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Understanding and quantifying damage by air pollution and leaf blast.

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INTERNATIONAL RICE RESEARCH INSTITUTE

Understanding and quantifying damage by air pollution and leaf blast

L. Bastiaans and M. J. Kropff¹

Potential yields are obtained in situations with ample water supply, nutrients, and other resources, and in the absence of weeds, pests, and diseases. Potential yield depends on site-specific conditions (radiation, temperature) and crop physiological characteristics (crop architecture, assimilate allocation). These factors determine potential growth.

Yield decreases to the attainable yield when one or more resources (water, nutrients) limit crop growth. Next to these growth-determining and -limiting factors, we can distinguish growth-reducing factors (air pollutants, diseases). Actual yield rarely meets the attainable level in their presence.

Mechanistic simulation models for crop growth were used to evaluate the effect of growth-reducing factors on plant growth and crop production. The two case studies are based on a quantitative analysis of the effect of these factors on plant physiological processes.

CASE STUDY 1: IMPACT OF SO₂ ON BROAD BEAN (*VICIA FABEA* L.) YIELD

Sulfur dioxide (SO₂) is a major air pollutant in industrialized areas that can damage vegetation. Three categories of SO₂ injury exist for plants: acute, chronic, and subtle.

Acute injury results from less than one day of exposure to high SO₂ concentrations and appears as irreversible, visible leaf necrosis. Chronic injury (chlorotic or necrotic damage) results from long-term exposure (days to years) to variable SO₂ concentrations. Older leaves are generally damaged, followed by early abscission.

Subtle injury changes physiological and biochemical processes. These changes cause reduced (or stimulated) growth without visible injury. Evidence shows that subtle injury reduces crop yield and influences vegetation composition. Widespread concern exists that sublethal concentrations of SO₂ affect agricultural crops and vegetation.

This study attempted to quantitatively explain the effects of SO₂ on crop growth and production through the foliar uptake of SO₂ and the interference of SO₂ metabolites with physiological processes.

Experiments at different levels of biological organization (field crop growth and biological processes) were conducted with broad bean (*Vicia faba* L. cv. *minica*) (Kropff 1989c). This experiment was directly coupled to developing mechanistic models that relate phenomena observed at the different levels of organization (crop and organ).

Photosynthesis and respiration determine the growth rate of closed crop canopies. Effects of short-term SO₂ exposure on these processes were analyzed by gas exchange measurements (Kropff 1987). SO₂ affected photosynthesis only at high radiation levels. The inhibition level increased rapidly after fumigation; a stationary state followed after about 1 h.

Mesophyll resistance to CO₂ diffusion increased as a direct result of SO₂ exposure, causing a rapid reduction in photosynthesis after fumigation began. The decrease in net photosynthesis indirectly affected stomatal resistance.

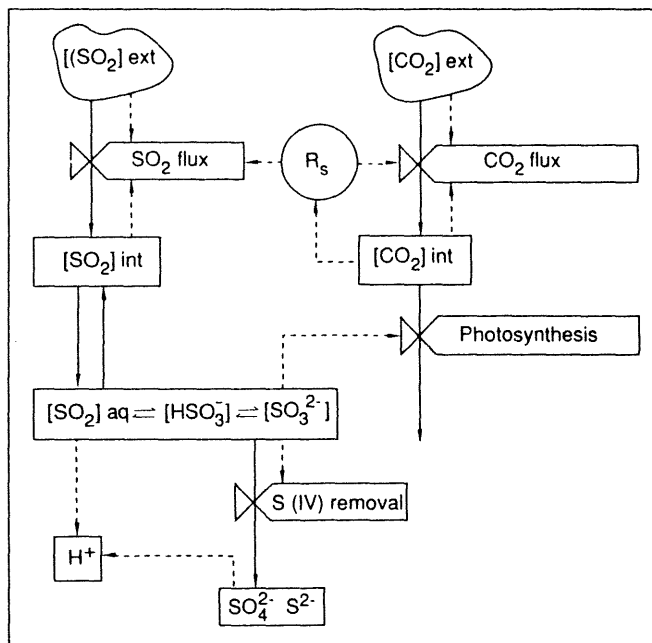
Effects on photosynthesis could be quantitatively explained by an inhibitory effect of SO₂ on CO₂ binding to ribulose-bis phosphate carboxylase/oxygenase. Effects on light reactions of photosynthesis and SO₂ effects on cellular pH and translocation of sugars are not responsible for the observed reductions in photosynthesis by SO₂ during short exposures (Kropff 1987).

A model, based on this analysis, was developed for the flux of atmospheric SO₂ into leaves and the effects of SO₂ metabolites (S [IV] compounds) on leaf photosynthesis and stomatal resistance (Kropff 1989a). The model (Fig. 1) contains two parameters describing biochemical characteristics, a time coefficient for S(IV) oxidation, and a parameter describing the sensitivity of photosynthesis for S(IV).

The model accurately described rapid photosynthetic reduction by SO₂ and rapid recovery following fumigation. A summarized version of a model for SO₂ flux into leaves and effects on photosynthesis was used to estimate values for the two model parameters by combined nonlinear regression of two equations (Kropff 1989b).

Parameter estimates agreed with experimentally determined values. Model results indicated that differences in

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1. A relational diagram of the model for fluxes of SO_2 and CO_2 into the leaf and the effects of S(IV) on photosynthesis. Boxes represent state variables (amounts), circles contain intermediate variables, valve symbols represent rate variables, solid lines indicate flows of material, and broken lines show flows of information. R_s represents stomatal resistance.

photosynthetic sensitivity of plants were mainly due to differences in the rate of S(IV) oxidation and leaf thickness. This approach was useful in explaining effects of temperature and humidity on photosynthetic depression by SO_2 (Kropff et al 1990).

The effect of short-term exposure of SO_2 on broad bean canopy photosynthesis was measured using mobile equipment in the field. Canopy photosynthesis was only affected at high radiation levels; fumigating with $800 \mu\text{g SO}_2/\text{m}^3$ reduced it by up to 6%. A model for canopy photosynthesis was extended with a submodel for SO_2 effects on leaf photosynthesis. Model performance was evaluated with empirical data. The model accurately simulated diurnal canopy photosynthesis and SO_2 effects (Kropff and Goudriaan 1989).

The effects of SO_2 on broad bean growth and production were determined under field conditions using a newly developed open-air exposure system (Kropff et al 1989a,b). The treated plots were exposed to mean SO_2 concentrations of $165 \mu\text{g}/\text{m}^3$ in 1985, $62 \mu\text{g}/\text{m}^3$ in 1986, and $74 \mu\text{g}/\text{m}^3$ in 1988. The background concentration was about $10 \mu\text{g SO}_2/\text{m}^3$.

Crop growth rate was depressed at the end of pod filling in 1985 and 1988. SO_2 exposure reduced total dry matter production by 17% in 1985 and 9% in 1988; it reduced seed yield by 23% in 1985 and 10% in 1988. Reduced pod dry weight resulted in reduced yield.

Dry matter was not analyzed until the end of the growing season in 1986 because *Botrytis fabae* severely infected the control plot during pod filling. *B. fabae* also slightly infected control plots in 1985 and 1988.

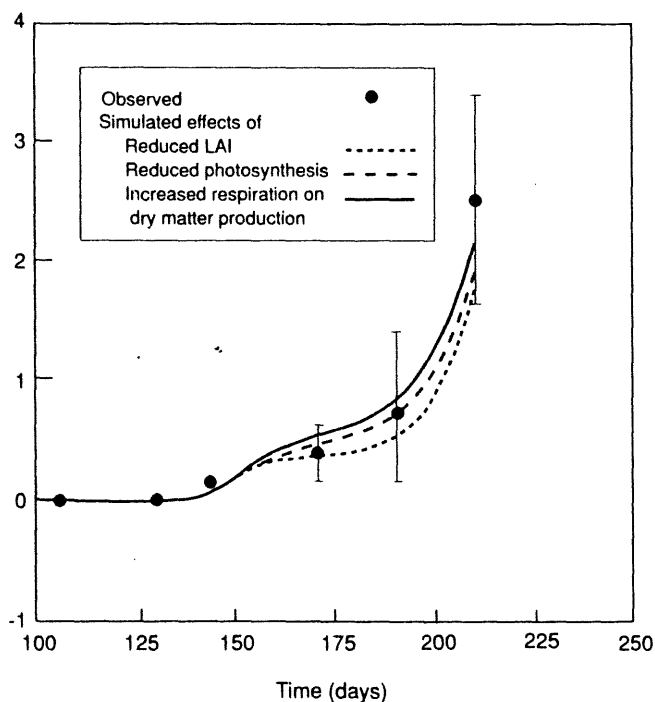
Little infection was observed in the exposed experimental plots, indicating a suppressing effect of SO_2 on the disease. Significant reductions of dry matter growth rate were not observed during vegetative and early reproductive phases in any of the experiments. SO_2 did not affect plant height, internode number, or pod number. Specific leaf area was slightly reduced in the SO_2 -exposed plants at the end of the growing season. Leaf area development was strongly affected during the pod-filling period in 1985 and 1988 as a result of leaf injury and defoliation in the fumigated plots (Kropff et al 1989a,b).

A mechanistic simulation model interpreted the observed effects of SO_2 on growth and production of broad bean (Kropff 1990). It consisted of an elementary crop growth model extended with microclimate submodels and the submodel for foliar uptake of SO_2 and effects on leaf photosynthesis.

Direct effects of SO_2 on leaf photosynthesis explained about 10% of the observed yield loss (Fig. 2). Maintenance respiration of leaves increased by 30% in the 1988 experiment, explaining another 10% of the reduced yield. Chronic SO_2 injury explained the majority of the reduction in total dry matter production. Yield loss was caused by dry matter loss through leaf abscission and a reduced growth rate due to the canopy absorbing less radiation. The model accurately simulated total SO_2 -S uptake of the fumigated crops (an important component of SO_2 dry deposition).

The mechanistic backgrounds of chronic effects were studied by determining the impact of SO_2 on regulating intracellular pH (Kropff 1991). When SO_2 is stored as sulfate and not assimilated in organic compounds, an equivalent

Dry matter (t/ha)



2. Observed and simulated difference in total dry matter production for control and fumigated crop in 1985.

amount of H^+ has to be buffered. Metabolic processes remove these H^+ ions.

A conceptual model was developed to describe the processes involved. H^+ can be neutralized by OH^- ions produced either in the leaves when organic compounds assimilate sulfate and nitrate, or by decarboxylation of organic anions (a biochemical pH stat mechanism that balances the pH). A biochemical pH stat (pH balance mechanism) produces these organic anions by removing OH^- from cellular solutions when sulfate and nitrate are reduced, or when differences in the uptake of non-nitrogen-containing cations and inorganic anions are counterbalanced by H^+ extrusion from roots.

Nitrate-grown plants produce large amounts of OH^- in leaves as a result of nitrate reduction. These plants have a much higher capacity for H^+ removal than N_2 -fixing plants (like broad bean) or ammonium-grown plants.

The increased sulfate in the SO_2 -exposed broad bean shoots was equivalent in charge to the decreased organic anion content. This content was measured as the difference between inorganic cation content (C) and inorganic anion content (A).

It is proposed that the metabolic buffering capacity of leaf cells is related to sulfate and nitrate reductions and organic anion import, rather than to the organic anion content in leaf cell vacuoles.

The appearance of chronic SO_2 injury (leaf damage) at the end of the growing period is discussed in relation to the impact of SO_2 on the processes involved in regulating intracellular pH. Further research at the cellular level is required for a quantitative understanding of these chronic effects.

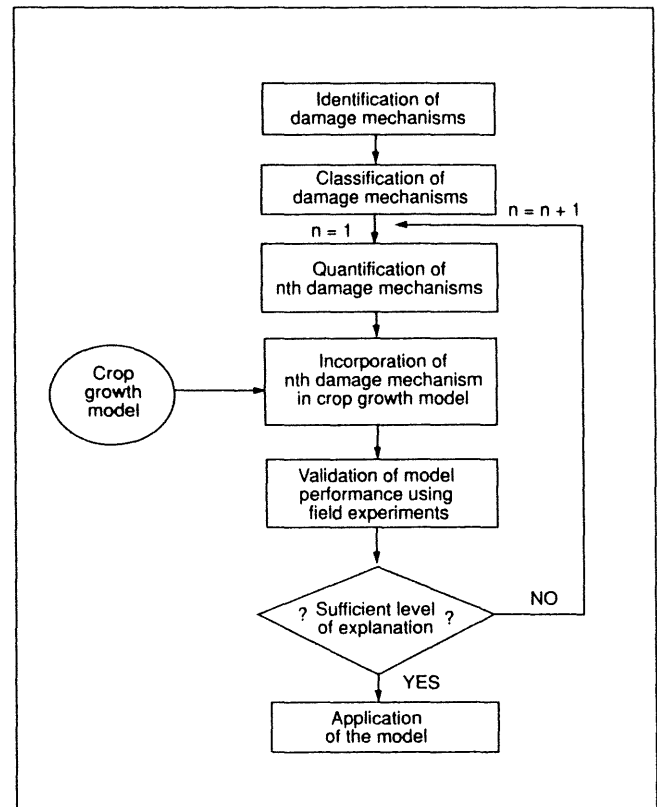
CASE STUDY 2: IMPACT OF LEAF BLAST ON RICE YIELD

Rice blast is caused by *Pyricularia oryzae* Cavara. It constrains rice production in temperate lowland, tropical upland, and rainfed lowland areas. Infection during the vegetative phase results in elliptically shaped lesions, mainly on leaves (leaf blast). Infection of the neck node or parts of the panicle (panicle blast) occurring after flowering directly affects yield. This study examines only leaf blast effects.

Several studies have been conducted to determine empirical damage functions for the effect of leaf blast, panicle blast, or combinations of both on rice yield (for review: Ou 1985, Teng et al 1991).

Several problems arise with leaf blast studies. The level of leaf blast changes over time; correlation studies demand summarization in one or two variables. Leaf blast—unlike panicle blast—indirectly affects yield by affecting crop growth before flowering. It is difficult to exclude panicle blast in experiments studying leaf blast effects. It is also difficult to apply the derived equations to other situations; this limits use.

A different approach was used in this study. Pathogen effects on plant physiological processes were quantified and a mechanistic crop growth model (Fig. 3) was used to evaluate effects on crop growth and rice production (Bastiaans 1991a).



3. Flow diagram optimizing the number of damage mechanisms introduced into a crop growth model to explain yield reduction.

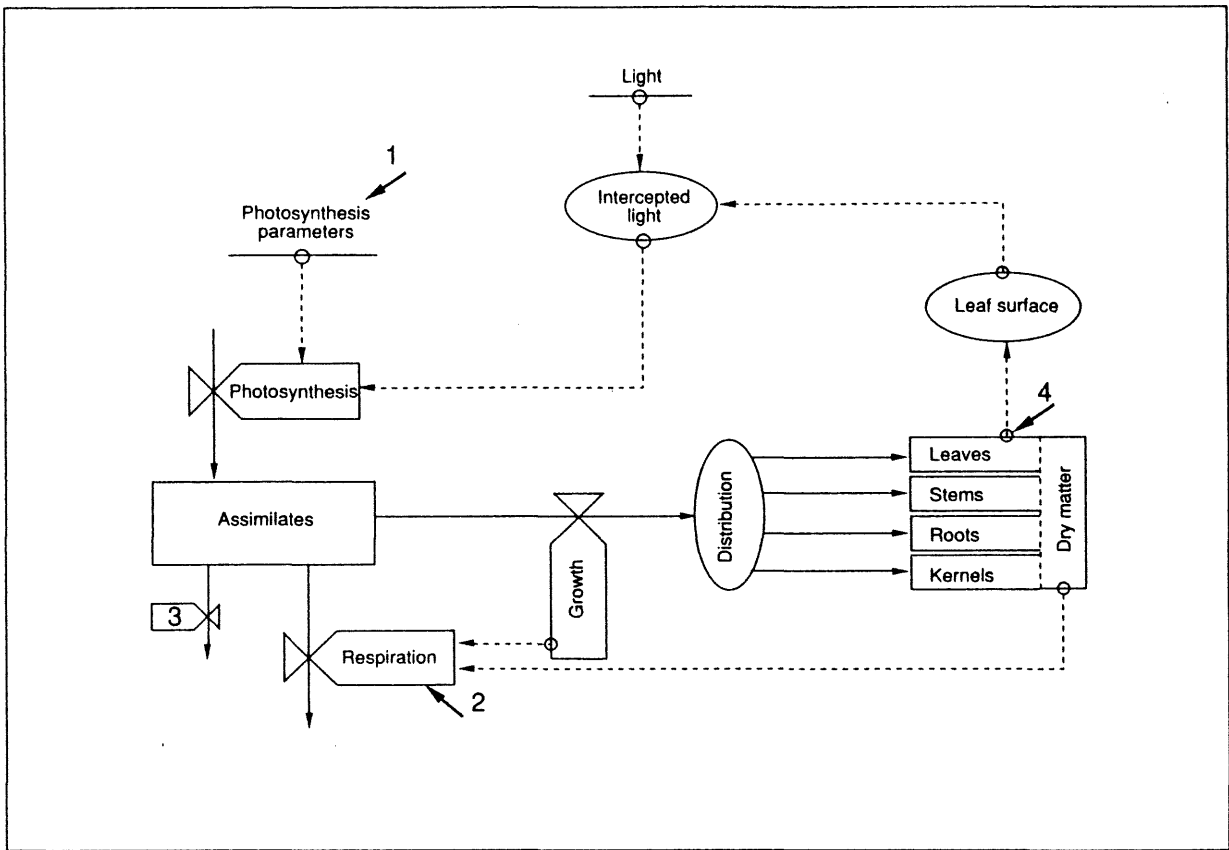
Four potential leaf blast damage mechanisms were identified (Fig. 4): photosynthesis rate is reduced, respiration rate of infected leaves is increased, the pathogen consumes assimilates produced by the plant, and leaf senescence is accelerated. Leaf photosynthesis effects were emphasized.

Pathogen effects can exceed lesion area (Livne 1964, Rabbinge et al 1985). No data were found in the literature on this aspect of blast in rice.

Gas exchange measurements were used to analyze the effect of blast in rice and determine the pathogen's effect on respiration.

Reduced photosynthesis in *P. oryzae*-infected leaves surpassed the reduction in green leaf area at both high and low light intensities (Fig. 5). By assuming a virtual lesion (consisting of the visual lesion and surrounding halo in which photosynthesis was inhibited), the measured effect could be described. The ratio between the area occupied by virtual and that occupied by visual lesion (beta) characterizes the effect on leaf photosynthesis (Bastiaans 1991b). Beta was 3-4 for the blast-rice pathosystem. The disease markedly increased dark respiration (Fig. 6).

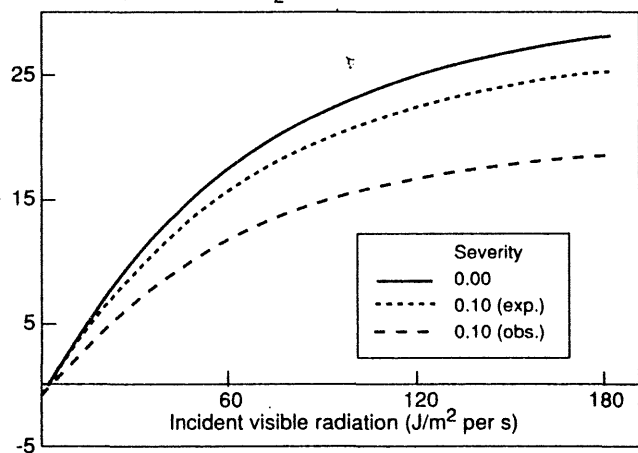
Quantified damage mechanisms were introduced into a mechanistic crop growth model (MACROS; Penning de Vries et al 1989). A temporary validation was made with unpublished field data (Fig. 7).



4. Relational diagram of a model for crop production, indicating potential damage mechanisms of leaf blast: 1) reduced rate of photosynthesis, 2) increased rate of respiration, 3) consumption of assimilates, and 4) increased leaf senescence.

Simulation results were compared with observed data at flowering because panicle blast appeared in the field experiments. At that growth stage the simulated reduction in shoot dry weight slightly underestimated the observed growth reduction in the field. Model calculations demonstrated the

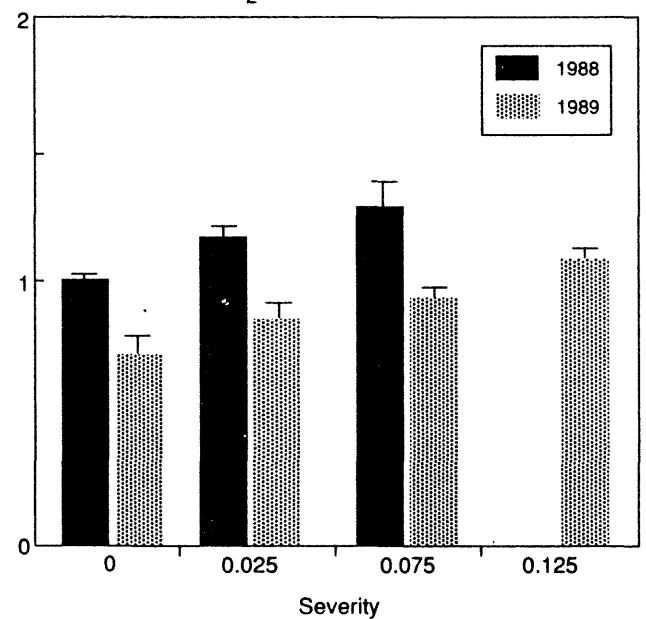
importance of determining the vertical disease distribution in the field.



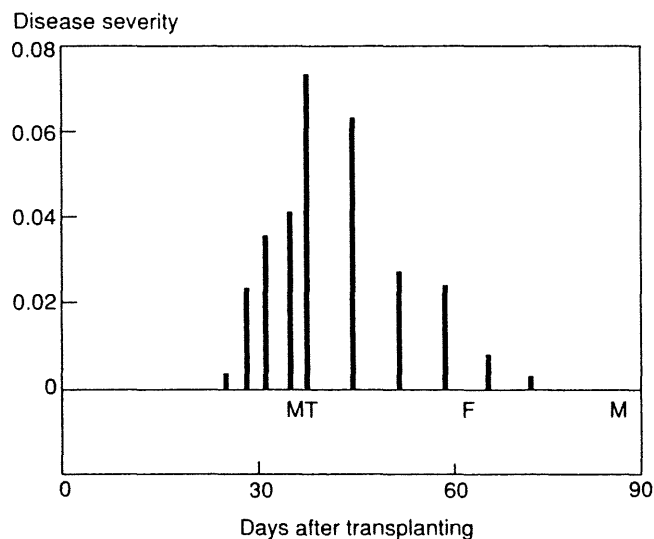
5. Measured net CO₂ assimilation light response curves for healthy and blast-infected leaves (severity = 0.1). The dotted lines refer to the observed effect on photosynthesis (obs.) and the expected effect (exp), based on reduced green leaf area.

importance of determining the vertical disease distribution in the field.

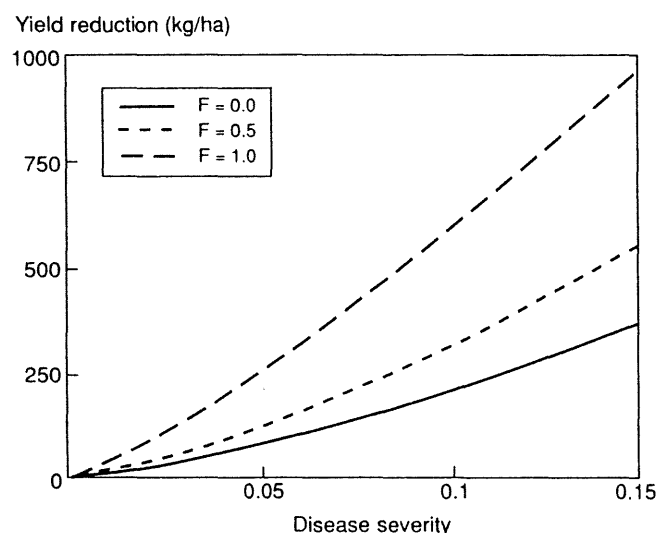
Dark respiration (kg CO₂/ha)



6. Measured rates of dark respiration (standard error of mean) of healthy leaves and leaves infected with *P. oryzae*.



7. Typical development pattern of leaf blast severity, as observed in a field experiment (data from C. Q. Torres).



8. Reduction in kernel yield due to a leaf blast epidemic before flowering. Simulated results of a model in which the fraction (F) to which redistribution contributed to fulfill N demand of grains was varied (F = 0, no redistribution; F = 1, only redistribution).

The model was also used to evaluate consequences of reduced shoot dry weight at flowering on yield (see table). Simulation indicated that light interception was hardly affected. Modern rice varieties generally have leaf area exceeding that needed for light interception. Leaves after flowering

Simulated effect of a leaf blast epidemic before flowering on dry matter accumulation at flowering and maturity.

	Healthy	Diseased
At flowering		
Shoot dry weight (t/ha)	7.0	5.4
Stem reserves (t/ha)	1.2	1.0
Green area index (ha/ha)	7.1	5.6
At maturity		
Kernel yield (t/ha)	5.3	5.2

are also an important N source for spikelet filling. A reduced leaf area implies reduced N storage capacity. N redistribution from remaining leaf areas will most likely accelerate, reducing canopy photosynthesis.

A dynamic model of N redistribution coupled to the MACROS model (as described by Penning de Vries et al [1990]) was used to quantify the effect on yield (Fig. 8). This simulation study indicated that reduced crop growth before flowering may affect yield; it also emphasized the importance of determining N in leaf blast experiments. Present field experiments are testing the formulated hypothesis.

When we finish validation, we must decide whether the model (with two of the identified damage mechanisms) reasonably explains yield reduction. If not, more damage mechanisms should be included. Although criterion for deciding is subjective, there is no need to quantify other damage mechanisms if 90% or more of reduced yield is explained.

The model can be used to extrapolate once it adequately explains yield reduction. It can also identify critical growth stages for the presence of blast, support the determination of damage relations, and help determine the disease's economic impact.

REFERENCES CITED

- Bastiaans L (1991a) Quantifying the effect of rice leaf blast on leaf photosynthesis, crop growth, and final yield using an ecophysiological model of crop growth. Pages 89-99 in Rice blast modeling and forecasting. International Rice Research Institute, P.O. Box 933, Manila, Philippines.
- Bastiaans L (1991b) 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.
- Kropff M J (1987) Physiological effects of sulphur dioxide. I. The effect of SO₂ on photosynthesis and stomatal regulation of *Vicia faba* L. *Plant Cell Environ.* 10:753-760.
- Kropff M J (1989a) Modelling short term effects of sulphur dioxide. I. A model for the flux of SO₂ into leaves and effects on leaf photosynthesis. *Neth. J. Plant Pathol.* 95:195-213.
- Kropff M J (1989b) Modelling short term effects of sulphur dioxide. II. Quantification of biochemical characteristics determining the effect of SO₂ on photosynthesis of leaves. *Neth. J. Plant Pathol.* 95:214-224.
- Kropff M J (1989c) Quantification of SO₂ effects on physiological processes, plant growth and crop production. Ph D thesis, Agricultural University, Wageningen. 201 p.
- Kropff M J (1990) Effects of long-term open-air fumigation with SO₂ on a field crop of broad bean (*Vicia faba* L.). III. Quantitative analysis of damage components. *New Phytol.* 115:357-365.
- Kropff M J (1991) Long-term effects of sulphur dioxide on plants. SO₂ metabolism and regulation of intracellular pH. *Plant Soil* 131:234-245.
- Kropff M J, Goudriaan J (1989) Modelling short term effects of sulphur dioxide. III. The effect of SO₂ on photosynthesis of leaf canopies. *Neth. J. Plant Pathol.* 95:265-280.
- Kropff M J, Mooi J, Goudriaan J, Smeets W, Leemans A, Kliffen C, Van der Zalm A J A (1989a) The effects of long-term SO₂

- exposure on a field crop of broad bean (*Vicia faba* L.). I. Depression of growth and yield. *New Phytol.* 113:337-344.
- Kropff M J, Mooi J, Goudriaan J, Smeets W, Leemans A, Kliffen C (1989b) The effects of long-term SO₂ exposure on a field crop of broad bean (*Vicia faba* L.). II. Effects on growth components, leaf area development and elemental composition. *New Phytol.* 113:345-351.
- Kropff M J, Smeets W, Meijer E, Van der Zalm A J A, Bakx E J (1990) Effects of sulphur dioxide on photosynthesis: the role of temperature and humidity. *Physiol. Plant.* 80:655-661.
- Livne A (1964) Photosynthesis in healthy and rust-affected plants. *Plant Physiol.* 39:614-621.
- Ou S H (1985) Rice diseases. 2d ed. Commonwealth Mycological Institute, Kew, Surrey, England. 380 p.
- 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. Simulation Monographs Series. PUDOC, Wageningen.
- Penning de Vries F W T, Van Keulen H, Alagos J C (1990) Nitrogen redistribution and potential production in rice. Pages 513-520 in International Congress of Plant Physiology. S. K. Sinha, P. V. Lane, S. C. Bhargava, and R. K. Agrawal, eds. Society for Plant Physiology and Biochemistry, Water Technology Centre, Indian Agricultural Research Institute, New Delhi, India.
- Rabbinge R, Jorritsma I T M, Schans J (1985) Damage components of powdery mildew in winter wheat. *Neth. J. Plant Pathol.* 96:17-28.
- Teng P S, Klein-Gebbinck H W, Pinnschmidt H (1991) An analysis of the blast pathosystem to guide modeling and forecasting. Pages 1-30 in Rice blast modeling and forecasting. International Rice Research Institute, P.O. Box 933, Manila, Philippines.