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Full Length Article

Effects of *Magnaporthe oryzae* on Photosynthesis and Yield of Different Rice Genotypes

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Abstract

Effects of Magnapor the Oryzae (*M. oryzae*) on photosynthesis, yield and yield components of 3 rice genotypes were investigated to clarify the mechanism of rice resistance to blast. R725, R720 and R727 were selected as the rice materials, which inoculated with five *M. oryzae* fungal races (ZA5, ZA17, ZC8, ZG1 and ZF2), and had different resistance to blast. Chlorophyll fluorescence data proposed that *M. oryzae* could harm the photosystem II response focus, restrained photosynthetic electron transport. Henceforth, the overabundance vitality couldn't be dispersed by warm or different structures and light insurance was debilitated, prompting diminishes in photosynthetic rate and rice yields. Moreover, the damaging impacts of *M. oryzae* on rice were subject to the two genotypes and contagious races. The analysis of optimum regression equations presented that panicle per plant (PPP), chlorophyll a/b (Chl a/b), actual photochemical efficiency of PSII (ΦPSII), potential photochemical efficiency (Fv/Fo), 1000 grain weight (TGW), and intercellular CO_2 concentration (*Ci*) were associated with rice yield after inoculation with different *M. oryzae* fungal races. Photosynthetic apparatus of R727 had most powerful tolerance to *M. oryzae* among all genotypes.Cultivation pattern could be changed in a timely approach to improve the disease resistance of rice plants and reduce utilization of chemical pesticides.

Keywords: *Magnaporthe oryzae*; Photosynthetic parameters; Photosynthetic pigment contents; Yield; Yield components

Abbreviation and Symbols: Pn Net photosynthetic rate (CO_2μmol/(m^2·S)); Ci Intercellular CO_2 concentration (μ mol/mol); Gs Stomatal conductance (mmol/(m^2·S)); E Transpiration rate (g/(m^2·h)); Fv/Fo Represented PSII activity; Fv/Fm PSII maximum quantum yield; Fv'/Fm' Excitation capture efficiency of open center; ΦPS II PSII effective quantum yield; qP Photochemical quenching coefficient; NPQ Non-photochemical quenching coefficient; Chl a Chlorophyll a (mg/kg); Chl b Chlorophyll b (mg/kg); Car Carotenoid (mg/kg); Chl a+b Total chlorophyll (mg/kg); Chl a/b Chlorophyll a/b ratio; PPP Panicle per plant (panicle); SSR Seed set rate (%); PL Panicle length (cm); TGW 1000 grain weight (g); YPP Yield per plant (g); GN Grain number per panicle

Introduction

Rice (*Oryza sativa* L.) is the most important staple food crop in the world and feeds more than 50% of the world's population (Bloom, 2000). As the farmland is decreasing and the world population is increasing, there is an urgent need to secure rice production and increase grain yield in current rice-breeding programs. Rice blast, caused by *Magnaporthe oryzae* (*M. oryzae*), is one of the most devastating fungal diseases, inducing 10% to 30% annual reduction in yield of rice (Skamnioti and Gurr, 2009). Protecting rice from blast is of great importance to develop Green Super Rice. As described previously, a Green Super Rice should possess the properties of resistances to multiple insects and diseases, high nutrient efficiency, and drought resistance, promising to greatly reduce the consumption of pesticides, chemical fertilizers, and water (Zhang, 2005). Currently, the most cost-efficient approach to control this disease is breeding and planting blast resistant rice. Thus, understanding the physiological response of *Magnaporthe oryzae* infection on host plant is necessary to screen accessions for resistance to blast disease in rice breeding (Howard and Valent, 1996).

Crop yield is directly related to biomass production, which mainly relies on the photosynthesis functions of green tissue (Johnson, 1987). Photosynthesis has been considered to be one of the most sensitive physiological processes to several abiotic and biotic stresses (Berry and

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Bjorkman, 1980; Bastiaans, 1991, 1993; Elings *et al*., 1999; Perez *et al*., 2014). Pathogens affect plant physiological function by negatively influencing the leaf gas exchange or lowering the efficiency of the photosynthesis (Shtienberg, 1992). The photosynthetic efficiency of a plant has been reported to be reduced by pathogens infections (Bastiaans, 1993; Garry *et al*., 1998; Elings *et al*., 1999; Gao *et al*., 2011; Debona *et al.,* 2014; Perez *et al*., 2014; Rios *et al.,* 2014). Lots of attempts have been made (Bastiaans, 1993; Bastiaans and Roumen, 1992) to elucidate the relationships between crop yield and photosynthesis in the presence of blast damage to understand the mechanism of yield reduction induced by blast infection intensively. However, the interaction between rice and the blast pathogen has not been fully investigated, particularly with regard to photosynthetic apparatus. In recent years, chlorophyll fluorescence has been used to explore the interaction between plants and pathogens (Rolfe and Scholes, 2010; Gorbe and Calatayud, 2012), which has been shown to potentially determine a cultivar's resistance to a disease pathogen (Chaerle *et al*., 2004; Perez-Bueno *et al.,* 2006; Berger *et al*., 2007; Bauriegel *et al.,* 2011; Pineda *et al*., 2011; Belin *et al*., 2013). Chlorophyll fluorescence analysis is quick, non-invasive, non-destructive, highly sensitive and accurate to assess *in vivo* photosynthesis (Genty *et al*., 1989). However, it is not clear whether it can be used to evaluate yield components and resistance to a specific pathogen such as *M. oryzae* in rice-breeding programs.

In this study, five fungal races of *M. oryzae* conidia were inoculated on three elite rice restorer lines (which have cytoplasmic male sterility and were used in three-line hybrid rice breeding). During the heading stage, to measure plant gas exchange, it is also necessary to explore the effects of the fungi on photosynthesis and yield component except for investigating the plant response to biotic and abiotic stresses by chlorophyll fluorescence extensively. Thus, it is meaningful to fill the knowledge gap in responses of rice photosynthetic apparatus to blast and gain a better understanding of mechanisms of rice resistance to blast that can be incorporated into rice-breeding research programs. The specific goal of the study was to assess the relationship between photosynthesis rate, stomatal conductance, chlorophyll fluorescence parameters, and yield components of rice genotypes.

Materials and Methods

Plants and Pathogens

Three rice genotypes (elite restorer lines used in three line hybrid rice breeding) with variable resistance to leaf blast disease viz., R725 (susceptible), R720 (moderately resistant) and R727 (highly resistant) were provided by Rice Research Institute (RRI) at Southwest University of Science and Technology (SWUST) Mianyang city, according to a test for rice leaf blast resistance by the Plant Protection Station of Sichuan Province, China (PPSS).

Five fungal races of *M. oryzae viz*., ZA5, ZA17, ZC8, ZG1 and ZF2 were provided by the RRISWUST. Activated strains of *M. oryzae* were inoculated in petri dishes and maintained at 28°C. When the mycelium had completely covered the media, the inoculum was placed on two layers of gauzes and kept wet for three days. Three days after incubation, fungal conidia were harvested from the petri dishes and re-suspended into sterile water containing 0.02% Tween 20. The spore density was adjusted to 5.0×10^5 conidia mL^{-1} with sterile distilled water.

Experimental Design and Pathogen Inoculation

A greenhouse pot experiment using these three rice genotypes was conducted between March and September, 2012 at the RRISWUST. Rice seeds were directly sown in each pot (diameter × depth of pot is 10 cm × 25 cm) with soil containing 198.0 $mg \cdot kg^{-1}$ full nitrogen, 80.3 $mg \cdot kg^{-1}$ available nitrogen, 43.3 $mg \cdot kg^{-1}$ available phosphorus and 76.2 $mg \cdot kg^{-1}$ available potassium (the amounts of nutrients were present in the planting medium). A total of 24 pots per genotype were divided into 6 treatment groups including one blank control without inoculation and each group had four replications. These pots were arranged in a completely randomized design in chamber and re-randomized once a week to minimize position effects. Four-leaf stage plants were thinned to four plants per pot 20 days after sowing, and got routine management. The greenhouse temperature was kept at 25 to 28°C under natural light conditions.

At the heading stage, top leaves of each genotype were sprayed with 25 mL inoculum suspension， and control (CK) was sprayed with 25 mL sterile water for one fungal race, respectively. To increase leaf wetness duration, pots were covered with plastic for 24 h after inoculation.

Measurement of Photosynthetic Parameters

Leaf gas exchange measurements were made on fully expanded flag leaves of each plant using a portable photosynthesis measurement system (GFS-3000, Walz, Germany) from 9:00 a.m. to11:00 a.m. at the seventh day after inoculation. The measurement conditions were as follows: flow rate of 750 $\mu mol \cdot s^{-1}$, leaf area of 4 cm^2, light intensity of 800 $\mu mol \cdot m^{-2} \cdot s^{-1}$, environmental CO_2 concentration of 500±25 ppm and environmental temperature of 26 ± 1°C. Subsequently, four gas exchange parameters of plants including net photosynthetic rates (*Pn*), intercellular CO_2 concentration (*Ci*), stomatal conductance (*Gs*), and transpiration rate (*E*) were measured and recorded.

Chlorophyll fluorescence analyses were performed on fully expanded flag leaves of each plant from 9:00 a.m. to 11:00 are seven days after inoculation by using Dual-PAM-100 measuring systems (Walz, Germany). Before measurement, the rice plants were exposed to darkness for 20 min. Then the leaves were initially exposed to the weak modulated measuring beam (12 $\mu mol \cdot m^{-2} \cdot s^{-1}$) to estimate Fo, followed by exposure to a saturating white light (10,000 $\mu mol \cdot m^{-2} \cdot s^{-1}$) to produce a reduction of the PS II reaction center, at which point Fm was measured. Thirty seconds after the saturation pulse, continuous actinic light (168 $\mu mol \cdot m^{-2} \cdot s^{-1}$) was applied to measure the steady-state fluorescence yield Fs. Saturation pulses were then triggered every 20 s over a period of 300 s. Four important chlorophyll fluorescence parameters including Fv/Fm (Fv/Fm = 1-Fo/Fm), Fv/Fo (Fv/Fo = Fm/Fo-1), photochemical quenching coefficient (qP) and non-photochemical quenching coefficient (NPQ) were obtained (Roháček, 2002).

Measurement of Photosynthetic Pigment Contents

Flag leaves used for measuring the photosynthetic gas exchange were harvested and the pigment contents (chlorophyll and carotenoid) were determined by the method described by (Hiscox and Israelstam, 1979). Fifty milligram of leaf tissue of each plant was collected and individually incubated in 20 mL 95% ethanol solution until leaf tissue became colorless. The absorbance of extract was measured using a Hitachi U-2001 spectrophotometer (Hitachi, Japan) at three wavelengths (665, 649 and 470 nm). Then chlorophyll A (Chl a), chlorophyll B (Chl b) and carotenoid concentrations were calculated according to the method described by (Chappelle et al., 1992).

Measurement of Yield Components

Rice grain was harvested at maturity stage. All plants were used for measurement of yield related traits that included panicle number per plant, panicle length, seed setting rate, 1000 grain weight, grain number per panicle and yield per plant.

Data Analysis

Data were statistically analyzed with Excel 2003 and SPSS22.0 for Windows (IBM Corporation). Analysis of variance was conducted using the Univariate General Linear Model in SPSS22.0. Duncan's test was used for multiple comparison and differences were considered significant at $p \leq 0.05$. Regression analysis was conducted for selected variables.

Results

Effects of *M. oryzae* on Photosynthetic Gas Exchange

Data obtained from this study showed that several important parameters indicating photosynthetic gas exchange of leaves in rice plants inoculated with *M. oryzae* exhibited various changes compared with non-inoculated rice plants. *Pn* of leaves in R725, R720 and R727 rice plants was reduced after inoculated with different fungal races. For example, inoculated with ZA5 in R725 and R727and inoculated with ZC8 in R720, *Pn* showed largely decreased.

Ci of leaves in three rice genotypes inoculated with *M. oryzae* was significantly higher when compared to that in non-inoculated plants. Obviously, the *Ci* of R727 increased less than that of R725 and R720. Taking ZF2 as an example, the *Ci* of R725, R720 and R727 inoculated with ZF2 increased by 21.5, 18.3 and 5.1%, respectively, compared with the corresponding non-inoculated plants. On the contrary, the *Gs* of leaves inoculated with *M. oryzae* dramatically decreased compared with the corresponding no-inoculated plants, and the extent of the decrease in *Gs* also depended on rice genotypes and fungal races of *M. oryzae*.

For transpiration rate (*E*), there were also obvious differences between rice plants inoculated with *M. oryzae* and the corresponding non-inoculated plants. *E* was drastically lowered for all three rice genotypes inoculated with ZG1 and ZF2 compared with the control. In general, the *E* value of R727 rice plants decreased to a less extent than R725 and R720 rice plants.

Pn, Net photosynthetic rates; *Ci*, intercellular CO_2 concentration; *Gs*, stomatal conductance; *E*, transpiration rates; *Fv/Fo*, represented PSII activity; *Fv/Fm*, PSII maximum quantum yield; *Fv'/Fm'* ,excitation capture efficiency of open centers; $\Phi_{PS\ II}$, PSII effective quantum yield; qP, photochemical quenching coefficient; NPQ, non-photochemical quenching coefficient. Values represents the means of four rice plants, and different letters indicate significant difference at $p < 0.05$ by Duncan's new multiple range tests. CK represents non-inoculated rice plants.

Effects of *M. oryzae* on Chlorophyll Fluorescence

Data in this study also indicated that the differences in the chlorophyll fluorescence parameters between inoculated and non-inoculated rice plants were dependent on the rice varieties and *M. oryzae* fungal races (Table 1). The *Fv/Fo* ratio of inoculated rice plants was decreased compared with the control non-inoculated rice plants. The *Fv/Fo* ratio in R725 inoculated with ZA5, ZG1 and ZF2 was reduced by 12.54%, 15.00% and 3.6%, respectively. Additionally, the *Fv/Fo* ratio of R720 and R727 inoculated with ZC8 were also decreased by 6.33% and 4.62% compared with the non-inoculated rice plants, respectively. The changes in the *Fv/Fm* were also dependent on the rice varieties and the different fungal races of *M. oryzae*. The *Fv/Fm* of inoculated plant was observed less than that of the non-inoculated plant. The *Fv/Fm* was observed in R725 inoculated with ZG1, R720 inoculated with ZC8, and R727 inoculated with ZF2 decreased by 3.55%, 2.00% and 2.24%, respectively.

The change pattern of Φ_{PSII}, *Fv'/Fm'* and qP, was roughly similar. After incubated with ZA5 and ZF2 in R725, the Φ_{PSII}, Fv'/Fm' and qP of leaves were no significant changes, indicating that ZA5 and ZF2 were minimal effect on the photochemical efficiency of R725. When ZG1

Table 1: Photosynthetic parameters in three rice genotypes after inoculated with five fungal races

Genotypes	Parameters	Treatments					
		ZA5	ZA17	ZC8	ZG1	ZF2	CK
R725	*Pn*(CO_2*μmol/*(m^2*·S))*	9.38d	11.71b	10.45c	9.81d	9.54d	12.35a
	Ci(μ mol/mol)	271.2c	290.9b	304a	308.7a	280.4bc	235.5d
	Gs(mmol/(m^2*S))*	108.2d	151.8b	149.6b	116.4c	87.1e	156a
	E (g/(m^2*·h))*	4.529b	5.31a	3.76c	3.306d	3.293d	5.671a
	Fv/Fo	4.017d	4.287c	4.351bc	3.904e	4.427b	4.593a
	Fv/Fm	0.795cd	0.8109b	0.8131b	0.7931d	0.8015c	0.8223a
	Fv'/Fm'	0.7436b	0.7607ab	0.7427b	0.7409b	0.7649ab	0.7758a
	$\Phi_{PS\ II}$	0.6244ab	0.6008bc	0.607bc	0.5782c	0.608bc	0.6555a
	qP	0.8048b	0.7898b	0.8168b	0.794b	0.7905b	0.845a
	NPQ	0.33d	0.2825e	0.3845b	0.2755e	0.3648c	0.4193a
R720	*Pn*(CO_2*μmol/*(m^2*·S))*	8.83d	13.7b	7.67e	10.61c	11.04c	15.62a
	Ci(μ mol/mol)	367.4a	343.1b	344.1b	311c	347.2b	307.6c
	Gs(mmol/(m^2*S))*	123.4d	205.5b	92.3f	136.9c	113.4e	238.8a
	E(g/(m^2*·h))*	4.719b	5.155ab	2.88d	2.668d	3.77c	5.605a
	Fv/Fo	4.328ab	4.262b	4.14c	4.308b	4.311b	4.42a
	Fv/Fm	0.8123ab	0.8139a	0.8025b	0.8074ab	0.8021b	0.8185a
	Fv'/Fm'	0.7544ab	0.769a	0.7476ab	0.7335a	0.76ab	0.7671a
	$\Phi_{PS\ II}$	0.6125b	0.5738c	0.6195b	0.5833c	0.6127b	0.6565a
	qP	0.7993b	0.7465c	0.829b	0.7513c	0.8065b	0.8785a
	NPQ	0.407c	0.3215d	0.367cd	0.602b	0.3668cd	0.6938a
R727	*Pn*(CO_2*μmol/*(m^2*·S))*	7.1d	7.92c	9.02b	8.54bc	9.02b	10.94a
	Ci(μ mol/mol)	322.1b	325.9b	339.1a	318.2bc	326.6b	311.5c
	Gs(mmol/(m^2*S))*	114e	140d	153.3c	204.8b	113.7e	214a
	E(g/(m^2*·h))*	4.47ab	3.528c	3.273c	4.31b	2.33d	4.848a
	Fv/Fo	4.089a	4.014bc	3.882d	3.973c	3.968c	4.07ab
	Fv/Fm	0.8033b	0.8004b	0.7949b	0.8015b	0.7988b	0.8131a
	Fv'/Fm'	0.732a	0.6719c	0.727a	0.6909bc	0.7091ab	0.7368a
	$\Phi_{PS\ II}$	0.5959b	0.4828e	0.5847bc	0.5764cd	0.5614d	0.6263a
	qP	0.8143b	0.7185d	0.8043bc	0.7848c	0.7925bc	0.8503a
	NPQ	0.3973d	0.639b	0.46cd	0.638b	0.5015c	0.7845a

Values represents the means of four rice plants, and different letters indicate significant difference at $p < 0.05$ by Duncan's new multiple range tests. CK represents non-inoculated rice plants, same as following tables

inoculating in R720, the Φ_{PSII}, *Fv'/Fm'* and qP were all decreased, indicating that ZG1 may comprehensive effect on photochemical efficiency of R720. When R727 treated with ZA17, Φ_{PSII}, *Fv'/Fm'* and qP of the leaves of R727 had maximal changes, and they were decreased by 22.91%, 8.81% and 15.5%, respectively.

Table 2: Photosynthetic pigment contents in three rice genotypes after inoculated with five fungal races

Genotypes	Parameters	Treatments					
		ZA5	ZA17	ZC8	ZG1	ZF2	CK
R725	Chl a (mg/kg)	3.27b	2.877c	3.331b	3.025c	3.198b	3.862a
	Chl b(mg/kg)	0.979a	0.842c	0.936ab	0.841c	0.881bc	0.997a
	Car(mg/kg)	0.775a	0.701b	0.739ab	0.69b	0.765a	0.803a
	Chl a+b(mg/kg)	4.249b	3.719d	4.268b	3.866cd	4.079bc	4.859a
	Chl a/b	3.341d	3.422cd	3.557bc	3.598bc	3.635b	3.875a
R720	Chl a(mg/kg)	3.014f	3.145e	3.337c	3.589b	3.217d	3.881a
	Chl b(mg/kg)	0.971c	1.002bc	1.048b	1.173a	1.035b	1.17a
	Car(mg/kg)	0.719d	0.72d	0.757c	0.81b	0.776c	0.879a
	Chl a+b(mg/kg)	3.985f	4.146e	4.386c	4.762b	4.252d	5.051a
	Chl a/b	3.105b	3.151ab	3.184ab	3.062b	3.108b	3.317a
R727	Chl a(mg/kg)	2.372d	2.533b	2.484bc	2.29e	2.447cd	3.073a
	Chl b(mg/kg)	0.707bc	0.72b	0.724b	0.663c	0.686bc	0.851a
	Car(mg/kg)	0.596b	0.611ab	0.6b	0.582b	0.609ab	0.639a
	Chl a+b(mg/kg)	3.078d	3.254b	3.209bc	2.953e	3.133cd	3.924a
	Chl a/b	3.357b	3.516ab	3.441ab	3.455ab	3.568a	3.609a

NPQ reflects unused light energy for heat dissipation, which was absorbed by antenna pigments of PSII (Maxwell and Johnson, 2000). The heat dissipation of R727 was significantly higher than the other two varieties. NPQ of leaves of rice plants inoculated with different fungal races was significantly reduced compared with the control, and the maximum decreases were 34.29% (R725 inoculated with ZG1), 53.66% (R720 inoculated with ZA17) and 49.36% (R727 inoculated with ZA5), respectively.

Effects of *M. oryzae* on Photosynthetic Pigment Contents

There was obvious difference in photosynthetic pigment contents of leaves between five fungal races and CK treatments (Table 2). Chl a+b of R727 inoculated with ZF2 decreased compared with CK, and Chl b was similar, as a result of a lower Chl a/b compared with CK. The Chl a and Chl b of R725 inoculated with ZA17 were lower than other treatments, so the Chl a+b of R725 was minimal and decreased by 23.46% compared with CK. All five fungal races could significantly reduce the Chl a content of R720 leaves, and the decrease level ranged from 7.52% to 22.34%. In addition to ZG1, the other four fungal races all could significantly reduce Chl b content of R720. Moreover, Chl a+b and Chl a/b exhibited a significant reduction in three genotypes after fungal races treatments in comparison with

Table 3: Yield related traits in three rice genotypes after inoculated with five fungal races

Genotypes	Parameters	Treatments					
		ZA5	ZA17	ZC8	ZG1	ZF2	CK
R725	PPP(panicle)	4.7c	5.7bc	6.7b	9.3a	6.3b	9.7a
	SSR(%)	50.51b	85.89a	87.04a	82.67a	86.59a	89.48a
	PL(cm)	22.2c	25.5a	25.6a	23.7bc	23.5bc	24.5ab
	TGW(g)	24.1c	27.33a	25.67b	26.37ab	27.43a	27.57a
	YPP(g)	10.69e	17.98b	16.24c	12.51d	11.2e	19.73a
	GN	116.3a	116.7a	114.0a	120.1a	113.3a	126.7a
R720	PPP(panicle)	6.7b	4.7b	5.0b	6.0b	10.7a	10.7a
	SSR(%)	86.87a	84.63ab	83.53b	85.09ab	84.85ab	87.36a
	PL(cm)	21.3bc	22.7a	21.9abc	22.6ab	20.7c	23.1a
	TGW(g)	29.67ab	28.63b	30.07a	28.97b	29.47ab	30.37a
	YPP(g)	16.3c	16.45c	14.14d	16.26c	19.61b	25.62a
	GN	102.4a	105.7a	113.1a	110.3a	107.6a	113.3a
R727	PPP(panicle)	5.3c	4.7c	7.3b	9.3a	8.7ab	9.7a
	SSR (%)	66.73a	62.24a	46.9b	62.19a	62.21a	67.12a
	PL(cm)	19.1bc	20.7ab	17.9c	19.3bc	19c	21.3a
	TGW(g)	24.97a	24.57a	22.8b	25.27a	24.53a	25.3a
	YPP(g)	10.83cd	10.62d	11.74bc	11.5cd	12.55b	15.53a
	GN	95.7a	93a	96.3a	98a	96a	96a

PPP, Panicle per plant; SSR, Seed set rate; PL, Panicle length; TGW, 1000-grain weight; YPP, Yield per plant; GN, Grain number per panicle . Values represents the means of four rice plants, and different letters indicate significant difference at $p < 0.05$ by Duncan's new multiple range tests. CK represents non-inoculated rice plants

Table 4: Analysis of variance (significance) of photosynthetic parameters, photosynthetic pigment contents, and yield related traits of three rice genotypes after inoculated with five fungal races

Characteristic Parameters		Source of Variation		
		G	F	G × F
Photosynthetic parameters	Pn	**	**	**
	Ci	**	**	**
	Gs	**	**	**
	E	**	**	**
	Fv/Fo	**	**	**
	Fv/Fm	**	**	**
	Fv'/Fm'	**	**	*
	$\Phi_{PS II}$	**	**	**
	qP	ns	**	**
	NPQ	**	**	**
Photosynthetic pigment contents	Chl a	**	**	**
	Chl b	**	**	**
	Car	**	**	**
	Chl a+b	**	**	**
	Chl a/b	**	**	*
Yield related traits	PPP	ns	**	**
	SSR	**	**	**
	PL	**	**	**
	TGW	**	**	**
	YPP	**	**	**
	GN	**	ns	ns

G, genotype; F: fungal race. Level of statistical significance: * $P < 0.05$; ** $P < 0.01$; and ns: not significant

CK. The effect of ZA5 on chlorophyll content of R720 was similar to R725. Compared with CK, Chl a+b and Chl a/b were decreased by 20.99% and 6.32%, respectively. ZA5 can also significantly reduce Chl a and Chl b contents of R727. The largest effect on chlorophyll content of R727 was ZG1. Chl a and Chl b were decreased by 25.41% and 22.35% compared with CK, respectively.

Under the impact of *M. oryzae*, Car (carotenoid content) of rice leaves was fewer changes, while Car of R720 all significantly reduced, with decrease range of 8.0-18.2%. Especially, among five fungal races, ZG1 could significantly reduce Car of three rice plants, which were decreased by 13.75%, 7.95% and 9.38% compared with CK, respectively.

Chl a, chlorophyll a; Chl b, chlorophyll b; Car, carotenoid; Chl a+b, total chlorophyll; Chl a/b, Chl a/b ratio. Values represents the means of four rice plants and different letters indicate significant difference at $p < 0.05$ by Duncan's new multiple range tests. CK represents non-inoculated rice plants.

Effects of *M. oryzae* on Yield Components

Different fungal races of *M. oryzae* to effect on yield and yield components were significantly in R725, R720 and R727 (Table 3). ZA5 also significantly affected PPP (panicle per plant), PL (panicle length) and YPP (yield per plant) of all genotypes. Compared with CK, yield and yield components in R725 treated with ZA5 were decreased remarkably by 45.82% (YPP), 51.55% (PPP), 9.39% (PL), 43.55% (SSR), 12.59% (TGW), and 8.21% (GN). ZF2 had slight effects on yield components in R720, only showing significant effects on PL (10.39%) and YPP (23.46%). ZC8 expressed lower effect on TGW (0.99%) but showed the greatest impact on PPP (53.27%) and YPP (44.81%) in R720. ZC8 showed remarkable effect on yield and yield components except GN in R727, and they were decreased by 24.74% (PPP), 15.96% (PL), 30.13% (SSR), 9.88% (TGW) and 24.40% (YPP) compared with CK, respectively.

Analysis of Variance and Correlation for Photosynthesis and Yield

Analysis of variance for photosynthetic parameters, photosynthetic pigment contents, and yield components by differential fungal races treatments were summarized in Table 4. For photosynthesis parameters and yield related traits, the results showed significant effects for all main factors [fungal race (F), and genotype (G)], except qP and PPP which exhibited no significant effects for genotype. In addition, GN showed significant effect only for genotype. Significant interacting effects of the main treatment factors were observed in all parameters except GN.

Table 5: Mean yield components and photosynthetic parameters across all genotypes for five fungal

Photosynthetic parameters and yield related traits	Treatments					
	ZA5	ZA17	ZC8	ZG1	ZF2	CK
YPP(g)	12.61e	15.02b	14.04c	13.42d	14.45c	20.29a
PPP(panicle)	5.6cd	5.0d	6.3c	8.2b	8.6b	10.0a
SSR(%)	68.04d	77.59b	72.49c	76.65b	77.88b	81.32a
PL(cm)	20.89c	22.94a	21.79b	21.86b	21.07bc	22.96a
TGW(g)	26.24cd	26.84bc	26.18d	26.87bc	27.14ab	27.74a
GN	104.9a	105.1a	107.8a	109.4a	105.8a	112.0a
Chl a (mg/kg)	2.885d	2.852d	3.05b	2.968c	2.954c	3.605a
Chl b(mg/kg)	0.885bcd	0.855d	0.903b	0.892bc	0.867cd	1.006a
Chl a+b(mg/kg)	3.771de	3.706e	3.954b	3.86c	3.821cd	4.611a
Chl a/b	3.268c	3.363bc	3.394b	3.372b	3.437b	3.601a
Car(mg/kg)	0.697bc	0.677c	0.699bc	0.694bc	0.717b	0.774a
Pn(CO_2μmol/(m^2·S))	8.44e	11.11b	9.05d	9.65c	9.87c	12.97a
Ci(μ mol/mol)	320.2b	320.0b	329.1a	312.6c	318.1bc	284.9d
Gs(mmol/(m^2·S))	115.2e	165.8b	131.8d	152.7c	104.7f	202.9a
E(g/(m^2·h))	4.573b	4.664b	3.304cd	3.428c	3.131d	5.375a
Fv/Fo	4.145cd	4.188c	4.124d	4.062e	4.235b	4.361a
Fv/Fm	0.8034bc	0.8085b	0.8035bc	0.8007c	0.8008c	0.8180a
Fv'/Fm'	0.7433b	0.734bc	0.7392b	0.7219bc	0.7445b	0.7599a
$\Phi_{PS\ II}$	0.6108b	0.5524e	0.6038bc	0.5793d	0.5938c	0.6461a
qP	0.8061bc	0.7516e	0.8167b	0.7767d	0.7965c	0.8579a
NPQ	0.3781d	0.4143c	0.4038cd	0.5052b	0.4110c	0.6325a

Table 6: Correlation analysis of yield components and photosynthetic parameters under Magnaporthe Oryzae treatments

	PPP	SSR	PL	TGW	YPP	GN	Chl a	Chl b	Car	Chl a+b	Chl a/b	Pn	Ci	Gs	E	Fv/Fo	Fv/Fm	Fv'/Fm'	ΦPS II	qP
SSR	0.66																			
PL	0.26	0.66																		
TGW	0.77	0.886*	0.49																	
YPP	0.37	0.886*	0.77	0.60																
GN	0.77	0.54	0.66	0.54	0.43															
Chl a	0.77	0.31	0.37	0.31	0.26	0.886*														
Chl b	0.60	0.09	0.31	0.14	0.09	0.77	0.943**													
Car	0.829*	0.49	0.03	0.49	0.37	0.49	0.71	0.60												
Chl a+b	0.771	0.314	0.371	0.314	0.257	0.886*	1.000**	0.943**	0.714											
Chl a/b	0.886*	0.771	0.429	0.657	0.657	0.771	0.771	0.543	0.829*	0.771										
Pn	0.429	0.943**	0.829*	0.771	0.943**	0.486	0.2	0.029	0.257	0.2	0.6									
Ci	-0.714	-0.771	-0.6	-0.943**	-0.486	-0.657	-0.371	-0.257	-0.314	-0.371	-0.543	-0.714								
Gs	0.086	0.429	0.943**	0.314	0.6	0.543	0.314	0.371	-0.086	0.314	0.2	0.657	-0.486							
E	-0.086	0.257	0.657	0.257	0.429	0.143	0.029	0.2	-0.086	0.029	-0.086	0.486	-0.371	0.829*						
Fv/Fo	0.429	0.771	0.314	0.657	0.771	0.086	0.086	-0.029	0.6	0.086	0.543	0.714	-0.429	0.2	0.371					
Fv/Fm	-0.058	0.319	0.667	0.058	0.667	0.203	0.232	0.319	0.174	0.232	0.203	0.522	-0.058	0.754	0.783	0.493				
Fv'/Fm'	0.6	0.486	-0.029	0.486	0.429	0.143	0.371	0.314	0.886*	0.371	0.6	0.314	-0.257	-0.086	0.143	0.829*	0.319			
$\Phi_{PS\ II}$	0.486	0.029	-0.086	0.143	0.029	0.257	0.6	0.714	0.771	0.6	0.371	-0.086	-0.086	0.029	0.257	0.371	0.348	0.771		
qP	0.543	0.086	0.029	0.086	0.143	0.429	0.771	0.829*	0.829*	0.771	0.543	-0.029	-0.029	0.086	0.143	0.314	0.406	0.714	0.943**	
NPQ	0.543	0.771	0.886*	0.771	0.657	0.771	0.429	0.314	0.143	0.429	0.543	0.829*	-0.886*	0.771	0.486	0.314	0.319	0.029	-0.086	-0.029

*Correlation is significant at the 0.05 level (2-tailed)
**Correlation is significant at the 0.01 level (2-tailed)
Correlation coefficients obtained by Spearman's rho

The average yield related traits after five fungal races treatments are mirrored by the photosynthetic capacity for the same treatments (Table 5). Yield per plant of plant inoculated with all fungal races was significantly less than CK. For photosynthetic parameters, Pn was the main influencing factor of yield according to correlation analysis (Table 6), since there was a significant association of Pn with NPQ and yield component SSR. Additionally, SSR was the main factor to influence YPP.

Regression Analysis between Photosynthetic Parameters and Yield under Different Fungal Races

After treated with five fungal races of *M. oryzae* and sterile water (CK), multiple linear regression analysis was performed to explore the relationship between photosynthetic parameters and yield. Yield per plant was selected as the dependent variable and other parameters were selected as independent variables, the optimum regression equations were established after regression analysis. Described as follows:

CK, $Y= -10.5+ 23.3X_1(\text{Chl b}) + 0.6X_2(\text{Pn})$, $R^2 = 0.99$
ZA5, $Y= -37.7 + 3.8X_1(\text{PPP}) + 8.8X_2(\text{Chl a/b})$, $R^2 = 0.99$
ZA17, $Y= -19.7+ 62.8X (\Phi_{PSII})$, $R^2 = 0.99$
ZC8, $Y= -25.5+ 9.6X (\text{Fv/Fo})$, $R^2 = 0.99$
ZG1, $Y= -21.9+ 1.3X (\text{TGW})$, $R^2 = 0.98$
ZF2, $Y= 21.8 + 3.1X_1(\text{PPP}) - 0.103X_2(Ci)$, $R^2 = 0.94$

The results showed that Chl b and Pn were two most important factors affecting the yield per plant in plant without any fungal infection. The main limiting factors of ZA5 were PPP (panicle per plant) and Chl a/b, the main limiting factor of ZA17 was Φ_{PSII}, the main limiting factor of ZC8 was Fv/Fo, the main limiting factor of ZG1 was a yield component TGW (1000 grain weight) and the main limiting factor of ZF2 were PPP and Ci. The results also suggested that most factors were positively correlated to the yield, except *Ci* that was negatively correlated with yield.

Discussion

After treated with five *M. oryzae* fungal races, the chloroplasts were injured to a certain extent. Disease-resistant genotype was slightly injured than susceptible genotype, suggesting that chloroplasts of resistant genotype were more tolerant to *M. oryzae* infection than those of susceptible genotype (Xing and Zheng, 2008). The chlorophyll, embedded in the thylakoid membranes of chloroplasts, was the material basis for photosynthesis, whose contents reflect the photosynthetic intensity in plants (Huang *et al.*, 2004). In our study, chlorophyll contents in different resistant genotypes to rice blast were reduced after inoculated with *M. oryzae*. Each fungal race could significantly reduce the photosynthetic pigment contents of plant leaves, causing low efficiency of light absorption and transmission and a reduction of *Pn*, as a result of photosynthesis inhibition. Car (Carotenoid content) which has strong antioxidant effect was also an important optical absorption complex factor in plants (Huang *et al*., 2004). Car has been partly destroyed by *M. oryzae* in leaves, and its capacity for light absorption and free radical scavenging was decreased, resulting in a reduction of protective effects of chlorophyll and photosynthetic efficiency.

Two main factors have been reported to be responsible for the decline of *Pn*. The stomatal factor was one contributor, which includes the number and size of stoma (Cornic and Briantais, 1991). The other contributor was non-stomatal factor, such as intrinsic enzyme activities and photosynthetic components (Lal *et al*., 1996). Our results showed that inoculation of ZA5 could significantly reduce the *Pn* and *Gs* of R725 and R720, while significantly increase Ci. As it was reported previously, the reduction of photosynthesis in R725 and R720 was not caused by stomatal limitation, but by the decreased carboxylation efficiency (Huang *et al.,* 2004), which suggested that *M. oryzae* could damage the photosynthetic mechanisms of leaf and then inhibit photosynthesis. Stress has been shown to reduce the chloroplast activity, Rubisco activity and RuBP carboxylase regeneration (Scafaro *et al*., 2012). *M. oryzae* acting as an inhibiting factor could affect photochemical activity and obstruct CO_2 utilization. In addition, *Pn* was found to be significantly reduced in our study, but the leaf tissues showed asymptomatic, indicating that blast severity is not an acceptable indicator for predicting *M. oryzae*-induced *Pn* reduction, as described previously (Debona *et al*., 2014).

Fv/Fo, potential photochemical efficiency of PSII, was proportional to the activity of the water-splitting complex on the donor side of the PSII (Kalaji *et al.,* 2011). *Fv/Fm* is the maximum quantum yield of PSII and reflects the energy conversion efficiency of PSII reaction centers. Changes in *Fv/Fm* represents the photochemical efficiency of PSII that is one of the most important indicators for photosynthesis (Kalaji *et al*., 2011). *Fv/Fo* and *Fv/Fm* of rice leaves were decreased after inoculated with *M. oryzae*. Reduction of *Fv/Fo* indicated that photochemical activity of chloroplast was inhibited and PSII reaction center was damaged. In this study, reduction in *Fv/Fo* level (15.00%) was significantly higher than that in *Fv/Fm* (2.95%), so *Fv/Fo* was better to indicate the effects of *M. oryzae* on photosystem than Fv/Fm under experimental conditions. Φ_{PSII}, actual photochemical reaction efficiency of PSII, reflects the electron transfer efficiency between PSII and PSI. It was also connected by carbon assimilation, photorespiration and O_2-dependent electron flow. Fv'/Fm' reflects photochemical capture efficiency of PSII reaction center, and qP indicates the share of light energy for photochemical electron transfer, which was absorbed by antenna pigments of PSII (Maxwell and Johnson, 2000). Namely Φ_{PSII}, Fv'/Fm' and qP directly reflect the light capturing capability and efficiency of the photochemical reaction (Maxwell and Johnson, 2000). The declines of qP indicated that the open proportion of PSII reaction centers and participatory electron of CO_2 fixation were decreased, leading to a reduction of the photosynthetic electron transport capacity. Then the dark reaction of leaf was blocked, carbon assimilation capacity was decreased, and electron transfer was blocked, finally resulting in photosynthetic rate decline (Dannehl *et al*., 1996), which changed basically same to *Pn*. Meanwhile NPQ was significantly reduced, indicating that the leaves could no longer dissipate excess excitation energy by launching the heat dissipation mechanisms to protect the photosynthetic apparatus from damage of *M. oryzae* conidia (Long *et al*., 2013). It also showed that rice blast fungus *M. oryzae* may destroy PSII reaction center and inhibit photosynthetic electron transport from the oxidizing side of PSII to PSII reaction center. Simultaneous measurements of chlorophyll fluorescence and plant gas exchange allowed a better understanding of the mechanism of deleterious effect of *M. oryzae* on photosynthetic apparatus.

Inoculation with *M. oryzae* caused a decrease in both photosynthesis rates and PSII activity, and the later was evaluated by chlorophyll fluorescence analysis. The deleterious effects of blast pathogen relied on rice genotype and fungal race. Furthermore, the result of chlorophyll fluorescence analysis could help to better understand the responses of different rice genotypes infected by *M. oryzae*. Chlorophyll fluorescence parameters indicated that photosynthetic apparatus of R727 had most powerful tolerance to *M. oryzae* among all genotypes.

Effects of different fungal races of *M. oryzae* on rice yield components were obviously different. Similar with photosynthetic parameters, the performance in virulent gene and toxicity of different fungal races were different in *M. oryzae* (Li *et al*., 2011). ZA5 showed the maximum impacts on PPP, PL, SSR, TGW and YPP of R725. This result meant that R725 was the most sensitive genotype to ZA5. The optimal regression model showed that Chl b, Pn, Chl a/b, Φ_{PSII}, Fv/Fo, TGW, PPP and Ci were the main limiting factors for rice production after inoculation of *M. oryzae*. It also suggested that the sensitivity of rice genotypes to *M. oryzae* was different, and the rice blast resistance genes were also different (Lin *et al*., 2007). Correlation analysis among yield, yield components and photosynthetic parameter showed that *Pn* was significantly positively correlated with YPP and SSR under all treatments. Consistent with previous research, net photosynthetic rate at the filling stage was significantly positively correlated with the seed setting rate (Zhang *et al*., 2011).

Conclusion

Based on the association of fungal races with rice genotypes, cultivation pattern could be changed in a timely approach to improve the disease resistance of rice plants and reduce utilization of chemical pesticides, which was extremely important for environmental protection.

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