

Effects of leaf blast on growth and production of a rice crop.

1. Determining the mechanism of yield reduction

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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 rate 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 fraction 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 uptake was not responsible for the yield reduction observed. Consequently, the reduction in grain yield was solely determined by a reduced carbohydrate supply.

Additional keywords: *Pyricularia oryzae*, *Oryza sativa*, crop loss.

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 peaks around maximum tillering, followed by a gradual decline 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 filling of the sink occurs after flowering (Evans, 1975). Leaf blast thus mainly affects grain yield indirectly.

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

rate 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 tissue contributes considerably to N supply for grain filling. A reduced amount of accumulated N in the crop at flowering may thus eventually limit carbohydrate supply during grain filling. 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.

Material and methods

Plant material and inoculation. From December 1990 till April 1991 (dry season) 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 m² (12 × 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 × 0.20 m. Frequency and timing of inoculations and fungicide applications varied per treatment to establish three levels of leaf blast (Table 1). Inoculum (*P. oryzae*; isolate P06-6) 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.

Table 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

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 applied at their recommended rates to repress the leaf blast epidemic (Table 1).

Fertilizer inputs consisted of a basal N-P-K application (60-50-50 kg ha⁻¹) 1 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 later on 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) at its recommended rate 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 the disease developed most rapidly. Sample size was 18 hills (0.72 m²) before flowering (63 DAT) and 24 hills (0.96 m²) from flowering till maturity. Six hills were used for detailed observations. The remaining hills were cut to pieces, oven-dried and weighed, for a more accurate determination of accumulated total shoot 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 sample of approximately 100 leaves. 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 °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 m² harvest area per plot was oven-dried and weighed. Grain yield (rough rice) was expressed at 14% moisture. Six rice hills were processed separately and used for yield component analysis (no. of panicles m⁻², no. of spikelets panicle⁻¹, 1000 grain weight, fraction filled grains).

Results

Disease development. The earliest blast lesions appeared five days after the first inoculation with *P. oryzae* in treatment C (Table 1). 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. 1). Starting from 34 DAT, fungicides were applied to hamper a further development of the disease (Table 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 successful, 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) 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 a stagnation in the increase in total and green leaf area, starting at about 30 DAT (Fig. 2). Total leaf area in the inoculated crops remained more or less constant for about

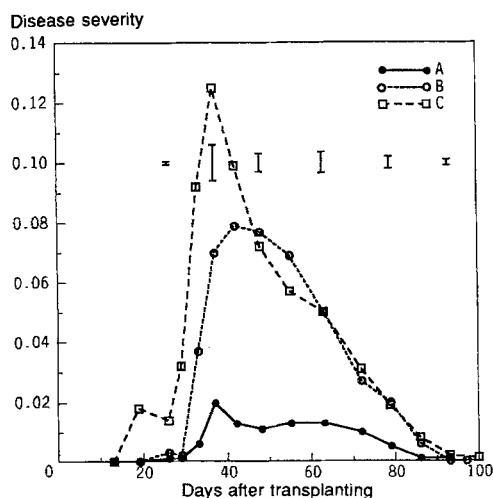


Fig. 1. Time course of severity of rice leaf blast in a control crop (A) and in crops inoculated with *Pyricularia oryzae* (B, C). Vertical bars represent standard error of difference of means.

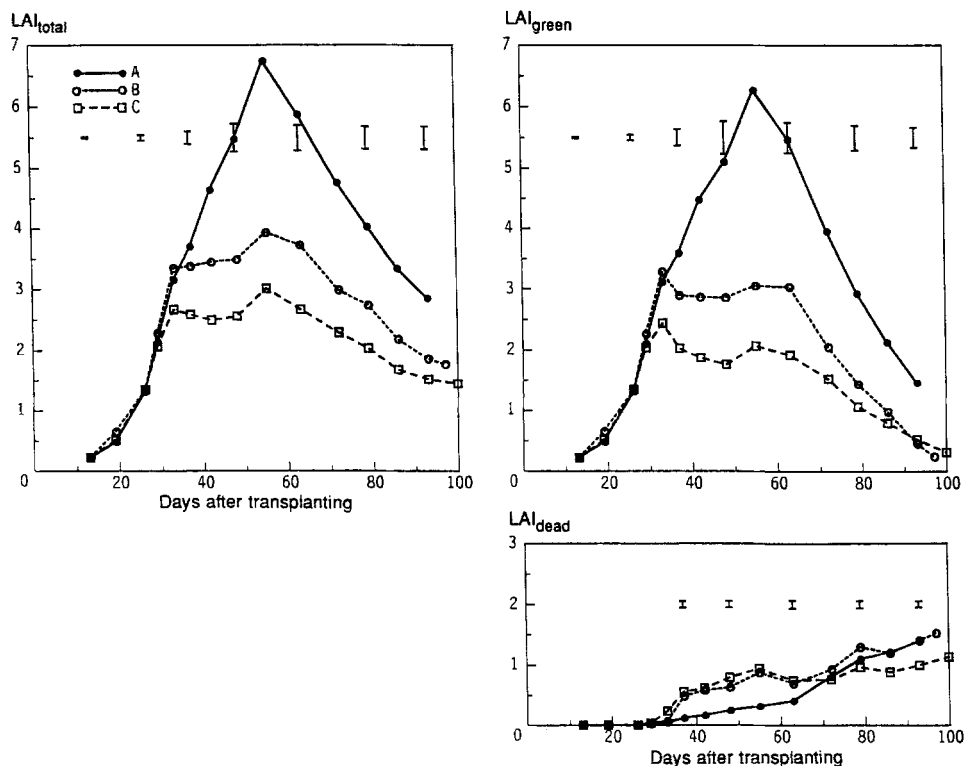


Fig. 2. Time course of total (LAI_{total}), green (LAI_{green}) and dead (LAI_{dead}) leaf area ($ha\ ha^{-1}$) of rice in a control crop (A) and in crops inoculated with *Pyricularia oryzae* (B, C). Vertical bars represent standard error of difference of means.

25 days, while the LAI of the control crop increased. From 35 DAT on, the premature senescence of heavily infested leaf tissue caused a clear increase in the amount of dead leaf area.

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 ($0.047\ d^{-1}$) was identical to the RDR of treatment C ($0.046\ d^{-1}$), whereas the RDR of treatment B was slightly higher ($0.060\ d^{-1}$) (standard error of difference of means (SED) = $0.005\ d^{-1}$).

Specific leaf area (SLA) of green leaf tissue was not affected by blast (Fig. 3).

Dry matter production and distribution. The time course of dry matter production is given in Fig. 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 linear 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 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. Average growth rate in the inoculated crops (99 and $82\ kg\ dry\ matter\ ha^{-1}d^{-1}$ for treatment B and C, respectively)

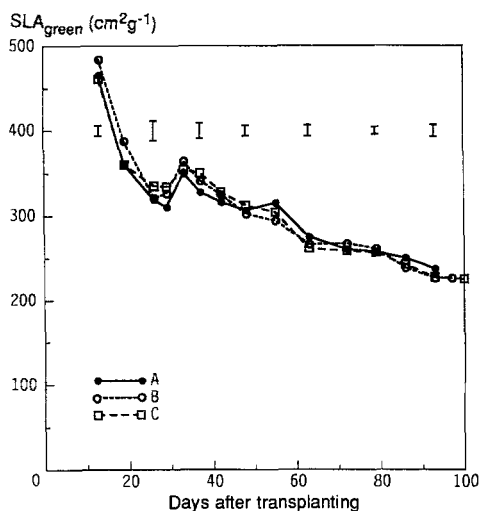


Fig. 3. Time course of specific leaf area of green tissue (SLA_{green} ; $cm^2 g^{-1}$) of rice in a control crop (A) and in crops inoculated with *Pyricularia oryzae* (B, C). Vertical bars represent standard error of difference of means.

remained significantly lower than in the control crop ($175 kg dry matter ha^{-1}d^{-1}$) ($SED = 11 kg dry matter ha^{-1}d^{-1}$). 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 Fig. 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 Fig. 4. A distinction was made between leaf blades, stems (including leaf sheaths) and panicles. Distribution of dry weight over leaf and stem was not 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 32, 30 and 31% for treatment A, B and C, respectively ($SED = 3\%$).

Yield and yield components. Grain yield was markedly reduced in the inoculated crops and this reduction reflected the reduction in dry matter production (Table 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). 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-productive tillers.

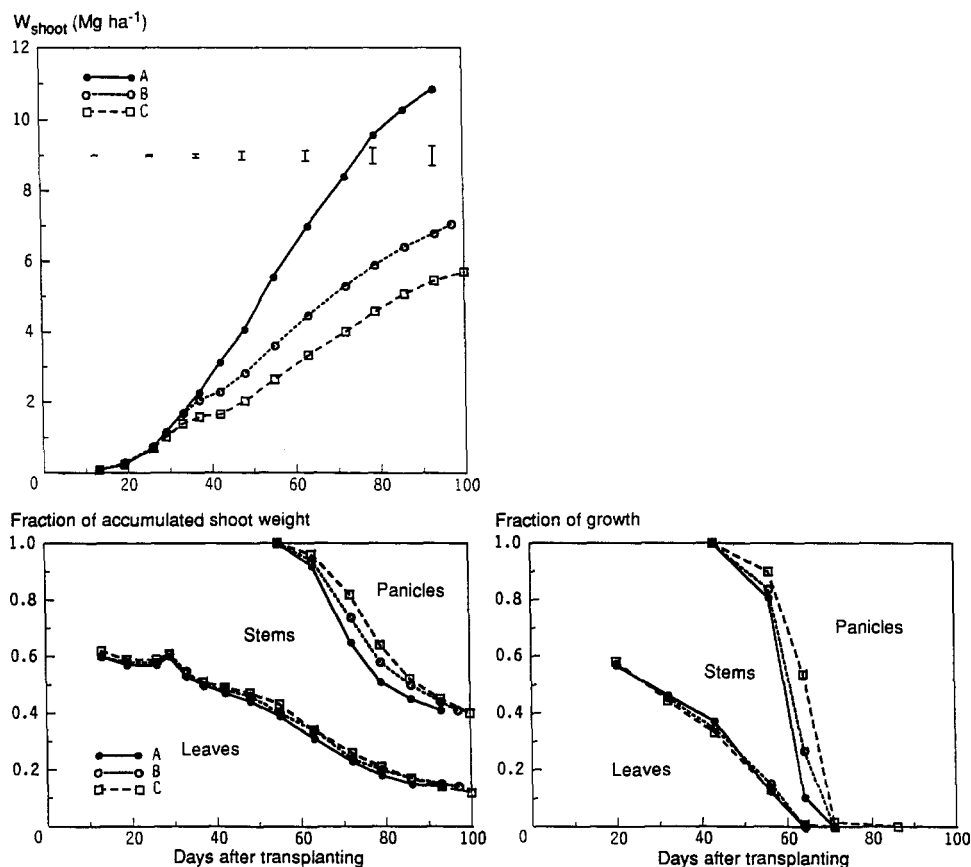


Fig. 4. Time course of total above ground dry matter (W_{shoot} ; Mg ha^{-1}) of rice in a control crop (A) and in crops inoculated with *Pyricularia oryzae* (B, C). Vertical bars represent standard error of difference of means. Distribution of the accumulated dry matter over the various shoot organs and the distribution pattern of newly produced dry matter are also presented as a function of time.

Table 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) ¹	7.1 (65) (b)	5.7 (52) (c)
Grain yield (Mg ha^{-1}) ²	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)
fraction filled grains	0.85 (100) (a)	0.80 (94) (b)	0.78 (92) (b)
1000-grain weight (g) ²	21.1 (100) (a)	20.1 (95) (b)	19.7 (93) (b)

¹ Means in the same row followed by the same letter are not significantly different according to *t*-test ($P < 0.05$).

² Rough rice at 140 g moisture kg^{-1} .

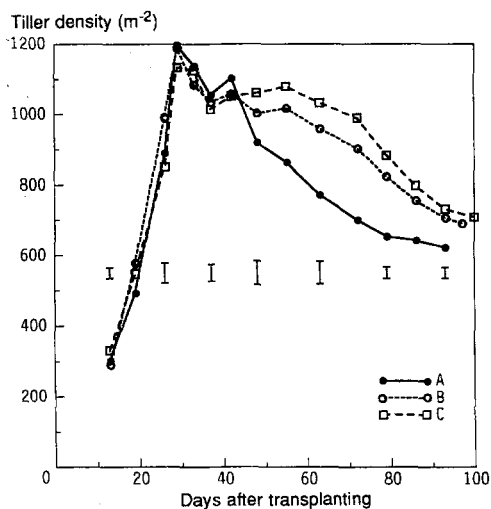


Fig. 5. Time course of total tiller number (m^{-2}) of rice in a control crop (A) and in crops inoculated with *Pyricularia oryzae* (B, C). Vertical bars represent standard error of difference of means.

N-crop status and translocation. N content of green leaf tissue was determined throughout the season (Fig. 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. 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) ($\text{SED} = 11 \text{ kg N ha}^{-1}$). Although N uptake in the inoculated crops was reduced, shoot N content was higher (N-content; Table 3). The same was true for the N content of green leaf tissue, dead leaf tissue, stem material, and the panicle. The distribution of N over the various shoot organs at flowering was affected as a result of the disease (F_N ; Table 3). 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 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 and Van Keulen, 1980). In the inoculated crops a

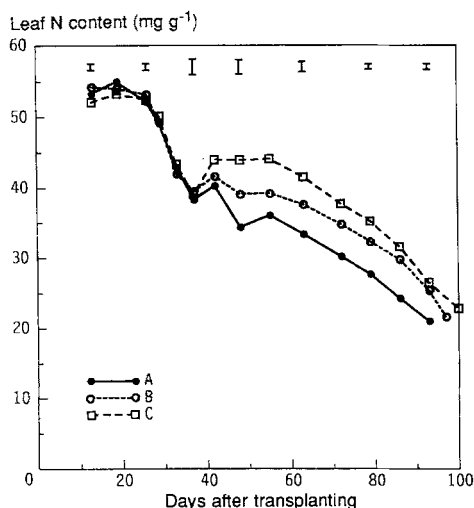


Fig. 6. Time course of N content of green leaf tissue (mg g^{-1}) of rice in a control crop (A) and in crops inoculated with *Pyricularia oryzae* (B, C). Vertical bars represent standard error of difference of means.

clear increase in the relative contribution of the stem to the overall N reallocation was observed (Table 4).

Table 3. Nitrogen content (N-content; 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-content			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 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
Leaf			
N translocatable at flowering (kg ha ⁻¹)	50	28	19
N translocatable at maturity (kg ha ⁻¹)	7	2	2
Estimated N reallocation from leaf tissue (kg ha ⁻¹)	43	26	17
Stem			
N translocatable at flowering (kg ha ⁻¹)	39	32	27
N translocatable at maturity (kg ha ⁻¹)	10	10	8
Estimated N reallocation from stem tissue (kg ha ⁻¹)	29	22	19
Uptake			
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

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). Leaf area formation decreased subsequently. The accelerated senescence of heavily infested leaf tissue, further enhanced the reduction in green leaf area. 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, 1993b).

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, 1988). 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. The effect of leaf blast on shoot/root-ratio was not investigated.

Leaf blast reduced the number of spikelets per m² 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 reallocation 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, differences in N uptake could not be responsible for the yield reduction observed.

Grain yield was reduced with 2.1 and 2.8 Mg dry matter ha⁻¹ in treatment B and treatment C, respectively. The analysis demonstrates that this 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. The relative contribution of stem reserves to the overall grain production was not affected by blast. In both healthy and inoculated crops this component was responsible for about 30% of total grain production. From this observation it can be concluded that in the inoculated crops 30% of the reduction in grain yield (0.6 and 0.8 Mg dry matter ha⁻¹ for treatment B and C, respectively) was due to a reduced supply from the stem reserves. The remaining reduction in grain yield (1.5 and 2.0 Mg ha⁻¹, respectively) is caused by a reduced supply of newly produced assimilates. Since leaf blast did not affect the duration of the grain filling period, this reduction is solely due to a reduced rate of carbohydrate production. Based on the duration of the grain filling period (30 days) and a conversion efficiency of 0.68 kg dry matter (kg CH₂O)⁻¹ (Penning de Vries et al., 1989), the reduction in the average carbohydrate supply of newly produced assimilates during grain filling can be estimated at 75 and 100 kg CH₂O ha⁻¹d⁻¹ for treatment B and C, respectively. This 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 this long-term effect of the disease on yield formation.

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