Wheat Resistance to Fusarium Head Blight is Associated With Changes in Photosynthetic Parameters

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Abstract

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Fusarium head blight (FHB) is an important wheat disease worldwide; however, its effects on the physiological parameters in plants with different levels of FHB resistance remain unclear. Here, we evaluated the effects of *Fusarium graminearum* infection on yield and the photosynthesis-associated parameters P_n , G_s , and C_i of wheat flag leaves and determined the influence of FHB resistance. The FHB-resistant wheat genotype L699 and its susceptible sister line L661 were point- and spray-inoculated. Photosynthesis-associated parameters were subsequently measured using a modulated photosynthesis system, and FHB intensity was evaluated. Compared with L661, FHB caused more significant reductions in the net

photosynthetic rate and stomatal conductance of flag leaves in L699. However, FHB caused a larger reduction in the 1000-grain weight and total grain weight per spike in L661 compared with L699. Independence sample *t* test showed that FHB resistance was significantly higher in L699 compared with L661. We concluded that under the conditions of the present study, FHB had a significantly greater effect on net photosynthesis in the resistant line compared with the susceptible line; however, it had a greater impact on yield components in the susceptible line. These results provide a new insight into the physiological cost of host resistance to FHB.

Wheat (*Triticum aestivum* L.) accounts for approximately 20% of the calories consumed by humans. Fusarium head blight (FHB), mainly caused by *Fusarium graminearum* Schwabe and *F. culmorum* WG Smith, is an economically important fungal disease in many wheat-growing areas and seriously threatens wheat production worldwide (21). Several FHB outbreaks in wheat and barley (*Hordeum vulgare* L.) from 1991 to 1997 resulted in estimated total direct losses of approximately \$1.3 billion and cumulative losses of \$4.8 billion in the United States (1). From 1998 to 2000, the direct economic losses due to FHB infection of wheat in the northern Great Plains and the central United States were estimated at \$734 million (24), while the total economic losses due to FHB reached \$2.7 billion in the United States during the same time period (23).

In China, FHB epidemics have historically occurred in the middle to lower valleys of the Yangtze River, including Jiangsu, Zhejiang, Anhui, and Hubei provinces, and the northeast spring wheat-growing area. In these areas, seven severe and 10 moderate epidemics of FHB were reported from 1951 to 1990 (35). In recent years, FHB has become increasingly severe in the southwest region of China (36). For example, in 2004, the epidemic area reached 292,000 ha in Sichuan, and the proportion of FHB-infected spikes ranged from 10 to 61% (29). A serious FHB epidemic occurred in 2012 in the Yellow and Huai River valleys, including southern Shandong, Henan, Shanxi, Hebei, and northern parts of Jiangsu,

Anhui, and Hubei provinces, which are the most important wheat-growing areas of China (14). Another complication of FHB is the accumulation of mycotoxins produced by *Fusarium* spp., especially deoxynivalenol, in wheat grain, which can cause acute food poisoning in humans and animals after they eat infected grain (7,38).

Although crop management practices and application of chemicals may reduce the damage caused by FHB, the development of genetically resistant cultivars is the most effective approach to combat this disease (1). In the past, efforts have been directed toward the identification of new sources of resistant germplasm because such material is required for the development of FHB-resistant cultivars (4,22). However, few studies have been conducted to investigate the physiological response of wheat to *Fusarium* inoculation and the influence of FHB resistance on this response.

The infection of plant tissue with fungal pathogens is closely linked to changes in metabolic pathways such as photosynthesis (9). Different plant organs have diverse tasks and biological functions. For example, one of the crucial functions of the leaf as a “source” tissue is to synthesize energy-rich molecules via photosynthesis for the transport of carbon, whereas a developing seed is a carbohydrate “sink” (30). It is well known that the FHB pathogen infects spike tissues and thus affects kernel development (5). Kernels are the most important nonphotosynthetic sink of the wheat plant. The relationship between photosynthetic sources and nonphotosynthetic sinks is maintained in a dynamic balance (15,19), and changes in this balance that occur when plant pathogens attack are likely to manifest as changes in photosynthesis-related parameters due to the regulation of cellular signaling homeostasis (27,34). In tomato plants infected with *F. oxysporum*, the level of chlorophyll fluorescence has been used to indicate disease severity (32). This suggests that certain physiological phenotypes could be associated with disease resistance, and measurements of such phenotypes could presumably provide some important information about the effects of host FHB resistance on the physiological mechanisms of the wheat plant. In addition, functional and

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comparative bioinformatics studies have shown that many genes involved in photosynthesis play key roles in protection against both *F. graminearum* and *F. culmorum* (9,11,12). These findings indicate that wheat FHB resistance is related to photosynthetic parameters. However, to date, the relationship between FHB and photosynthetic parameters has not been determined. Understanding this relationship will be valuable for determining the costs of FHB resistance.

In the present study, a new FHB-resistant wheat line L699 and its susceptible sister line L661 were used to study the effects of *F. graminearum* infection on photosynthesis-associated parameters and yield components. The use of sister lines contrasting in their reactions to FHB for studying the effect of FHB resistance on these parameters significantly reduces the differences in genetic backgrounds between the two lines. Photosynthetic traits, including the net photosynthetic rate (P_n), stomatal conductance (G_s), and intercellular CO_2 concentration (C_i), were investigated using the Li-6400 photometer system. In addition, grain weight per spike and 1000-kernel weight were also measured because they may also be affected by FHB (28). The overall aims of the present study were to i) determine the changes in photosynthetic parameters and yield components after inoculation with *F. graminearum*, ii) investigate the physiological effects of *F. graminearum* inoculation on wheat flag leaves, and iii) determine whether changes in physiological responses to FHB were influenced by FHB resistance.

Materials and Methods

Plant material and resistance screening. Two wheat sister lines, L661 and L699 (Reg. No. GP-974, PI 672540), were selected from a segregating $F_{6:7}$ recombinant inbred line of the cross MY11/YU25 (13). L699 has strong resistance to both stripe rust caused by *Puccinia striiformis* Westend. f. sp. *tritici* and powdery mildew caused by *Erysiphe graminis* f. sp. *tritici*, which is conferred by the *YrYU25* (*YrL693*) and *Pm40* genes, respectively, from YU25 (10,16,18). L661 is resistant only to powdery mildew. In addition, field observations showed that L699 is highly resistant to FHB and that L661 is FHB susceptible (36).

More than 600 seeds of each genotype were sown during the 2009–2010 and 2010–2011 wheat-growing seasons in a field at the Ya'an Agricultural Research Station (27°17' N latitude, 120°16' E longitude, approximately 620 meters above sea level) of Sichuan Agricultural University in southwest China, where the climate is temperate and rainy with a yearly average temperature of 15 to 17°C and yearly average precipitation of 1,520 mm (19). All experiments used a randomized complete block design with three replications. Each plot consisted of 3-m-long rows with 0.5-m spacing between rows, and 30 cm between plants.

In this study, we sprayed a macroconidial suspension containing 200 macroconidia/ μl on the spikes of approximately 200 plants. These plants were randomly chosen from each plot at anthesis to screen for type I resistance. A single spore-derived isolate of *F. graminearum* No. 4 (kindly provided by Professor Zhengqiang Ma at Nanjing Agricultural University, Nanjing, Jiangsu Province, China) was used to prepare conidial suspensions as follows: the *F. graminearum* conidia were placed into V8 juice agar and grown for 1 to 2 weeks at room temperature. Next, falcate conidia collected from the plates were transferred into liquid mung bean medium and cultured at 25°C for 3 days with shaking at 150 rpm. Finally, the conidial suspension was filtered through Miracloth, centrifuged at 8,000 rpm for 10 min, placed in an ice bucket for transport to the field, and used for inoculation within 5 h. Heads from the main stem were randomly marked to evaluate FHB resistance. Although the number of heads investigated varied depending on the genotype and year, at least 64 spikes were evaluated per genotype in each year. The disease incidence (DI) was calculated as the percentage of heads with visible symptoms for two independent experiments (in 2010 and 2011 cropping seasons). Diseased spikelets were counted, and the mean percentage of diseased spikelets (PDS) was calculated at 7, 14, 21, and 28 days after inoculation.

To determine type II resistance, 5 μl of a macroconidial suspension (200 macroconidia/ μl) was injected into two opposite florets

of a spikelet at early anthesis, and the spikes from the main stem of approximately 200 plants per genotype were randomly marked and used for inoculation. The inoculated spikes were covered with plastic bags for 3 days to maintain high relative humidity. At least 77 spikes per genotype were evaluated in each year. For each genotype, DI and PDS were recorded (including the inoculated spikelets) on a 0 (no disease) to 1 (100% infected spikelets) scale (with increments of 0.1) at 7, 14, 21, and 28 days after inoculation. All inoculated spikes were harvested and processed individually by hand to avoid loss of seriously diseased grains. *Fusarium*-damaged kernels (FDK) were distinguished by their obviously shriveled shape, light weight, and chalky white (or occasionally pink) color. These parameters were also evaluated from 70 randomly selected uninoculated spikes in each plot from each experiment (2010 and 2011 growing seasons).

The area under the disease progress curve (AUDPC) was calculated using the PDS collected from each plant, and the AUDPC value for each genotype was calculated from the mean of all the observed plants using a previously described equation (2).

Measurement of photosynthetic parameters and yield components.

Ten plants of each genotype (L661 and L699) were randomly selected from among the spray inoculation, point inoculation, and control plants. Net photosynthetic rates and related physiological parameters of each plant were measured twice at 7 days and 21 days after inoculation, respectively. The mean value of three measurements per plant represented a replicate sample, and the mean from all 10 plants represented the value for a given genotype at a given time point. The measurements were made in the middle of the flag leaf (3). P_n , G_s , and C_i were measured using a Li-6400 photometer (LiCor, Lincoln, NE), with air temperatures from 21 to 24°C and vapor pressure deficits (VPD) from 0.55 to 0.65 kPa. The actinic light intensity was 1,000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Each measurement took approximately 30 s.

The seeds of the plants marked for photosynthetic measurement were harvested individually by hand. The number of seeds per spike and the number of infected seeds per spike were counted, and the percentage of infected seeds was calculated. After the seeds were dried in an oven, grain weight per spike and 1000-grain weight were determined based on the mean of the 10 marked spikes.

Statistical analysis. Significant differences in the mean disease severity, physiological parameters, and yield traits of randomly selected plants from three replications between the two wheat lines (L699 and L661) were determined separately for each inoculation method in each year using an independent samples *t* test with IBM SPSS Statistics 19 software (SPSS Inc., Chicago, IL). In addition, significant differences in the mean physiological parameters and yield traits between both the point- and spray-inoculated and the uninoculated plants of the same genotypes were also determined by the same program.

Results

FHB resistance of host plants. All wheat lines showed visible FHB symptoms after either point or spray inoculation. The PDS after 7 and 21 days, DI, AUDPC, and FDK are shown in Table 1. In two independent experiments, *t* test of the inoculated plants randomly selected from three replications showed that L699 had significantly lower disease severity than L661, and the differences between L699 and L661 for all measurements of FHB infection were significant at ($P < 0.01$). More importantly, some L699 plants did not show obvious symptoms at the inoculation point, whereas all inoculated spikelets of L661 had visible symptoms after 14 days.

Effects of FHB on photosynthetic parameters. Photosynthetic traits are usually evaluated using comprehensive photosynthetic parameters such as P_n , G_s , and C_i . The data for these parameters are shown in Figure 1. P_n is the most important photosynthetic parameter and is most sensitive to stresses such as disease infection. The differences in the photosynthetic parameters between uninoculated L699 and L661 wheat lines were not significant at the $P = 0.05$ level in the two independent experiments at both 7 days and 21 days after flowering. Spray-inoculated L699 plants showed a significant ($P < 0.01$) decrease in P_n at 7 days in 2010 and at 7 and 21 days in 2011 compared with uninoculated plants, whereas P_n was significantly

Table 1. Disease incidence (DI), percentage of diseased spikelets (PDS), area under the disease progress curve (AUDPC), and *Fusarium*-damaged kernels (FDK) evaluated by inoculating wheat plants with *F. graminearum* in field experiments in 2010 and 2011^a

Parameter	Year	Point inoculation		Spray inoculation	
		L661	L699	L661	L699
PDS1 ^b	2010	0.096 ± 0.002	0	0.002 ± 0.001	0
	2011	0.138 ± 0.004	0	0.004 ± 0.002	0
PDS2 ^c	2010	0.283 ± 0.013	0.078 ± 0.005**	0.075 ± 0.007	0.048 ± 0.004**
	2011	0.357 ± 0.017	0.085 ± 0.006**	0.145 ± 0.012	0.034 ± 0.007**
AUDPC	2010	5.829 ± 0.183	1.248 ± 0.083**	2.089 ± 0.126	1.196 ± 0.078**
	2011	6.731 ± 0.176	1.487 ± 0.057**	2.394 ± 0.166	0.974 ± 0.041**
PDK	2010	0.097 ± 0.008	0.062 ± 0.008**	0.043 ± 0.005	0.020 ± 0.002**
	2011	0.162 ± 0.018	0.076 ± 0.006**	0.059 ± 0.007	0.016 ± 0.003**
DI	2010	1	0.876	0.781	0.660
	2011	0.983	0.934	0.834	0.592

^a In point inoculation experiments, 77 L661 spikes and 105 L699 spikes in 2010, and 89 L661 spikes and 94 L699 spikes in 2011, were observed. In spray inoculation experiments, 64 L661 spikes and 103 L699 spikes in 2010, and 72 L661 spikes and 81 L699 spikes, were observed. The data are presented as the mean ± SE; ** = significantly different from L661 at $P < 0.01$.

^b PDS at 7 days after inoculation.

^c PDS at 21 days after inoculation.

Fig. 1. *Fusarium* head blight inoculation via both spraying and injection of *Fusarium graminearum* had different effects on the photosynthetic parameters of wheat plants in two experiments conducted in 2010 and 2011. Net photosynthetic rate (P_n) in 2010 (A) and 2011 (B); stomatal conductance (G_s) in 2010 (C) and 2011 (D); intercellular CO_2 concentration (C_i) in 2010 (E) and 2011 (F). The data are presented as the means ± SE ($n = 10$). * = significantly different from uninoculated plants of the same genotype at $P < 0.05$; ** = significantly different from uninoculated plants of the same genotypes at $P < 0.01$; † = significantly different from L661 inoculated with same method at $P < 0.05$; ‡ = significantly different from L661 inoculated with same method at $P < 0.01$.

lower ($P < 0.01$) in point-inoculated L699 compared with uninoculated L699 plants at all time points investigated (Fig. 1A and B). Although the change in P_n in L661 plants was initially similar to that observed for L699, both spray and point inoculation had little effect on the P_n of L661. The reduction in P_n observed with spray inoculation in 2010 was not significant ($P = 0.461$). Inoculation had contrasting effects on P_n between L661 and L699; the P_n of L699 was significantly ($P < 0.05$) lower than that of L661 at 7 days in both 2010 and 2011 and at 21 days in 2011.

G_s also plays a key role in plant adaptation to changing environmental conditions and to infection. The G_s values were significantly ($P < 0.01$) lower at 7 days after inoculation in both spray- and point-inoculated L699 plants than in uninoculated plants in the two independent experiments, whereas changes in L661 in response to inoculation were not significant at the same time point (Fig. 1C and D). In L699, both spray and point inoculation led to lower G_s values compared with the uninoculated L699 plants in both experiments. In L661, inoculation also reduced G_s ; however, the reduction was very small compared with that observed in L699 (Fig. 1C and D). In both experiments, the G_s value at 7 days after inoculation was significantly lower in L699 than in L661, regardless of whether inoculation was performed via spraying or injection (Fig. 1C and D). Thus, G_s in L699 was more sensitive to infection than G_s in L661.

C_i is balanced by both P_n and G_s ; thus, a comparison of the change in C_i with the changes in both P_n and G_s between genotypes may provide useful information regarding how photosynthetic indices respond to disease stress. C_i of the inoculated L661 plants was significantly ($P < 0.05$) higher compared with that of uninoculated plants at 7 days after inoculation; however, the change in inoculated L699 plants was not significant (with the exception of L699 plants inoculated by injection in 2010) (Fig. 1E and F). The effects of *F. graminearum* infection on C_i in the two genotypes at 21 days after inoculation were similar, although there were some differences between the two inoculation methods.

Effect of FHB on yield components. Yield components such as 1000-grain weight and total grain weight per spike are usually useful parameters for determining responses of different genotypes to disease infection. Uninoculated L699 and L661 plants had similar 1000-grain weight and grain weight per spike in the two experiments (Fig. 2). In both experiments, spray inoculation caused a significant

($P < 0.05$) reduction in 1000-grain weight and grain weight per spike in L661 plants but not in L699 plants (Fig. 2). Although point inoculation led to a significant decrease in 1000-grain weight and grain weight per spike in both L661 and L699, L661 had a greater reduction in these yield components than L699, and L699 had significantly ($P < 0.01$) higher 1000-grain weight and grain weight per spike than L661 in the point inoculation experiment (Fig. 2). FHB infection by either spray or point inoculation had a greater negative effect on the yield components in L661 compared with L699.

Discussion

In the present study, we aimed to characterize the effects of *F. graminearum* infection on photosynthetic and yield traits between two genotypes with contrasting levels of FHB resistance. We also evaluated the physiological cost of host FHB resistance in wheat. Our results show that FHB infection had a smaller effect on photosynthetic parameters and a larger negative effect on yield components in the FHB-susceptible genotype than in the resistant genotype, suggesting that host FHB resistance has a greater physiological cost and a more modest yield cost.

L699 had significantly ($P < 0.01$) lower PDS (at 7 and 21 days after FHB inoculation), DI, AUDPC, and FDK in both experiments than L661, suggesting that L699 had stronger resistance of both type I and type II than L661. Thus, L699 was employed as the resistant genotype and L661 was employed as the susceptible genotype to determine the differential effects of FHB infection on photosynthetic parameters and yield components.

FHB infection affects photosynthetic parameters such as P_n and G_s . Theoretically, the physiological cost of host FHB resistance can be measured by the changes in the photosynthetic parameters after FHB infection. Unfortunately, studies on the physiological cost of FHB resistance are still scarce. It has been shown that *F. graminearum* infection changes the allocation of carbon to various organs (8). Thus, the photosynthetic parameters in flag leaves may be altered when spikes are attacked by *F. graminearum*. Although the location of the *F. graminearum* attack is the spike, this attack would alter the photosynthetic activity via feedback regulation mechanisms. Therefore, differences in the photosynthetic parameters may reveal differences in the costs of FHB resistance in different genotypes after inoculation with *F. graminearum*.

Fig. 2. Inoculation with *Fusarium graminearum* had a more negative effect on the yield components of susceptible wheat plants (L661) than resistant (L699) plants. (A) 1000-grain weight. (B) Grain weight per spike. The data are presented as the means $\pm$ SE. * = significantly different from uninoculated plants of the same genotype at $P < 0.05$; ** = significantly different from uninoculated plants of the same genotypes at $P < 0.01$; † = significantly different from L661 inoculated with same method at $P < 0.05$; ‡ = significantly different from L661 inoculated with same method at $P < 0.01$.

In the two independent experiments (2010 and 2011), P_n , the most important parameter of photosynthesis, decreased significantly ($P < 0.01$) in the FHB-resistant line L699 within 7 days after spray and point inoculation, whereas in L661, the reduction in P_n was trivial. A previous expression profiling study of the soybean response to infection by *Pseudomonas syringae* showed similar results, i.e., infection led to a greater reduction in photosynthesis during the resistance response than during the susceptible response (37). This result suggested that host FHB resistance may be associated with a P_n cost.

Because stomata play a vital role in the regulation of gas exchange and water loss, stomatal function is likely related to physiological processes such as photosynthesis and respiration as well as the ability of plants to cope with pathogen infection (25). Therefore, G_s -mediated plant disease resistance has been proposed as the most common form of nonhost resistance associated with plant fitness (6,26,33). *F. graminearum* infection by either spraying or injection resulted in a significant ($P < 0.01$) decrease in G_s in the FHB-resistant line L699, but not in the FHB-susceptible line L661, within 7 days of inoculation. G_s and the activity of the photosynthetic apparatus are the two main factors influencing P_n (19). An analysis of the disease data and the photosynthetic parameters suggests that P_n in L661 may be regulated mainly by stomatal factors; however, P_n in L699 is not. This actively regulated physiological mechanism has been considered as part of the host resistance mechanism mediated by host resistance genes (33).

In this study, L661 and L699 had similar values for physiological parameters and yield components under the control conditions (without inoculation) due to the similar genetic background of these lines. Indeed, only 39 (2.26%) of the 1,726 loci amplified by 781 SSR primers were polymorphic between the two lines (unpublished data). In L699, the point-inoculated plants showed obvious reductions in P_n and G_s at 7 and 21 days after inoculation compared with the uninoculated plants, whereas the corresponding changes were very trivial in L661. In addition, the spray-inoculated L699 plants also showed reduced P_n and G_s at both 7 and 21 days after inoculation compared with the uninoculated plants. Thus, changes in P_n and G_s between the two genotypes suggested a large physiological cost for host FHB resistance, especially at 7 days after *F. graminearum* infection. At this time point, both P_n and G_s were significantly ($P < 0.05$) lower in the FHB-resistant line L699 compared with uninoculated L699, whereas the decrease was trivial in L661.

In contrast, 1000-grain weight and grain weight per spike were sharply reduced for both the point- and spray-inoculated plants and the uninoculated control L661 plants, whereas in L699, the reductions were smaller than those in L661. Although *F. graminearum* infection of FHB-resistant L699 plants resulted in a decrease in photosynthetic parameter values, these plants maintained a higher yield. On the contrary, *F. graminearum*-infected FHB-susceptible L661 plants exhibited higher photosynthetic parameter values, although their yield was lower. This finding may be explained by alterations in the source-sink relationship (31). This result also further indicated that *F. graminearum* infection might activate the non-flag-leaf photosynthetic organs, such as the spike (19), which may serve as a “buffer” during abiotic stress (20). These findings suggest that FHB resistance has a more negative effect on 1000-grain weight and grain weight per spike and a less negative effect on photosynthetic parameters. Therefore, the cost of resistance may be higher in terms of photosynthesis than the cost in terms of yield.

Further analysis of the relationships among P_n , G_s , and C_i suggests that the reduced P_n in L699, which may be actively regulated (in contrast to passive stomatal regulation), may be an effective physiological mechanism for host FHB resistance. Therefore, the study of the relationship between photosynthetic parameters and yield components may facilitate the elucidation of the mechanism underlying resistance to FHB in wheat. In conclusion, we found that *F. graminearum* infection had greater effects on the photosynthetic parameters of flag leaves and weaker effects on the related yield components, which provides new insight into the consequences of FHB resistance.

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