

Leaf photosynthetic characteristics and photosystem II photochemistry of rice (*Oryza sativa* L.) under potassium-solubilizing bacteria inoculation

M. YAGHOUBI KHANGHAHI*, H. PIRDASHTI*, H. RAHIMIAN**, G.H. NEMATZADEH***, M. GHAJAR SEPANLOU#, E. SALVATORI##, and C. CRECCHIO####, +

Department of Agronomy, Genetics and Agricultural Biotechnology Institute of Tabarestan and Sari Agricultural Sciences and Natural Resources University, 9th km of Farah Abad Road, 4818168984, Sari, Māzandarān, Iran*

Department of Plant Pathology, Sari Agricultural Sciences and Natural Resources University, 9th km of Farah Abad Road, 4818168984, Sari, Māzandarān, Iran**

Department of Plant Breeding, Genetics and Agricultural Biotechnology Institute of Tabarestan and Sari Agricultural Sciences and Natural Resources University, 9th km of Farah Abad Road, 4818168984, Sari, Māzandarān, Iran***

Department of Soil Sciences, Sari Agricultural Sciences and Natural Resources University, 9th km of Farah Abad Road, 4818168984, Sari, Māzandarān, Iran#

Department of Environmental Biology, Sapienza University of Rome, Piazzale Aldo Moro 5, 00185 Rome, Italy##

Department of Soil, Plant and Food Sciences, University of Bari Aldo Moro, Via Amendola 165/a, 70125 Bari, Italy####

Abstract

The current research was performed to investigate the effects of three potassium-solubilizing bacteria (KSB) strains (*Pantoea agglomerans*, *Rahnella aquatilis*, and *Pseudomonas orientalis*) on leaf photosynthetic characteristics in rice (*Oryza sativa* L. cv. Pajohesh). A pot and a field experiment were conducted in a paddy field. The results indicated that the KSB inoculums significantly enhanced chlorophyll (Chl) *a*, Chl *a+b*, SPAD value, and stomatal conductance as compared to the control in both experiments, especially when applied along with half the recommended dose of the potassium chemical fertilizer. KSB inoculations, alone or combined with K fertilizer, significantly increased the value of photochemical quenching, photosynthetic electron transport rate, and the effective quantum efficiency as compared to the control. In conclusion, these native KSB strains could be used as inoculants to reduce consumption of K chemical fertilizer and improve the efficiency of photosynthesis for rice production under the flooding irrigation conditions.

Additional key words: chlorophyll florescence; grain yield; photosynthetic pigments; potassium uptake; potassium utilization.

Introduction

Rice (*Oryza sativa* L.) is one of the principal food crops worldwide. Globally, around 163 million hectares of rice paddy field were cultivated in 2016. Asia accounts for 90% of global rice production and consumption and a paddy production of nearly 678 million tones (FAO 2016). Iran is also an important area for rice cultivation with a total rice production of 2.9 million tones, about 40% of it is

produced in Mazandaran province in northern Iran (FAO 2016, Yaghoubi Khanghahi *et al.* 2018a).

Rice growth and productivity depends considerably on several factors, especially soil fertility and soil nutrient contents (Yaghoubi Khanghahi *et al.* 2018b). Potassium (K) is an essential nutrient to improve rice growth and grain yield (Carmes Filho *et al.* 2017). K also plays key roles to maintain stronger photosynthetic ability with high resistance to photoinhibition and to keep PSII reaction center

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*Corresponding author; e-mail: carmine.crecchio@uniba.it

Abbreviations: Chl – chlorophyll; ChlF – chlorophyll fluorescence; DAT – days after transplanting; ETR – electron transport rate; F – steady-state fluorescence; F_0 – minimal fluorescence yield of the dark-adapted state; F_0' – minimal fluorescence yield of the light-adapted state; F_m – maximal fluorescence yield of the dark-adapted state; F_m' – maximal fluorescence yield of the light-adapted state; F_v – variable fluorescence; F_v/F_m – maximal quantum yield of PSII photochemistry; KSB – potassium solubilizing bacteria; NPQ – nonphotochemical quenching; q_L – coefficient of photochemical fluorescence quenching assuming that all reaction centers share a common light-harvesting antenna; q_N – nonphotochemical quenching coefficient; q_P – photochemical quenching coefficient; $Y_{(NO)}$ – quantum yield of regulated energy dissipation; $Y_{(NPQ)}$ – quantum yield of light-induced nonphotochemical quenching; Φ_{PSII} – effective quantum yield of PSII photochemistry.

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less damaged and a significantly higher net stomatal conductance in rice (Jia *et al.* 2008). Rice absorbs large quantities of K which is greater than any other essential nutrients, such as nitrogen (N) and phosphorus (P) (Krishna 2014). Average nutrient acquisition and accumulation by rice is around 22.2 kg N, 3.1 kg P, and 26.6 kg K per ton of grain yield (Krishna 2014).

K deficiency disrupts the leaf photosynthetic function and results in lower rates of net photosynthesis, stomatal conductance, Rubisco activity, and especially declines the grain yield in rice (Zhao *et al.* 2016). Evaluations of chlorophyll (Chl) fluorescence (ChlF) are used as a powerful tool for nondestructive testing of photosynthetic energy conversion efficiency in crops (Salvatori *et al.* 2014, Yaghoubian *et al.* 2016). This technique has been widely used to study the response of crops to environmental stimuli, such as effects of low K on the photosynthetic apparatus of crops both in a controlled environment and in the field (Zhao *et al.* 2016).

Nowadays, farmers usually use injudicious application of chemical fertilizers to overcome deficiency of nutrients and reach maximum agricultural productivity (de Souza *et al.* 2015). The global average of total consumption of N, P, and K fertilizers is 107 kg ha⁻¹ (Meena *et al.* 2017) and their use efficiency is approximately 30–60% for N, less than 20% for P, and 30–50% for K (Fageria *et al.* 2014). However, negligible application of K chemical fertilizer has been recorded due to lack of awareness of its importance in crop production and its high price as compared to other chemical fertilizers (Zhao *et al.* 2016, Meena *et al.* 2017). On the other hand, imbalanced or overdose use of chemical fertilizers has the adverse impacts on soil and water quality and food safety (Bakhshandeh *et al.* 2015). Therefore, interest has grown in ecofriendly and cost-effective agrotechnologies to enhance crop production and reduce the chemical fertilizers input while minimizing negative effects on the environment and food (Pii *et al.* 2016, Yaghoubi Khanghahi *et al.* 2018a). For this purpose, the utilization of plant growth-promoting rhizobacteria (PGPR) could be considered as a sound strategy in rice cultivation systems (Yaghoubi Khanghahi *et al.* 2018a). These beneficial bacteria, such as K-solubilizing bacteria (KSB) play an important role in nutrient solubilization, mobilization, mineralization, dissolving, and uptake of nutrients (Meena *et al.* 2017, Nath *et al.* 2017). The KSBs are able to convert the insoluble or mineral structural K compounds into an available form of K in soils (Nath *et al.* 2017). Direct and indirect mechanisms of PGPR are biological nitrogen fixation, organic matter mineralization, phytohormone productions, *e.g.*, auxins, cytokinins, and gibberellins; biological control against soil-borne pathogens, cellulose degradation, starch hydrolysis, production of hydrogen cyanide, antibiotic, siderophore, and certain volatile organic compounds (Pii *et al.* 2015, Meena *et al.* 2017). The majority of credible group of PGPR belongs to genera *Acinetobacter*, *Azadirachta*, *Azotobacter*, *Azospirillum*, *Bacillus*, *Burkholderia*, *Pantoea*, *Pseudomonas*, *Rahnella*, *Rhizobium*, *Serratia*, and *Streptomyces* sp. (Bakhshandeh *et al.* 2014, Scagliola *et al.* 2016, Yaghoubi Khanghahi *et al.* 2018c).

Research has focused on soil–plant–microbe interaction in recent decades (Meena *et al.* 2017). So far numerous bacterial species, mostly associated with the crop rhizosphere, have been tested and found to be beneficial for plant growth, yield, and crop quality, but there is no information about the effect of KSB inoculations (alone or combined with K chemical fertilizer) on photosynthetic pigments and ChlF parameters. Therefore, the major objective of the present study was to investigate the effects of three native KSB strains proposed by Yaghoubi Khanghahi *et al.* (2018b), *Pantoea agglomerans*, *Rahnella aquatilis*, and *Pseudomonas orientalis*, on leaf photosynthetic pigments, stomatal conductance, and ChlF parameters in rice plant. Our hypothesis is that the inoculation by native KSB strains is able to enhance significantly the photosynthetic performance of rice plants by raising the efficiency of K utilization, thus improving crop yield and concurrently reducing consumption of K chemical fertilizer.

Materials and methods

Three KSB strains of *P. agglomerans* (*Pa*), *R. aquatilis* (*Ra*), and *P. orientalis* (*Po*) were isolated from the paddy rhizosphere soil across Mazandaran province in northern Iran. The soil characteristics, isolation of KSB, their potassium solubilizing ability, and identification methods are fully described in Yaghoubi Khanghahi *et al.* (2018b). The current supplementary research was performed to measure their capabilities on photosynthetic performance and crop yield of rice plants. The levels of potassium fertilizer, commercial biofertilizer and KSBs inoculation applied in pot and field experiments are listed in the text table further (+: inoculation with KSBs, -: inoculation without KSBs).

The field experiment was conducted in a paddy field of Mazandaran province (Sari, located at 36°3'N, 53°04'E, altitude of 11 m below the average of sea level, with long-term annual precipitation mean of 780.7 mm and long-term annual temperature mean of 18.1°C) with Mediterranean climate conditions (according to Domarten classification), in a randomized complete block design (RCBD) with three replications. Nine square meter plots (3 × 3 m) were arranged and 25-d-old seedlings (about 20–25 cm in height) were transplanted in the plots at a spacing of 20 × 20 cm. In order to prevent water penetration through plots, a fixed distance of 100 cm was determined among plots. The chemical and physical properties of the soil (at a depth of 0–30 cm) are presented in Table 1S (*supplement*).

Pot experiment was performed in a completely randomized design (CRD), in pots filled with 6 kg of sterile soil. Rice seedlings (135) were used in the pot experiment (15 treatments × 3 replications × 3 seedlings per pot), and the total duration of the experiment was 121 d. Experimental soil was collected from rice growing area, where field experiment was conducted, and sterilized using an autoclave (high pressure at 103421 Pa, 121°C for 60 min, twice before use). The pots were kept outside and therefore the growing conditions were similar to the field experiment.

Commercial K biofertilizer (CB)	<i>Pseudomonas</i> <i>orientalis</i> (Po)	<i>Rahnella</i> <i>aquatilis</i> (Ra)	<i>Pantoea</i> <i>agglomerans</i> (Pa)	K chemical fertilizer	NP chemical fertilizers	Abbreviation
–	–	–	–	–	–	Control (–NPK)
–	–	–	–	–	100% N, 100% P	NP
–	–	–	–	50%	100% N, 100% P	NP½K
–	–	–	–	100%	100% N, 100% P	NPK
–	–	–	+	–	100% N, 100% P	NP + Pa
–	–	+	–	–	100% N, 100% P	NP + Ra
–	+	–	–	–	100% N, 100% P	NP + Po
+	–	–	–	–	100% N, 100% P	NP + CB
–	–	–	+	50%	100% N, 100% P	NP½K + Pa
–	–	+	–	50%	100% N, 100% P	NP½K + Ra
–	+	–	–	50%	100% N, 100% P	NP½K + Po
+	–	–	–	50%	100% N, 100% P	NP½K + CB
–	–	+	+	50%	100% N, 100% P	NP½K + Pa + Ra
–	+	–	+	50%	100% N, 100% P	NP½K + Pa + Po
–	+	+	–	50%	100% N, 100% P	NP½K + Ra + Po

Inoculants: The three KSB strains were grown in nutrient broth medium (NB, Merck, Germany; 8 g l⁻¹) by inoculating 100 µl of a 10⁸ CFU ml⁻¹ bacterial suspension in 2 l of NB medium under agitation at 100 × g on an orbital shaker (Model 3031; GFL, Germany) for 48 h at 30°C to a final density of 10⁷ CFU ml⁻¹. Rice seedlings (cv. Pajohesh, an improved cultivar) were inoculated with each bacterial suspension at room temperature (25°C) for 5 h (Bakhshandeh *et al.* 2017). Control rice seedlings were also treated in the same way with noninoculated NB medium before transplanting in the field and pot. In addition, a commercial K biofertilizer (formulated by Zist Fanavar Sabz Company, Iran) including two isolates of *Pseudomonas koreensis* and *P. vancouverensis* was tested to compare with the native KS bacteria.

Chemical fertilization: Based on the results of the soil test, urea (46% N) was used as N fertilizer equivalent to 160 kg ha⁻¹. P and K chemical fertilizers were added through triple superphosphate (46% P₂O₅) and potassium sulphate (44% K₂O) equivalent to 120 and 95 kg ha⁻¹, respectively, as basal fertilizer before transplanting. Two thirds of the urea fertilizer application were also added during a land preparation before planting, while the rest was applied 30 d after transplanting. A water depth of 3 cm was kept to all pots and plots from transplanting time until two weeks before harvest maturity.

Chlorophyll content: The relative Chl content (SPAD value), and Chl *a*, Chl *b*, and carotenoids (Car) contents were measured by a portable Chl meter (SPAD-502, Minolta, Japan), and by the method described by Porra (2002), respectively. Three rice seedlings were selected for measuring from each plot and pot (3 rice seedlings × 45 plots/pots = 135 rice seedlings). The youngest expanded leaves of each treatment were selected as the materials (*n* = 9 leaves). Measurements were made at the anthesis stage (62 d after transplanting, 62 DAT), from 10–13 h. The leaves surface temperature was around 27°C.

For Chl *a*, Chl *b*, and Car determinations, fresh samples of leaves (1.0 cm²) were extracted by incubation in methanol at room temperature for 24 h in darkness and determined at the visible wavelengths of 665.2 (A_{665.2}), 652.4 (A_{652.4}), and 470 (A₄₇₀) nm using a spectrophotometer (SPEKOL 1300, Analytic, Jena, Germany) (Yaghooubian *et al.* 2016). The contents of Chl *a*, Chl *b*, and Car were calculated by the following equations:

$$\text{Chl } a \text{ } [\mu\text{g ml}^{-1}] = 162.72 A_{665.2} - 9.16 A_{652.4}$$

$$\text{Chl } b \text{ } [\mu\text{g ml}^{-1}] = 34.09 A_{652.4} - 15.28 A_{665.2}$$

$$\text{Car } [\mu\text{g ml}^{-1}] = (1,000 A_{470} - 1.8 \text{ Chl } a - 85.02 \text{ Chl } b)/198$$

Chl fluorescence (ChlF) and stomatal conductance (g_s) were measured with the same leaves and times as for SPAD measurements. ChlF was measured by using a pulse amplitude modulated fluorometer (PAM-2500, Walz, Germany), as described by Genty *et al.* (1989). The samples were acclimated to dark for 30 min before the measurements. The leaf was then exposed to low intensity light [$< 0.1 \mu\text{mol}(\text{photon}) \text{ m}^{-2} \text{ s}^{-1}$, red light]. Afterwards, a saturating light pulse [$> 8,000 \mu\text{mol}(\text{photon}) \text{ m}^{-2} \text{ s}^{-1}$, white light] was turned on for 1 s (one pulse). The maximum quantum yield of PSII was evaluated on dark-adapted leaves as $F_v/F_m = [(F_m - F_0)/F_m]$ where F_0 is the basal fluorescence, F_v the variable fluorescence, and F_m is the maximum fluorescence. The effective quantum efficiency Φ_{PSII} was evaluated as $(F_m' - F)/F_m'$, where F is the steady-state fluorescence and F_m' is the maximum fluorescence measured in light-exposed leaf samples. The photosynthetic electron transport rate [ETR, $\mu\text{mol}(\text{electron}) \text{ m}^{-2} \text{ s}^{-1}$], the quantum yield of light induced nonphotochemical quenching [$Y_{(\text{NPQ})} = (F/F_m') - (F/F_m)$], the quantum yield of nonregulated energy dissipation [$Y_{(\text{NO})} = F/F_m$], the non-photochemical quenching [$\text{NPQ} = (F_m/F_m') - 1$], coefficient of nonphotochemical fluorescence quenching (q_N), coefficient of photochemical fluorescence quenching based on a model of separate photosynthetic units (q_P),

and coefficient of photochemical fluorescence quenching assuming that all reaction centers share a common light-harvesting antenna (q_L) (Bilger and Björkman 1990), were also calculated. A portable porometer (KR1301, Korea Tech, Korea) was used to determine the stomatal conductance [g_s , $\text{mmol}(\text{H}_2\text{O}) \text{ m}^{-2} \text{ s}^{-1}$].

Grain yield and K concentration: Grain yield was measured by removing 1 m^2 of rice plants from each plot (25 plants in each treatment) and two rice plants from each pot at harvest time (94 DAT). The grain was oven-dried at 70°C and dry mass was recorded after 72 h. Moreover, rice straw was dried and was used to determine K concentration at the anthesis stage (62 DAT) by flame photometer (PFP7, Jenway, UK).

Statistical analysis: Analysis of variance (ANOVA) and the least significant difference (LSD) test were performed using the MSTAT-C software (version 1.42, Michigan State University, USA) to compare the differences between treatments means at a 0.05 level. The correlation (Pearson, 2 tailed) and regression (multiple linear regression, enter method) analyses were done using SPSS software (Statistical Product and Service Solutions, version 16, IBM, New York, USA).

Results

Grain yield and K accumulation in straw: The maximum rice grain yield was recorded in the NPK (632.3 g m^{-2}) and $\text{NP}\frac{1}{2}\text{K}+\text{Ra}+\text{Po}$ (659.1 g m^{-2}) treatments in the pot and field experiments, respectively. While the lowest yield was found in the control treatment (–NPK) treatment of both experiments (447.7 and 431.2 g m^{-2} , respectively), single KSB inoculations (without K chemical fertilizer) insignificantly increased the grain yield as compared to the NP treatment in the pot experiment. By contrast, this difference was significant in the field experiment. In addition, these findings showed that the inoculation with *R. aquatilis* had more positive effects on grain yield than other strains, especially, by applying half the recommended dose of K chemical fertilizer (Fig. 1A,C). Based on the pot experiment results, the maximum value of K accumulation in straw was observed in $\text{NP}\frac{1}{2}\text{K}+\text{Pa}+\text{Ra}$, NPK, and $\text{NP}\frac{1}{2}\text{K}+\text{Ra}$ treatments equal to 10.81, 10.73, and 10.71 g m^{-2} , respectively (Fig. 1). The straw K content in the field experiment was also highly influenced by K fertilizer application alone or combined with KSB inoculations. K uptake by straw was significantly influenced by $\text{NP}\frac{1}{2}\text{K}+\text{Pa}+\text{Ra}$ treatment which were about 2.5, 2.2, and 1.5 times of those in –NPK, NP, and $\text{NP}\frac{1}{2}\text{K}$ treatments, respectively (Fig. 1B,D).

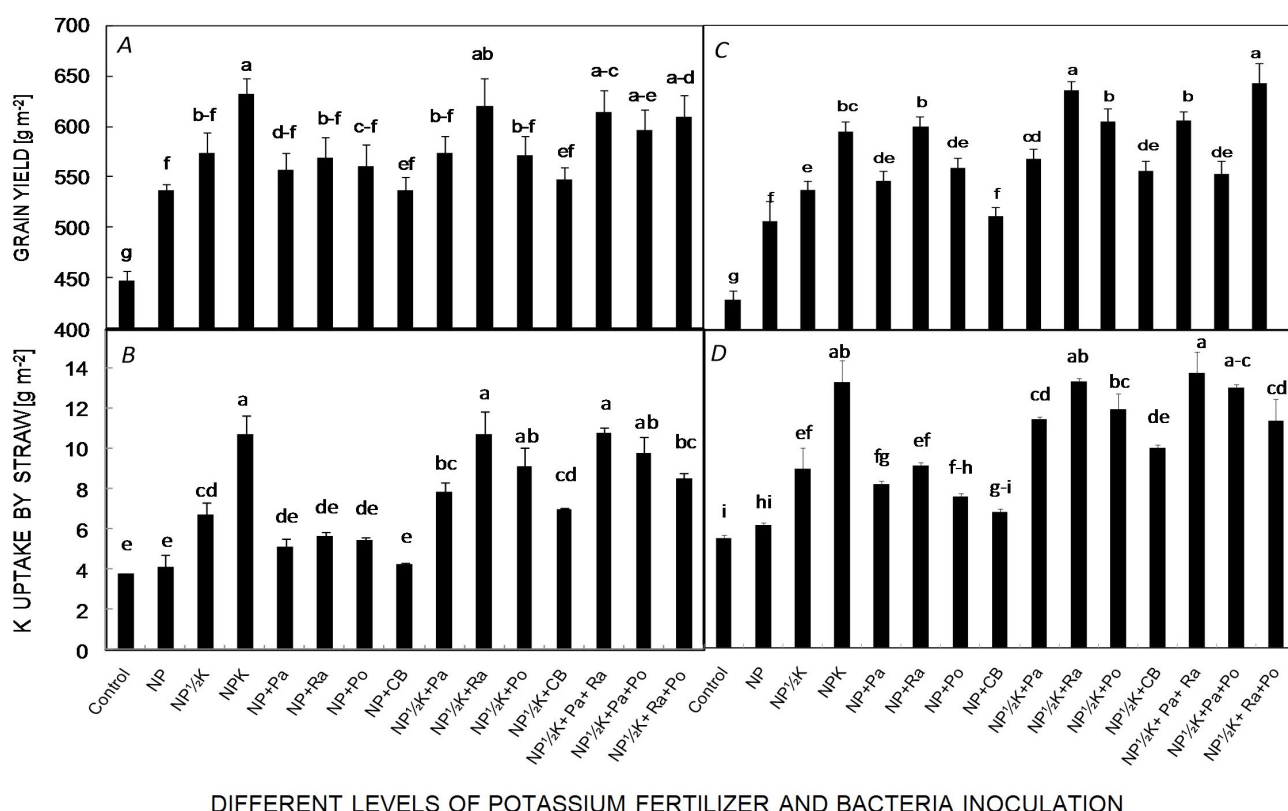


Fig. 1. The response of grain yield (A,C) and K concentration in straw (B,D) to potassium solubilizing bacteria (KSB) inoculations and K chemical fertilizer application in pot (left panel) and field (right panel) experiments. Means in each trait and each experiment followed by the same letter(s) are not significantly different based on the least significant difference (LSD) test at 0.05 probability level.

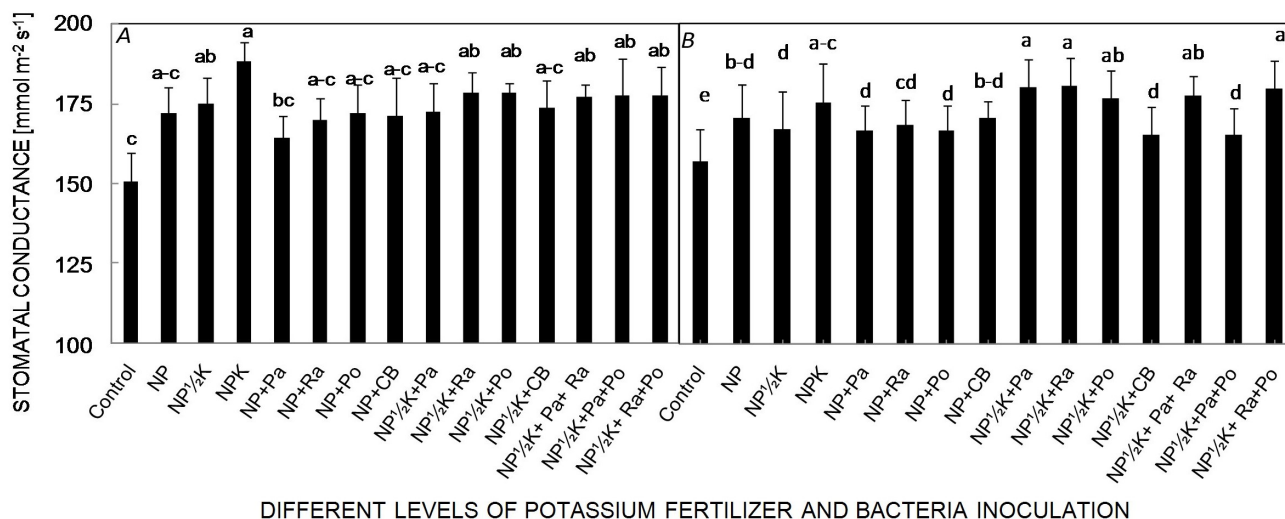


Fig. 2. The response of stomatal conductance to potassium solubilizing bacteria (KSB) inoculations and K chemical fertilizer application in pot (A) and field (B) experiments. Means in each experiment followed by the same letter(s) are not significantly different based on the least significant difference (LSD) test at 0.05 probability level.

Stomatal conductance and photosynthetic pigment contents: The g_s varied from 150.7 (control) to 188.3 mmol m⁻² s⁻¹ (NPK) in the pots, and 214 (control) to 261.5 mmol m⁻² s⁻¹ (NP½K+Ra) in the field experiment (Fig. 2). The highest amounts of Chl *a* were 8.1 and 8.3 mg g⁻¹(FM) at NPK application in the pot and field experiments, respectively. Nevertheless, there were no statistically significant differences between NPK and NP½K+Ra treatment in both experiments and NP½K+Pa+Po treatment in the field. Accordingly, Chl (*a+b*) reached the maximum value equal to 10.46 and 10.70 mg g⁻¹(FM) in NPK treatment which was about 25.4 and 20.5% more than the control (-NPK) in the pot and field experiments, respectively (Fig. 3A,E). The difference was not statistically significant between all of the treatments in term of Chl *b* and Chl *a/b* in both experiments (Table 1). These values varied from 1.82 to 2.30 and 3.18 to 3.62 mg g⁻¹(FM) in the pot, and from 1.95 to 2.41 and 3.12 to 3.70 mg g⁻¹(FM) in the field experiment, respectively. Also, KSB inoculations, alone or combined with NPK fertilizer treatment, decreased the Car content in both experiments (Table 1). There was an increasing trend in the SPAD value by application of chemical fertilizer and KSB inoculations as compared to the control (Table 1).

Chl fluorescence parameters: As observed for ChlF, all the considered parameters, except for F_v/F_m , $Y_{(NO)}$ in both experiments, and for q_L in the pots, were affected by treatments. However, KSB inoculations, alone or combined with K fertilizer, significantly increased the value of ETR as compared to the control, but the highest value was obtained from NPK chemical fertilizer equal to 7.22 in the pot and 7.37 in the field experiment (Fig. 3C,G). On the other hand, there was not statistically significant difference between treatments in term of F_v/F_m and $Y_{(NO)}$. These values varied from 0.777 (control) to 0.804 (NPK) and 0.057 (NP½K) to 0.066 (control) in the pot and from 0.783 (control) to 0.810 (NP+Po) and 0.053 (NP½K+Po)

to 0.068 (control) in the field experiment, respectively (Table 2, Fig. 3B,F). Application of KSB inoculations and K fertilizer also induced $Y_{(NPQ)}$ and NPQ to decrease significantly as compared to the control. The minimum value of $Y_{(NPQ)}$ (0.14) and NPQ (1.5) were recorded by NPK treatment application in the pot experiment. Nevertheless, in the field experiment, these parameters reached the lowest value equivalent to 0.14 (NPK) and 1.5 (NP½K+Ra+Po) which was 0.66 and 0.92 times as much as those in control (Fig. 3B,C,F,G). The highest value of q_N was obtained from the control in both experiments (0.718 and 0.720, respectively). In opposite, the minimum q_P was belonging to the control treatment which was significantly lower than the inoculation and chemical fertilization treatments in both experiments. The NP½K+Po treatment had the greatest impact on q_L in the field experiment which was 1.28 and 1.17 times those in the control and NP treatments, respectively. Nevertheless, there was no statistically significant difference between treatments in terms of q_L in the pot experiments (Table 1). In the pot experiments, the highest value of Φ_{PSII} was observed under NPK treatment (0.798) which was 10.8% more than that in the control. The field experiment results indicated that the inoculation with *P. orientalis* coupled with ½ K fertilizer (NP½K+Po) had more positive effects on Φ_{PSII} than other treatments. Accordingly, the value of Φ_{PSII} varied from 0.711 to 0.796 in the field experiment (Fig. 3D,H).

Correlation and regression analysis: The Pearson's correlation coefficients showed that there were highly significant correlations between the K concentration in straw and Chl *a*, SPAD value, g_s , $Y_{(NO)}$, ETR, q_N , F_v/F_m , Φ_{PSII} , and grain yield in both experiments, NPQ in the pot experiment and $Y_{(NPQ)}$, q_P and q_L in the field experiment (Table 2). The results of multiple linear regressions between grain yield and some main parameters of ChlF are shown in the Table 3. This multiple linear regression model with eight explanatory variables had an R squared

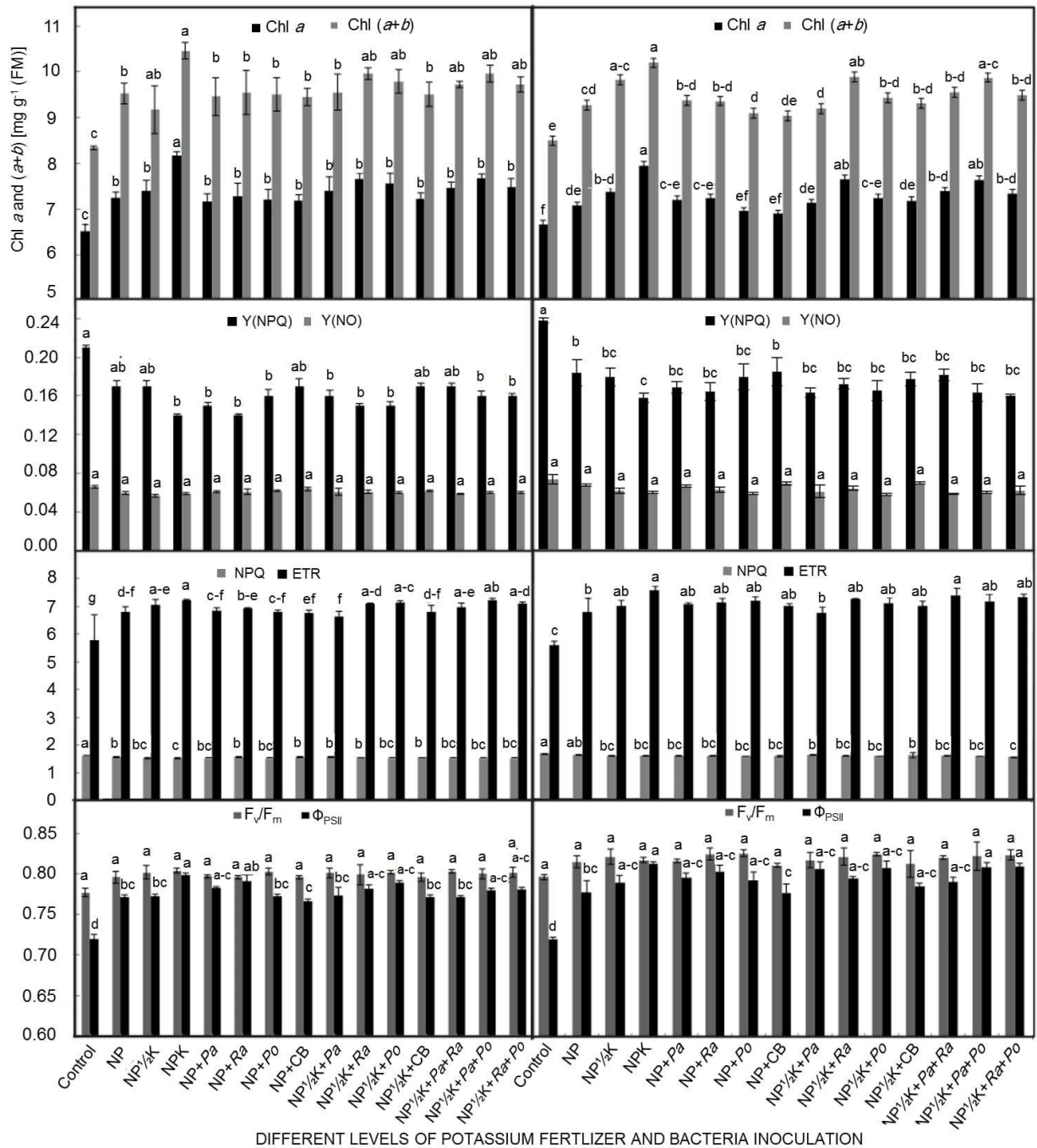


Fig. 3. The response of chlorophyll *a* (Chl *a*), total chlorophyll (*a+b*) (A,E), quantum yield of light induced nonphotochemical quenching (Y_(NPQ)), quantum yield of regulated energy dissipation (Y_(NO)) (B,F), nonphotochemical quenching (NPQ), electron transport rate (ETR) (C,G), photochemical efficiency of PSII (F_v/F_m) and effective quantum efficiency of PSII (Φ_{PSII}) (D,H) to potassium solubilizing bacteria (KSB) inoculations and K chemical fertilizer application in pot (left panel) and field (right panel) experiments. Means in each trait and each experiment followed by the same letter(s) are not significantly different based on the least significant difference (LSD) test at 0.05 probability level.

value of 0.894 and 0.895 in the pot and field experiments, respectively. Therefore, 89.4 and 89.5% of the variation in % grain yield can be explained by this model. According to the results, linear regression significantly was fitted to model the relationship between stomatal conductance and

ETR at the anthesis stage in the pot ($P < 0.01$) and field ($P < 0.05$) experiments. These coefficients of determination (r^2) of the equations were 0.63 and 0.29 in the pot and field experiments, respectively (Fig. 4).

Table 1. Amount of chlorophyll *b* (Chl *b*), ratio of Chl *a/b*, carotenoid content, SPAD value, coefficient of photochemical fluorescence quenching based on a model of separate photosynthetic units (q_p), coefficient of nonphotochemical fluorescence quenching (q_N), and coefficient of photochemical fluorescence quenching assuming that all reaction centers share a common light-harvesting antenna (q_L), as influenced by KSB inoculations and K chemical fertilization in rice. Values are means \pm SE, $n = 3$. Means in each column and each experiment followed by the same letter(s) are not significantly different based on the least significant difference (LSD) test at 0.05 probability level. *, ** – significant at $P < 0.05$ and $P < 0.01$ levels, respectively; ns – not significant.

Treatments	Chl <i>b</i> [mg g ⁻¹ (FM)]	Chl <i>a/b</i>	Carotenoids [mg g ⁻¹ (FM)]	SPAD	q_p	q_L	q_N
Pot experiment							
Control (–NPK)	1.82 \pm 0.11 ^a	3.62 \pm 0.31 ^a	1.67 \pm 0.06 ^{ab}	36.37 \pm 0.11 ^d	0.926 \pm 0.007 ^c	2.303 \pm 0.079 ^a	0.718 \pm 0.002 ^a
NP	2.28 \pm 0.11 ^a	3.19 \pm 0.11 ^a	1.69 \pm 0.05 ^a	40.57 \pm 0.17 ^{a-c}	0.968 \pm 0.008 ^{ab}	2.496 \pm 0.068 ^a	0.704 \pm 0.001 ^{ab}
NP½K	2.31 \pm 0.35 ^a	3.32 \pm 0.41 ^a	1.55 \pm 0.05 ^{a-c}	41.53 \pm 0.28 ^{ab}	0.963 \pm 0.011 ^{ab}	2.548 \pm 0.137 ^a	0.697 \pm 0.002 ^b
NPK	2.30 \pm 0.08 ^a	3.55 \pm 0.09 ^a	1.47 \pm 0.11 ^{a-c}	42.25 \pm 0.57 ^a	0.992 \pm 0.008 ^a	2.519 \pm 0.106 ^a	0.691 \pm 0.001 ^b
NP + <i>Pa</i>	2.30 \pm 0.26 ^a	3.18 \pm 0.29 ^a	1.50 \pm 0.03 ^{a-c}	40.31 \pm 0.18 ^{a-c}	0.982 \pm 0.002 ^{ab}	2.491 \pm 0.022 ^a	0.699 \pm 0.001 ^b
NP + <i>Ra</i>	2.25 \pm 0.23 ^a	3.29 \pm 0.29 ^a	1.49 \pm 0.12 ^{a-c}	41.14 \pm 0.21 ^{a-c}	0.993 \pm 0.010 ^a	2.516 \pm 0.153 ^a	0.702 \pm 0.002 ^{ab}
NP + <i>Po</i>	2.30 \pm 0.23 ^a	3.20 \pm 0.32 ^a	1.53 \pm 0.07 ^{a-c}	40.90 \pm 0.57 ^{a-c}	0.962 \pm 0.006 ^{ab}	2.321 \pm 0.066 ^a	0.696 \pm 0.000 ^b
NP + CB	2.27 \pm 0.13 ^a	3.18 \pm 0.20 ^a	1.36 \pm 0.07 ^c	39.29 \pm 0.13 ^c	0.962 \pm 0.005 ^{ab}	2.320 \pm 0.072 ^a	0.702 \pm 0.002 ^{ab}
NP½K + <i>Pa</i>	2.14 \pm 0.27 ^a	3.57 \pm 0.47 ^a	1.41 \pm 0.09 ^{bc}	40.70 \pm 0.52 ^{a-c}	0.966 \pm 0.018 ^{ab}	2.416 \pm 0.275 ^a	0.700 \pm 0.002 ^b
NP½K + <i>Ra</i>	2.29 \pm 0.09 ^a	3.35 \pm 0.16 ^a	1.39 \pm 0.112 ^c	42.01 \pm 0.39 ^{ab}	0.979 \pm 0.019 ^{ab}	2.443 \pm 0.222 ^a	0.700 \pm 0.006 ^b
NP½K + <i>Po</i>	2.24 \pm 0.05 ^a	3.36 \pm 0.12 ^a	1.42 \pm 0.13 ^{bc}	41.90 \pm 0.37 ^{ab}	0.983 \pm 0.001 ^{ab}	2.464 \pm 0.020 ^a	0.697 \pm 0.000 ^b
NP½K + CB	2.28 \pm 0.14 ^a	3.18 \pm 0.15 ^a	1.48 \pm 0.08 ^{a-c}	40.02 \pm 0.25 ^{bc}	0.968 \pm 0.005 ^{ab}	2.398 \pm 0.046 ^a	0.702 \pm 0.002 ^{ab}
NP½K + <i>Pa</i> + <i>Ra</i>	2.26 \pm 0.06 ^a	3.31 \pm 0.13 ^a	1.55 \pm 0.11 ^{a-c}	40.40 \pm 0.68 ^{a-c}	0.959 \pm 0.004 ^b	2.442 \pm 0.052 ^a	0.697 \pm 0.000 ^b
NP½K + <i>Pa</i> + <i>Po</i>	2.29 \pm 0.19 ^a	3.39 \pm 0.31 ^a	1.51 \pm 0.09 ^{a-c}	42.20 \pm 0.47 ^a	0.975 \pm 0.007 ^{ab}	2.480 \pm 0.064 ^a	0.698 \pm 0.002 ^b
NP½K + <i>Ra</i> + <i>Po</i>	2.25 \pm 0.02 ^a	3.33 \pm 0.10 ^a	1.33 \pm 0.13 ^c	39.26 \pm 0.59 ^c	0.979 \pm 0.011 ^{ab}	2.460 \pm 0.134 ^a	0.697 \pm 0.002 ^b
<i>ANOVA</i> (Mean square)							
K treatments	0.046 ^{ns}	0.064 ^{ns}	0.031 [*]	6.872 ^{**}	0.001 [*]	0.020 ^{ns}	0.000 [*]
Field experiment							
Control (–NPK)	1.95 \pm 0.11 ^a	3.58 \pm 0.21 ^a	1.74 \pm 0.02 ^a	37.39 \pm 1.02 ^c	0.908 \pm 0.012 ^b	2.134 \pm 0.101 ^c	0.720 \pm 0.002 ^a
NP	2.35 \pm 0.11 ^a	3.14 \pm 0.10 ^a	1.55 \pm 0.11 ^{a-c}	41.60 \pm 0.88 ^{a-c}	0.957 \pm 0.009 ^a	2.332 \pm 0.074 ^{bc}	0.704 \pm 0.001 ^{ab}
NP½K	2.41 \pm 0.36 ^a	3.41 \pm 0.46 ^a	1.61 \pm 0.04 ^{ab}	43.33 \pm 1.12 ^{ab}	0.963 \pm 0.10 ^a	2.518 \pm 0.106 ^{ab}	0.698 \pm 0.004 ^{ab}
NPK	2.40 \pm 0.08 ^a	3.46 \pm 0.08 ^a	1.33 \pm 0.07 ^{cd}	43.31 \pm 1.70 ^{ab}	0.995 \pm 0.013 ^a	2.736 \pm 0.176 ^a	0.692 \pm 0.001 ^b
NP + <i>Pa</i>	2.32 \pm 0.18 ^a	3.26 \pm 0.24 ^a	1.40 \pm 0.02 ^{b-d}	41.18 \pm 1.04 ^{a-c}	0.976 \pm 0.011 ^a	2.405 \pm 0.103 ^{a-c}	0.700 \pm 0.001 ^{ab}
NP + <i>Ra</i>	2.27 \pm 0.19 ^a	3.36 \pm 0.30 ^a	1.46 \pm 0.03 ^{b-d}	42.07 \pm 1.14 ^{ab}	0.975 \pm 0.014 ^a	2.474 \pm 0.163 ^{a-c}	0.696 \pm 0.002 ^{ab}
NP + <i>Po</i>	2.30 \pm 0.16 ^a	3.17 \pm 0.24 ^a	1.29 \pm 0.02 ^d	41.82 \pm 0.94 ^{ab}	0.961 \pm 0.010 ^a	2.599 \pm 0.214 ^{ab}	0.694 \pm 0.002 ^{ab}
NP + CB	2.31 \pm 0.09 ^a	3.12 \pm 0.17 ^a	1.37 \pm 0.11 ^{b-d}	40.03 \pm 0.70 ^{bc}	0.959 \pm 0.008 ^a	2.321 \pm 0.117 ^{bc}	0.700 \pm 0.004 ^{ab}
NP½K + <i>Pa</i>	2.21 \pm 0.29 ^a	3.48 \pm 0.52 ^a	1.39 \pm 0.16 ^{b-d}	42.23 \pm 1.17 ^{ab}	0.987 \pm 0.016 ^a	2.646 \pm 0.273 ^{ab}	0.702 \pm 0.002 ^{ab}
NP½K + <i>Ra</i>	2.39 \pm 0.09 ^a	3.46 \pm 0.12 ^a	1.28 \pm 0.13 ^d	45.33 \pm 0.90 ^a	0.969 \pm 0.020 ^a	2.463 \pm 0.284 ^{a-c}	0.696 \pm 0.007 ^{ab}
NP½K + <i>Po</i>	2.35 \pm 0.04 ^a	3.21 \pm 0.09 ^a	1.34 \pm 0.09 ^{cd}	43.69 \pm 1.29 ^{ab}	0.979 \pm 0.020 ^a	2.745 \pm 0.359 ^a	0.693 \pm 0.001 ^b
NP½K + CB	2.27 \pm 0.14 ^a	3.30 \pm 0.12 ^a	1.36 \pm 0.10 ^{cd}	42.89 \pm 1.81 ^{ab}	0.967 \pm 0.010 ^a	2.322 \pm 0.071 ^{bc}	0.702 \pm 0.002 ^{ab}
NP½K + <i>Pa</i> + <i>Ra</i>	2.32 \pm 0.02 ^a	3.32 \pm 0.11 ^a	1.56 \pm 0.14 ^{a-c}	41.64 \pm 1.49 ^{a-c}	0.964 \pm 0.012 ^a	2.656 \pm 0.185 ^{ab}	0.699 \pm 0.003 ^{ab}
NP½K + <i>Pa</i> + <i>Po</i>	2.40 \pm 0.21 ^a	3.70 \pm 0.27 ^a	1.37 \pm 0.09 ^{b-d}	43.59 \pm 1.05 ^{ab}	0.984 \pm 0.011 ^a	2.683 \pm 0.183 ^{ab}	0.694 \pm 0.000 ^{ab}
NP½K + <i>Ra</i> + <i>Po</i>	2.29 \pm 0.06 ^a	3.34 \pm 0.08 ^a	1.29 \pm 0.08 ^d	41.73 \pm 1.34 ^{ab}	0.983 \pm 0.004 ^a	2.574 \pm 0.184 ^{ab}	0.697 \pm 0.002 ^{ab}
<i>ANOVA</i> (Mean square)							
K treatments	0.039 ^{ns}	0.052 ^{ns}	0.054 [*]	10.02 [*]	0.001 [*]	0.096 [*]	0.000 [*]

Discussion

Based on our previous research, *P. agglomerans*, *R. aquatilis*, and *P. orientalis* solubilized about 45 and 60 $\mu\text{g ml}^{-1}$ of K from insoluble K-bearing mineral source (mica powder) after 28 d from inoculation, respectively (more details in Yaghoubi Khanghahi *et al.* 2018b). The current study was performed to assess the potential effects of

these KSB strains (applied alone or combined with half the recommended dose of the K chemical fertilizer) to improve the leaf photosynthetic capacity of rice. The results showed that the KSB inoculations not only enhanced the rice K accumulation, but also increased the grain yield, especially, when they were applied with ½ K chemical fertilizer. These findings are in agreement with Bakhshandeh *et al.* (2018), who reported that the mineral

Table 2. Pearson's correlation coefficients (r) between K uptake by straw and different photosynthetic variables and grain yield as influenced by KSB inoculations and K chemical fertilizer application ($n = 15$). Chl a – chlorophyll a ; $Y_{(NPQ)}$ – quantum yield of light-induced nonphotochemical quenching; $Y_{(NO)}$ – quantum yield of regulated energy dissipation; NPQ – nonphotochemical quenching; ETR – photosynthetic electron transport rate; q_p – coefficient of photochemical fluorescence quenching based on a model of separate photosynthetic units; q_N – coefficient of nonphotochemical fluorescence quenching; q_L – coefficient of photochemical fluorescence quenching assuming that all reaction centers share a common light-harvesting antenna; F_v/F_m – maximum quantum yield of photosystem II; Φ_{PSII} – effective quantum efficiency of PSII. * and ** – significant at $P < 0.05$ and $P < 0.01$ levels, respectively; ns – not significant.

Variable	r (pot experiment)	r (field experiment)
Chl a	0.814**	0.825**
Carotenoids	-0.418 ^{ns}	-0.462 ^{ns}
SPAD value	0.602*	0.715**
Stomatal conductance	0.775**	0.666**
$Y_{(NPQ)}$	-0.464 ^{ns}	-0.631*
$Y_{(NO)}$	-0.565*	-0.686**
NPQ	-0.633*	-0.491 ^{ns}
ETR	0.664*	0.653**
q_p	0.437 ^{ns}	0.682**
q_N	-0.620*	-0.609*
q_L	0.388 ^{ns}	0.770**
F_v/F_m	0.605*	0.538*
Φ_{PSII}	0.531*	0.658**
Grain yield	0.839**	0.788**

Table 3. Multiple linear regressions (enter method) between grain yield and some photosynthetic variables in rice under KSB inoculations and K chemical fertilizer application. Chl a – chlorophyll a ; F_v/F_m – maximum quantum yield of PSII; Φ_{PSII} – effective quantum efficiency of PSII; $Y_{(NPQ)}$ – quantum yield of light-induced nonphotochemical quenching; NPQ – nonphotochemical quenching; q_p – coefficient of photochemical fluorescence quenching based on a model of separate photosynthetic units; q_N – coefficient of nonphotochemical fluorescence quenching; ETR – photosynthetic electron transport rate. * and ** – significant at $P < 0.05$ and $P < 0.01$ levels, respectively; ns – not significant.

Dependent variable	Independent variables	Standardized coefficients (Beta)	
		Pot	Field
Grain yield	Chl a	0.67*	0.64*
	F_v/F_m	2.73*	7.53**
	Φ_{PSII}	3.40*	24.82**
	$Y_{(NPQ)}$	-0.88 ^{ns}	-3.04**
	NPQ	-2.40 ^{ns}	0.24 ^{ns}
	q_p	1.72 ^{ns}	-21.13**
	q_N	3.69 ^{ns}	0.54 ^{ns}
	ETR	0.02 ^{ns}	0.35 ^{ns}
Adjusted R square		0.894**	0.885**

nutrient uptake, especially K, by plant enhanced under PGPR inoculation treatments. In this regard, Bakhshandeh *et al.* (2017) showed in rice that the PGPR inoculation significantly enhanced K uptake by leaves, stem, and roots up to 77, 53, and 75% as compared to the control, respectively. In other study, Yaghoubi Khangahi *et al.*

(2018a) showed that rice plants inoculated with KSB had higher K concentration in grain as compared to the non-inoculated plants. Previous investigations have shown that the nutrient uptake by rice plant was in response to inoculations with K-solubilizing microorganisms significantly increased through both direct (the ability of solubilizing insoluble silicate compounds minerals in the rhizosphere and plant hormone production) and indirect mechanisms (synthesis of antibiotics, enzymes, fungicidal compounds, and competition with detrimental microorganisms) (Bakhshandeh *et al.* 2015, Priyanka *et al.* 2017).

In the present study, photosynthetic pigments [Chl a , Chl $(a+b)$, and Car] and SPAD value were affected by application of NPK fertilizer and KSB inoculations. Accordingly, low K resulted in decreased contents of Chl a and SPAD value in plants under the control and NP treatments. Similarly, Shah *et al.* (2017) investigated the Chl and SPAD measurement during nutrient stress in wheat and reported that the limited nutrient supply resulted in decreased pigment content per unit area, as well as in the total amount produced per plant. It has already been reported that the optimal N, P, and K supply is considered essential for the biosynthesis of plant photosynthetic pigments (Yong *et al.* 2010). Furthermore, K is the most abundant cellular cation and plays important roles in plant cellular homeostasis by contributing to charge balance, osmotic adjustment, and enzyme catalysis (Marschner 1995). On the other hand, linear models related to SPAD value and rice leaf Chl content at anthesis time were determined with high coefficients of determination in the pot ($r^2=0.69$) and field ($r^2=0.60$) experiments (data not shown). This finding supports the results of other studies by Wakiyama (2016) and

Kumagai *et al.* (2009) in rice plant.

However, Shah *et al.* (2017) reported that the K fertilizer application enhanced Chl content and SPAD value as compared to that of the plants without fertilization, but the impact of KSB inoculations on photosynthetic pig-

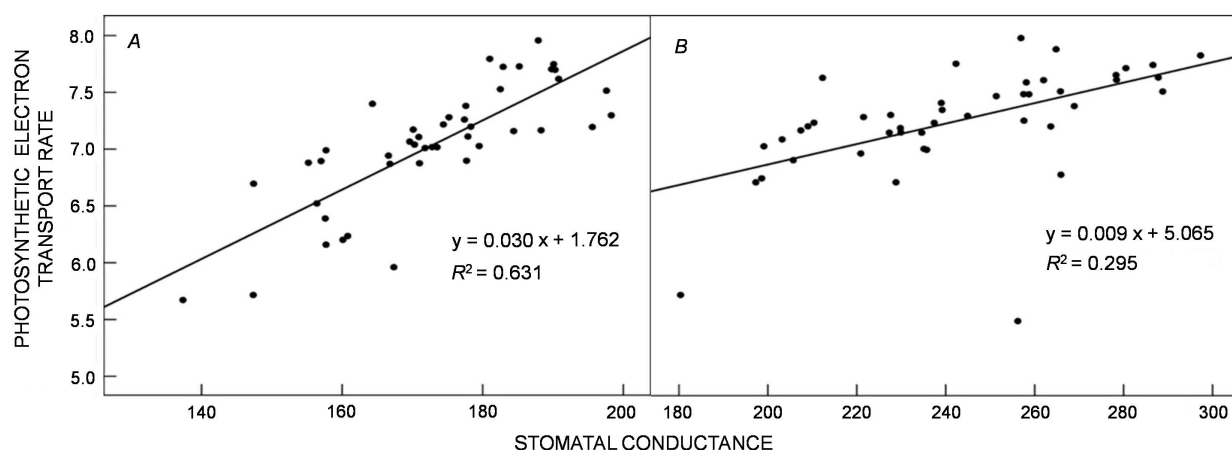


Fig. 4. The relationship between stomatal conductance and photosynthetic electron transport rate in response to potassium solubilizing bacteria (KSB) inoculations and K chemical fertilizer application in pot (A) and field (B) experiments.

ments, stomatal conductance, and ChlF in rice plants has not been characterized. Bakhshandeh *et al.* (2015) in a pot experiment studied the effects of phosphate-solubilizing bacteria (PSB) on rice seedlings and showed that the total Chl and Car contents increased by 8.5 and 9.2%, respectively, when rice seeds were inoculated with the *Enterobacter* sp. as compared to the control. Similar results were presented by Panhwar *et al.* (2011), who reported that the leaf Chl content in rice was enhanced by *Bacillus* sp. inoculation. Bakhshandeh *et al.* (2018) also reported that SPAD value in rice seedlings increased by 8.6–12.0% under KSB inoculations as compared to noninoculated seedlings.

On the other hand, Chl *b* and Chl *a/b* showed no significant changes. This may be caused by the different sensitivity of Chl *a* and *b* under external environment (Sayyad-Amin *et al.* 2016). Previous study has also reported that the Chl *a* may be 2 to 4 times higher than Chl *b*, according to the growth stage and environmental conditions (Maina and Wang 2015).

Compared with the controls, the g_s in leaves increased by NPK fertilization and KSB inoculations. This result is in agreement with Jin *et al.* (2011) and Jia *et al.* (2008), who reported that the g_s and electron transfer energy in rice leaves increased under K fertilization. Zhao *et al.* (2016) also reported K deficiency disrupted the g_s . In previous studies, the decrease in g_s was considered as the main action that depressed plant leaf photosynthetic capacity under K-deficient conditions (Peng *et al.* 2006).

The parameters of $Y_{(NPQ)}$, NPQ, and ETR were significantly affected by the applied treatments. Inoculation of KSB strains alone or combined with NPK chemical fertilizer increased ETR, while both $Y_{(NPQ)}$ and NPQ decreased as compared to the control in both pot and field experiments. Ratio of F_v/F_m was used for characterizing potential photochemical efficiency of PSII. This parameter is the maximum efficiency at which light absorbed by PSII is used for reduction of quinone A (Q_A), as the first quinone acceptor, and is used as a sensitive indicator of plant photosynthetic performance (Maxwell and Johnson 2000).

The results in our study showed that the ratio of F_v/F_m varied from 0.78 to 0.80 and 0.78 to 0.81 in the pot and field experiments, respectively. It has already been proved that the value of F_v/F_m is usually from 0.79 (Chojak-Kozniewska *et al.* 2018) to 0.85 (Kalaji and Guo 2008) when seedlings are not influenced by environmental conditions. Accordingly, Φ_{PSII} significantly increased by inoculation and fertilization treatments as compared to the control. KSB inoculation and K fertilization could increase Φ_{PSII} and maintain relatively high photochemical efficiency and strong photosynthetic capacity. This ratio is the one most widely used in research employing the fluorescence technique and is directly correlated with the photochemical efficiency of PSII (Torres Netto *et al.* 2002). Similarly, it has already been reported that the F_v/F_m is known to be quite insensitive to many environmental stress factors, including nutrient deficiency (Živčák *et al.* 2008), while the effective quantum yield of PSII is far more responsive also to mild stress conditions (Salvatori *et al.* 2017). Since Φ_{PSII} is directly related to the CO_2 assimilation rate (Kramer *et al.* 2004), increased Φ_{PSII} in this study could lead to higher CO_2 assimilation and contribute to enhanced grain yield.

The value of ETR significantly increased when the K uptake by straw increased by applied treatments. Maxwell and Johnson (2000) investigated the changes of ChlF under laboratory conditions and reported that the ETR value highly correlated with CO_2 assimilation rate in crops. Therefore, in the present study, the increment of rice growth and grain yield under inoculation and K fertilization may be attributed to ETR enhancement and elevation of CO_2 assimilation (Yaghoubian *et al.* 2016). According to the results, bacterial inoculants could increase the ETR value as compared to the control. This finding agrees with the results of Li *et al.* (2013), who reported that soil microorganisms could relieve the inhibition of the PSII reaction center and enhance the value of ETR, and then improve the process of photochemical and light transformation.

The $Y_{(NPQ)}$ is the yield for dissipation by downregulation and $Y_{(NO)}$ is the yield of other nonphotochemical losses and

reflects no light-induced quenching processes (Kramer *et al.* 2004). According to the results, $Y_{(NPQ)}$ in both pot and field experiments were sensitive to K deficiency in the control as compared to other treatment. It seems that K deficiency decreased the light-saturation points. In that condition, absorption of light energy by PS that was in excess of the capacity of the photosynthesis can lead to a significant increase of NPQ in the stressed leaves of rice. (Jia *et al.* 2008).

However, the results of several studies indicated that the photosynthetic capacities of higher plants change dramatically in response to different supplies of K (Weng *et al.* 2007, Jia *et al.* 2008), but we did not find any document that would report the effect of KSB on ChlF parameters. The underlying mechanisms of the effects of leaf K concentration on photosynthesis are still not fully understood; however, it has been suggested that the activity of Rubisco is an important limiting factor of photosynthesis in rice leaves (Weng *et al.* 2007). K affects the photosynthesis process at many levels, such as synthesis of ATP, activation of the enzymes involved in photosynthesis, CO_2 uptake, balance of the electric charges required for photophosphorylation in chloroplasts and acting as the counter ion to light-induced H^+ flux across the thylakoid membranes (Marschner 1995).

The multiple linear regressions were used to explain which of the ChlF parameters could be more useful to predict the grain yield under the K fertilization and KSB inoculations in both experiments. Accordingly, Chl *a*, F_v/F_m , and Φ_{PSII} in both experiments and $Y_{(NPQ)}$ and q_P in the field experiment can significantly affect the grain yield. Based on the correlation analysis results, K concentration in straw at anthesis showed a significant correlation with some parameters, such as Chl *a*, Φ_{PSII} , and grain yield. These findings are in agreement with the results of Xue *et al.* (2016), who reported the positive correlations between K concentration in plant tissues and grain yield. Similarly, Ntanos and Koutroubas (2002) reported that the grain yield significantly correlated with nutrient uptake and concentration in rice plant. Bakhshandeh *et al.* (2015) also found an increase in leaf Chl content when rice seeds were inoculated with *R. aquatilis*. They reported these increases may have resulted in improved nutrient uptake, photosynthetic pigment contents, and finally an increase in the grain yield. These results are also in agreement with Jia *et al.* (2008), who showed the ChlF parameters were markedly affected by K deficiency. It means that any K deficiency likely leads to a reduced content of leaf pigments, retarded plant growth, and low net primary productivity (Zhang *et al.* 2003).

ETR seems to be more independent from g_s in the field experiment as compared to the pots. In fact, ETR in pots were lowered more rapidly than in the field when g_s decreased. It has been reported that the decrease of ETR led to the generation of excess excitation energy, which can exacerbate photoinhibition under stress (Wang *et al.* 2016). ETR is known as an indicator of electron transport to acceptors other than CO_2 in alternative processes, such as photorespiration and Mehler reactions (Jiang *et al.* 2006). It seems that the rice plants grown in the field

had a greater potential to maintain their ETR capability under lower g_s values and to replace photosynthesis with photorespiration as an electron-consuming process (Flexas *et al.* 2002) and a protective role against photoinhibition (Jiang *et al.* 2006) under K-deficient conditions.

There were some differences between the results achieved by the pot and field experiments in term of SPAD value, g_s , K uptake by straw, grain yield, $Y_{(NPQ)}$, NPQ, and Φ_{PSII} . Accordingly, the lowest values of the $Y_{(NPQ)}$ and NPQ parameters in the pot experiment were obtained with NPK, while the lowest values of these indices in the field experiment were obtained from $NP\frac{1}{2}K+Pa+Ra$ and $NP\frac{1}{2}K+Ra+Po$ treatments, respectively. It seems that soil bacterial activities in the field experiment were higher than that in the pot experiment. The reason for this difference may be the use of sterilized soil in the pots. In addition, the pot experiments usually are performed under environmental conditions which seldom or never occur in the field experiments (de Vries 1980) such as stagnant flood conditions that could decrease microbial biomass and activity (Unger *et al.* 2009) and rice growth (Kuanar *et al.* 2017).

R. aquatilis and *P. orientalis* had greater impacts on photosynthetic pigments content and ChlF parameters (especially Φ_{PSII}) than other strains. Results also showed that the commercial K biofertilizer ($NP+CB$ and $NP\frac{1}{2}K+CB$ treatments) had lower effects on the studied traits, such as K concentration in straw, grain yield, ETR, g_s , and Φ_{PSII} than those in native KSB inoculations. This result could be explained by a lower adaptation to the crop micro-environmental conditions (Tabassum *et al.* 2017). Therefore, nonnative strains, when applied as a commercial biofertilizer, cannot compete with the existing native bacterial community for establishment and persistence in the soil. It has already been reported that the native PGPRs isolated from rhizospheric soil may be more useful than others because they are already competent, adapted, and dominant in a particular geographical area (Bergottini *et al.* 2015). Also, crops are defended both by chemicals and by specific immune responses to nonnative strains (Bever *et al.* 2012).

Based on the results, the three native KSB strains can be used as a viable alternative to increase K concentration in plants, especially when $\frac{1}{2}$ K chemical fertilizer was applied. These findings are in agreement with the results of several studies that proved the application of PGPRs in nutrient management strategies aimed at decreasing chemical fertilizer consumption and consequently, promoting environmentally friendly crop production (Meena *et al.* 2017). It has already been reported that the application of biofertilizer can reduce the cost of K chemical fertilizers about 50 to 60% (Chandra *et al.* 2002) and enhance the K fertilizer efficiency (Bahadur *et al.* 2014).

In conclusion, the results of this study showed that the inoculation with three native KSB strains of *P. agglomerans*, *R. aquatilis*, and *P. orientalis* isolated from rice paddy soils could be considered as an effective way to enhance K uptake by rice seedlings, ChlF parameters, Chl *a* content, and stomatal conductance. Therefore, these KSBs strains, as potential inoculants, can help to minimize use

of K chemical fertilizer for rice production by increasing the efficiency of photosynthesis in the flooding irrigation conditions.

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