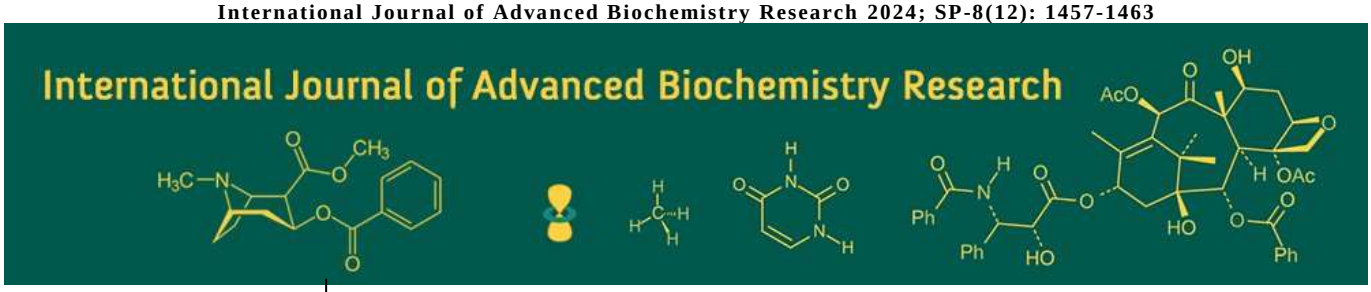

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Comparing the changes in physiological parameters in two rice genotypes due to infection with bakanae disease caused by *Fusarium fujikuroi*

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Abstract
Rice is a primary nutritional source for a significant portion of the global population. Despite notable advancements in rice production and productivity over the past five decades, a substantial portion of the annual yield is lost due to various biotic and abiotic stress factors. Among these, bakanae disease has emerged as a serious threat to rice cultivation. Stress factors significantly impact physiological parameters such as leaf gas exchange activities in rice plants. This study investigated the effects of bakanae disease on leaf gas exchange activities in two contrasting rice genotypes, one resistant and the other susceptible. The results revealed that pathogen inoculation inhibited germination, increased plant height in the susceptible genotype, while the resistant genotype remained largely unaffected. Initially, photosynthesis rates increased in inoculated plants but subsequently declined compared to control plants, with a more pronounced reduction observed in the susceptible genotype. Similar trends were observed in transpiration rates and stomatal conductance. In control plants of both genotypes, no significant changes in these parameters were observed over time. Further research is essential to elucidate the mechanisms underlying these physiological responses, which could provide valuable insights into the complex nature of host resistance.

Keywords: Rice cultivation, Bakanae disease, leaf gas exchange activities, abiotic and biotic stress

Introduction
Rice (*Oryza sativa* L.) is the staple food crop for about half of the population of world. It is a major source of food along with wheat and maize throughout the world. Despite the significant increase in rice production and productivity witnessed in the last five decades, a significant proportion of rice production is lost every year due to various abiotic (*viz*., high or low temperature, drought and salinity) and biotic (*viz*., pathogen infection and insect herbivory) stress factors (Kreye *et al*., 2009; Devine, 2009) [27, 14]. Diseases like bacterial blight (*Xantomonas oryzae* pv. *oryzae*), sheath blight (*Rhizoctonia solani*), blast (*Magnaporthe oryzae*), brown spot (*Biplolaris oryzae*), bakanae or foot rot (*Fusarium fujikuroi*), stem rot (*Sclerotium oryzae*) and false smut (*Ustilaginoidea virens*) are of major economic significance. Among these bakanae disease caused by *Fusarium fujikuroi* is emerging as a serious threat to production of rice (Singh and Sunder, 2012) [40]. Bakanae disease was first identified during 1828 in Japan. In India, Thomas (1931) [44] described it as foot rot disease. Hori (1898) [21] first time demonstrated the fungus *Fusarium heterosporium* Nees induced the bakanae symptom in rice plants. The disease is incited by *Fusarium fujikuroi* Nirenberg (Anamorph) (Teleomorph: *Gibberella fujikuroi* Sawada, Wollen worth). This disease is emerging as a major threat to rice cultivation in India, Japan, Taiwan and Thailand (Webster and Gunnell, 1992; Bashyal *et al.*, 2016; Saremi, 2005; Kini *et al.*, 2002) [46, 3, 39, 26]. It causes 20 to 50% crop loss in Japan (Ito and Kimura, 1931) [23], 3.7 to 14.7% in Thailand (Kanjanasoon, 1965) [25]. In India, the prevalence and incidence of bakanae disease has been reported very recently particularly in basmati rice cultivars (Bashyal *et al*., 2014; Gupta *et al*., 2014) [2, 20]. The yield losses ranging from 15-25% have been reported from UP, Assam, AP, TN, Haryana and Punjab states of India (Pavgi and Singh, 1964; Rathaiah *et al*., 1991; Pannu *et al*., 2012; Sunder *et al*., 2014) [32, 34, 31, 42]. The disease produces different kind

of symptoms including seedling blight, root rot, crown rot, stunting, and the most classical symptoms of etiolation, hypertrophy effect or excessive elongation of infected plants, foot rot, seedlings rot, grain sterility, grain discoloration. Pathogen infection impacts plants photosynthesis by causing leaf yellowing, which leads to a reduction in chlorophyll content and decreases the photosynthetically active leaf area. This results in the down-regulation of CO2 fixation rates in the remaining green tissues (Bingham *et al*., 2009) [7]. The decline in photosynthetic efficiency has been linked to several factors, including self-shading, stomatal limitations, and other metabolic disruptions (Boote *et al*., 1983; Johnson, 1987; Bowden *et al*., 1990; Bassanezi *et al*., 2002) [8, 27, 10, 4]. Consequently, the loss of photosynthetic capacity under disease conditions has been strongly associated with reduced plant growth and yield (Schwartz *et al*., 1981; Widin and Schipper, 1981; Spitters *et al*., 1990) [50, 47, 41]. Genotypic variation in rice has long been reported for WUE, measured either as intrinsic WUE, i.e. the ratio of net photosynthesis rate to stomatal conductance (A/gs) or by carbon isotope discrimination (Δ) (Samejima, 1985; Dingkuhn *et al*., 1991) [35, 16]. Dingkuhn *et al*. (1991) [16] found that Δ was highly correlated with in situ measurements of A/gs. Varietal differences in stomatal response to decreasing leaf water potential have also been reported (Dingkuhn *et al*., 1989) [15]. Comparing WUE values of tropical japonica with those of indica cultivars based on leaf gas exchange rates (A/E) under irrigated conditions, Peng *et al*. (1998) [33] found that indica cultivars had generally higher E than tropical japonica lines, and the A/E ratio was 25–30% higher for the tropical japonica than for indica. Moreover, lower Δ values in the tropical japonica compared to indica confirmed the observed differences in A/E. Impa *et al*. (2005) [22] confirmed the relationship between gravimetrically determined WUE and Δ among rice germplasm, indicating that WUE is genetically variable in rice and hence can be exploited through breeding. Plants infected with pathogens exhibit increased respiration rates and reduced light-use efficiency, alongside a decline in photosynthetic activity. Pathogen infection causes the down-regulation of most genes related to photosynthesis and chloroplast synthesis, as well as their transcriptional activity (Bozso, 2009) [11]. During the grain-filling period, the majority of carbon stored in mature rice grains is derived from CO2 assimilation, with the flag leaf serving as the primary site of photosynthesis (Yoshida, 1981; Murchie *et al*., 1999) [49, 30]. Any reduction in the photosynthesis rate of the flag leaf during this critical period can significantly limit grain yield (Dingkuhn *et al*., 1989) [15]. Plants possess several mechanisms to regulate water use with water availability. Regulation of diffusive conductances is known to affect WUE by modulating both transpiration and photosynthesis rates. Regulation of photosynthetic rates also strongly affects WUE. The fractionation of carbon isotopes during photosynthesis depends on biochemical and physical phenomena, mainly associated with CO_2 diffusion and carboxylation reactions. In fact, the depletion of the heavy isotope 13 C in plant tissues, with respect to its abundance in the atmospheric CO_2, is directly related to the ratio of Cc to atmospheric CO_2 concentration (Ca); this ratio represents the equilibrium between the availability and the requirement of CO_2 at the leaf level, that is the set point for gas exchange activity (Ehleringer, 1993) [18]. Understanding the physiological changes of a pathogen's host during the infection process can help to predict the effects of diseases on crop growth and yield (Bastiaans, 1993; Boote *et al*., 1980) [6, 9]. Photosynthesis, a major driver of crop yield, is the key physiological process affected by foliar pathogens (Bassanezi *et al*., 2002; Bastiaans, 1991; Dallagnol *et al*., 2011; Debona *et al*., 2014; Resende *et al*., 2012) [4, 5, 12, 13, 35]. Therefore, the proper assessment of the photosynthetic performance of plants under pathogen infection can provide crucial insight into the mechanisms underlying their interactions, with the potential for identifying novel strategies for crop protection (Rolfe and Scholes 2010) [37]. There is an imminent need to investigate the detailed physiological functions under bakanae infection for better understanding of plant physiology during pathogen infection in the rice genotypes having varying degree of resistance against the pathogen. The present state of knowledge on photosynthetic leaf gas exchange traits in bakanae infected rice is preliminary and the responses of some of the important gas exchange characteristics including stomatal conductance to CO_2, leaf transpiration rate and internal CO_2 concentration have not yet been investigated in detail during bakanae infection in rice. The present study has, therefore, been designed to study the impact of bakanae infection on various physiological parameters related to leaf gas exchange activities in order to understand dynamic responses in leaf assimilation physiology in rice genotypes having contrasting response to disease infection.

Material and Methods

a) Pathogen and plant material: The experiment was conducted at division of Plant Pathology, ICAR- Indian Agricultural Research Institute, New Delhi. *Fusarium fujikuroi*, the causative pathogen, was isolated and purified from infected field samples. The purified pathogen culture was then mass-produced on autoclaved sorghum in a BOD incubator maintained at 25±2 ºC. The study utilized two rice genotypes with contrasting levels of disease resistance: PB1121 (susceptible) and GP50 (resistant).

b) Inoculum preparation and inoculation: The pathogen inoculum was prepared by mixing the sorghum-based pathogen culture with distilled water and manually mashing it. The mixture was then filtered through muslin cloth, and the spore concentration was adjusted to 10^6 spores per milliliter. Seeds of both genotypes were inoculated by immersing them in the spore suspension for 24 hours. A separate set of seeds was immersed in distilled water for 24 hours to serve as a control. Following inoculation, the seeds were sown in plastic pro trays filled with autoclaved soil. All treatments were conducted in triplicate.

c) Plant growth and disease assessment: After sowing the plants were kept under glass house conditions. The germination percentage in each treatment was recorded seven days after inoculation. The disease scoring was done at 7, 14 and 21 days post inoculation and disease incidence was calculated. The average height of plants was also measured at every interval *viz.* 7, 14 and 21 days post inoculation. Each observation was taken in three replications.

d) Evaluation of physiological changes: The IRGA LI-6400XT Portable Photosynthesis System was used to record the physiological parameters. The physiological

parameters such as Transpiration rate, stomatal conductance, photosynthesis rate and internal CO_2 concentration were recorded as per manufacturer's protocol. To setup the IRGA instrument, the sensor head was connected to the console by uncoiled cable and the CO_2 cartridge was attached. Before using the instrument, calibration was done and before each observation zeroing was done (Evans and Santiago, 2014) [19]. The leaf area standard was set 2 ×3 cm leaf chamber, light source (6400-02B LED light) and the flow rate of 300-400 µmol m^{-2} s^{-1}. The CO_2 entering the leaf chamber was 415 µmol mol^{-1} that maintains 400 µmol mol^{-1} in the leaf chamber head (Mujawamariya *et al.*, 2018) [29]. The leaf was securely placed in the head chamber, ensuring there were no leaks. Physiological parameters were allowed to stabilize to minimize variability caused by environmental fluctuations. Measurements were taken once the values for photosynthesis and stomatal conductance reached a steady state.

Transpiration rate

The rate of transpiration depicted as E is calculated as differences in H2O concentration, based on the readings of the IRGAs in the reference and sample circuits, as per following formula: $E = F (W_e-W_o)/L_a$. Where, W_e and W_o are the H2O mole fraction at the chamber entrance and output respectively; F-flow and L_a- the leaf area surface (m^2).

Stomatal conductance

The transpiration rate (E) and relative humidity in the substomatal cavity is used to calculate the stomatal conductance to water vapour (gs) by using the first Fick's law of diffusion (Douthe *et al.*, 2018) [17], as per following formula: $gsw = E/(Wi– Wa)$. Where, Wi -H_2O in the substomatal cavity, Wa- H_2O in the atmosphere (chamber head) and E- rate of transpiration.

Photosynthesis rate

The difference of CO_2 and water flux between reference and sample circuit is measured and is used to calculate rate of photosynthesis (A_N) or rate of CO_2 assimilation (Douthe *et al.*, 2018; von Caemmerer and Farquhar, 1981) [17, 45].

$$A_N = u_e \frac{C_e - C_o}{L_a} - C_o EAn$$

Where, C_e and C_o are the CO_2 mole fraction at the chamber entrance and output, respectively; u_e is the incoming flow air (mol air s^{-1}), La is the leaf area surface (m^2), and E is the transpiration rate (mol H2O m^{-2} s^{-1}).

Internal CO_2 concentration: Stomatal conductance is expressed as gsw in terms of H_2O and gsc in terms of CO_2. The CO_2 concentration in the substomatal cavities (Ci) is calculated from CO_2 concentration in the atmosphere, rate of photosynthesis and stomatal conductance in terms of CO_2 by using following formula: $Ci = Ca – A_N/gsc$. Where, Ca is the atmospheric CO_2 (in chamber head) (Von Caemmerer and Farquhar, 1981) [45].

Statistical data analysis: The differences between treatment means for various growth and physiological parameters were analyzed using one-way ANOVA and the Student's t-test. A significance level of ($p< 0.05$ \) was used to determine statistical significance. The physiological data were analyzed using OPSTAT software.

Results and Discussion

Germination percentage and growth parameters: The germination percentage was assessed seven days after inoculation. The highest germination rate (93.33%) was observed in the control plants of the resistant genotype (GP50), while the lowest germination rate (78.67%) was recorded in the *Fusarium fujikuroi*-inoculated susceptible genotype (PB1121) (Table 1). No significant difference in germination was found between inoculated and non-inoculated plants of the resistant genotype, whereas a significant reduction in germination was observed in the inoculated plants of the susceptible genotype compared to its control. Similar results were reported by Yadav *et al.* (2020) [48], who found that Fusarium inoculation led to seed colonization, thereby inhibiting germination and reducing germination rates. Plant height was consistently highest in the inoculated plants of the susceptible genotype PB1121 across all time intervals compared to its control. A significant difference in plant height was observed between inoculated and non-inoculated PB1121 plants, attributed to stem elongation induced by pathogen infection. In contrast, no significant difference in plant height was noted between inoculated and control plants of the resistant genotype GP50, as no disease symptoms were observed. Root length was significantly reduced in the pathogen-inoculated plants of PB1121 compared to its control, likely due to *Fusarium fujikuroi* infection causing tissue blockage and impaired root growth. However, no significant difference in root length was recorded between control and inoculated plants of the GP50 genotype (Table 1). These findings align with those reported by Yadav *et al.* (2020) [48].

Table 1: Germination percentage and different growth parameters of two rice genotypes (PB1121 and GP50) inoculated with *Fusarium fujikuroi* and control at different time interval

Treatment	Germination %	Plant Height (cm)			Root length (cm)		
		7 DPI	14 DPI	21 DPI	7 DPI	14 DPI	21 DPI
PB1121 (I)	78.67	19.67	25.33	27.67	5.33	7.67	8.33
PB1121 (C)	91.67	15.33	20.33	23.33	6.67	9.33	10.33
GP50 (I)	91.33	13.33	17.67	20.33	4.67	6.33	7.33
GP50 (C)	93.33	13.67	17.33	19.67	4.33	6.67	7.67
S.E. (m) ±	2.73	0.49	0.62	0.78	0.34	0.36	0.36
CD	8.21	1.47	1.86	2.34	1.02	1.08	1.08

Disease incidence and Area under Disease Progress Curve: Highest disease incidence was observed in the PB1121 inoculated with *Fusarium fujikuroi* at all-time intervals. At 21 DPI pathogen inoculated PB1121 plants

showed a disease incidence of 85.91%. Whereas no to very little disease was observed in pathogen inoculated GP50 plants (Fig. 1). At 21 DPI pathogen inoculated GP50 plants showed a disease incidence of 3.33%. No disease incidence was observed in the non-inoculated plants of both genotypes. After 21 days post inoculation highest AUDPC (885.88) was observed in pathogen inoculated PB1121 plants whereas at same time point an AUDPC of 23.34 was observed in pathogen inoculated GP50 plants (Table 2).

Table 2: Disease incidence and Area under Disease Progress Curve of two rice genotypes (PB1121 and GP50) inoculated with *Fusarium fujikuroi* and control at different time interval

Genotypes	Disease Incidence			AUDPC
	7DPI	14DPI	21DPI	
PB1121 (I)	29.78	68.71	85.91	885.88
PB1121 (C)	0	0	0	0
GP50 (I)	0	1.67	3.33	23.34
GP50 (C)	0	0	0	0
S.E. (m) ±	1.67	2.78	3.22	25.687
CD	5.00	8.34	9.66	77.061

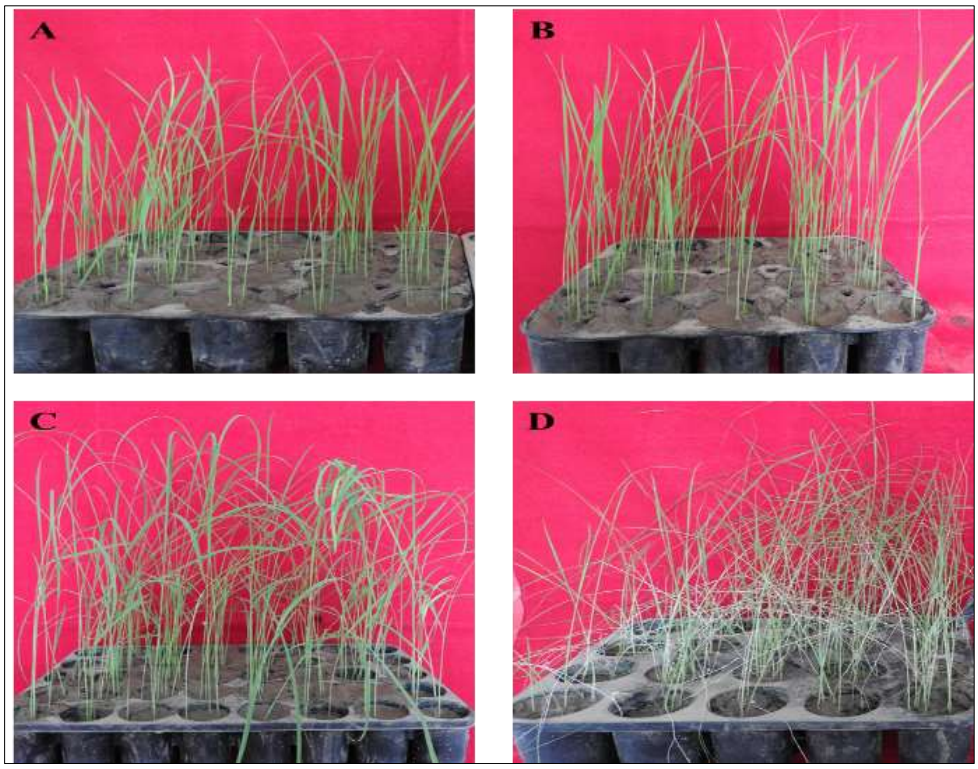

Fig 1: Two rice genotypes (PB1121 and GP50) showing contrasting reaction to *Fusarium fujikuroi* infection. Where, A= GP50 control, B= GP50 inoculated, C= PB1121 control and D= PB1121 inoculated

Physiological parameters: IRGA readings were taken at three different time intervals *viz.* 7, 14 and 21 days post inoculation in between 10-11 a.m. and on the basis of that different physiological parameters such as photosynthesis rate, transpiration rate, stomatal conductance, and internal CO_2 concentration etc. were measured in inoculated and control plants of both genotypes (GP50 and PB1121).

Photosynthesis rate: At 7 days post-inoculation (DPI), the rate of photosynthesis was initially higher in inoculated plants of both genotypes; however, it later declined in these plants compared to their respective controls. The net carbon assimilation rate dropped significantly in the pathogen-inoculated susceptible genotype (PB1121) compared to the control, with the lowest photosynthesis rate observed at 21 DPI (5.27 µmol m^{-2} s^{-1}) in the inoculated PB1121 plants (Fig. 2 A), corresponding to the severity of the disease. In GP50, the photosynthesis rate initially showed a slight increase before declining, but the reduction was not as pronounced as in the susceptible genotype. No significant changes in photosynthesis were observed in the non-inoculated plants of either genotype. These findings are consistent with the results reported by Kumar *et al*. (2013) [28] and Tatagiba *et al*. (2015) [43]. The reduced photosynthesis rate in inoculated plants is likely due to decreased activity of Rubisco and carbonic anhydrase, reduced mesophyll conductance to CO_2 diffusion, increased respiratory and photorespiratory activities, and biochemical damage (Ribeiro *et al*., 2004) [36].

Stomatal conductance: The stomatal conductance was observed to be decreasing in inoculated plants as compared to their non-inoculated counterparts in both genotypes. However the rate of decrease was low in resistant genotype whereas, it was very high in susceptible genotype. The lowest stomatal conductance activity was recorded in pathogen inoculated PB1121 plants at 21 DPI (0.14 mol m^{-2} s^{-1}) (Fig. 2 B). No significant difference was observed in

control plants of both resistant and control genotypes. Our findings are in accordance with the findings of Kumar *et al*., 2013 [28].

Transpiration rate: The transpiration rate was initially observed to increase in pathogen-inoculated plants compared to their non-inoculated counterparts at 7 DPI. However, it began to decline in inoculated plants relative to their control counterparts in both resistant and susceptible genotypes. The reduction in the resistant genotype was minimal, whereas the susceptible genotype showed a significant and rapid decline. The lowest transpiration rate was recorded at 21 DPI (0.26 mmol m^{-2} s^{-1}) in the inoculated susceptible genotype. No significant changes in transpiration rate were observed in the control plants of either genotype (Fig. 2 C). These findings align with previous studies by Kumar *et al*. (2013) [28], Alves *et al.* (2011) [1], and Resende *et al.* (2012) [15].

Internal CO_2: Highest internal CO_2 (275 µmol m^{-2} s^{-1}) was observed in PB1121 inoculated plants at 21 DPI. The internal CO_2 activity was initially decreasing in inoculated plants but it was reported to increase at later stages. In control plants no significant changes were observed in both genotypes (Fig. 2 D). Tatagiba *et al* (2015) [43] also observed similar results in their experiment.

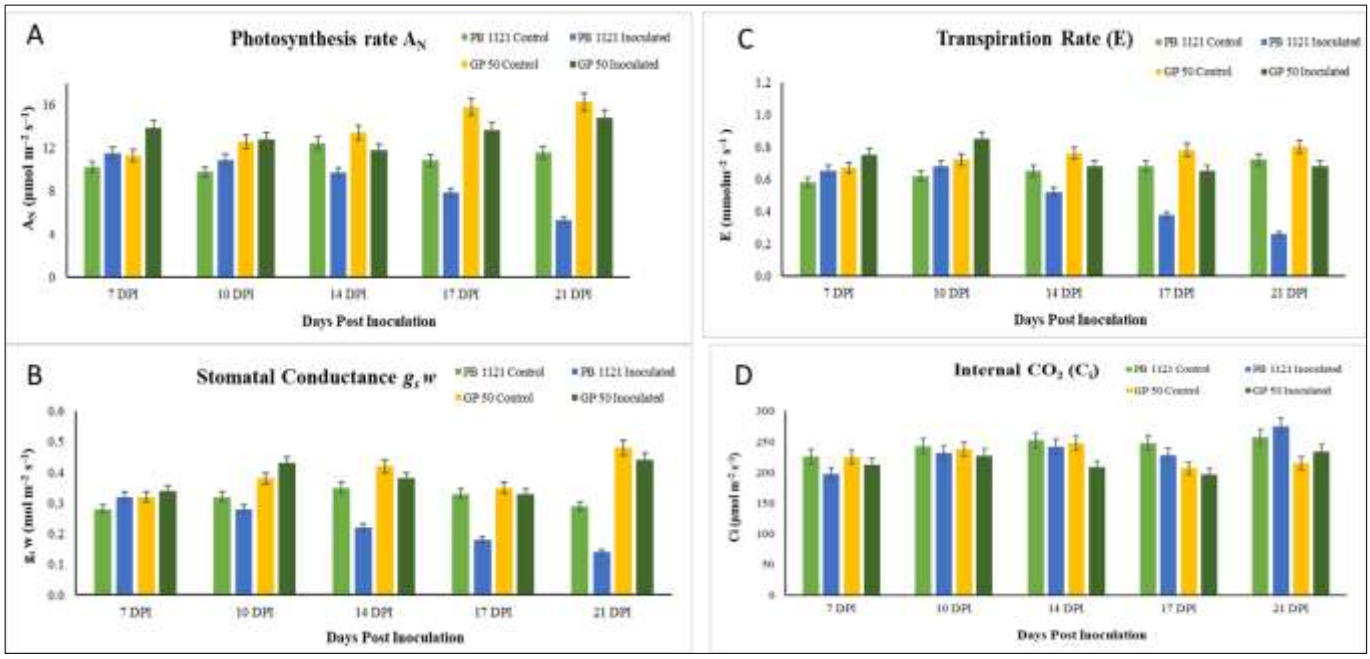

Fig 2: Physiological parameters of two rice genotypes (PB1121 and GP50) inoculated with *Fusarium fujikuroi* and control at different time interval. A: Photosynthesis rate; B: Stomatal Conductance; C: Transpiration Rate; D: Internal CO_2.

Conclusions

The study findings indicate that disease severity significantly impacts the leaf gas exchange activities of plants. Genotypes with differing responses to pathogen infection exhibit distinct physiological changes when challenged by the pathogen. Infected plants generally experience a decline in the photosynthesis rate or net carbon assimilation, attributed to various underlying factors. However, in resistant genotypes with little to no disease, these factors have minimal impact, resulting in no significant changes. Similarly, other physiological activities such as transpiration rate, water use efficiency, internal CO_2 concentration, and stomatal conductance are affected differently based on the genotype's susceptibility to the pathogen.

Fututre Scope

Further studies are required to gain a deeper understanding of the mechanisms underlying each physiological parameter and the factors influencing these processes. Such research could provide valuable insights into the host's defense mechanisms and aid in developing more robust resistance sources.

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Conflict of Interest: None.

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