillering (29 DAT), and stem elongation (43 DAT), respectively. The outcomes of this study are illustrated for a maximum disease severity of 0.10 only, since the simulations with a maximum severity of 0.05 and 0.15 yielded comparable results. After the onset of an epidemic, disease severity was increased according to a logistic growth curve, reaching its maximum value after 14 days. From then onwards new infections were excluded and disease severity dropped gradually (Fig. 7.5A). After an early epidemic both the death of infected leaf tissue and the formation of new leaf tissue contributed to the decrease in disease severity. The crop outgrew the disease, resulting in a fast decrease in disease severity. In case of a late epidemic the reduction in disease severity was solely brought about by the death of infected leaf tissue. This resulted in a slower decline in disease severity.

All epidemics resulted in a reduced amount of leaf area during ripening (Fig. 7.5B). However, the causes for the reduction in LAI differed markedly. With late epidemics, disease induced leaf senescence was the main cause of the reduction in leaf area (Fig. 7.6). With early epidemics disease induced leaf senescence was less important, since LAI at the time of infection was still small. In this situation the reduction in leaf area resulted mainly from the effect of the disease on crop growth rate and the reduction in leaf area formation that goes with it. After a late epidemic the reduction in LAI was smaller than with the earlier epidemics, resulting in a higher LAI during ripening (Fig. 7.5B). However, during the same period, leaf blast severity (Fig. 7.5A) and the fraction dead leaf area (Fig. 7.5C) of the crop infected last were higher than those of the earlier infected crops.

Two types of senescence contributed to the amount of dead leaf tissue in the inoculated crops; disease induced and age related senescence. With early epidemics, this led to two separate flushes in the fraction dead leaf area, of which the first was caused by disease induced senescence, and the second by age related senescence (Fig. 7.5C). With late epidemics, both flushes overlapped partly, leading to a high fraction of dead leaf area during ripening.

The time course of dry matter accumulation is given in Figure 7.5D. The growth pattern of infected crops was strongly determined by the onset time of
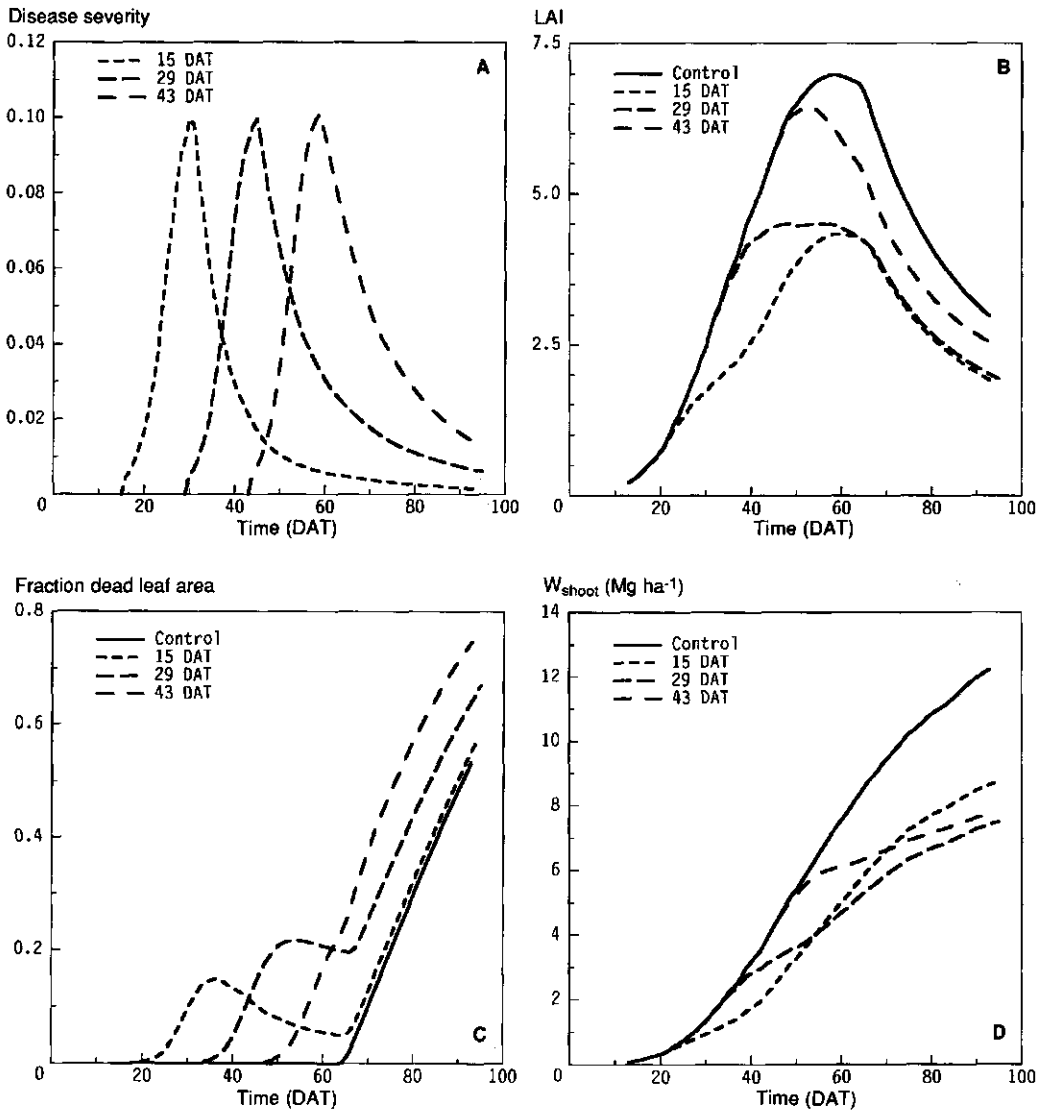
Figure 7.5 Results of a simulation study to examine the effect of various leaf blast epidemics on crop production (A = disease severity; B = leaf area index; C = fraction dead leaf area; D = total shoot dry weight). Simulations were made for leaf blast epidemics with a maximum disease severity of 0.10 and different onset times (15, 29 and 43 days after transplanting (DAT)). The logistic increase in disease severity during the first 14 days after the onset of an epidemic was introduced as a forcing function.

the epidemic. The early epidemic caused an early reduction in the rate of dry matter accumulation. However, after a period with a clear inhibition of crop growth, the crop was able to recover. With the late epidemic the growth was undisturbed during the first six weeks after transplanting, but the reduction in

94
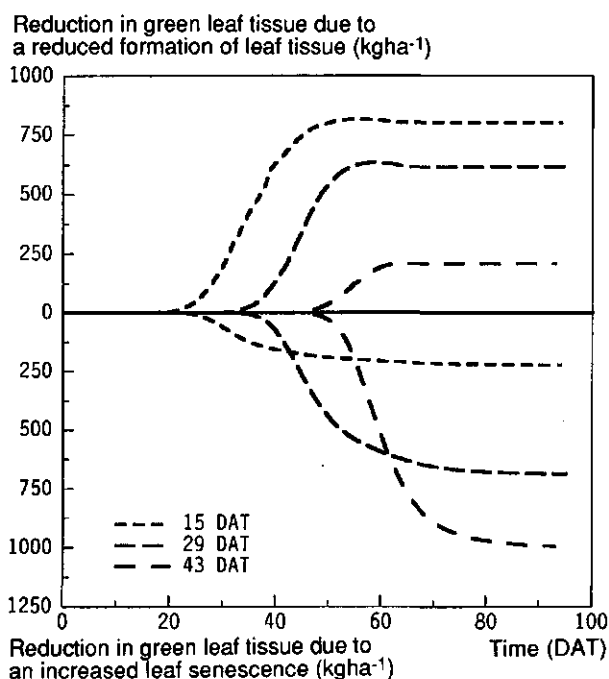
Figure 7.6 Simulated reduction in dry weight of green leaf tissue ($W_{leaf,green}$; kgha^{-1}) of rice crops infected with leaf blast as compared to dry weight of green leaf tissue of an healthy rice crop. A distinction was made between the reduction due to a reduced formation of leaf tissue (upper curves) and the reduction due an increased leaf senescence (lower curves). Simulations were made for leaf blast epidemics with a maximum disease severity of 0.10 and different onset times (15, 29 and 43 days after transplanting). Natural leaf senescence was not considered.

crop growth rate that appeared after the onset of the epidemic was maintained till maturity. The reduction in total dry matter production varied between 29 and 39%. The smaller reduction in case of an early infection was mainly due to a smaller reduction in radiation use efficiency (Table 7.1). The reduction in cumulative radiation interception due to leaf blast was independent of the onset time of the epidemic. Differences in grain yield between the infected crops were more pronounced than the differences in total shoot dry weight (Table 7.1). This was caused by a clear reduction in harvest index of the crop infected last. The low growth rate of this crop during the ripening phase caused a moderate kernel filling and consequently a low harvest index.

95

Reduction in development rate

Heavy epidemics starting before maximum tillering (33 DAT) caused a prolonged growth duration (Fig. 7.7A). The magnitude of the prolongation depended on onset time of the epidemic and disease severity. The prolonged growth duration enabled the crop to partly recover from the adverse effects of the disease. This is illustrated in Figure 7.7B (shaded areas), where the simulated reduction due to leaf blast is compared with the simulated reduction that would occur without an extended growth duration. Clearly the extended growth duration enabled a partial compensation of the adverse effect of the disease on grain yield.

Reduction in radiation use efficiency

Simulation was used to estimate the importance for yield reduction of the effects that directly affect the RUE of the crop. For this purpose the relevant damage mechanisms were removed from the crop growth model, and the reduction in grain yield due to epidemics starting at 15, 29 and 43 DAT, was determined once more. Removing the effect of leaf blast on leaf photosynthetic rate and respiration and not accounting for assimilate uptake by the pathogen led to a considerable smaller reduction in grain yield (Table 7.2). The decrease in yield reduction varied between 30 and 50%, depending on the onset time of the epidemic. In a further analysis only one of the relevant damage mechanisms was removed, to estimate the contribution of each damage mechanism to yield

Table 7.1 Simulated dry matter production and grain yield of a healthy rice crop, and of crops infected by *Pyricularia oryzae*. Grain yield is analyzed in terms of cumulative radiation interception (PARCUM; (MJ PAR)$^{-1}$ha^{-1}), radiation use efficiency (RUE; g dry matter (MJ PAR)$^{-1}$) and harvest index. Simulations were made for leaf blast epidemics with a maximum disease severity of 0.10 and different onset times (15, 29 43 days after transplanting (DAT)). (PAR = photosynthetically active radiation)

		Onset time of the epidemic		
	Control	15 DAT	29 DAT	43 DAT
Shoot weight (Mg ha^{-1})	12.2	8.7	7.5	7.7
PARCUM ((MJ PAR) ha^{-1})	450.	363.	351.	360.
RUE (g dry matter (MJ PAR)$^{-1}$)	2.71	2.39	2.13	2.15
Grain yield (Mg ha^{-1})	6.6	4.8	3.8	3.3
Harvest index	0.54	0.55	0.51	0.43
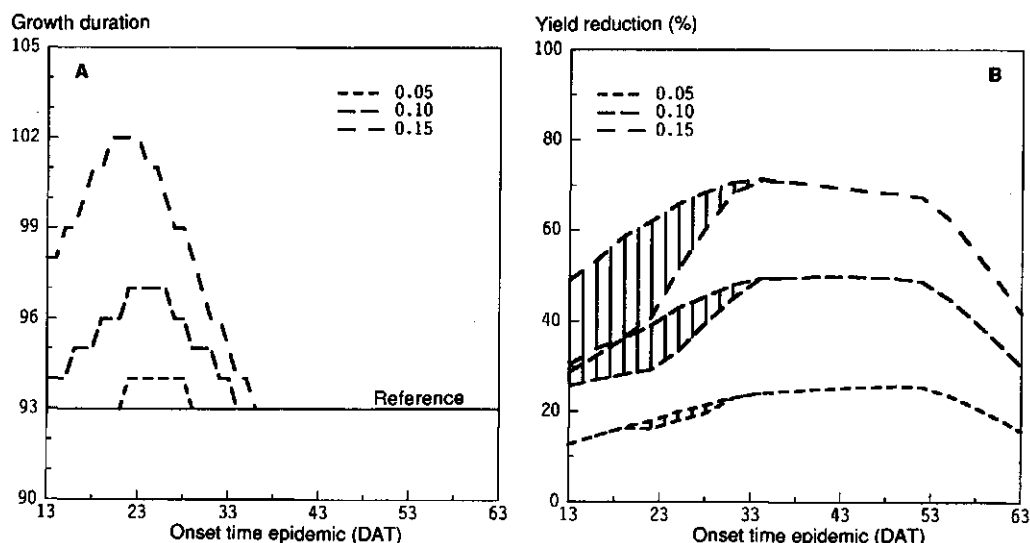
Figure 7.7 Simulated growth duration of a rice crop (number of days from transplanting till maturity) as affected by leaf blast epidemics (A), and the partial compensation of yield reduction that is caused by an extended growth duration (B; upper line = yield reduction without extended growth duration; lower line = yield reduction with extended growth duration). The various leaf blast epidemics were characterized by onset time (horizontal axis; days after transplanting (DAT)) and maximum disease severity (0.05, 0.10 and 0.15).

Table 7.2 Simulated reduction in grain yield (Mg ha^{-1}) for crops infected by *Pyricularia oryzae*. The contribution of the various damage mechanisms of leaf blast to the reduction in rice production was estimated according to the procedure described in the text. Primary effects on radiation interception (RI) are caused by lesion coverage and leaf senescence. The contribution of the various primary effects on radiation use efficiency (RUE) were determined separately. Simulations were made for leaf blast epidemics with a maximum disease severity of 0.10 and various onset times (15, 29 and 43 days after transplanting (DAT)).

	Onset time of the epidemic		
	15 DAT	29 DAT	43 DAT
Total reduction due to leaf blast	1.8 (1.00)	2.8 (1.00)	3.3 (1.00)
Reduction due to primary effects on RI	0.9 (0.50)	1.7 (0.63)	2.3 (0.69)
Reduction due to primary effects on RUE	0.9 (0.50)	1.1 (0.37)	1.0 (0.31)
Contribution of the various primary effects on RUE			
- Reduced leaf photosynthetic rate	53%	48%	44%
- Increased leaf maintenance respiration	3%	4%	3%
- Assimilate uptake by the pathogen	44%	48%	53%

97

reduction separately. This analysis demonstrated that the contribution of the reduction in leaf photosynthetic rate and the assimilate uptake by the pathogen were almost equally important. The increased leaf maintenance respiration hardly contributed to the yield reduction in rice due to leaf blast. The reduction due to the three damage mechanisms combined was almost equal to the sum of the individual reductions (data not shown). This indicates that the effect of the identified damage mechanisms is additive.

7.4 Discussion

Previous research focused on the effects of leaf blast on physiological processes in rice and the development of a crop growth simulation model in which these effects are considered. In the present paper this model was used to study the effect of blast disease on rice yield formation by means of dynamic simulation. In the model, the development of the disease was introduced as a forcing function. This means that the influence of the crop and prevailing weather conditions on the epidemiological development of the disease were ignored. In reality the development rate of the disease is to a large extent determined by the crop, directly by level of resistance, crop development stage, and N status, and indirectly by the crop's effect on microclimate. Consequently, the simulated results only represent the impact of the disease on crop production, without considering the actual probability of the occurrence of the disease. Adult plant resistance is a major feature of the leaf blast-rice pathosystem. Ageing leaves become gradually more resistant and leaves emerging on physiologically older plants obtain this property faster (Yeh and Bonman, 1986; Koh et al., 1987; Roumen et al., 1992). As a consequence, the rice crop is most susceptible to leaf blast during early development phases of the crop. After heading the panicle is susceptible to infection by *P. oryzae*. Late epidemics of leaf blast may therefore enhance the development of neck blast, by providing inoculum. These epidemiological aspects were not accounted for in the present study.

Contribution of various damage mechanisms to yield reduction.

Leaf blast in rice is a pathosystem in which the disease affects radiation interception (RI) and radiation use efficiency (RUE). Pathosystems in which the reduction in crop production is exclusively determined by a reduction in cumulative radiation interception are also reported, for example,

98

Phytophthora infestans on potato (Haverkort and Bicamumpaka, 1986; van Oijen, 1991b). Other examples of pathosystems that are reported to affect RI and RUE are *Cercospora* sp. leafspot in peanuts (Boote et al., 1980) and *Verticillium dahliae* in potato (Bowden and Rouse, 1991). Lesion coverage and leaf senescence are identified as the damage mechanisms that directly affect radiation interception. However, the contribution of these damage mechanisms to yield reduction can not simply be estimated from the observed reduction in cumulative radiation interception. This is illustrated in Figure 7.8, where a distinction is made between the direct effects of the disease on crop growth rate (primary effects) and the effects that are induced by previous reductions in crop growth rate (secondary effects). A primary effect on radiation use efficiency may cause a secondary effect on radiation interception, through its adverse effect on leaf area formation. Consequently, the reduction in cumulative radiation interception can not be fully attributed to the primary effects on radiation interception. The model offers an elegant way of estimating the importance of the various primary effects of the disease to yield reduction, by simply removing the relevant damage mechanisms. The results show that the direct effects of the disease on radiation interception are responsible for 50 to 70% of the reduction in rice production. The direct effects on radiation use efficiency are responsible for the remaining part of yield reduction. This part of the reduction is mainly caused by the reduction in leaf photosynthetic rate and assimilate uptake by the pathogen for spore production. The analysis confirms that the increased respiration of infected leaf tissue is of no importance for yield reduction (Bastiaans and Kropff, 1993). The model thus is a tool that helps to set priorities for physiological research.

Disturbed growth pattern

The dependence of the allocation pattern of newly produced assimilates on the development stage of the crop causes a shift in the secondary effects of the disease with development stage (Fig. 7.8). Consequently, clear differences occur between early and late epidemics with respect to the way the reduction in grain yield is established. With early epidemics the formation of new leaf area is reduced. This leads to a smaller leaf area during ripening, although by that time disease symptoms are hardly present anymore. Lim and Gaunt (1985) observed a similar mechanism of yield reduction in the pathosystem barley-mildew in case of early epidemics, and called it the long-term effect of the disease. With late epidemics the reduction in crop growth rate caused a poor kernel filling. Consequently, the harvest index of the crop decreased.
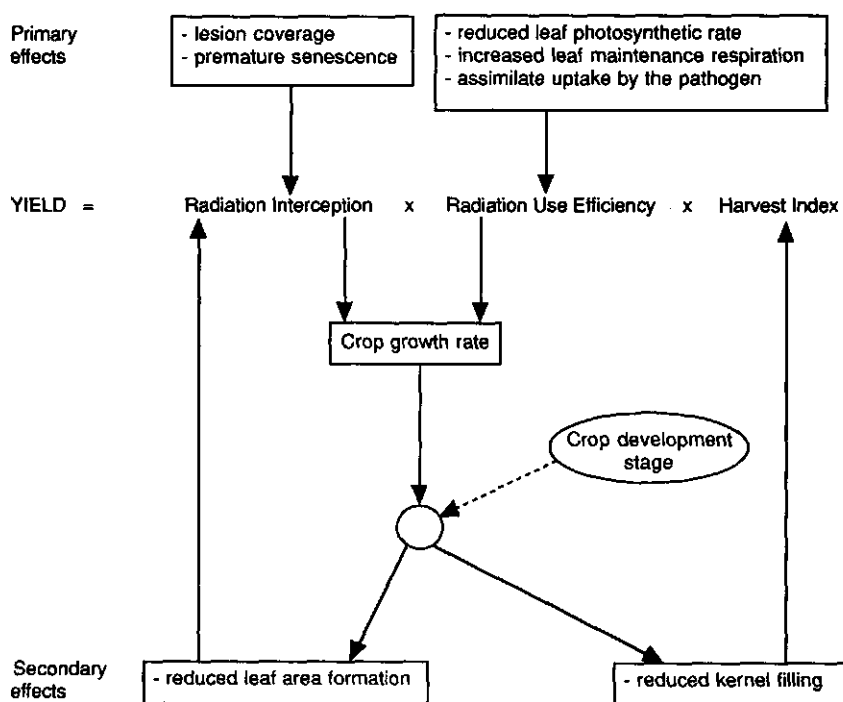
Figure 7.8 Schematic representation of the effect of leaf blast on yield formation. A distinction is made between the direct effects of the disease on crop growth rate (primary effects) and the effects that result from previous reductions in crop growth rate (secondary effects). The nature of secondary effects depends on the crop development stage.

The prolonged tillering and extended growth duration after early infections enables a partial compensation for the adverse effects of leaf blast on crop production. A prolonged tillering, however, will be accompanied by a larger variability in the development of individual tillers (Goto, 1965; Bastiaans, 1993b). In extreme situations the difference between maturity of early and late tillers will lead to the harvest of a crop which is not completely mature. Postponement of the harvest will lead to shedding of kernels from overripe panicles. Since the model does not consider differences in development rate between individual tillers, the advantage of the extended growth duration may in some cases be less than predicted by the model.

Sensitive periods

The present results demonstrate that for a fixed disease development, rice is most sensitive to epidemics of leaf blast starting during the middle of the pre-

100

flowering phase. Epidemics early in the vegetative phase allow the crop to outgrow the disease and to limit the effects of the disease on crop production. Epidemics starting in the late reproductive phase, just prior to flowering, do not have sufficient time to fully develop their unfavourable effect on crop production. This points at an interesting difference between foliar diseases and weeds. For weeds it has been shown that their starting position relative to the crop is of primary importance for the magnitude of crop loss (Kropff et al., 1984). Crop and weed compete for the same resources, which explains the importance of the relative starting positions in this situation. The present study demonstrates that biological constraints operating at a higher trophic level maintain their yield-reducing potential much longer.

The study demonstrates that rice is most vulnerable to foliar injury between mid tillering and flowering. A simulation study of a clipping experiment in rice showed a similar pattern (Teng and Savary, 1992). Although damage due to foliar diseases and clipping can not simply be compared, both studies demonstrate that there is not a single development stage during which the disease has a dominating effect on the magnitude of yield reduction. Consequently, critical point models are inappropriate to describe yield reduction in rice due to leaf blast. The model presented in this study enables the quantification of yield reduction for various epidemics. Therefore, the model is an appropriate tool in constructing damage functions, which are of primary importance for the construction of damage thresholds for supervised disease control.

Empirical damage functions are derived by applying regression analysis to field data. The models directly relate a measure of disease intensity to yield loss, without considering the causes of yield reduction. For this reason, the question remains whether empirical damage functions are specific for the conditions in which they were derived, or whether they have a more general applicability. In the present study the effect of leaf blast on growth and production of a rice crop was studied according to the methodology developed by Rabbinge and Rijsdijk (1981), further referred to as the ecophysiological approach to yield loss assessment. This approach tries to explain yield reduction by quantitative insight in the processes underlying damage. For that reason, experimental work was conducted at different levels of biological organization, the plant and the crop. The experimental work was directly coupled to the development of an explanatory model relating phenomena observed at different levels of organization. The study resulted in a better understanding of yield reduction by leaf blast and in a model that can be used to estimate yield reduction due to leaf blast for epidemics at different crop development stages and under variable environmental conditions.

An alternative method to quantify yield reduction is the approach in which the yield of healthy and infected crops is linearly related to the cumulative amount of radiation intercepted by the green leaf area of the crop. This approach was successfully applied to various pathosystems (Haverkort and Bicamumpaka, 1986; Waggoner and Berger, 1987). Implicitly, the approach assumes that the effect of a disease on crop production is limited to a reduction in leaf photosynthetic area. The results of the present study, however, demonstrate that leaf blast in rice is a pathosystem in which yield reduction results form a reduced cumulative radiation interception and a reduced radiation use efficiency. The reduction in radiation use efficiency was mainly caused by a reduction in leaf photosynthetic rate of infected leaf tissue and by assimilate uptake of the pathogen for spore production. The contribution of these effects to the overall reduction in yield was estimated at 30-50%. The results of the present study thus demonstrate that the radiation interception approach is not applicable to leaf blast in rice.

Requirements for an ecophysiological approach

An ecophysiological analysis of yield loss is not yet a common part of studies on yield loss due to pathogenic stress. This is partly due to the fact that the approach and its requirements differ from more traditional approaches to estimate yield loss due to a disease. The experience gained in the present study on the pathosystem leaf blast-rice is used to illustrate the specific requirements of the ecophysiological approach.

Crop growth model

The core of the present approach is an ecophysiological model for crop growth. The simulation model is used to integrate the observations at the process level and to determine their consequences at the systems level. Over the years, the availability of crop growth models has improved. However, very few models have been designed to include disease and pest constraints. For the straightforward introduction of a damage mechanism, the model should possess a sufficient level of detail at the site of interaction between crop and disease. In this study for instance, it was demonstrated that the disease reduces the photosynthetic rate of infected leaf tissue. Experimental data were used to derive a relation between leaf blast severity and leaf photosynthetic rate. In the model, the assimilation response of individual leaves and the radiation profile in the canopy are used to calculate canopy photosynthesis. The existence of such a detailed assimilation routine enabled the straightforward introduction of the relations obtained at the process level. This example illustrates that for foliar diseases affecting leaf photosynthetic rate, a model with a fixed radiation use efficiency of the canopy is not appropriate.

Most of the available crop growth models are able to calculate crop production for production situations where crop growth is not limited by a lack of water and nutrients, but only determined by incident radiation, temperature and some physiological characteristics of the crop. Shortage of water and nutrients reduces yield from its potential to its attainable level. The simulation of the consequences of water and nutrient shortage for crop growth and production requires the introduction of 1) relations that describe or simulate the availability of water and nutrients to the crop and 2) relations that describe the effect of these growth limiting factors on physiological, morphological and phenological plant processes. Research in this area is still on its way. Therefore, the ecophysiological approach to crop loss assessment is applied to potential production situations. In the present study, for instance, the effect of leaf blast

on crop production was studied for irrigated rice production systems. In the tropics however, leaf blast is an important constraint to rice production when the crop is grown under upland conditions. For this production system the present study is a first step. The utilization of these models for upland and rainfed conditions requires the cooperation with scientists from other disciplines, such as soil science, agrohydrology and plant nutrition.

Equipment

In the ecophysiological approach, experiments are done at two levels of integration. Process research at the plant level is used to determine quantitative relations between the presence of the disease and its effect on various plant processes. This type of research may require expensive, high tech equipment. Obtaining a relation between disease severity and leaf photosynthetic rate, for instance, required the availability of an infrared gas analyzer. This type of equipment is not available at every research institute, it is expensive and its maintenance may cause difficulties. These problems are important in developing countries, and may retard the application of the ecophysiological approach to crop loss assessment in these countries.

Education

Since 1980, hardware and software limitations are no longer hampering the widespread application of systems analysis. As a bottle-neck remained the shortage of scientists trained in this field, caused by a lack of possibilities for a proper education in systems analysis (ten Berge, 1993). In crop protection, current education of plant pathologists is another limiting factor for the use of systems analysis for crop loss assessment. In the present approach, a central position is given to the crop. This is not in line with the traditional training of plant pathologists, where a central role is given to the biology of the organisms responsible for disease. The physiology and epidemiology of the disease-causing organisms are the main fields of interest. This pathogen-oriented education may hamper the application of the ecophysiological approach to crop loss assessment.

Applications of the explanatory model

During the study experimental work at the process and the systems level was combined with the development of an ecophysiological model for simulation of leaf blast effects on growth and production of a rice crop. Besides giving a better understanding of yield reduction, the extended simulation model is a concrete result of the present study. The model primarily is a tool for the translation of the occurrence of leaf blast into the consequences of the disease for growth and production of rice. Some of the potential applications of the model for crop protection purposes are discussed.

Priority setting in research and breeding

Most of the funding organizations for agricultural research are operating on limited budgets. Therefore, they require a reliable estimate of the significance of a certain research program before they decide to support it. For crop protection in general, a determinant for the importance of a research program is the damage caused by the concerning pathogen. Methods that enable a reliable estimation of yield loss are therefore of primary importance. The general strategy of loss appraisal involves two phases. The first phase is a survey to assess the intensity of the disease in the fields of the region under consideration. The second phase is the translation of disease occurrence into yield loss. For this second phase the model can be a useful tool.

The model can also be used for determining priorities at a much lower level of integration. This was shown in Chapter 7, where the model was used to determine the contribution of the various damage mechanisms to yield reduction. The analysis demonstrated that a lower radiation use efficiency is mainly caused by the reduction in leaf photosynthetic rate and the assimilate uptake by the pathogen for spore production. The increased respiration of infected leaf tissue was of no importance to yield reduction. These outcomes may help to set priorities within the ecophysiological research conducted with this pathogen.

In a study on late blight of potato, van Oijen (1991c) used a simulation model of blight epidemiology to determine the most suitable components of resistance for breeding purposes. Field experiments were used to determine the genetic variation for the various components of partial resistance, like infection efficiency, latent period and lesion growth rate. The model was then used to estimate the consequences of the available genetic variation in the identified components of resistance for disease development. The simulation results led to

106

the identification of the components that were most promising for breeding resistance against late blight in potato. A similar procedure could be used to determine the most appropriate components of tolerance to a disease for breeding purposes. A first step would be to identify the various components of tolerance, which can be is defined as the ability of the host to endure the presence of the pathogen with reduced disease symptoms and/or damage (Parlevliet, 1979). For leaf blast, β, the parameter that characterizes the effect of the disease on leaf photosynthetic rate of the remaining green leaf tissue, was identified as one of the components of tolerance. The lack of genetic variation in this parameter among cultivars led to the conclusion that β is not a suitable selection criterion in breeding rice for tolerance to leaf blast. The increased rate of leaf senescence after infection, as determined in Chapter 6, is another component of tolerance. It expresses the ability of the host to maintain functional leaf area after infection. The relation between premature leaf senescence and disease severity was only determined for cultivar IR50. If genetic variation among cultivars for this component of tolerance exists, the model would be an appropriate tool to determine the consequences of the genetic variation for crop growth and production. This type of model thus is a suitable tool for the selection of components of tolerance for breeding purposes. A combination model, consisting of an epidemiological model for the disease and a growth model for the crop, would even enable a comparison between the suitability of components of resistance and components of tolerance for breeding purposes.

Crop protection at the farm level

Chapter 7 showed how the model can be used for the determination of sensitive periods of the rice crop with respect to leaf blast. The simulation study demonstrated that between mid-tillering and flowering no differences appear with respect to the sensitivity of rice to leaf blast. During this entire development phase the disease is able to cause considerable reductions in rice production. Regular field observations are thus required to determine the actual disease pressure and to decide whether a crop protection measure is required. Damage thresholds, defined as the lowest level of disease that justifies the application of a disease control measure from an economic point of view, are a useful device to support this type of decision. For the construction of damage thresholds phytopathological knowledge is combined with an economical analysis of costs and benefits. The phytopathological knowledge consists of

epidemiological knowledge and damage functions. Epidemiological knowledge is required to estimate the future development of the disease. Damage functions enable the translation of the expected disease development into its consequences for yield. Finally, the costs of a control measure are compared with the financial gain of the avoided yield reduction. The model developed in this study enables the determination of damage functions and thus is a useful device for the construction of damage thresholds for supervised disease control.

Summary

Systems analysis was used to understand and quantify yield reduction in rice (*Oryza sativa*) due to leaf blast (*Pyricularia oryzae*). The study started at the whole plant level, by determining the effect of the disease on photosynthesis and respiration by means of CO_2 exchange measurements (Chapters 1 to 3). The lesions that developed after infection by *P. oryzae* decreased the rate of CO_2 assimilation at light saturation (P_{max}) and the initial light use efficiency (ε) beyond the visual borders of the lesion. To relate the photosynthesis parameters to disease severity, 'virtual lesions' were introduced in which CO_2 assimilation is absent, while in the remaining leaf tissue it is unaffected (Chapter 1). This concept resulted in a standard function to describe the relation between disease severity and photosynthesis which is characterized by a single parameter, β, the ratio between virtual and visual lesion size. The effect of leaf blast on P_{max} and ε was characterized by β-values of 3.7 ± 0.6, and 3.0 ± 0.7, respectively. A comparison of three rice cultivars did not reveal any differences in β among cultivars (Chapter 2). Leaf dark respiration increased after infection by *P. oryzae* (Chapter 3).

The effect of leaf blast on photosynthesis of a rice canopy was determined with mobile equipment in the field (Chapter 4). Canopy CO_2 exchange rate (CER) was significantly reduced in crops inoculated with *P. oryzae*. The experimentally obtained data were used to evaluate the performance of a model for the effects of leaf blast on canopy photosynthesis. The model comprised photosynthesis and respiration routines of a mechanistic crop growth model, extended with submodels for the effect of leaf blast on leaf photosynthetic rate and respiration. Canopy photosynthesis and the effect of leaf blast on CER were accurately simulated with the model. Analysis showed that the reduction in canopy photosynthesis was mainly due to the adverse effect of leaf blast on leaf photosynthetic rate and to shading by dead leaf tissue resulting from disease induced premature senescence. The increased respiration hardly contributed to the observed reduction in canopy photosynthesis of inoculated crops. A sensitivity analysis demonstrated the importance of the vertical distribution of the disease in the canopy. Lesions in the top of the canopy contributed more to the reduction in canopy photosynthesis than lesions in lower canopy layers, as a result of the higher contribution of the top layers to the photosynthesis of the

canopy.

The effect of leaf blast on growth and production of a rice crop was determined under field conditions (Chapter 5). The treated plots were inoculated during the tillering phase of the crop, resulting in severe epidemics of leaf blast around maximum tillering. Analysis demonstrated that apart from carbon economy, the disease also affected N uptake and sink formation. Sink size was reduced through a reduction in spikelet number and grain weight. Since the number of filled grains was also reduced, it was concluded that the reduction in grain yield was exclusively source determined. Nitrogen uptake of the inoculated crops before flowering was reduced compared to the N uptake of the control crop, whereas the uptake of N after flowering was negligible in both healthy and inoculated crops. Redistribution from vegetative tissue was therefore the main source of N for grain growth. The higher N content of the shoot organs of the inoculated crops during ripening demonstrated that the reduced N supply was not a limiting factor during grain growth. Consequently, the reduction in grain yield was solely determined by a reduced carbohydrate supply.

The reduction in crop growth rate was analyzed in more detail by using two crop growth models with different complexity (Chapter 6). The first model demonstrated that leaf blast reduces the dry matter production of rice by decreases in cumulative radiation interception and radiation use efficiency. Analysis with a more detailed mechanistic crop growth model demonstrated that during the first two weeks after the onset of the disease, the observed reduction in radiation use efficiency of the crop could not be adequately explained by the effects of leaf blast on leaf photosynthetic rate and respiration. This period coincides with the most active period for sporulation. Carbohydrate withdrawal by the pathogen for spore production is therefore the most suitable explanation for the unexplained part of the reduction in radiation use efficiency of the crop. Accordingly, the model was extended with a submodel for carbohydrate uptake of the pathogen for sporulation.

In Chapter 7, the extended model was used to estimate the contribution of the various damage mechanisms to the overall reduction in rice production. Lesion coverage and premature senescence caused direct effects on radiation interception and were responsible for 50 to 70% of the reduction in yield. The direct effects on radiation use efficiency were responsible for the remaining part of yield reduction. From the effects that reduce the radiation use efficiency of the crop, the reduction in leaf photosynthetic rate and the carbohydrate uptake by the pathogen were equally important. The contribution of the increased respiration of infected leaf tissue to yield reduction was negligible. The simulation study further demonstrated that in between mid-tillering and

flowering no differences appear with respect to the sensitivity of rice to leaf blast.

Een systeemanalytische aanpak werd gebruikt om het effect van de brandvlekkenziekte, veroorzaakt door de schimmel *Pyricularia oryzae*, op de groei en de opbrengst van een rijstgewas (*Oryza sativa*) zowel kwalitatief als kwantitatief te kunnen verklaren. De studie richtte zich in eerste instantie op het niveau van de individuele plant (hoofdstuk 1-3). Door meting van de CO_2 uitwisselingssnelheid van individuele bladeren werd het effekt van de ziekte op fotosynthese en ademhaling gemeten. De vlekken die op het blad gevormd werden na infektie door *P. oryzae* bleken zowel de initiële lichtbenuttings-efficiëntie (ε) als de fotosynthesesnelheid bij lichtverzadiging (P_{max}) van rijst bladeren sterker te beïnvloeden dan verwacht op basis van het door hen bezette deel van het bladoppervlak. Om de fotosynthese-parameters aan de bedekkingsgraad te relateren werd het begrip virtuele lesie geïntroduceerd (hoofdstuk 1). Een virtuele lesie is opgebouwd uit de zichtbare lesie en een omringende halo, waarin de fotosynthesesnelheid nul is. In het overblijvende gedeelte van het blad wordt de fotosynthese onaangetast verondersteld. De grootte van de virtuele lesie wordt zodanig gekozen dat de gemeten reduktie in CO_2 uitwisselingssnelheid er volledig door verklaard kan worden. Dit concept resulteerde in een standaardfunktie voor de beschrijving van de relatie tussen bedekkingsgraad en fotosynthesesnelheid, die gekarakteriseerd wordt door slechts één parameter. Deze parameter, β, geeft de verhouding weer tussen het oppervlak van de virtuele en het oppervlak van de zichtbare lesie. Metingen toonden aan dat het effekt van de brandvlekkenziekte op P_{max} en ε weergegeven kan worden met β-waarden van respectievelijk 3.7 ± 0.6 en 3.0 ± 0.7. Een vergelijking tussen drie rijst rassen toonde aan dat de β-waarde niet afhankelijk is van het ras (hoofdstuk 2). De lesies bleken bovendien de ademhalingssnelheid van het geïnfekteerde blad te verhogen (hoofdstuk 3).

Het effekt van de brandvlekkenziekte op de fotosynthesesnelheid van een rijstgewas werd in het veld gemeten, met behulp van mobiele apparatuur (hoofdstuk 4). In de geïnoculeerde veldjes werd een duidelijke reduktie in gewasfotosynthese gemeten. Een model voor de invloed van de brandvlekkenziekte op de fotosynthese van een rijstgewas werd opgesteld, door aan de fotosynthese- en de ademhalingsroutines van een bestaand model submodellen voor de effekten van de ziekte op bladfotosynthese en ademhaling

toe te voegen. De gemeten fotosynthese werd met het model zowel voor de gezonde als voor de geïnoculeerde gewassen bevredigend gesimuleerd. Een analyse van de resultaten van het model maakte duidelijk dat de reduktie in gewasfotosynthese voornamelijk toegeschreven kon worden aan het negatieve effekt van de ziekte op de bladfotosynthese en aan de beschaduwing die veroorzaakt werd door voortijdig afgestorven bladeren bovenin het gewas. Met een gevoeligheidsanalyse werd het belang van de verticale verdeling van de ziekte in het gewas aangetoond. Lesies bovenin het gewas bleken een grotere invloed op de fotosynthesesnelheid van het gewas te hebben dan lesies in het onderste deel van het gewas. Dit verschil bleek volledig toe te schrijven te zijn aan de grotere bijdrage van de bovenste gewaslagen aan de fotosynthese van het gewas.

Onder veldomstandigheden werd de invloed van de brandvlekkenziekte op de groei en produktie van een rijstgewas bepaald (hoofdstuk 5). De behandelde veldjes werden hierbij gedurende de uitstoelingsfase van het gewas geïnoculeerd. Dit resulteerde in een hoge aantastingsgraad rond het eind van de uitstoeling, waarna de ziekte geleidelijk uit het gewas verdween. Een eerste analyse maakte duidelijk dat naast het effekt van de ziekte op de koolstofhuishouding van het gewas er ook sprake was van een effekt op de stikstofopname en de aanleg van opslagorganen. De opslagcapaciteit van het gewas werd gereduceerd door een vermindering van het aantal korrels en een verlaging van het korrelgewicht. Echter, omdat de ziekte ook de fraktie gevulde korrels verminderde, werd gekonkludeerd dat de verminderde graanopbrengst volledig was toe te schrijven aan de verminderde produktiecapaciteit van het gewas. Voor de bloei bleek de stikstofopname van geïnoculeerde gewassen aanmerkelijk lager te zijn dan de stikstofopname van het gezonde gewas, terwijl de stikstofopname na de bloei in beide gevallen nagenoeg verwaarloosbaar was. Herverdeling van stikstof uit vegetatieve plantedelen was dan ook de voornaamste stikstofbron voor de korrelgroei. Het hogere stikstofgehalte in de bovengrondse organen van geïnfekteerde planten, gemeten tijdens de korrelvullingsfase, toonde aan dat de verminderde stikstofopname geen belemmerende faktor was gedurende de korrelvulling. Dientengevolge kon de reduktie in graanopbrengst volledig worden toegeschreven aan een verminderd aanbod van assimilaten.

De reduktie in de opbrengst van het gewas werd nader geanalyseerd met behulp van twee gewasgroei-modellen (hoofdstuk 6). Met behulp van het eerste model werd aangetoond dat de brandvlekkenziekte de droge-stofproduktie verlaagt door middel van een reduktie in de hoeveelheid onderschept licht en een reduktie in de efficiëntie waarmee dit licht omgezet wordt in droge stof. Analyse met een meer gedetailleerd mechanistisch gewasgroeimodel toonde aan

dat, gedurende de eerste weken na het begin van de epidemie, de reduktie in lichtbenuttingsefficiëntie van het gewas niet volledig verklaard kon worden met behulp van het eerder gemeten effekt van de ziekte op de fotosynthese- en de ademhalingssnelheid van individuele bladeren. Uit literatuuronderzoek bleek dat deze periode samenvalt met de periode waarin de schimmel actief sporuleert. Onttrekking van assimilaten aan het groeiproces van de plant door de schimmel lijkt dan ook de meest aannemelijke verklaring voor het feit dat de lichtbenuttingsefficiëntie van het gewas sterker geremd werd dan verwacht. Op basis van deze resultaten werd het model uitgebreid met een submodel waarin de onttrekking van assimilaten voor sporulatie gesimuleerd wordt.

In hoofdstuk 7 werd het mechanistisch gewasgroeimodel gebruikt om de bijdrage van de verschillende schademechanismen aan de totale opbrengst-derving te schatten. Bedekking van groen blad door brandvlekken en een vervroegde bladafsterving verlaagden op een direkte wijze de lichtonder-schepping. Beide komponenten tezamen waren verantwoordelijk voor 50 tot 70% van de verlaging in korrelopbrengst. Het resterende deel van de verlaging in korrelopbrengst werd veroorzaakt door direkte effekten van de ziekte op de lichtbenuttingsefficiëntie van het gewas. Van deze effekten waren de verlaging in bladfotosynthesesnelheid en de opname van assimilaten voor sporulatie nagenoeg even belangrijk. De verhoogde ademhaling droeg nauwelijks bij aan de opbrengstverlaging. De studie maakte verder duidelijk dat vanaf het midden van de uitstoelingsfase tot aan de bloei er nauwelijks verschillen bestaan in de gevoeligheid van het rijstgewas voor aanwezigheid van de brandvlekkenziekte.

References

Ahn, S.W. & Ou, S.H., 1982. Quantitative resistance of rice to blast disease. *Phytopathology* 72: 279-282.

Akita, S., Parao, F.T. & Coronel, V.P., 1987. Physiological response of rice to light and to nitrogen. In: *Weather and Rice*. International Rice Research Institute, Los Baños, Philippines. p. 82-91.

Anderson, A.L., Henry, B.W. & Tullis, E.C., 1947. Factors affecting infectivity, spread and persistence of *Pyricularia oryzae* Cav.. *Phytopathology* 37: 94-110.

Azcón-Bieto, J., 1983. Inhibition of photosynthesis by carbohydrates in wheat leaves. *Plant Physiology* 73: 681-686.

Azcón-Bieto, J. & Osmond, C.B., 1983. Relationship between photosynthesis and respiration. The effect of carbohydrate status on the rate of CO_2 production by respiration in darkned and illuminated wheat leaves. *Plant Physiology* 71: 574-581.

Bastiaans, L., 1991. Ratio between virtual and visual lesion size as a measure to describe reduction in leaf photosynthesis of rice due to leaf blast. *Phytopathology* 81: 611-615.

Bastiaans, L., 1993a. Effects of leaf blast on photosynthesis of rice. 1. Leaf photosynthesis. *Netherlands Journal of Plant Pathology* 99: *in press*

Bastiaans, L., 1993b. Effects of leaf blast on growth and production of a rice crop. 1. Determining the mechanism of yield reduction. *Netherlands Journal of Plant Pathology* 99: *accepted*

Bastiaans, L., 1993c. Effects of leaf blast on growth and production of a rice crop. 2. Analysis of the reduction in dry matter production of rice due to leaf blast, using two models with different complexity. *Netherlands Journal of Plant Pathology* 99: *accepted*

Bastiaans, L. & Kropff, M.J., 1993. Effects of leaf blast on photosynthesis of rice. 2. Canopy photosynthesis. *Netherlands Journal of Plant Pathology* 99: *in press*

Berge, H.F.M. ten, 1993. Building capacity for systems research at national agricultural research centres: SARP's experience. In: Penning de Vries, F.W.T., Teng, P.S. & Metselaar, K. (Eds), *Systems approaches for agricultural development*. Kluwer Academic Publishers, Dordrecht, The Netherlands. p. 515-538.

Björkman, O., 1981. Responses to different quantum flux densities. In: Lange, L.O., Nobel, P.S., Osmond, C.B. & Ziegler, H. (Eds), *Encyclopedia Plant Physiology, New series. Volume 12A: Physiological Plant Ecology I: Responses to the Physical Environment*. Springer Verlag, Berlin. p. 57-107.

Blackman, V.H., 1919. The compound interest law and plant growth. *Annals of botany* 33: 353-360.

Boote, K.J., Jones, J.W., Mishoe, J.W. & Berger, R.D., 1983. Coupling pests to crop growth simulators to predict yield reductions. *Phytopathology* 73: 1581-1587.

Boote, K.J., Jones, J.W., Smerage, G.H., Barfield, C.S. & Berger, R.D., 1980. Photosynthesis of peanut canopies as affected by leafspot and artificial defoliation.

Agronomy Journal 72: 247-252.

Bowden, R.L. & Rouse, D.I., 1991. Chronology of gas exchange effects and growth effects of *Verticillium dahliae* infection in potato. *Phytopathology* 81: 301-310.

Brouwer, R., 1962. Nutritive influences on the distribution of dry matter in the plant. *Netherlands Journal of Agricultural Science* 10: 399-408.

Buchanan, B.B., Hutcheson, S.W., Magyarosy, A.C. & Montalbini, P., 1981. Photosynthesis in healthy and diseased plants. In: Ayres P.G. (Ed.), *Effects of disease on the physiology of the growing plant*. Cambridge University Press, Cambridge. p. 13-28.

Burrell, M.M. & Rees, T., 1974. Carbohydrate metabolism of rice leaves infected by *Pyricularia oryzae*. *Physiological Plant Pathology* 4: 489-496.

Bushnell, W.R. & Allen, P.J., 1962. Respiratory changes in barley leaves produced by single colonies of powdery mildew. *Plant Physiology* 37: 751-758.

Chatterton, N.J., 1973. Product inhibition of photosynthesis in alfalfa leaves as related to specific leaf weight. *Crop Science* 13: 284-285.

Cook, M.G. & Evans, L.T., 1983. Nutrient responses of seedlings of wild and cultivated *Oryza* species. *Field Crops Research* 6: 205-218.

Daamen, R.A., 1989. Assessment of the profile of powdery mildew and its damage function at low disease intensities in field experiments with winter wheat. *Netherlands Journal of Plant Pathology* 95: 85-105.

Dingkuhn, M., Schnier, H.F., De Datta, S.K., Wijangco, E. & Doerffling, K., 1990. Diurnal and developmental changes in canopy gas exchange in relation to growth in transplanted and direct seeded flooded rice. *Australian Journal of Plant Physiology* 17: 119-134.

Ephrath, J.E., Shteinberg D., Drieshpoun, J., Dinoor, A. & Marani, A., 1989. *Alternaria alternata* in cotton (*Gossypium hirsutum*) cv. Acala: effects on gas exchange, yield components and yield accumulation. *Netherlands Journal of Plant Pathology* 95: 157-166.

Evans, L.T., 1975. The physiological basis of crop yield. In: Evans, L.T. (Ed.), *Crop physiology; some case histories*. Cambridge University Press, London. p. 327-355.

Gaunt, R.E., 1978. Crop physiology: disease effects and yield loss. In: *Proceedings of the APPS workshop on epidemiology and crop loss assessment*. Lincoln College, New Zealand. p. 9/1-12.

Genstat 5 reference manual, 1987. Clarendon Press, Oxford. 749 pp.

Goto, K., 1965. Estimating losses from rice blast in Japan. In: *The rice blast disease*. The Johns Hopkins Press, Baltimore, Maryland. p. 195-202.

Goudriaan, J., 1982. Potential production processes. In: Penning de Vries, F.W.T. & Laar, van H.H. (Eds), *Simulation of plant growth and crop production*. Simulation monographs, Pudoc, Wageningen, p. 98-113.

Goudriaan, J., 1986. A simple and fast numerical method for the calculation of daily totals of crop photosynthesis. *Agricultural and Forest Meteorology* 38: 251-255.

Goudriaan, J., 1988. The bare bones of leaf angle distribution in radiation models for canopy photosynthesis and energy exchange. *Agricultural and Forest Meteorology* 43: 155-169.

Haverkort, A.J. & Bicamumpaka, M., 1986. Correlation between intercepted radiation and yield of potato crops infested by *Phytophthora infestans* in central Africa. *Netherlands Journal of Plant Pathology* 92: 239-247.

Jeanguyot, M., 1983. Rice blast and its control. *Mémoires et travaux de l'IRAT no. 3*. IRAT. 53 pp.

Johnson, K.B., 1987. Defoliation, disease and growth: a reply. *Phytopathology* 77: 1495-1497.

Justesen, J.H. & Tammes, P.M.L., 1960. Studies on yield losses I. The self-limiting effect of injurious or competitive organisms on crop yield. *Tijdschrift over Planteziekten* 66: 281-287.

Kaiser, W.M., 1987. Effects of water deficit on photosynthetic capacity. *Physiologia Plantarum* 71: 142-149.

Kato, H. & Kozaka, T., 1974. Effect of temperature on lesion enlargement and sporulation of *Pyricularia oryzae* in rice leaves. *Phytopathology* 64: 828-830.

Kato, H., Sasaki, T. & Koshimizy, Y., 1970. Potential for conidium formation of *Pyricularia oryzae* in lesions on leaves and panicles of rice. *Phytopathology* 60: 608-612.

Katsube, T. & Koshimizu, Y, 1970. Influence of blast disease on harvests in rice plant. 1. Effects of panicle infection on yield components and quality. *Bulletin of the Tohoku National Agricultural Experiment Station* 39: 55-96.

Kim, C.K., Yoshino, R. & Lee, E.J., 1987. Epidemiological studies of rice blast disease caused by *Pyricularia oryzae* Cavara. II. Sporulation and conidia release from naturally infected lesions. *Korean Journal of Plant Protection* 26: 37-41.

Koh, Y.J., Hwang, B.K. & Chung, H.S., 1987. Adult-plant resistance of rice to leaf blast. *Phytopathology* 77: 232-236.

Kropff, M.J., 1989. Quantification of SO_2 effects on physiological processes, plant growth and crop production. *Ph.D. thesis, Wageningen Agricultural University*, The Netherlands. 201 pp.

Kropff, M.J. & Goudriaan, J., 1989. Modelling short term effects of sulphur dioxide. 3. Effects of SO_2 on photosynthesis of leaf canopies. *Netherlands Journal of Plant Pathology* 95: 265-280.

Kropff, M.J., Vossen, F.J.H., Spitters, C.J.T. & Groot, W. de, 1984. Competition between a maize crop and a natural population of *Echinochloa crus-galli* (L.). *Netherlands Journal of Agricultural Science* 35: 525-528.

Ku, S.B., Edwards, G.E.& Smith, D., 1978. Photosynthesis and nonstructural carbohydrate concentration in leaf blades of *Panicum virgatum* as affected by night temperature. *Canadian Journal of Botany* 56: 63-68.

Kuribayashi, K. & Ichikawa, H., 1952. Studies on forecasting of the rice blast disease. Special report, *Nagano Agricultural Experiment Station* 13, 1-229.

Lim, L.G. & Gaunt, R.E., 1986. The effect of powdery mildew (*Erysiphe graminis* f. sp. *hordei*) and leaf rust (*Puccinia hordei*) on spring barley in New Zealand. I. Epidemic development, green leaf area and yield. *Plant Pathology* 35: 44-53.

Louwerse, W. & van Oorschot, J.L.P., 1969. An assembly for routine measurements of photosynthesis, respiration and transpiration of intact plants under controlled conditions. *Photosynthetica* 3:305-315.

Mackill, A.O. & Bonman, J.M., 1986. New hosts of *Pyricularia oryzae*. *Plant Disease* 70: 125-127.

Madden, L.V., 1983. Measuring and modelling crop losses at the field level. *Phytopathology* 73: 1591-1596.

Marshall, B. & Biscoe, P.V., 1980. A model for C_3 leaves describing the dependence of net photosynthesis on irradiance. I. Derivation. *Journal of Experimental Botany* 31: 29-39.

119

Matshushima, S., 1970. *Crop science in rice.* Fuji Publishing Co., Ltd., Tokyo, Japan. 379 p.

McCree, K.J., 1970. An equation for the rate of respiration of white clover plants grown under controlled conditions. In: *Prediction and measurement of photosynthetic productivity.* Pudoc, Wageningen. p. 221-229.

McCree, K.J., 1974. Equations for the rate of dark respiration of white clover and grain sorghum, as functions of dry weight, photosynthetic rate, and temperature. *Crop Science* 14: 509-514.

Monteith, J.L., 1977. Climate and the efficiency of crop production in Britain. *Philosophical Transactions of the Royal Society of London, Series B* 281: 277-294.

Neales, T.F. & Incoll, L.D., 1968. The control of leaf photosynthesis rate by the level of assimilate concentration in the leaf: a review of the hypothesis. *Botanical Review* 34: 107-125.

Nonhebel, S., 1992. Use of weather data in crop growth simulation models. In: Scaife, A. (Ed.), *Proceedings of the Second Congress of the European Society for Agronomy.* ESA UK Congress Office, Wellesbourne, UK. p. 156-165.

Oijen, M. van, 1990. Photosynthesis is not impaired in healthy tissue of blighted potato plants. *Netherlands Journal of Plant Pathology* 96: 55-63.

Oijen, M. van, 1991a. Leaf area dynamics of potato cultivars infected by *Phytophthora infestans. Netherlands Journal of Plant Pathology* 97: 345-354.

Oijen, M. van, 1991b. Light use efficiencies of potato cultivars with late blight (*Phytophthora infestans*). *Potato Research* 34: 123-132.

Oijen, M. van, 1991c. Identification of the major characteristics of potato cultivars which affect yield loss caused by late blight. *Ph.D. thesis, Wageningen Agricultural University,* The Netherlands. 116 pp.

Ou, S.H., 1985. *Rice diseases.* Commonwealth Mycological Institute, Kew, Surrey, England. 2nd Edition, 380 pp.

Padhi, B., Chakrabarti, N.K. & Nayak, S.K., 1978. Effect of blast on the photosynthetic activity of rice seedlings. *Biologia Plantarum* 20: 418-420.

Padmanabhan, S.Y., 1965. Estimating losses from rice blast in India. In: *The rice blast disease.* The Johns Hopkins Press, Baltimore, Maryland. p. 203-221.

Parlevliet, J.E., 1979. Components of resistance that reduce the rate of epidemic development. *Annual Review of Phytopathology* 17: 203-222.

Parton, J.P. & Logan, J.A., 1981. A model for diurnal variation in soil and air temperature. *Agricultural Meteorology* 23: 205-216.

Penning de Vries, F.W.T., 1972. Respiration and growth. In: Rees, A.R., Cockshull, K.E., Hand, D.W. & Hurd, R.J. (Eds), *Crop Processes in Controlled Environments.* Academic Press, London. p. 327-347.

Penning de Vries, F.W.T., 1975. The cost of maintenance processes in plant cells. *Annals of Botany* 39: 77-92.

Penning de Vries, F.W.T., Jansen, D.M., ten Berge, H.F.M. & Bakema, A., 1989. *Simulation of ecophysiological processes of growth in several annual crops.* PUDOC, Wageningen, the Netherlands. 271 pp.

Penning de Vries, F.W.T., van Keulen, H. & Alagos, J.C., 1990. Nitrogen redistribution and potential production in rice. In: *Proceedings of the International Congress of Plant Physiology,* New Delhi, India. Society for Plant Physiology & Biochemistry, New Delhi.

120

p. 513-520.

Rabbinge, R. & Bastiaans, L., 1989. Combination models, crop growth and pests and diseases. In: Rabbinge, R., Ward, S.A. & van Laar, H.H. (Eds), *Simulation and systems management in crop protection.* Pudoc, Wageningen. p. 217-239.

Rabbinge, R., Jorritsma, I.T.M. & Schans, J., 1985. Damage components of powdery mildew in winter wheat. *Netherlands Journal of Plant Pathology* 91: 235-247.

Rabbinge, R. & Rijsdijk, F.H., 1981. Disease and crop physiology: a modeller's point of view. In: Ayres, P.G., (Ed.), *Effects of disease on the physiology of the growing plant.* Cambridge University Press, Cambridge. p. 201-220.

Ralston, M.L. & Jennrich, R.I., 1979. DUD, a derivative-free algorithm for nonlineair least squares. *Technometrics* 1: 7-14.

Roermund, H.J.W. van & Spitters, C.J.T., 1990. Simulation of yield reduction by leaf rust in winter wheat, applied to the analysis of genetic variation in partial resistance. *Netherlands Journal of Plant Pathology* 96: 17-28.

Rossing, W.A.H., 1991. Simulation of damage in winter wheat caused by the grain aphid *Sitobion avenae.* 2. Construction and evaluation of a simulation model. *Netherlands Journal of Plant Pathology* 97, 25-54.

Rossing, W.A.H., Oijen, M. van, Werf, W. van der, Bastiaans, L. & Rabbinge, R., 1992. Modelling the effects of foliar pests and pathogens on light interception, photosynthesis, growth rate and yield of field crops. In: Ayres, P.G., (Ed.), *Pests and pathogens: plant responses to foliar attack.* Bios Scientific Publishers Ltd., Oxford, UK. p. 161-180.

Rossman, A.Y., Howard, R.J. & Valent, B., 1990. *Pyricularia grisea,* the correct name for the rice blast fungus. *Mycologia* 82: 509-512.

Rotem, J., Bashi, E. & Kranz, J., 1983. Studies of crop loss in potato blight caused by *Phytophthora infestans. Plant Pathology* 32: 117-122.

Roumen, E.C., 1992. Effect of leaf age on components of partial resistance in rice to leaf blast. *Euphytica* 63: 271-279.

Roumen, E.C., 1993. Partial resistance in rice to blast and how to select for it. *Ph.D. thesis, Wageningen Agricultural University,* The Netherlands. 108 pp.

Roumen, E.C., Bonman, J.M. & Parlevliet J.E., 1992. Leaf age related partial resistance to *Pyricularia oryzae* in tropical lowland rice cultivars as measured by the number of sporulating lesions. *Phytopathology* 82: 1414-1417.

Ryle, G.J.A., Cobby, J.M. & Powell, C.E., 1976. Synthetic and maintenance respiratory losses of $^{14}CO_2$ in uniculm barley and maize. *Annals of Botany* 40: 571-586.

Samborski, D.J. & Shaw, M., 1956. The physiology of host-parasite relations. II. The effect of *Puccinia graminis tritici* Eriks. & Henn. on the respiration of the first leaf of resistant and susceptible species of wheat. *Canadian Journal of Botany* 34: 601-619.

Schans, J., 1993. Population dynamics of potato cyst nematodes and associated damage to potato. *Ph.D. thesis, Wageningen Agricultural University,* The Netherlands. 115 pp.

Shaw, M. & Samborski, D.J., 1957. The physiology of host-parasite relations. III. The pattern of respiration in rusted and mildewed cereal leaves. *Canadian Journal of Botany* 35: 389-407.

Siddiqui, M.Q. & Manners, J.G., 1971. Some effects of general yellow rust (*Puccinia striiformis*) infection on ^{14}carbon assimilation and growth in spring wheat. *Journal of Experimental Botany* 22: 792-799.

Smedegaard-Petersen, V., 1984. The role of respiration and energy generation in diseased and disease resistant plants. In: Wood, R.K.S. & Jellis, G.J. (Eds), *Plant diseases: infection, damage and loss.* Blackwell Scientific Publications, Oxford. p. 73-85.

Smedegaard-Petersen, V. & Tolstrup, K., 1985. The limiting effect of disease resistance on yield. *Annual Review of Phytopathology* 23: 475-490.

Spiertz, J.H.J. & van Keulen, H., 1980. Effects of nitrogen and water supply on growth and grain yield of wheat. *Proceedings 3rd International Wheat Conference,* Madrid, Spain. p. 595-610.

Spitters, C.J.T., 1986. Separating the diffuse and direct component of global radiation and its implications for modelling canopy photosynthesis. Part II: Calculation of canopy photosynthesis. *Agricultural and Forest Meteorology* 38: 231-242.

Spitters, C.J.T., Roermund, van H.J.W., Nassau, van H.G.M.G., Schepers, J. & Mesdag, J., 1990. Genetic variation in partial resistance to leaf rust in winter wheat: disease progress, foliage senescence and yield reduction. *Netherlands Journal of Plant Pathology* 96: 3-15.

Spitters, C.J.T., Toussaint, H.A.J.M. & Goudriaan, J., 1986. Separating the diffuse and direct component of global radiation and its implications for modeling canopy photosynthesis. Part I: Components of incoming radiation. *Agricultural and Forest Meteorology* 38: 217-229.

Tamari, K. & Kaji, J., 1954. Biochemical studies of the blast fungus (*Pyricularia oryzae* Cav.), the causative fungus of the blast disease of rice plants. I. Studies on the toxins produced by blast fungus. *Journal of the Agricultural Chemical Society of Japan* 28: 254-258.

Teng, P.S., Klein-Gebbinck, H.W. & Pinnschmidt, H., 1991. An analysis of the blast pathosystem to guide modelling and forecasting. In: *Rice blast modeling and forecasting.* International Rice Research Institute, Los Baños, Philippines. p. 1-30.

Teng, P.S. & Savary, S., 1992. Implementing the systems approach in pest management. *Agricultural Systems* 40: 237-264.

Thornley, J.H.M., 1970. Respiration, growth and maintenance in plants. *Nature* 227: 304-305.

Toriyama, K., 1975. Recent progress of studies on horizontal resistance in rice breeding for blast resistance in Japan. In: G.E. Gàlvez (Ed.), *Proceedings of a Seminar on Horizontal Resistance to the Blast Disease of Rice, CIAT series CE 9.* Cali, Colombia. p. 65-100.

Torres, C.Q., 1986. Effect of plant age on the expression of resistance to *Pyricularia oryzae* Cav. in upland rice varieties. *Ph.D. thesis, University of the Philippines at Los Baños, Laguna, Philippines.* 82 pp.

Toyoda, S. & Suzuki, N., 1957. Histochemical studies on the lesions of rice blast caused by *Pyricularia oryzae* Cav. III. Changes in the respiration of infected tissues. *Annals of the Phytopathological Society of Japan* 22: 173-177.

Tsai, W.H., 1988a. Estimation of rice yield losses caused by panicle blast disease. *Journal of Agricultural Research of China* 37: 86-90.

Tsai, W.H., 1988b. Estimation of yield losses caused by leaf blast disease. *Journal of Agricultural Research of China* 37: 207-210.

Upmeyer, D.J. & Koller, H.R., 1973. Diurnal trends in net photosynthetic rate and carbohydrate levels of soybean leaves. *Plant Physiology* 51: 871-874.

von Caemmerer, S. & Farquhar, G.D., 1981. Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. *Planta* 153: 376-387.

Waggoner, P.E. & Berger, R.D., 1987. Defoliation, disease and growth. *Phytopathology* 77: 393-398.

Werf, van der W., 1988. Yellowing viruses in sugarbeet; epidemiology and damage. *Ph.D.*

thesis, Wageningen Agricultural University, The Netherlands. 152 pp.

Wit, C.T. de & Keulen, H. van, 1987. Modelling production of field crops and its requirements. *Geoderma* 40: 253-265.

Yeh, W.H. & Bonman, J.M., 1986. Assessment of partial resistance to *Pyricularia oryzae* in six rice cultivars. *Plant Pathology* 35: 319-323.

Yoshida, S., 1981. *Fundamentals of rice crop science.* International Rice Research Institute, Los Baños, Laguna, Philippines. 269 pp.

Yoshii, H., 1937. Pathological studies of rice blast caused by *Pyricularia oryzae*. III. Pathohistological observations of diseased plants. *Annals of the Phytpathological Society of Japan* 7: 289-304.

Zadoks, J.C., 1961. Yellow rust on wheat, studies in epidemiology and physiologic specialization. *Tijdschrift over Planteziekten* 67: 69-256.

Zadoks, J.C., 1973. Modelling the models. *Introduction to Symposium: Developing models for measuring crop losses (handout).* 2nd International Congres of Plant Pathology, Minneapolis.

Zadoks, J.C., 1989. EPIPRE, a computer-based decision support system for pest and disease control in wheat: its development and implementation in Europe. In: Leonard, K.J. & Fry, W.E. (Eds), *Plant disease epidemiology. Volume 2: Genetics, resistance, and management.* McGraw-Hill Publishing Company, New York. p. 3-29.

Zadoks, J.C., Chang, T.T. & Konzak, C.F., 1974. A decimal code for the growth stages of cereals. *Weed Research* 14: 415-421.

Zadoks, J.C. & Schein, R.D., 1979. *Epidemiology and plant disease management.* Oxford University Press, New York. 427 pp.

Kropff, M.J., Bastiaans, L. & Goudriaan, J., 1987. Implications of improvements in modelling canopy photosynthesis in SUCROS (a simple and universal crop growth simulator). *Netherlands Journal of Agricultural Science* 35: 192-194.

Kropff, M.J., Joenje, W., Bastiaans, L., Habekotté, B., van Oene, H. & Werner, R., 1987. Competition between a sugar beet crop and populations of *Chenopodium album* L. and *Stellaria media* L.. *Netherlands Journal of Agricultural Science* 35: 525-528.

Rabbinge, R. & Bastiaans, L., 1989. Combination models, crop growth and pests and diseases. In: Rabbinge, R., Ward, S.A. & van Laar, H.H. (Eds), *Simulation and systems management in crop protection.* Pudoc, Wageningen. p. 217-239.

Rabbinge, R., Zadoks, J.C. & Bastiaans, L., 1989. Population models. In: Rabbinge, R., Ward, S.A. & van Laar, H.H. (Eds), *Simulation and systems management in crop protection.* Pudoc, Wageningen. p. 83-97.

Bastiaans, L., 1990. Incorporation of damage mechanisms of leaf blast into crop growth model MACROS. In: Teng, P.S. & Yuen, J.E. (Eds), *Proceedings workshop on modelling pest-crop interactions.* Research Extension Series 120, International Benchmark Sites Network for Agrotechnology Transfer (IBSNAT), University of Hawaii. p. 38-39.

Bastiaans, L., 1991. Ratio between virtual and visual lesion size as a measure to describe reduction in leaf photosynthesis of rice due to leaf blast. *Phytopathology* 80: 611-615.

Bastiaans, L., 1991. Quantification of the effect of leaf blast on leaf photosynthesis, crop growth, and final yield using an ecophysiological model of crop growth. In: *Proceedings International Rice Research Conference*, Seoul, 1990. Rice Blast Modelling and Forecasting, IRRI, Philippines. p. 89-99.

Bastiaans, L. & Kropff, M.J., 1991. Understanding and quantifying damage by air pollution and leaf blast. In: Penning de Vries, F.W.T., Kropff, M.J., Teng, P.S. & Kirk, G.J.D. (Eds), *Systems simulation at IRRI.* IRRI Research Paper Series 151, IRRI, Los Baños, Philippines. p. 21-26.

Reddy, P.R., Nayak, S.K. & Bastiaans, L., 1991. Simulation of the effect of bacterial blight disease on crop growth and yield of rice. In: Penning de Vries, F.W.T., van Laar, H.H. & Kropff, M.J. (Eds), *Simulation and systems analysis for rice production (SARP).* Pudoc, Wageningen. p. 340-347.

Werf, van der W., Bastiaans, L., Rossing, W.A.H. & Rabbinge, R., 1991. Modelling crop response to growth reducing factors. In: *Proceedings of the international symposium on biotic stress of barley in arid and semi-arid environments*, Big Sky, Montana. p. 87-102.

Rossing, W.A.H., van Oijen, M., van der Werf, W., Bastiaans, L. & Rabbinge, R., 1992. Modelling the effects of foliar pests and pathogens on light interception, photosynthesis, growth rate and yield of field crops. In: Ayres, P.G. (Ed.), *Pests and pathogens: plant responses to foliar attacks.* Bios Scientific Publishers Ltd., Oxford, UK. p.161-180.

Bastiaans, L., 1993. Effect of leaf blast on photosynthesis of rice. 1. Leaf photosynthesis. *Netherlands Journal of Plant Pathology* 99: *in press.*

Bastiaans, L., 1993. Effects of leaf blast on growth and production of a rice crop. 1. Determining the mechanism of yield reduction. *Netherlands Journal of Plant Pathology* 99: *accepted*

Bastiaans, L., 1993. Effects of leaf blast on growth and production of a rice crop. 2. Analysis of the reduction in dry matter production of rice due to leaf blast, using two models with different complexity. *Netherlands Journal of Plant Pathology* 99: *accepted*

Bastiaans, L. & Kropff, M.J., 1993. Effect of leaf blast on photosynthesis of rice. 2. Canopy photosynthesis. *Netherlands Journal of Plant Pathology* 99: *in press.*

Bastiaans, L. & Roumen, E.C., 1993. Effect on leaf photosynthetic rate by leaf blast for rice cultivars with different types and levels of resistance. *Euphytica* 66: 81-87.

Bastiaans, L., Rabbinge, R. & Zadoks, J.C., 1993. Understanding and modeling leaf blast effects on crop physiology and yield. In: *Proceedings of an international symposium on rice blast disease.* University of Wisconsin, Madison: *in press.*

Curriculum vitae

Lammert Bastiaans werd op 17 augustus 1959 geboren te Eexterveen. In 1976 behaalde hij het HAVO diploma aan de Rijksscholengemeenschap Winkler Prins te Veendam. In 1980 rondde hij zijn studie aan de Rijks Hogere Landbouwschool te Groningen af, in de landbouwkundige differentiatie (akkerbouw). In hetzelfde jaar startte hij aan de Landbouwhogeschool te Wageningen met een studie plantenziektenkunde. In 1987 slaagde hij cum laude voor het doctoraalexamen met als hoofdvakken fytopathologie en theoretische teeltkunde en als bijvak onkruidkunde.

Aansluitend aan zijn studie werd hij aangesteld als Assistent in Opleiding bij de vakgroep Theoretische Produktie-ecologie van de Landbouwuniversiteit Wageningen, waar hij het onderzoek voor dit proefschrift verrichtte. Het onderzoek werd uitgevoerd als onderdeel van het 'Systems analysis and simulation for rice production' (SARP) - project, een project opgezet door de vakgroep, het Centrum voor Agrobiologisch Onderzoek (CABO-DLO) en het International Rice Research Institute (IRRI) op de Filippijnen. In 1992 werd hij binnen hetzelfde project aangesteld als coördinator gewasbescherming en initieerde hij schade-onderzoek naar bacterial leaf blight en de rijststengelboorder. Sinds maart 1993 is hij aangesteld bij het Nederlands Graan Centrum als wetenschappelijk onderzoeker Agro-ecologie en als zodanig gedetacheerd bij de sectie kwantitatieve ecologie van het Instituut voor Planteziektenkundig Onderzoek (IPO-DLO).