



Full Length Article

Effects of Bacterial Leaf Blight on Photosynthesis and Chlorophyll *a* Fluorescence in Susceptible and Resistant Rice Cultivars

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Abstract

Bacterial leaf blight (BLB) caused by *Xanthomonas oryzae* pv. *oryzae* is a serious disease affecting rice. Understanding of the effects of this disease on photosynthesis and chlorophyll (Chl) *a* fluorescence is important in rice management. We studied the effect of BLB on enzyme activities, photosynthetic rate (P_n) and Chl *a* fluorescence transient in susceptible Neiwuyou 8015 and resistant Shenzhou 98 rice cultivars. BLB had a negative effect on rice net photosynthesis (P_n) and stomatal conductance (G_s). Superoxide dismutase (SOD), polyphenol oxidase (PPO), phenylalanine ammonia lyase (PAL) activities, malondialdehyde (MDA) contents were increased while Chl content was decreased, indicating that rice photosynthetic functions were damaged by BLB. The effect of BLB on photosynthesis was greater in susceptible rice than in resistant rice. A significant difference of Chl *a* fluorescence transient curves was observed between BLB treatments and healthy ones. Parameters measured in transient rice Chl *a* fluorescence showed the photosynthetic reaction center was inactive after BLB. These findings will help in evaluating rice resistance and may be useful for rice disease management. © 2021 Friends Science Publishers

Keywords: Bacterial leaf blight; Chlorophyll content; Enzyme activities; OIJP curves; Stomatal conductance; Resistance

Introduction

Rice (*Oryza sativa* L.) is one of the most important food crops in the world (Wang and Luo 1998). However, rice is susceptible to many diseases, such as bacterial leaf blight (BLB) caused by *Xanthomonas oryzae* pv. *oryzae*. BLB occurs at almost all rice growth stages. It causes wilting, leaf rolling and yellowing and the seedling death. The disease is a threat to rice production and cause a significant yield reduction (Rajarajeswari and Muralidharan 2006; Noh *et al.* 2007).

Plants have physiological defenses against the negative effects caused by disease pathogens (Medhy 1994). Diseased plants may have changed enzyme activities that are used to overcome infections (Kumar *et al.* 2009; Harrach *et al.* 2013). The enzymes may help promote plant growth by keeping the reactive oxygen species level below a critical threshold. Research on rice BLB has mainly focused on resistance genes, disease detection and control

(Yasmin *et al.* 2017; Šebela *et al.* 2018; Chukwu *et al.* 2019). Internal defense changes against rice BLB such as antioxidant enzyme activities have seldom been reported.

Photosynthesis, associated with crop yield and quality, is important in disease management (Rojas *et al.* 2014). Crop photosynthesis is greatly influenced by disease infection (Selvaraj and Fofana 2012). Photosynthesis reduction may be caused by a disease that decreases leaf chlorophyll (Chl) content, light interception and photosynthetic leaf area (Prokopová *et al.* 2010; Zhao *et al.* 2011). Planting resistant cultivars can be an effective strategy for disease control. Evaluating disease resistance in a crop strain is important before widespread cultivation. Photosynthetic rates and chlorophyll *a* fluorescence may differ between resistant and susceptible genotypes.

Plant photosynthesis and Chl *a* fluorescence are indicator tools for disease monitoring (Kalaji *et al.* 2016), and the effects of BLB on photosynthesis have been studied. Kumar *et al.* (2013) reported that net photosynthetic rate

(P_n), stomatal conductance (G_s), and transpiration rate (T_r) in susceptible rice variety PB1 was significantly lower than in the resistant variety IRBB21 after BLB infection. Hu *et al.* (2018) reported that BLB greatly decreased the maximum rice photosynthetic rate, light saturation point and carboxylation efficiency. However, the resistance of rice plants to BLB on photosynthesis and chlorophyll *a* fluorescence was not studied. BLB effects on photosynthesis and Chl *a* fluorescence, and the mechanisms involved in these changes in resistant and susceptible rice are unclear. This study investigated photosynthesis, Chl *a* fluorescence aims to study BLB effect on photosynthetic functions; to determine photosynthesis differences of susceptible and resistant rice plants to BLB; and to assess the feasibility of Chl *a* fluorescence as a tool to monitor BLB disease.

Materials and Methods

Plant material and growth conditions

Glasshouse experiments were conducted in 2018 at the Zhejiang Academy of Agricultural Sciences, Hangzhou, Zhejiang Province, China. BLB susceptible (Neiwuyou 8015) and resistant (Shenzhou 98) rice cultivars were selected. Seedlings of rice at the three-leaf stage were obtained and transplanted into 40-L polyvinyl chloride pots on June 20. Five plants were cultivated in each pot. The cultivated soil had total N content 0.842 g kg^{-1} , pH (soil: water 1:5) 6.76, and organic matter content 13.53 g kg^{-1} . Available phosphorus and potassium contents were 24.28 g kg^{-1} and 56.75 g kg^{-1} , respectively. During the experiment, air temperature was 28°C , air relative humidity was 75%, and light intensity was $550 \mu\text{mol m}^{-2} \text{ s}^{-1}$.

Experimental design and inoculations

The experimental design was a randomized block with healthy (CK), slight (S1), moderate (S2) and serious (S3) disease grade treatments of two cultivars with 20 replications. The total number of pots was 160. On July 4, 2018, the upmost fully expanded leaves were inoculated using shearing off leaf tips with scissors dipped in a *Xanthomonas oryzae* pv. *oryzae* bacterial cell suspension. Five leaves were inoculated from each pot. CK (healthy) treatment was inoculated with deionized water. S1, S2 and S3 disease grades were created with 10^5 , 10^6 and 10^7 bacterial cells mL^{-1} . After inoculation, the rice was seal-covered with polyvinyl chloride for 7 days. On July 26, 2018, 20 leaves per treatment were sampled for antioxidant enzymes and Chl, leaf gas exchange and chlorophyll fluorescence measurements.

Enzyme activity, malondialdehyde and chlorophyll content measurement

The uppermost fully expanded leaves were collected, frozen

in liquid nitrogen and stored at -80°C for further analysis. Activities of superoxide dismutase (SOD), polyphenol oxidase (PPO), phenylalanine ammonia lyase (PAL), and malondialdehyde (MDA) content was measured as described by Debona *et al.* (2012). Chl content was determined using a SPAD-502 Plus reading.

Gas exchange measurements

P_n of the uppermost fully expanded leaves was measured using a portable photosynthesis system (CIRAS-II, PP Systems, Amesbury, MA, USA). Leaf chamber photosynthetic photon flux density was set at $1000 \mu\text{mol m}^{-2} \text{ s}^{-1}$ with a fixed atmospheric CO_2 concentration of $380 \mu\text{mol mol}^{-1}$. The air temperature was 25°C , and air humidity was 80% during the above measurements. Data of T_r , G_s , and intercellular CO_2 concentration (C_i) were automatically collected and transformed into MS Excel software.

Chlorophyll *a* fluorescence measurement

Chl *a* fluorescence transient (OJIP) induced by the pulse of saturating red light (peak at 650 nm, photons of $3000 \text{ m mol m}^{-2} \text{ s}^{-1}$) was measured using Multi-Function Plant Efficiency Analyser (M-PEA, Hansatech, UK) after the leaves adapted to the dark for about 30 min. The O, J, I and P point in the curve represented *a* fluorescence intensity recorded at 20 μs , 2 ms, 30 ms and the maximal value. The fluorescence intensity at 50 μs was considered as F_0 . The maximal fluorescence value is F_m and F_v/F_m is defined as the ratio of $(F_m - F_0)$ and F_m . V_j , V_i and S_m represented relative variable fluorescence at 2 ms and 30 ms, and the normalized area between F_m and F_0 in the OJIP curve.

Biophysical parameters induced from OJIP transient were calculated and used. (1) Flux ratio of PSII: $\phi(E_0)$, the quantum yield of electron transport. (2) Flux ratio of PSI: $\delta(R_0)$, the efficiency with which an electron can move from the reduced intersystem electron acceptors to the PSI end electron acceptors; $\phi(R_0)$, the quantum yield of electron transport from Q_A^- to the PSI end electron acceptors. (3) Specific energy fluxes per reaction center (RC): absorption (ABS/RC), trapping (TR_0/RC), electron transport (ET_0/RC), dissipation (DI_0/RC), and reduction of end acceptors at the PSI electron acceptor side (RE_0/RC). (4) Phenomenological energy fluxes per cross section (CS): absorption (ABS/CS_m), trapping (TR_0/CS_m), electron transport (ET_0/CS_m), and dissipation (DI_0/CS_m). (5) Performance index: PI_{ABS} , performance of absorption basis; PI_{Total} , performance of up to the PSI end electron acceptors.

Data analysis

Statistical analysis was conducted using S.P.S.S. 17.0 (SPSS Inc., Chicago, USA). Differences in physiological, photosynthesis and Chl *a* fluorescence parameter between healthy and BLB treatments (CK, S1, S2 and S3) were

analyzed using one-way analysis of variance. Multiple comparisons of the means were performed using Fisher's LSD (least significant difference) at the 0.05 level. Means in tables and graphs represent average values and standard errors are provided in the graphs.

Results

Enzyme activities and MDA content

Changes of activities of SOD, PPO, PAL, MDA and Chl content in Neiwuyou and Shenzhou 98 were measured after BLB occurred. After infection, antioxidant enzymes activities in SOD, PPO, PAL and MDA content increased gradually from S1 to S3, and were higher than those in CK. Significant differences ($P \leq 0.05$) between CK and most BLB treatments were observed (Table 1). Leaf Chl content in both rice cultivars decreased after BLB occurred and reached the minimum value in S3 disease treatment. SOD activity was higher and PPO, PAL, and Chl contents were lower in Neiwuyou 8015 than those in Shenzhou 98.

Photosynthetic gas exchange

The changes of P_n , T_r , G_s and C_i of CK, S1, S2 and S3 treatments in Neiwuyou 8015 and Shenzhou 98 plants are shown in Fig. 1. Compared with healthy plants (CK), P_n in the two rice plants decreased significantly ($P \leq 0.05$) from S1 to S3 after infection. In the most serious disease treatment (S3), P_n in Neiwuyou 8015 and Shenzhou 98 was 54.3 and 51.0% lower than that in CK. G_s in infected treatments was lower than in the healthy ones across the two rice cultivars and the differences also reached the significant level. In the S3 treatment, G_s in Neiwuyou 8015 and Shenzhou 98 reduced significantly and was lower 22.4 and 15.4% than that in CK. With BLB treatment increased from S1 to S3, T_r and C_i in both two rice cultivars decreased gradually and reached a minimum value in S3. No significant changes for C_i in Neiwuyou 8015 and Shenzhou 98 were observed after BLB infection.

Chlorophyll *a* fluorescence

Chl *a* fluorescence transient OIJP curves of CK, S1, S2, and S3 in Neiwuyou 8015 and Shenzhou 98 are shown in Fig. 2. The curves contained O, J, I and P steps and showed that I and P steps of the infection treatments were lower than those of the CK, and decreased gradually from S1 to S3 across the two cultivars. Comparatively, small differences in O steps and large differences in P steps were observed.

Parameters induced from the above OIJP curves in Neiwuyou 8015 and Shenzhou 98 were calculated and the relative values (Relative to CK, CK=1) are shown in Fig. 3. The spider plots showed that flux ratios of PSII such as ABS/RC, TRo/RC and DIO/RC were higher and RE_o/RC

were lower under BLB stress than those in CK. Almost all flux ratios of PSII and phenomenological fluxes per CS were slightly lower under BLB stress than those in CK. The parameters ϕ (E_o), ϕ (R_o), δ (R_o), V_j , and V_i (relative variable fluorescence at 2 ms and 30 ms) in S2, and S3 were higher than those in CK.

In the two rice cultivars, there were reduced values of F_m in BLB rice compared to the CK. F_0 in Neiwuyou 8015 decreased gradually from S1 to S3. There were no significant differences in F_0 between the CK and the infected treatments in Shenzhou 98 plants. No significant changes of S_m , indicating the pool size of the electron carrier, were observed.

Almost all the phenomenological fluxes expressed per cross section in ABS/CS_m, TRo/CS_m and ETo/CS_m in BLB infected Neiwuyou 8015 and Shenzhou 98 were lower than those in CK. The reduction of intersystem electron acceptors, PI_{abs} of the two rice cultivars, was lower in S1 and higher in S2, and S3 when compared to the CK.

Discussion

BLB has a negative effect on rice photosynthesis, and this was also observed in grape varieties (Shasmita *et al.* 2018). In the present study, after BLB infection, P_n in both the BLB susceptible rice Neiwuyou 8015 and resistant Shenzhou 98 was lower than that in the healthy ones. Debona *et al.* (2014) reported that the BLB susceptible rice cultivar BR 18 exhibited a greatly reduced net carbon assimilation rate compared with the partially resistant cultivar (BRS 229) after wheat was infected with *Pyricularia oryzae*. This may help maintain high yields in regions where BLB is widespread. G_s decreased and negligible changes in C_i were observed after infection across the above two rice cultivars. These results suggested that the reduced photosynthetic rate may be related to non-stomatal limitation factors. In the two rice cultivars, antioxidant enzyme activities increased and Chl content decreased after BLB arising, thus suggesting that rice photosynthetic functions may be impaired by the disease. The effect of BLB on Chl content is consistent with findings from other plants after disease infection (Bertamini *et al.* 2002; Lobato *et al.* 2010; Bermúdez-Cardona *et al.* 2015; Rios *et al.* 2014). Chl has a direct effect on plant photosynthesis. The reduced G_s and Chl content after BLB infection may be responsible for the decreased photosynthesis.

Chl *a* fluorescence transient occurs while the plant is in photosynthesis. It may reveal the inner photosynthetic physiological status and the mechanism of plants under stress (Maxwell and Johnson 2000). In this study, the I and P steps of OIJP curves in the BLB treatments were lower than those in controls, and decreased gradually from S1 to S3 in the two rice plants. The results were similar to rice infection with *Xanthomonas oryzae*pv (Shasmita *et al.* 2019), and suggest that OIJP curves can be useful for differentiating disease grades.

Table 1: Activities of superoxide dismutase (SOD), polyphenol oxidase (PPO), phenylalanine ammonia lyase (PAL), malondialdehyde (MDA) and chlorophyll (Chl) content in susceptible Neiwuyou 8015 and resistant Shenzhou 98 rice after bacterial leaf blight (BLB) infection

Cultivar	Treatment	SOD activity Ug ⁻¹ FW	PPO activity Ug ⁻¹ min	PAL activity Ug ⁻¹ min	MDA content nmol g ⁻¹ FW	Chl content SPAD
Neiwuyou 8015	CK	70.5c	1.95c	131b	5.02d	40.9a
	S1	81.3bc	2.39c	158ab	5.53c	37.3ab
	S2	92.4ab	3.95b	172a	6.78b	34.6b
	S3	99.5a	4.77a	189a	8.24a	23.9c
Shenzhou 98	CK	69.2c	2.33d	145c	5.21c	42.3a
	S1	75.6bc	4.15c	172bc	5.27c	42.2a
	S2	84.3ab	6.77b	199ab	5.75b	36.4b
	S3	90.1a	8.38a	220a	6.14a	33.9b

Mean values for various treatments in each rice cultivar followed by the same letter are not significantly different ($P \leq 0.05$) according to the LSD test

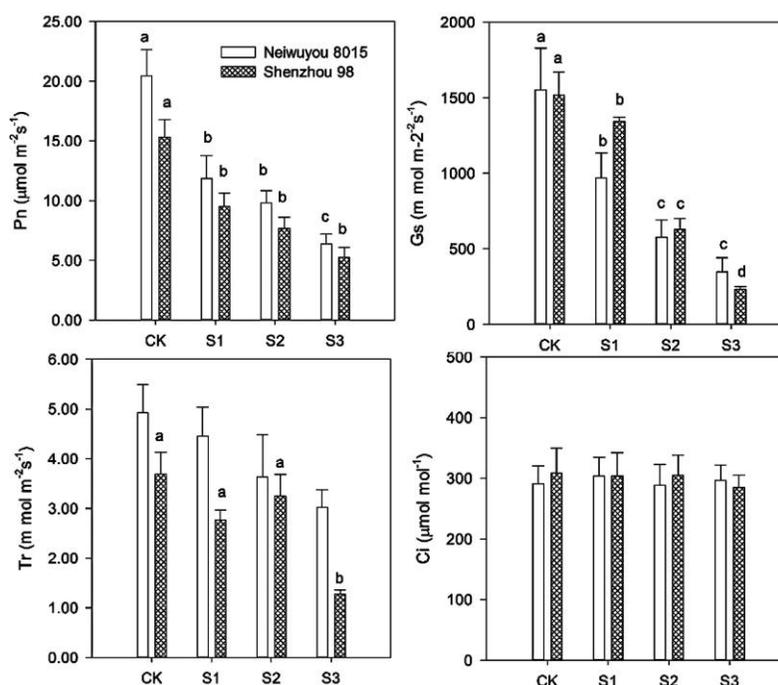


Fig. 1: Net photosynthetic rate (P_n), transpiration rate (T_r), stomatal conductance (G_s), and intercellular carbon dioxide concentration (C_i) of healthy (CK) and slight (S1), moderate (S2), and serious (S3) bacterial leaf blight (BLB) disease treatments imposed on BLB susceptible (Neiwuyou 8015) and resistant (Shenzhou 98) rice. Mean values for various treatments in each rice cultivar followed by the same letter were not significantly different ($P \leq 0.05$) according to the LSD test. No letters for the treatments in each cultivar indicated no significant differences between CK, S1, S2 and S3 treatments using variance analysis

For both rice cultivars stressed by BLB, F_v/F_m and F_0 showed minor reductions in comparison with the control treatments and indicated a delay in the occurrence of damage to the photosystems. Similar results were observed in soybean plants infected with *Phakopsora pachyrhizi* (Rios *et al.* 2018). However, the F_v/F_m of downy mildew affected *Plantago ovata* leaves was significantly reduced in slightly chlorotic and severely chlorotic leaves as compared with healthy leaves (Mandal *et al.* 2009). F_v/F_m as a disease stress indicator may require further evaluation.

Parameters induced from the OIIP curves may reflect the status of physiological photosynthesis and may have valuable applications in monitoring plant stress (Kalaji *et al.* 2016). Energy pipeline models (membrane model and leaf

model) were used to visualize the structure and function of PSII. In the membrane model, the energy fluxes affected by BLB were shown by the width of the corresponding arrows. In the present study, the increased ABS/RC was higher in BLB leaves than in the control, indicating an increase in the antenna size of rice PSII after infection. Lu *et al.* (2001) reported that inactivation of some PSII reaction centers could lead to an increase in ABS/RC due to the expression ABS/RC referring to the active PSII reaction centers. DI_0/RC also increased after BLB arising showing an increased quantity of dissipated energy. The energy could be considered as the excessive absorption of photons that could not be trapped by the RC and was released mainly in the form of heat (Strasser *et al.* 2000; Castro *et al.* 2011).

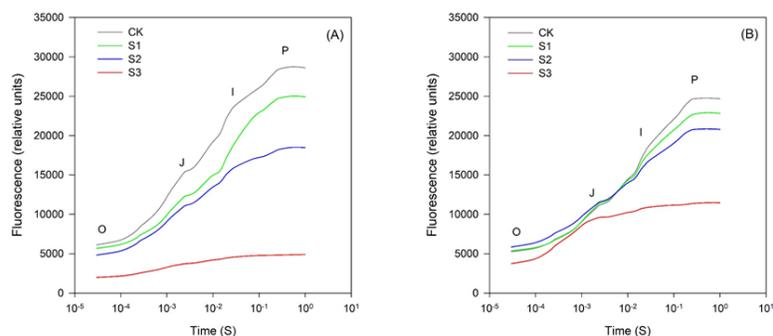


Fig. 2: Chlorophyll a fluorescence transient (OJIP) curves of healthy (CK) and slight (S1), moderate (S2) and serious (S3) bacterial leaf blight (BLB) disease treatments imposed on BLB susceptible Neiwuyou 8015 (A) and resistant Shenzhou 98 (B) rice

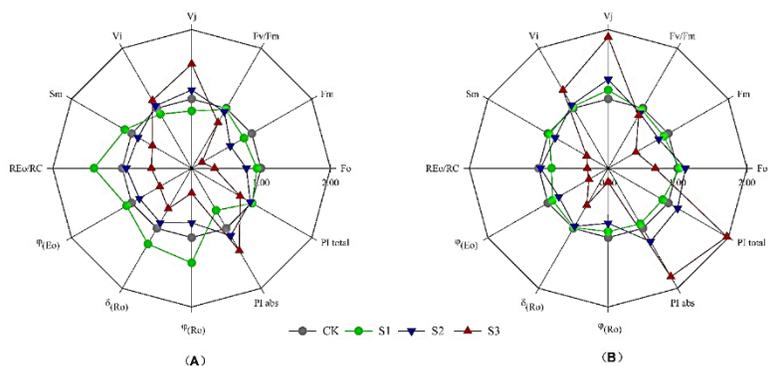


Fig. 3: Spider plots of parameters induced from chlorophyll a fluorescence transient (OJIP) curves of healthy (CK) and slight (S1), moderate (S2), and serious (S3) bacterial leaf blight (BLB) disease treatments imposed on BLB susceptible Neiwuyou 8015 (A) and resistant Shenzhou 98 (B) rice. CK (Control) = 1

In the leaf model, the number of the inactive PSII reaction centers per cross section indicated by closed circles in the BLB treatments was greater than that in the control, indicating that BLB inactivated the photosynthetic reaction center.

Higher ABS/RC, TRo/RC and DIo/RC and lower REo/RC, F_m , ABS/CS_m, TRo/CS_m and ETo/CS_m in rice plants affected with BLB compared with the control across the two rice cultivars indicated that photosynthetic reaction centers were inactive after BLB infection. The parameters tested offer potential application in disease monitoring. Considering the negative effect caused by other stresses, additional research in this area is needed.

Plant photosynthesis during disease stress may be related to disease resistance. In our experiment, P_n in BLB susceptible rice Neiwuyou 8015 was higher than in resistant Shenzhou 98 under the absence of BLB. However, more rapid reductions of P_n in Neiwuyou 8015 compared with Shenzhou 98 were observed when they were both infected with BLB. Similarly, G_s in Neiwuyou 8015 were lower than in Shenzhou 98. These results suggest that high disease resistance could help plants to maintain high photosynthesis under disease stress. Higher SOD activity and MDA content needed for self-defense in Neiwuyou 8015 were observed after BLB occurred. PAL and PPO activities of two rice

cultivars increased, but the increasing speed in Neiwuyou 8015 gradually slowed compared to Shenzhou 98. Similarly, Siddique *et al.* (2014) reported that SOD activities showed lower values in resistant genotypes. SOD activity increased in strawberry leaves infected by *Mycosphaerella fragariae* (Ehsani-Moghaddam *et al.* 2006). These results suggest that enzyme activities may be affected by plant resistance, these might be used as markers in the study of plant-pathogen interactions.

Decreased ABS/CS_m, TRo/CS_m and ETo/CS_m in the two rice cultivars from CK to S3 disease treatments are shown in Fig. 5. These results indicate that the resistance against BLB has almost no effect on the above parameters of PSII reaction centers per cross section, which may be used for the diagnosis of disease stress. In slight disease stress (S1), ABS/RC, TRo/RC, S_m , V_j , REo/RC, (Ro) and (Ro) of BLB resistant rice Shenzhou 98 were lower than those of susceptible rice (Fig. 3–5). Hence, these parameters could be used for differentiating the plant disease resistance. However, considering the difficulty in quantifying the disease severity, the response of the above parameters to disease stress needs more research.

Generally, higher Chl content denotes higher photosynthesis. Under BLB stress, Neiwuyou 8015 with lower BLB resistance had a lower Chl content and more

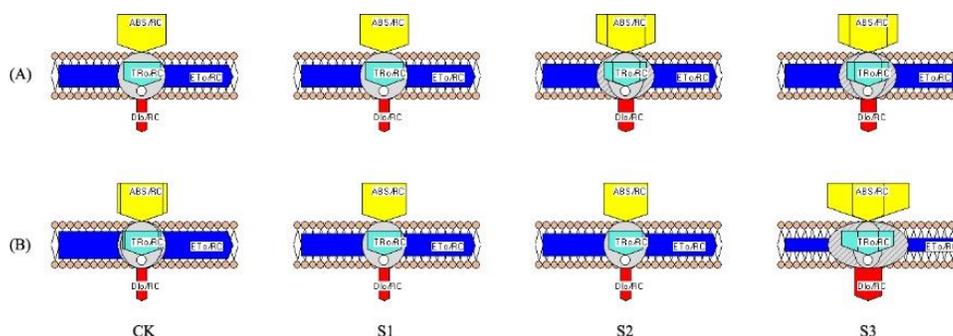


Fig. 4: Energy pipeline models of specific fluxes per reaction center (RC) of healthy (CK) and slight (S1), moderate (S2), and serious (S3) bacterial leaf blight (BLB) disease treatments imposed on BLB susceptible Neiwuyou 8015 (A) and resistant Shenzhou 98 (B) rice

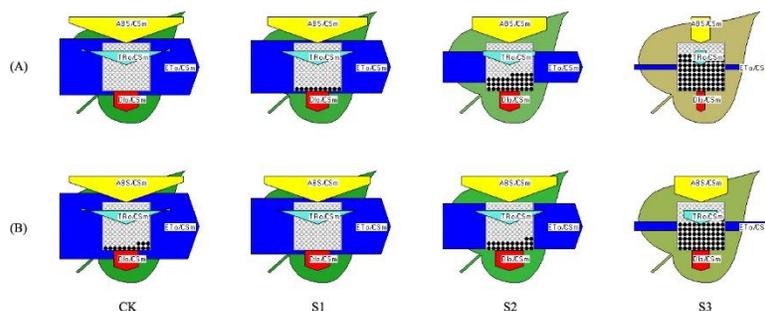


Fig. 5: Energy pipeline models of phenomenological fluxes per cross section (CS_m) of healthy (CK) and slight (S1), moderate (S2), and serious (S3) bacterial leaf blight (BLB) disease treatments imposed on BLB susceptible Neiwuyou 8015 (A) and resistant Shenzhou 98 (B) rice

reduction of Chl content than Shenzhou 98. Changes in energy flux induced by BLB stress were different between PSI and PSII. The fluxes of RE_0/RC , $o(Ro)$ and (Ro) of Neiwuyou 8015, not Shenzhou 98, in slight grade (S1) were higher than those in CK. Similarly, Stefanov *et al.* (2011) reported that (Ro) increased after heat stress. The result indicates that PSI was less damaged than PSII in BLB susceptible rice.

Conclusion

BLB had a negative effect on rice photosynthesis. Increased SOD, PPO and PAL activities, and MDA content and decreased Chl content and G_s indicated that rice photosynthetic functions were reduced by BLB. BLB had greater effects on the photosynthesis of a resistant rice cultivar than a susceptible cultivar. Significant differences of Chl *a* fluorescence transient curves existed between BLB treatments and healthy ones. Parameters induced from the rice Chl *a* fluorescence transient showed that the rice photosynthetic reaction center was inactive by BLB. These findings may enable rapid resistance evaluation of the plant cultivars and may be useful for plant disease management.

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Author Contributions

Aiping Shu, Zengbing Liu and Hao Hu conceived and designed the experiments; Wenxue Zhang, Guangrong Liu, and Zuzhang Li performed the experiments; Gang Sun and Hao Hu analyzed the data; Zengbing Liu wrote the paper.

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