










Article

Plant Growth-Promoting Rhizobacteria Improve Rice Response to Climate Change Conditions

Susana Redondo-Gómez ^{1,*}, Jennifer Mesa-Marín ¹, Jesús A. Pérez-Romero ², Vicente Mariscal ³, Fernando P. Molina-Heredia ³, Consolación Álvarez ³, Eloísa Pajuelo ⁴, Ignacio D. Rodríguez-Llorente ⁴ and Enrique Mateos-Naranjo ¹

- ¹ Departamento de Biología Vegetal y Ecología, Facultad de Biología, Universidad de Sevilla, 41012 Seville, Spain; jmesam@us.es (J.M.-M.); emana@us.es (E.M.-N.)
- ² Departamento de Biología, Instituto Universitario de Investigación Marina (INMAR), Universidad de Cádiz, 11510 Puerto Real, Spain; jesusalperezromero@gmail.com
- ³ Instituto de Bioquímica Vegetal y Fotosíntesis, cicCartuja, Universidad de Sevilla and CSIC, 41092 Seville, Spain; vicente.mariscal@ibvf.csic.es (V.M.); publio@us.es (F.P.M.-H.); consolacion@ibvf.csic.es (C.Á.)
- ⁴ Departamento de Microbiología y Parasitología, Facultad de Farmacia, Universidad de Sevilla, 41012 Seville, Spain; epajuelo@us.es (E.P.); irodri@us.es (I.D.R.-L.)
- * Correspondence: susana@us.es

Abstract: Rice is one of the most important crops in the world and is considered a strategic crop for food security. Furthermore, the excessive use of chemical fertilizers to obtain high yields causes environmental problems. A sustainable alternative includes taking advantage of beneficial bacteria that promote plant growth. Here, we investigate the effect of five bacterial biofertilizers from halophytes on growth, and we investigate photosynthetic efficiency in rice plants grown under saline conditions (0 and 85 mmol L⁻¹ NaCl) and future climate change scenarios, including increased CO₂ concentrations and temperature (400/700 ppm and 25/+4 °C, respectively). Biofertilizers 1–4 increased growth by 9–64% in plants grown with and without salt in both CO₂- temperature combinations, although there was no significant positive effect on the net photosynthetic rate of rice plants. In general, biofertilizer 1 was the most effective at 400 ppm CO₂ and at 700 ppm CO₂ +4 °C in the absence of salt. Inocula 1–5 also stimulated plant length at high CO₂ levels without salt. Finally, the positive effect of biofertilization was attenuated in the plants grown under the interaction between salt and high CO₂. This highlights the significance of studying biofertilization under stress interaction to establish the real potential of biofertilizers in the context of climate change conditions.

Keywords: bacterial consortium; efficiency of PSII photochemistry; elevated atmospheric CO₂; gas exchange; inoculation; PGPR; temperature



Citation: Redondo-Gómez, S.; Mesa-Marín, J.; Pérez-Romero, J.A.; Mariscal, V.; Molina-Heredia, F.P.; Álvarez, C.; Pajuelo, E.; Rodríguez-Llorente, I.D.; Mateos-Naranjo, E. Plant Growth-Promoting Rhizobacteria Improve Rice Response to Climate Change Conditions. *Plants* **2023**, *12*, 2532. <https://doi.org/10.3390/plants12132532>

Academic Editor: Carmen Bianco

Received: 30 May 2023

Revised: 20 June 2023

Accepted: 1 July 2023

Published: 3 July 2023



Copyright: © 2023 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

1. Introduction

Microorganisms are essential for the formation of soil structures in both natural and agricultural systems, and they are involved in fundamental processes such as the decomposition of organic matter and, in general, the cycle of C, N, P and S [1,2]. Some bacterial populations of the soil are capable of colonizing the rhizosphere or the interior of plants and stimulating growth, for which they are named plant growth-promoting rhizobacteria (PGPR) [2].

PGPR inoculants can carry out beneficial biological processes in agricultural systems with little or no negative impacts, as a natural solution [3]. This has led to a growing interest in developing PGPR-based biofertilizers for their application to different types of crops. PGPR promote plant growth through different mechanisms, such as [4–7] auxin production for root development (particularly indole-3-acetic acid, IAA), facilitation of nutrient uptake, atmospheric nitrogen fixation, siderophore production for iron uptake,

phosphorus solubilization, synthesis of the enzyme ACC deaminase (cleaves ethylene, which is essential in response to stress), and biofilm production (which improves bacterial adhesion to root tissue and facilitation of nutrient uptake). Biofertilizers usually consist of PGPR consortia since a single strain often does not show all the mechanisms to promote host growth [5,8].

Rice (*Oryza sativa* L.) is an essential food product for the human population; it is estimated that world rice production for 2023 will be 517 million t [9]. Furthermore, rice is considered a strategic crop due to its wide distribution in soils and climates worldwide, as well as in a scenario of climate change [1,10]. However, studies that evaluate the effect of PGPR on rice growth are still limited [11–14]. Some of these studies have evaluated PGPR consortia or isolates not only as an alternative to chemical fertilization [1], but also to alleviate salinity [11,14] or drought stresses [12] in rice plants. This is relevant due to the fact that salt stress is limiting cultivation on lands around the world [15]. Anyway, none of these studies have considered the effect of PGPR on growth under the interaction of several abiotic factors.

Studies assessing the effect of PGPR consortia on crops in combination with different abiotic stresses, such as salinity, temperature, and CO₂ concentration, are very scarce. However, these studies are important for establishing the effectiveness of the use of biofertilizers in the context of the world's changing climate [4,16]. In this context, halophytes are an excellent reservoir of halotolerant bacteria with plant growth-promoting traits that could be used for these studies [17].

Biofertilizers from halophytes have previously demonstrated their effectiveness in mitigating abiotic stress in different crops, including rice [4]. However, this previous study evaluated the effect of bacterial inoculants on growth, but not on the physiological response of crops. Therefore, our objective was to test the effects of five biofertilizers from halophytes on rice growth and physiological response under salinity stress (85 mM NaCl) since it has been previously shown that concentrations reduce the growth of rice [4], as do variations in atmospheric CO₂ concentration and air temperature (400 ppm and 25/14 °C and 700 ppm +4 °C).

2. Materials and Methods

2.1. Plant Materials, Growth Conditions, and Treatments

Rice seeds (*Oryza sativa* var. Puntal) were surface-disinfested in 0.5% (*w/v*) calcium hypochlorite for 20 min. Then, hypochlorite was removed by successive washing with sterilized tap water and germinated on a wet filter paper for 7 days. Germinated seedlings were transferred to 4 L closed tanks containing at least 20 plants, in +N BG110 medium [18]. Plants ($n = 24$) were grown in controlled-environment chambers at 400 ppm CO₂ with a diurnal regime of 16 h of light at 25 °C and 8 h of darkness at 14 °C, 80% relative humidity and 300 $\mu\text{mol m}^{-2} \text{s}^{-1}$ light flux (Aralab/Fitoclima 18.000 EH, Lisbon, Portugal). Treatments were established after 5 days of growth (see below).

Twenty-four different treatments were established ($n = 20$ per treatment): six biofertilization treatments (five rhizobacteria consortia + non-inoculated control), two salinity concentrations (0 and 85 mmol L⁻¹ NaCl), and two CO₂- temperature combinations—400 ppm CO₂ at 25/14 °C (16/8 h) and 700 ppm CO₂ at 29/18 °C (16/8 h).

The salinity treatment was imposed by adding the appropriate concentration of salt (0 or 85 mmol L⁻¹ NaCl) to the culture medium. This salt concentration was determined as the optimum for salt stress in rice in a previous analysis [4]. The conductivity of the tanks was monitored weekly with a conductivity meter (Probe GS3, Decagon, Pullman, WA, USA), and NaCl was added when necessary. The atmospheric CO₂ concentrations in the chambers were continuously recorded by CO₂ sensors (Aralab, Lisbon, Portugal) and maintained by supplying pure CO₂ from a compressed gas cylinder (Air Liquide, B50 35 K). Rhizobacterial inoculation was carried out the day after setting environmental treatments (salinity, CO₂ and temperature).

2.2. Consortia of Rhizobacteria

Five bacterial biofertilizers were used, which had been tested with eight crops: alfalfa, flax, maize, millet, wheat, strawberry, sunflower and rice [4]. They were constructed from rhizobacteria originally isolated from the rhizospheres of five different halophytes, commonly inhabiting salt marshes in southwestern Spain [16]. These five microbial consortia, containing three strains each, showed different PGPR activities likely promoting plant growth (see Figure 1).

Biofertilizers:

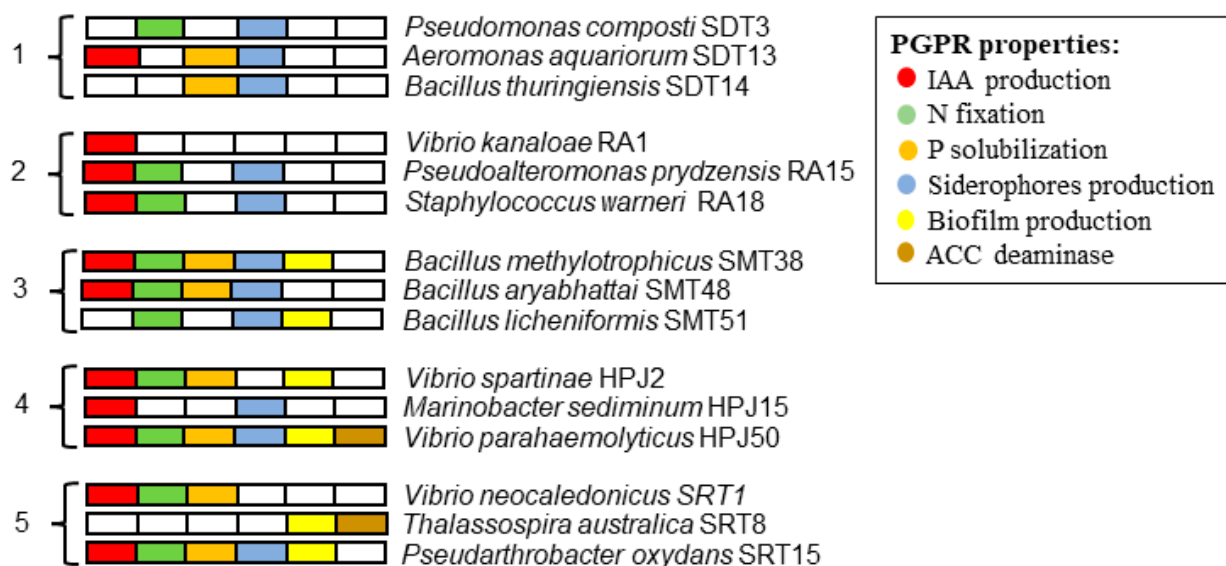


Figure 1. Plant growth-promoting rhizobacterial (PGPR) traits for the strains of biofertilizers used in this study. The rhizobacteria that compose biofertilizers were isolated from: 1, *Sporobolus montevidensis* (Arechav.) P.M. Peterson & Saarela; 2, *Allenrolfea occidentalis*; 3, *Sporobolus maritimus* (Curtis) P.M. Peterson & Saarela; 4, *Atriplex portulacoides*; and 5, *Salicornia europaea* (Information adapted with permission from Redondo-Gómez et al. [4]).

Bacterial suspension for inoculation was prepared as described previously [4]. In short, strains grown in TSB (Tryptone Soya Broth) medium were collected and resuspended in tap water to reach an OD_{600} of approximately 1.0 in order to produce a uniform bacterial concentration of all strains. The bacterial suspensions were mixed to produce the five final inoculant suspensions, as follows: strains SDT3, SDT13 and SDT14 were mixed to obtain Biofertilizer 1; strains RA1, RA15 and RA18 for Biofertilizer 2; strains SMT38, SMT48 and SMT51 for Biofertilizer 3; strains HPJ2, HPJ15 and HPJ50 for Biofertilizer 4 and strains SRT1, SRT8 and SRT15 were mixed in Biofertilizer 5. For plant inoculation, every 1.5 L pot was watered with 20 ml of the inoculant suspensions to get a final bacteria concentration of 10^5 CFU/ml (estimating that a suspension of OD_{600} 1 corresponds to approximately 10^8 CFU/ml).

2.3. Growth Measurements

After 20 d of growth in the different treatments, plant lengths ($n = 20$) were determined. Finally, the plants were harvested, and dry mass was determined after drying the samples at 80 °C for 48 h.

2.4. Gas Exchange

Gas exchange was measured in random tillers ($n = 5$) using an infrared gas analyser (LI-6400, LI-COR Inc., Lincoln, NE, USA; equipped with a light leaf chamber LI-6400-02B) in an open system one day before plant harvest. Net photosynthetic rate (A), stomatal

conductance (G_s) and instantaneous water use efficiency ($iWUE$; ratio between A and G_s) and intercellular CO_2 concentration (C_i), were determined at a photon flux density (PPFD) of $1000 \text{ mmol photons m}^{-2} \text{ s}^{-1}$ (with 15% blue light to maximize stomatal aperture), a CO_2 concentration surrounding the leaf of $400 \text{ mmol mol}^{-1}$ air, an air temperature of $24 \pm 1 \text{ }^\circ\text{C}$, a relative humidity of $45 \pm 5\%$, and a vapor pressure deficit of 2.0–3.0 kPa [19].

2.5. Chlorophyll Fluorescence

Chlorophyll fluorescence was measured in leaves ($n = 12$) from plants 20 d after treatment using a portable modulated fluorimeter (FMS-2; Hansatech Instruments Ltd., Kings Lynn, UK). Quantum efficiency of PSII photochemistry (F_v/F_m) was measured in leaves that were dark-adapted for 30 minutes using leaf clips designed for this purpose, and the maximum quantum efficiency of PSII photochemistry (F_v/F_m) was measured. Maximum efficiency of PSII was calculated as F_v/F_m (i.e., the quantum efficiency if all PSII centres were open) [20].

2.6. Statistical Analysis

Data were analysed using generalized linear models (GLMs). Statistical analysis was performed using the SPSS 26.0 statistical program (SPSS Inc., Chicago, IL, USA), using the Duncan test to establish the significance between treatments ($p < 0.05$). Before statistical analysis, to verify the assumptions of normality and homogeneity of the variances, Kolmogorov–Smirnov and Levene tests were used, respectively.

3. Results

3.1. Growth Measurements

Inoculation with the different consortia of rhizobacteria had a significant effect on rice plants under different salinity conditions (0 and 85 mmol L^{-1} NaCl) at $400 \text{ ppm } CO_2$ and $25 \text{ }^\circ\text{C}$ and $700 \text{ ppm } CO_2 + 4 \text{ }^\circ\text{C}$ (GLM, $p < 0.0001$; Figures 2 and 3). Bacterial inoculation increased plant growth at $400 \text{ ppm } CO_2$ at $25 \text{ }^\circ\text{C}$, regardless of saline treatment ($p < 0.0001$ for both with and without salt). Inoculum 1 showed the highest plant dry weight without salt compared to non-inoculated control plants by 9% (Figure 2A). Inocula 1–4 increased plant dry weight by 21–46% at 85 mmol L^{-1} NaCl and ambient CO_2 .

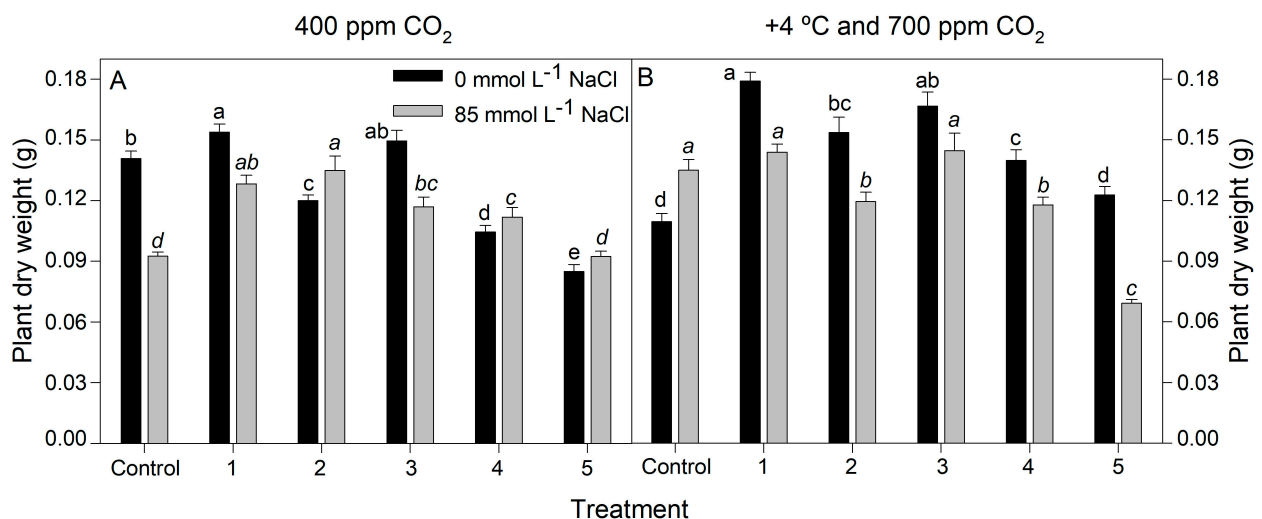


Figure 2. Dry weight of rice plants inoculated with rhizobacteria consortia, numbered 1 to 5 (control = non-inoculated plants), after 20 d of treatment at $400 \text{ ppm } CO_2$ (A) and at $+4 \text{ }^\circ\text{C}$ and $700 \text{ ppm } CO_2$ (B) with 0 and 85 mmol L^{-1} NaCl. Each value represents the mean of twenty replicates \pm SE. Different letters for each saline treatment (capital and italic letters for 0 and 85 mmol L^{-1} NaCl, respectively) indicate means that are significantly different from each other (GLM; Duncan test, $p < 0.05$).

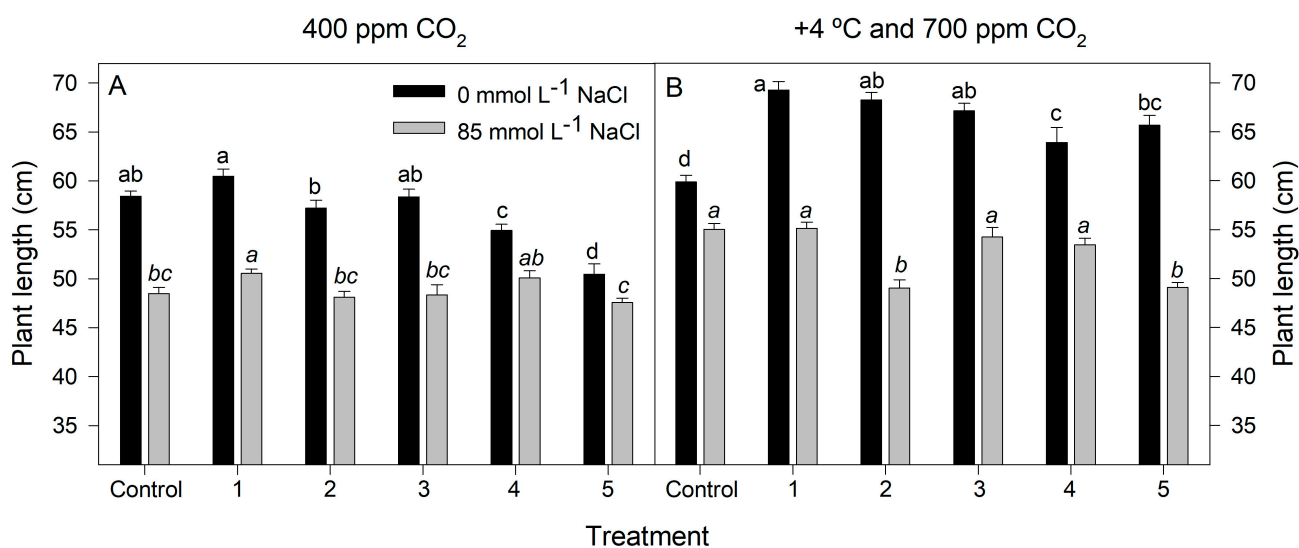


Figure 3. Length of rice plants inoculated with rhizobacteria consortia, numbered 1 to 5 (control = non-inoculated plants), after 20 d of treatment at 400 ppm CO₂ (A) and at +4 °C and 700 ppm CO₂ (B) with 0 and 85 mmol L⁻¹ NaCl. Each value represents the mean of twenty replicates ±SE. Different letters for each saline treatment (capital and italics letters for 0 and 85 mmol L⁻¹ NaCl, respectively) indicate means that are significantly different from each other (GLM; Duncan test, $p < 0.05$).

Overall, biofertilization improved the growth of rice plants by 28–64% in the absence of salt at high CO₂ and +4 °C ($p < 0.0001$). Nevertheless, there was not a significant effect from the dry weight of inoculated plants treated with 85 mmol L⁻¹ NaCl ($p < 0.0001$; Figure 2B). In the same way, there was not a significant effect on the length increase in plants grown without salt at 400 ppm CO₂ and 25 °C. However, in the presence of salt, plants treated with inoculum 1 showed an increased length by 4% with respect to the non-inoculated control ($p < 0.0001$; Figure 3A).

Finally, when the two treatments were combined (85 mmol L⁻¹ NaCl and high CO₂ and +4 °C), there was no beneficial effect of biofertilization on the length of the plants. However, in the absence of salt, the plants treated with inocula 1–5 significantly increased in length compared to the non-inoculated control by 7–16% ($p < 0.001$; Figure 3B).

3.2. Gas Exchange

In general, the values of the net photosynthetic rate (A) were higher at elevated CO₂ than those measured at ambient CO₂ (GLM, $p < 0.0001$; Figure 4). There was no positive effect from biofertilization on A of plants grown in the absence of salt and ambient CO₂; in fact, inoculum 5 had a negative effect on A (GLM, $p < 0.0001$; Figure 4A). Plants treated with biofertilizer 2 showed the highest A in the presence of salt, although there were no significant differences compared to control plants without inoculation ($p < 0.01$). This A value corresponded to a lower intercellular CO₂ concentration (C_i), but stomatal conductance (G_s) remained at values similar to those of the control (Figure 4B,C). In the same way, A values and inoculum 2 increased instantaneous water use efficiency (iWUE) by 23.5% at 85 mmol L⁻¹ NaCl (Figure 4D).

The trend described previously was also observed at 700 ppm CO₂ at +4 °C. Only in the presence of salt there was a beneficial effect from inoculation (GLM, $p < 0.0001$). Again, inoculum 2 improved A values by 19% compared to non-inoculated control plants (Figure 4E). This increase also corresponded to lower C_i values, while G_s remained unchanged with respect to the control (Figure 4F,G). Finally, plants treated with biofertilizer 2 showed the highest iWUE values (Figure 4H).

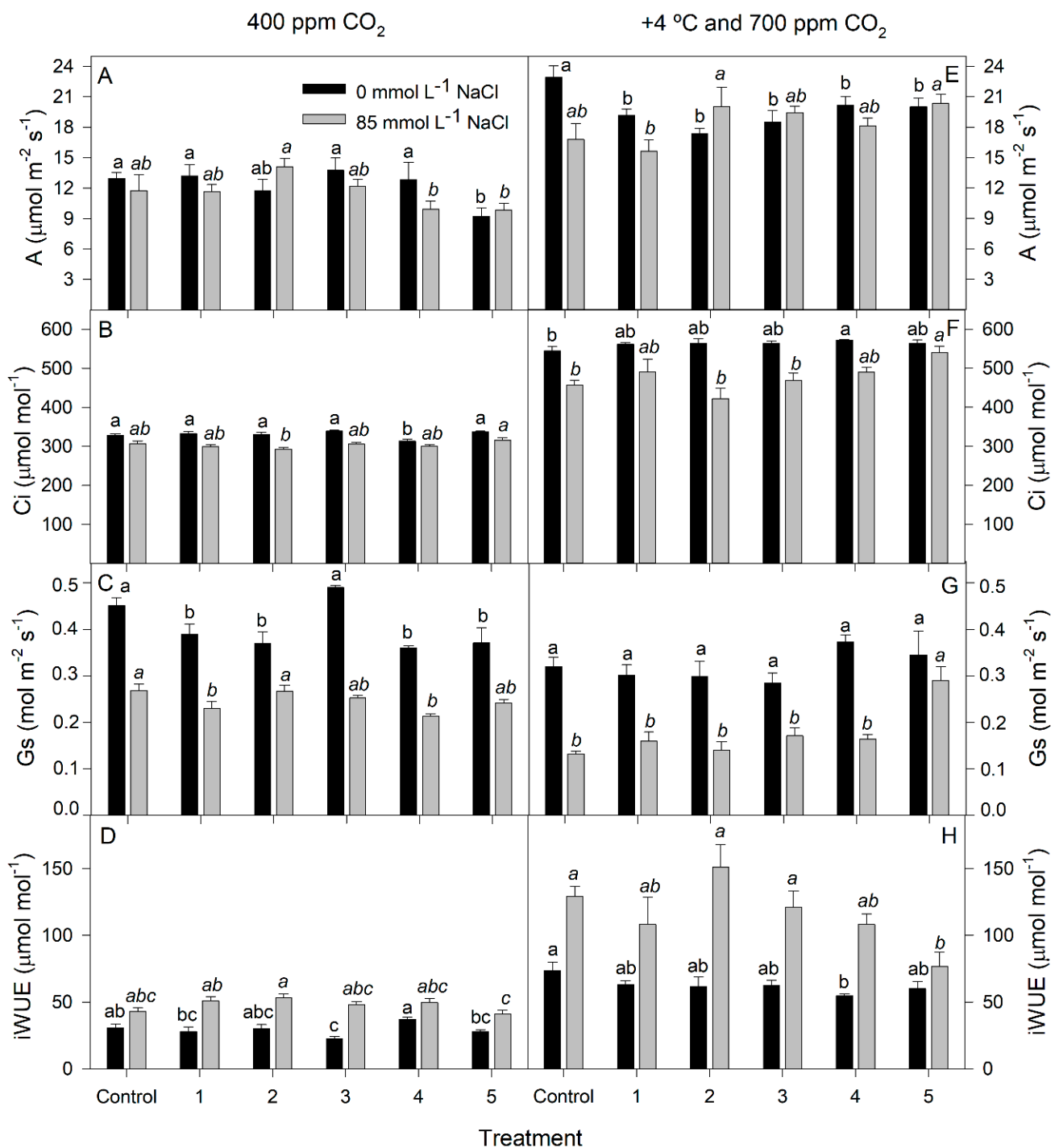


Figure 4. (A), Net photosynthetic rate (A,E); Ci, intercellular CO₂ concentration (B,F); Gs, stomatal conductance (C,G); and iWUE, instantaneous water use efficiency (D,H) of rice plants inoculated with rhizobacteria consortia, numbered 1 to 5 (control = non-inoculated plants), after 20 d of treatment at 400 ppm CO₂ (A–D) and at +4 °C and 700 ppm CO₂ (E–H) with 0 and 85 mmol L⁻¹ NaCl. Each value represents the mean of five replicates ±SE. Different letters for each saline treatment (capital and italic letters for 0 and 85 mmol L⁻¹ NaCl, respectively) indicate means that are significantly different from each other (GLM; Duncan test, *p* < 0.05).

3.3. Chlorophyll Fluorescence

Biofertilizer 1 was the only inoculant that produced a beneficial effect on photosystem II (PSII) activity in the rice plants grown at 400 ppm CO₂ and 25 °C since the maximum

quantum efficiency of PSII photochemistry (Fv/Fm) of plants treated with this inoculum was significantly higher than the non-inoculated control at 0 mmol L⁻¹ NaCl ($p < 0.0001$). This effect was not observed in the presence of salt ($p > 0.05$; Figure 5A) and was reversed at 700 ppm CO₂ +4 °C, having only a significant positive effect on Fv/Fm values in the presence of salt. Notably, inoculum 2 was the one producing an improvement PSII activity, recording a higher Fv/Fm value than the control ($p < 0.05$; Figure 5B). Finally, Fv/Fm values were lower at elevated CO₂ +4 °C than at ambient CO₂, regardless of saline treatment ($p < 0.0001$).

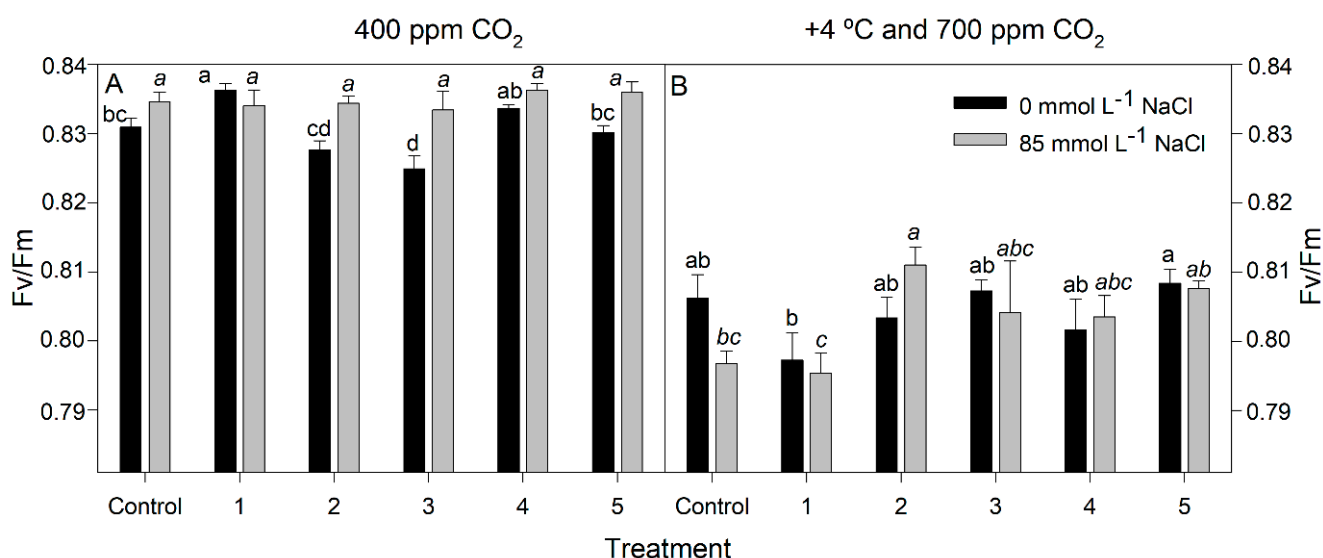


Figure 5. Maximum quantum efficiency of PSII photochemistry (Fv/Fm) of rice plants inoculated with rhizobacteria consortia, numbered 1 to 5 (control = non-inoculated plants), after 20 d of treatment at 400 ppm CO₂ (A) and at +4 °C and 700 ppm CO₂ (B) with 0 and 85 mmol L⁻¹ NaCl. Each value represents the mean of ten replicates \pm SE. Different letters for each saline treatment (capital and italics letters for 0 and 85 mmol L⁻¹ NaCl, respectively) indicate means that are significantly different from each other (GLM; Duncan test, $p < 0.05$).

4. Discussion

Both salinity and 700 ppm CO₂ +4 °C treatments were stressful conditions for rice plants, as they reduced plant growth and increased photoinhibition, that is, low Fv/Fm values. Our results are in agreement with previous results found for the Shiroudi rice variety, which reduced its total dry weight at 700 ppm CO₂ compared to plants treated with 360 ppm CO₂ [21]. Nonetheless, Cheng et al. [22] found that dry weight was higher for rice plants grown at high CO₂ concentration and high or low night temperatures (32 and 22 °C, respectively). In the same way, Feng et al. [23] observed a greater relative growth rate in rice seedlings at 700 ppm CO₂ and 27 °C than those grown at 450 ppm CO₂ and 23 °C, and this trend was maintained in the presence of 1.1 g Na L⁻¹. This is in line with our findings in the presence of salt for non-inoculated plants. We have reported an increase in plant dry weight at 700 ppm CO₂ +4 °C and 85 mmol L⁻¹ NaCl with respect to plants at ambient CO₂. This was not the case for the plant length since the lowest size was recorded in plants grown under the interaction of the two stressors. On the other hand, Kazemi et al. [21] concluded that the negative effects of salinity on rice plant growth were intensified by elevated CO₂ conditions, which enhanced cell membrane damage. The adverse effects of salinity are also intensified with increasing temperature [24].

Interestingly, the higher rate of net photosynthesis measured for the non-inoculated control at elevated CO₂ +4 °C did not correspond to higher dry weight with respect to the non-inoculated control at ambient CO₂. Carbon dioxide is expected to increase photosynthesis, dry matter production, and yield; decrease stomatal conductance rate and transpiration in C₃ and C₄ species; and improve the water use efficiency of plants [25].

However, high CO₂ suppresses photorespiration, which has been linked to nitrogen uptake capacity [26]. It has been reported that *Arabidopsis* mutants with impaired nitrate uptake capacity showed a greater effect on growth at elevated CO₂ concentrations than at lower concentrations [27], which was due to a reduction in the mutant's ability to assimilate nitrate at elevated CO₂. In our study, in the absence of salt and at 700 ppm CO₂ +4 °C, the effect on growth might be overall counteracted by biofertilization, as all consortia contained strains with nitrogen fixation capacity. Furthermore, photorespiration plays an important role in plant carbon metabolism and provides tolerance to stress in plants [28]. Photorespiration counteracts photoinhibition and reactive oxygen species (ROS) production under high light conditions [29,30], which cause lipid peroxidation and chlorophyll degradation [31]. In this way, we found lower Fv/Fm values, at 700 ppm CO₂ +4 °C with respect to ambient CO₂.

In the absence of stress, biofertilizer 1 was the only one stimulating the growth of the rice plants. In contrast, biofertilizers 1–4 increased rice growth in the presence of stressors, salinity, or high CO₂ +4 °C. Finally, no effect from biofertilization was registered in the plants grown under the stress interaction, high CO₂ +4 °C and 85 mmol L⁻¹. A previous study found that inoculation with *Bacillus pumilis*, *Pseudomonas pseudoalcaligenes* alone and in combination increased the plant dry weight of the GJ-17 rice variety in the presence and in the absence of salt [32]. In this way, biofertilizer 1 was the only one that contained a strain of the genus *Pseudomonas*. Redondo-Gómez et al. [4] already described that consortia obtained from halophytes were really useful for salt stress alleviation under stress conditions [16].

The present work highlights the use of microbial consortia from halophytes to alleviate plant growth under a combination of abiotic stresses, even if a low effect on the improvement of photosynthetic rate is observed. Nevertheless, there was no determining property in the inocula, but rather in the combination of them. This makes the use of a microbial consortium more useful than the use of independent strains [5,8]. Biofertilizers 3 and 4 are composed of two PGPR strains with the ability to produce biofilm, and therefore, they are capable of chelating different cations. In this way, bacteria can bind with the Na⁺ ion under salt stress by means of the secretion of exopolysaccharides (EPS), consequently reducing its toxicity in the soil [33]. However, these biofertilizers were not the most effective in stimulating plant growth at 400 ppm CO₂ and 85 mmol L⁻¹ NaCl; it was consortium 2 that exhibited greater IAA production than consortia 1, 3 or 5. Higher IAA production could stimulate root growth and improve the uptake of nutrients and water for the plant. The flow of water and nutrients has previously been reported to stabilize stomatal conductance and transpiration rate, improving photosynthetic rate, iWUE, and starch production, and therefore, stimulating plant growth under salinity conditions [13]. Indeed, we also observed higher iWUE values for plants treated with salt and biofertilizer 2 at ambient CO₂. Interestingly, biofertilizer 1, with a lower IAA production capacity, stimulated the growth of rice plants to the same extent as biofertilizer 2, although the first contained PGPR capable of solubilizing P and had greater siderophore production, which would also imply an improvement in the nutritional status of the plants. Finally, biofertilizer 5, which along with 4 was the most complete in terms of PGPR traits, only improved plant length at high CO₂ levels without salt.

5. Conclusions

Biofertilizers containing microbial consortia from halophytes proved to be effective in mitigating the negative effects of salinity and high CO₂ concentration and temperature on rice plants, although they did not show an effect when the interaction between these abiotic factors was tested. These biofertilizers improved plant growth and physiological response. Biofertilizers 1–4 stimulated plant growth in the presence of salt stress or high CO₂ +4 °C. Furthermore, these consortia kept photosynthetic rate, instantaneous water use efficiency, and the maximum quantum efficiency of PSII photochemistry of the rice plants at similar values to those of the control. The combination of strains in a consortium shows a synergistic effect that provides better PGPR features than the individual strains.

Studies that identify the effect of different stressors on crop are very scarce, and studies that consider inoculation with PGPR to mitigate the effects of these stressors are even more so. This highlights the significance of developing studies that consider stress interaction to establish the real potential of biofertilizers in the context of climate change conditions.

Finally, it would be necessary to analyse in the future biofertilizer effectiveness in field experiments and study their effect on crop production.

Author Contributions: S.R.-G. and E.M.-N. conceived the study, supervised, and acquired funding for the project. S.R.-G. performed data analysis and wrote the manuscript with input from E.M.-N., J.M.-M., V.M. with assistance from F.P.M.-H., J.A.P.-R. and C.Á., E.P. and I.D.R.-L. provided the bacterial inocula. All authors performed the experimental development. All authors have read and agreed to the published version of the manuscript.

Funding: This work has been supported by MINECO (CGL2016-75550-R, AEI/FEDER, UE).

Data Availability Statement: The data presented in this study are available on request from the corresponding author.

Acknowledgments: The authors thank the University of Seville Greenhouse General Services (CITIUS) for its collaboration. J.M.-M. acknowledges the European Social Fund and Junta de Andalucía for personal funding (Talento Doctores DOC_00725).

Conflicts of Interest: The authors declare that they have no conflict of interest.

References

- Ríos-Ruiz, W.F.; Torres Chávez, E.E.; Torres-Delgado, J.; Rojas-García, J.C.; Bedmar, E.J.; Valdez-Nuñez, R.A. Inoculation of bacterial consortium increases rice yield (*Oryza sativa* L.) reducing applications of nitrogen fertilizer in San Martin region, Peru. *Rhizosphere* **2020**, *14*, 100200. [[CrossRef](#)]
- Olanrewaju, O.S.; Glick, B.R.; Babalola, O.O. Mechanisms of action of plant growth promoting bacteria. *World J. Microbiol. Biotechnol.* **2017**, *33*, 197. [[CrossRef](#)]
- Adeleke, R.A.; Raimi, A.R.; Roopnarain, A.; Mokubedi, S.M. Status and prospects of bacterial inoculants for sustainable management of agroecosystems. In *Biofertilizers for Sustainable Agriculture and Environment*; Giri, B., Prasad, R., Wu, Q.S., Varma, A., Eds.; Springer Nature: Cham, Switzerland, 2019; pp. 137–172.
- Redondo-Gómez, S.; Mesa-Marín, J.; Pérez-Romero, J.A.; López-Jurado, J.; García-López, J.V.; Mariscal, V.; Molina-Heredia, F.P.; Pajuelo, E.; Rodríguez-Llorente, I.D.; Flowers, T.J.; et al. Consortia of plant-growth-promoting rhizobacteria isolated from halophytes improve response of eight crops to soil salinization and climate change conditions. *Agronomy* **2021**, *11*, 1609. [[CrossRef](#)]
- Mesa-Marín, J.; Mateos-Naranjo, E.; Rodríguez-Llorente, I.D.; Pajuelo, E.; Redondo-Gómez, S. Synergic Effect Rhizobacteria—Halophytes as a Rising Strategy to Face a Changing World. In *Halophytes and Climatic Change: Adaptive mechanisms and Potential Uses*; Hasanuzzaman, M., Shabala, S., Fujita, M., Eds.; CABI: Wallingford, UK, 2019; pp. 240–254.
- Thomas, L.; Singh, I. Microbial Biofertilizers: Types and Applications. In *Biofertilizers for Sustainable Agriculture and Environment*; Giri, B., Prasad, R., Wu, Q.S., Varma, A., Eds.; Springer Nature: Cham, Switzerland, 2019; pp. 1–19.
- Das, N.; Basak, L.V.G.; Salam, J.A.; Abigail, E.A. Application of biofilms on remediation of pollutants—An overview. *J. Microbiol. Biotechnol.* **2012**, *2*, 783–790.
- Du Jardin, P. Plant biostimulants: Definition, concept, main categories and regulation. *Sci. Hortic. Amst.* **2015**, *196*, 3–14. [[CrossRef](#)]
- FAO. *Crop Prospect and Food Situation*; Quaternary Global Report; FAO: Rome, Italy, 2023. [[CrossRef](#)]
- Fahad, S.; Adnan, M.; Noor, M.; Arif, M.; Alam, M.; Khan, I.A.; Basir, A. Major constraints for global rice production. In *Advances in Rice Research for Abiotic Stress Tolerance*; Hassanuzzaman, M., Fujita, M., Biswas, J.K., Eds.; Woodhead Publishing: Cambridge, UK, 2019; pp. 1–22.
- Khumairah, F.H.; Setiawati, M.R.; Fitriatin, B.N.; Simarmata, T.; Alfaraj, S.; Ansari, M.J.; Enshasy, H.A.; Sayyed, R.Z.; Najafi, S. Halotolerant Plant Growth-Promoting Rhizobacteria Isolated From Saline Soil Improve Nitrogen Fixation and Alleviate Salt Stress in Rice Plants. *Front. Microbiol.* **2022**, *13*, 905210. [[CrossRef](#)] [[PubMed](#)]
- Joshi, B.; Chaudhary, A.; Singh, H.; Kumar, P.A. Prospective evaluation of individual and consortia plant growth promoting rhizobacteria for drought stress amelioration in rice (*Oryza sativa* L.). *Plant Soil* **2020**, *457*, 225–240. [[CrossRef](#)]
- Shultana, R.; Zuan, A.T.K.; Yusop, M.R.; Saud, H.M.; Ayanda, A.F. Effect of salt-tolerant bacterial inoculations on rice seedlings differing in salt-tolerance under saline soil conditions. *Agronomy* **2020**, *10*, 1030. [[CrossRef](#)]
- Sultana, S.; Paul, S.C.; Parveen, S.; Alam, S.; Rahman, N.; Jannat, B.; Hoque, S.; Rahman, M.T.; Karim, M.M. Isolation and identification of salt-tolerant plant-growth-promoting rhizobacteria and their application for rice cultivation under salt stress. *Can. J. Microbiol.* **2020**, *66*, 144–160. [[CrossRef](#)]

15. Mandhania, S.; Madan, S.; Sawhney, V. Antioxidant defense mechanism under salt stress in wheat seedling. *Biol. Plant* **2006**, *50*, 227–231. [[CrossRef](#)]
16. Redondo-Gómez, S.; García-López, J.V.; Mesa-Marín, J.; Pajuelo, E.; Rodríguez-Llorente, I.D.; Mateos-Naranjo, E. Synergistic Effect of plant-growth-promoting rhizobacteria improves strawberry growth and flowering with soil salinization and increased atmospheric CO₂ levels and temperature conditions. *Agronomy* **2022**, *12*, 2082. [[CrossRef](#)]
17. Etesami, H.; Beattie, G.A. Mining halophytes for plant growth-promoting halotolerant. Bacteria to enhance the salinity tolerance of non-halophytic crops. *Front. Microbiol.* **2018**, *9*, 148. [[CrossRef](#)] [[PubMed](#)]
18. Álvarez, C.; Navarro, J.A.; Molina-Heredia, F.P.; Mariscal, V. Endophytic colonization of rice (*Oryza sativa* L.) by the symbiotic strain *Nostoc punctiforme* PCC 73102. *Mol. Plant Microbe Interact.* **2020**, *33*, 1040–1045. [[CrossRef](#)]
19. Mesa-Marín, J.; Pérez-Romero, J.A.; Redondo-Gómez, S.; Pajuelo, E.; Rodríguez-Llorente, I.D.; Mateos-Naranjo, E. Impact of plant growth promoting bacteria on *Salicornia ramosissima* ecophysiology and heavy metal phytoremediation capacity in estuarine soils. *Front. Microbiol.* **2020**, *11*, 553018. [[CrossRef](#)]
20. Maxwell, K.; Johnson, G.N. Chlorophyll fluorescence—A practical guide. *J. Exp. Bot.* **2000**, *51*, 659–668. [[CrossRef](#)]
21. Kazemi, S.; Eshghizadeh, H.R.; Zahedi, M. Responses of four rice varieties to elevated CO₂ and different salinity levels. *Rice Sci.* **2018**, *25*, 142–151. [[CrossRef](#)]
22. Cheng, W.; Sakai, H.; Yagi, K.; Hasegawa, T. Interactions of elevated [CO₂] and night temperature on rice growth and yield. *Agric. For. Meteorol.* **2009**, *149*, 51–58. [[CrossRef](#)]
23. Feng, Y.X.; Tian, P.; Li, C.Z.; Zhang, Q.; Trapp, S.; Yu, X.Z. Individual and mutual effects of elevated carbon dioxide and temperature on salt and cadmium uptake and translocation by rice seedlings. *Front. Plant Sci.* **2023**, *14*, 1161334. [[CrossRef](#)]
24. Collalti, A.; Ibrom, A.; Stockmarr, A.; Cescatti, A.; Alkama, R.; Fernández-Martínez, M.; Matteucci, G.; Sitch, S.; Friedlingstein, P.; Ciais, P.; et al. Forest production efficiency increases with growth temperature. *Nat. Commun.* **2020**, *11*, 5322. [[CrossRef](#)] [[PubMed](#)]
25. Lawlor, D.W.; Mitchell, R.A.C. The effects of increasing CO₂ on crop photosynthesis and productivity: A review of field studies. *Plant Cell Environ.* **1991**, *14*, 807–818. [[CrossRef](#)]
26. Busch, F.A.; Sage, R.F.; Farquhar, G.D. Plants increase CO₂ uptake by assimilating nitrogen via the photorespiratory pathway. *Nat. Plants* **2018**, *4*, 46–54. [[CrossRef](#)]
27. Takatani, N.; Ito, T.; Kiba, T.; Mori, M.; Miyamoto, T.; Maeda, S.; Omata, T. Effects of high CO₂ on growth and metabolism of *Arabidopsis* seedlings during growth with a constantly limited supply of nitrogen. *Plant Cell Physiol.* **2014**, *55*, 281–292. [[CrossRef](#)] [[PubMed](#)]
28. Voss, I.; Sunil, B.; Scheibe, R.; Raghavendra, A.S. Emerging concept for the role of photorespiration as an important part of abiotic stress response. *Plant Biol.* **2013**, *15*, 713–722. [[CrossRef](#)] [[PubMed](#)]
29. Takahashi, S.; Badger, M.R. Photoprotection in plants: A new light on photosystem II damage. *Trends Plant Sci.* **2011**, *16*, 53–60. [[CrossRef](#)] [[PubMed](#)]
30. Dusenge, M.E.; Duarte, A.G.; Way, D.A. Plant carbon metabolism and climate change: Elevated CO₂ and temperature impacts on photosynthesis, photorespiration and respiration. *New Phytol.* **2019**, *221*, 32–49. [[CrossRef](#)]
31. Schütz, M.; Fangmeier, A. Growth and yield responses of spring wheat (*Triticum aestivum* L. cv. Minaret) to elevated CO₂ and water limitation. *Environ. Pollut.* **2001**, *114*, 187–194. [[CrossRef](#)]
32. Jha, Y.; Subramanian, R.B.; Patel, S. Combination of endophytic and rhizospheric plant growth promoting rhizobacteria in *Oryza sativa* shows higher accumulation of osmoprotectant against saline stress. *Acta Physiol. Plant.* **2011**, *33*, 797–802. [[CrossRef](#)]
33. Arora, M.; Kaushik, A.; Rani, N.; Kaushik, C.P. Effect of cyanobacterial exopolysaccharides on salt stress alleviation and seed germination. *J. Environ. Biol.* **2010**, *31*, 701–704.

Disclaimer/Publisher’s Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.