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Inoculation of ACC Deaminase-Producing *Brevibacterium linens* RS16 Enhances Tolerance against Combined UV-B Radiation and Heat Stresses in Rice (*Oryza sativa* L.)

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Abstract: UV-B radiation and high temperature have detrimental effects on plant physiological and biochemical processes. The use of bacterial inoculants for stress alleviation has been regarded as a sustainable and eco-friendly approach. Hence, this study was conducted to evaluate the ability of 1-aminocyclopropane-1-caboxylate (ACC) deaminase-producing *Brevibacterium linens* RS16 in enhancing stress tolerance in rice against combined UV-B radiation and heat stresses. A combination of 0.5 Wm^{-2} UV-B radiation and 40 °C of temperature were imposed on rice plants for 5 days. The plants imposed with combined stress had shown significantly higher ethylene emissions compared to the plants grown under normal conditions. In addition, the stress imposition had shown negative effects on the photosynthetic traits, biomass, and genetic material of rice plants. The inoculation of bacteria had shown a 26.5% and 31.8% decrease in ethylene emissions at 3 and 4 days of stress imposition compared to the non-inoculated plants. Additionally, bacterial inoculation had also enhanced plant biomass and photosynthetic traits, and had proved to be effective in restricting DNA damage under stress conditions. Taken together, the current study has shown the effective strategy of enhancing stress tolerance against the interactive effects of UV-B radiation and heat stresses by regulation of ethylene emissions through inoculating ACC deaminase-producing bacteria.

Keywords: ACC deaminase; *Brevibacterium linens* RS16; DNA damage; ethylene; heat stress; UV-B radiation

1. Introduction

Industrial emissions during the past century have resulted in the depletion of the ozone layer and uncontrolled penetration of UV-B radiation in the Earth's atmosphere [1]. The adaptation of the Montreal Protocol has restricted the widening of the ozone hole [2] and the total recovery of the depleted ozone layer will take decades to revert back to the pre-industrial era [3,4]. The exposure to irradiation has shown significant effects on the physiological and biochemical processes of plants, such as a decrease in biomass and leaf area, DNA damage, stress ethylene emission, accumulation of reactive oxygen species and flavonoids, membrane disintegration, and cell death [5–8]. In addition, global warming is another threatening factor affecting the life cycle of plants and has shown negative impacts on the majority of plant physiological characteristics, such as photosynthesis, growth, and water loss due to enhanced transpiration, and pollen viability is also a matter

of concern [9–11]. The global temperature has already recorded a rise in 0.8 °C as of 2012 and it is expected to rise up to 1.5 °C, compared to the pre-industrial era, by the end of 21st century [12]. Rice (*Oryza sativa* L.) is a major crop that is grown in lower latitudinal regions, leading to its exposure towards a higher flux of UV due to the greater solar angle and longer duration of sunlight [13]. Additionally, these regions have also shown a steady increase in the rise of surface temperature in the past decade [14].

Researchers have previously focused on studying the interactive effect of UV-B radiation and heat stress on plants. For example, such combined stresses have shown changes in flavonoid and phenolic profiles in *Brassica oleracea* var. *sabellica* and *Picea abies* [15,16]; altered timelines of bud setting in male and female clones of *Populus tremula*, leading to decreasing chances of fertilization [17]; shown effects on growth and reproduction in *Salix myrsinifolia* [18]; and have enhanced volatile organic compound (VOC) emissions from *Populus tremula* [19]. However, these studies were specific to a few ornamental plants and vegetation native to Europe. Hence, studying the effect of combined UV-B radiation and heat stresses on a major food crop such as rice will be valuable in the field of agriculture.

The use of ACC deaminase-producing, plant growth-promoting bacteria (PGPB) has shown promising results in the enhancement of plant growth and stress alleviation under various environmental conditions [20–22]. However, there have been a lack of studies that explore the effectiveness of bacterial inoculation in enhancing stress tolerance under combined UV-B radiation and heat stresses. Such studies will address the potential strategy to enhance plant growth and productivity in the recent climate change scenario. *Brevibacterium linens* RS16 is a characteristic ACC deaminase-producing bacteria that has the ability to alleviate a varied range of stresses [21–23] and recently we reported its ability to enhance tolerance against UV-B radiation in rice by regulating ethylene emission levels [7]. Hence, this study was conducted to evaluate the ability of *B. linens* RS16 in enhancing the stress tolerance of rice against combined UV-B radiation and heat stresses by monitoring ethylene emission, photosynthetic traits, plant biomass, and DNA damage.

2. Materials and Methods

Rice (*O. sativa* L. ssp. *japonica* cv. Chucheongbyo) seeds were germinated by soaking them on water in a dark chamber at 30 °C for 72 h. The germinated seedlings were transplanted in a seedling tray and kept in a growth chamber (DS 54 GLP, DASOL Scientific Co., Ltd., Seoul, Korea) with 32 °C/28 °C, 16–8 h day/night conditions, and 70% relative humidity. The inoculum of *B. linens* RS16 was prepared by growing the bacterium in a nutrient broth until OD_{600}~0.8, washing three times in 0.03 M $MgSO_4$, and eventually resuspending in the same by maintaining OD_{600}~0.8. After 5 days of sowing in the seedling tray, a total of 30 rice seedlings were transplanted in a 60 mL pot containing 50 g of nursery soil (Doobaena, Nongkung Co., Jincheon-gun, Korea). The bacterial suspension (10 mL) was inoculated near the root zone of the transplanted seedlings. The non-inoculated plants were treated with 10 mL 0.03 M $MgSO_4$. The transplanted seedlings were grown for 2 days in the growth chamber and the subsequent treatments were applied.

UV-B radiation was applied at an intensity of 0.5 W m^{-2} using UV-B lamps (Sankyo Ultraviolet Co. Ltd., Kanagawa, Japan) (the spectral intensity of the fluorescence lamps and UV-B lamps are provided in Figure S1) for 6 h during the day (9 AM to 3 PM) and heat stress was applied by raising the temperature to 40 °C for 2 h at the 4th–6th h (1 PM to 3 PM) of UV-B irradiation treatment. Control plants were kept in a different growth chamber and grown without any irradiation or heat stress. Rice seedlings were harvested at 2, 3, 4, and 5 days after the stress treatment for measuring the ethylene emission, chlorophyll fluorescence, photosynthetic activity, DNA laddering, and phenolic content. Ethylene emission was measured by transferring the pots in a 1-L customized GC bottle and closing the lid for an additional 1 h in a stress condition, thereby collecting 1 mL of air from the headspace and injecting it into a gas chromatograph (dsCHROM 6200, Donam Instruments Inc., Korea) equipped with the Poropak-Q column. The photosynthetic rate was measured by using a portable photosynthesis system (LI-6800, Li-Cor, Lincoln, NE, USA) and the

data were recorded once the rate reached the steady state (in ca. 15–20 min after leaf enclosure). The leaf area was recorded by scanning the leaf enclosed in the measurement block at 300 dpi and analyzing the figure in Image J software. The photosynthetic rate was calculated according to von Caemmerer and Farquhar [24]. Chlorophyll fluorescence was recorded by measuring the ratio of F_v and F_m using a PAM fluorometer (PAM 2000, Heinz Walz GmbH, Effeltrich, Germany). The rice leaves were adapted to the dark for 20 min prior to the measurement of chlorophyll fluorescence. The maximum (F_m) and minimum (F_o) fluorescence were recorded using a 20 kHz saturating light pulse with 1100 µmol m^{-2} s^{-1} PPFD and the final calculation was done using the formula:

$$\frac{F_v}{F_m} = \frac{F_m - F_o}{F_m}$$

DNA damage due to the combined stress was determined by extracting the genomic DNA from the fresh leaves (0.5 g) of rice plants using the Wizard® Genomic DNA Isolation Kit (Promega, Madison, WI, USA) as per the manufacturer's protocol and running an electrophoresis using 0.8% agarose gel. The leaf samples were chosen from the region in which necrosis was the least present for eliminating biasness in the result. The intensity of the genomic DNA band was measured by using a Gel Doc (Biorad, CA, USA). The study was carried out in a randomized block design and the data obtained were subjected to a one-way analysis of variance (ANOVA). The significant differences between the means within the treatments were determined by Tukey's test at $p < 0.05$ using SAS package, Version 9.4.

3. Results and Discussions

3.1. Bacterial Inoculation Reduced Ethylene Emissions and Enhanced Plant Biomass under Combined UV-B Radiation and Heat Stresses

Elevated levels of ethylene are a typical response for various environmental stress conditions [25]. In this study, ethylene emissions from plants imposed with combined UV-B radiation and heat stresses were significantly higher compared to the plants grown under normal conditions at 2, 3, and 4 days after the stress treatment (Figure 1a). These results corroborate the previous studies in which elevated ethylene emissions were induced by UV-B radiation in rice plants [7] and heat stress in wheat [26] and soybean [27]. Additionally, the inoculation of *B. linens* RS16 resulted in a significant decrease in ethylene emissions compared to non-inoculated plants at 3 and 4 days after the stress imposition (Figure 1a). The inoculation of bacteria had shown a 26.5% and 31.8% decrease in ethylene emissions compared to non-inoculated plants at 3 and 4 days after the stress imposition, respectively. The decrease in ethylene emissions can be attributed to the ability of *B. linens* RS16 to produce ACC deaminase [23], which can scavenge the precursor of ethylene, ACC, and convert it into α-ketobutyrate and ammonia [20,25]. Interestingly, the non-inoculated stressed plants had shown significantly lower ethylene emissions compared to the other treatments. This may be due to the fact that those plants had shown leaf necrosis due to the stress imposition, as shown in Figure S2. Previous studies have shown that these stresses, when imposed individually on plants, can lead to leaf necrosis [26,28], which can be the reason for the accelerated death of leaf tissues of rice and, in turn, the decrease in ethylene emissions during prolonged exposure to combined stresses.

The elevated ethylene emissions have been broadly attributed to the decrease in plant biomass [20,25,29]. The combined UV-B radiation and heat stresses have also been observed to decrease plant growth [18]. Similarly, in this study, the combined stress resulted in a significant decrease in the dry weight of rice plants at 2, 3, 4, and 5 days after the stress treatment, irrespective of the bacterial inoculation, compared to the plants grown under normal conditions (Figure 1b). Conversely, the inoculation of *B. linens* RS16 resulted in a significant increase in the dry weight of the plants compared to the non-inoculated plants under normal and stress conditions at 3, 4, and 5 days after the stress treatment (Figure 1b). The inoculation had shown a 20.3%, 19.2%, and 11.9% increase in the dry weight of rice

plants compared to the non-inoculated plants under normal conditions at 3, 4, and 5 days after the stress treatment, respectively. In addition, the inoculated plants resulted in a 8.2%, 9.4%, and 7% increase in the plant dry weight compared to the non-inoculated plants under combined stress conditions at 3, 4, and 5 days after the stress imposition, respectively. Such an increase in the plant dry weight can be corroborated with previous studies in which the inoculation of *B. linens* RS16 was able to enhance the dry weight of rice [21] and canola [23] under salt stress conditions. In addition, *B. linens* RS16 has the ability to secrete hormones such as indole-acetic acid and cytokinins that are important for enhancing plant growth and for the ability to decrease stress ethylene levels through its ACC deaminase activity [23].

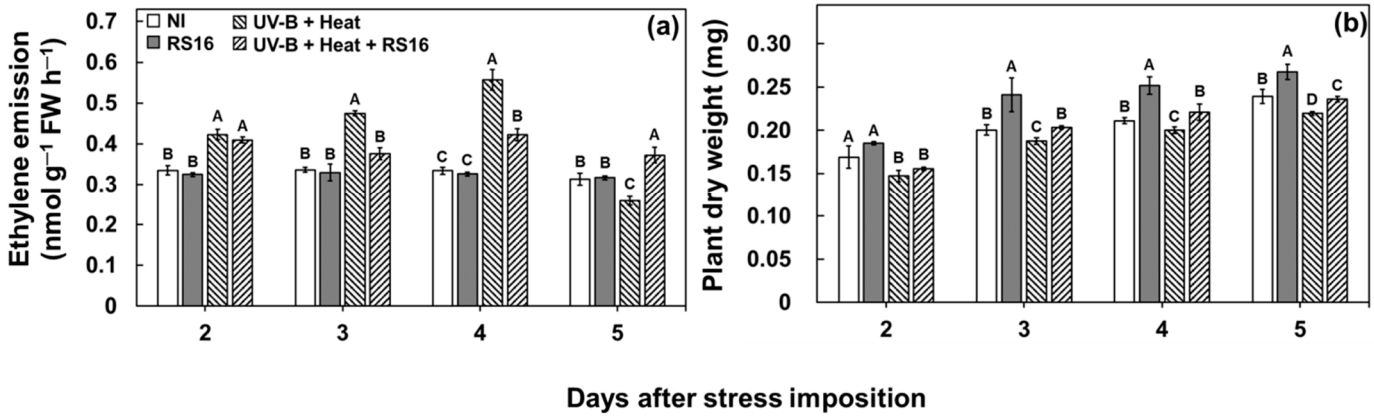

Figure 1. The effect of *B. linens* RS16 inoculation on ethylene emissions (**a**) and the dry weight (**b**) of rice plants imposed with combined UV-B radiation and heat stresses for 2, 3, 4, and 5 days. Different letters indicate significant differences, expressed as $p < 0.05$, among the treatments at each day.

3.2. Bacterial Inoculation Enhances Photosynthetic Traits under Combined UV-B Radiation and Heat Stresses

UV-B radiation and heat stress have been characterized as major factors in affecting photosynthesis in plants [30,31]. Plants grown under normal conditions have a F_v/F_m ratio of 0.8–0.83 and environmental stress decreases the ratio below 0.8 [32]. Similar inferences were drawn from the current study, wherein the chlorophyll fluorescence measured in terms of F_v/F_m were significantly decreased in rice plants imposed with combined UV-B radiation and heat stresses compared to the plants grown under normal conditions at 3, 4, and 5 days after the stress treatment (Figure 2a). These results corroborate with previous studies in which the imposition of UV-B radiation on peas and heat stress on rice had shown a decrease in chlorophyll fluorescence [22,33]. The decrease in chlorophyll fluorescence can be attributed to the severe impact on the functioning of photosystem II under these stress conditions [22,33]. However, the inoculation of ACC deaminase-producing bacteria had shown a significant increase in chlorophyll fluorescence compared to the non-inoculated plants at 3, 4, and 5 days after the stress treatment (Figure 2a). The bacterial inoculation had shown a 8%, 22.9%, and 17.9% increase in F_v/F_m measurements compared to the non-inoculated plants at 3, 4, and 5 days after the stress treatment. A similar effect was observed in the photosynthetic rate of plants imposed with combined stresses (Figure 2b). Additionally, the photosynthetic rate could not be measured from the non-inoculated plants at 4 and 5 days after the stress treatment. This can be due to the enhanced leaf necrosis pertained by the stress conditions that can be observed in Figure S2. The bacterial inoculation had shown a significantly higher photosynthetic rate in rice plants under normal and stress conditions (Figure 2a). The higher assimilation was observed in bacteria-inoculated plants throughout the experimental period for control conditions, whereas the higher assimilation rate was observed for bacteria-inoculated plants at 4 and 5 days after the combined stress treatment in rice plants. The increase in photosynthetic traits by the inoculation of *B. linens* RS16 was observed in rice and eucalyptus under salt and heat

stress, respectively [21,22]. Although the mechanism of ACC deaminase-producing bacteria regarding the enhancement of photosynthetic parameters still remains unclear, these results can be attributed to previous reports in which the PGPB inoculation assisted in increasing photosynthetic pigments under various environmental stress conditions [34,35]. In addition, the efficiency of ACC deaminase-producing bacteria in enhancing photosynthetic pigment concentrations under stress conditions suggests the ability of bacteria to nullify the adverse effects of combined UV-B radiation and heat stresses by enhancing the activity of electron transporters related to photosynthesis [36].

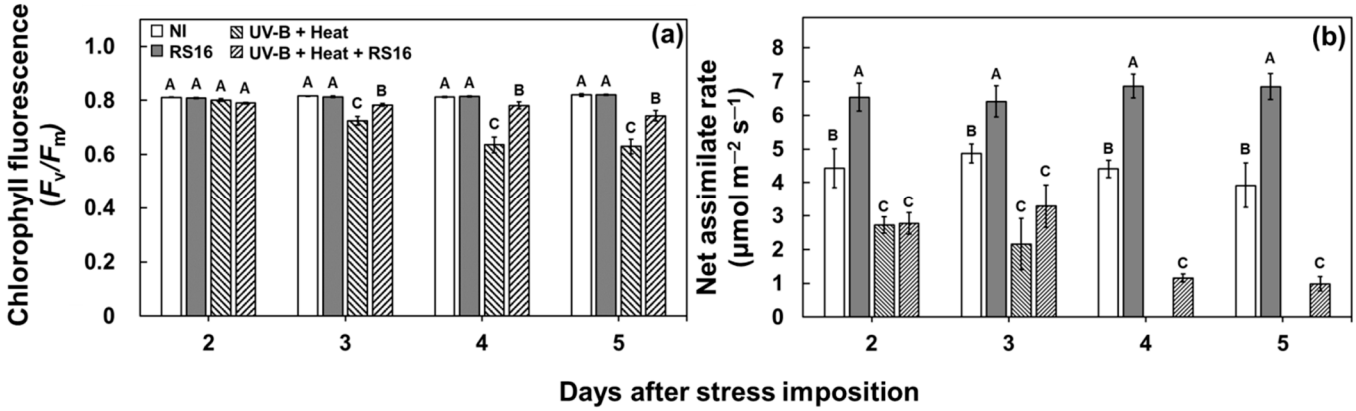

Figure 2. The effect of *B. linens* RS16 inoculation on chlorophyll fluorescence (**a**) and photosynthetic rate (**b**) of rice plants imposed with combined UV-B radiation and heat stresses for 2, 3, 4, and 5 days. Different letters indicate significant differences, expressed as $p < 0.05$, among the treatments at each day.

3.3. Combined Stress-Induced DNA Damage Was Alleviated by Bacterial Inoculation

The induction of DNA damage by UV-B radiation and heat stresses have been characterized previously [37,38]. The preliminary idea regarding DNA damage leading to programmed cell death is characterized by studying the effect of environmental stress on the DNA-laddering of the plant [38]. In this study, the DNA-laddering was evident in rice plants imposed with combined UV-B radiation and heat stresses (Figure 3a). In addition, the intensity signal from the genomic DNA loaded on the wells were lower for the stress imposed plants compared to the plants grown under normal conditions (Figure 3b). Furthermore, the genomic DNA of *B. linens* RS16 inoculated plants had shown higher intensity signals compared to the non-inoculated plants imposed with combined stresses. As it has been reported earlier, *B. linens* RS16 has the ability to secrete various enzymes such as phytoene desaturase, phytoene synthase, and ectoine synthase that are important for the synthesis of carotenoids, phytoene, and ectoine, which are important for stabilizing the DNA under environmental stress conditions [7]. Conversely, elevated ethylene emissions have been reported previously to accelerate DNA damage in cucumber [39] and the ability of ACC deaminase-producing *B. linens* RS16 in reducing ethylene emission levels could have minimized the effect of the combined stress on the rice genetic material.

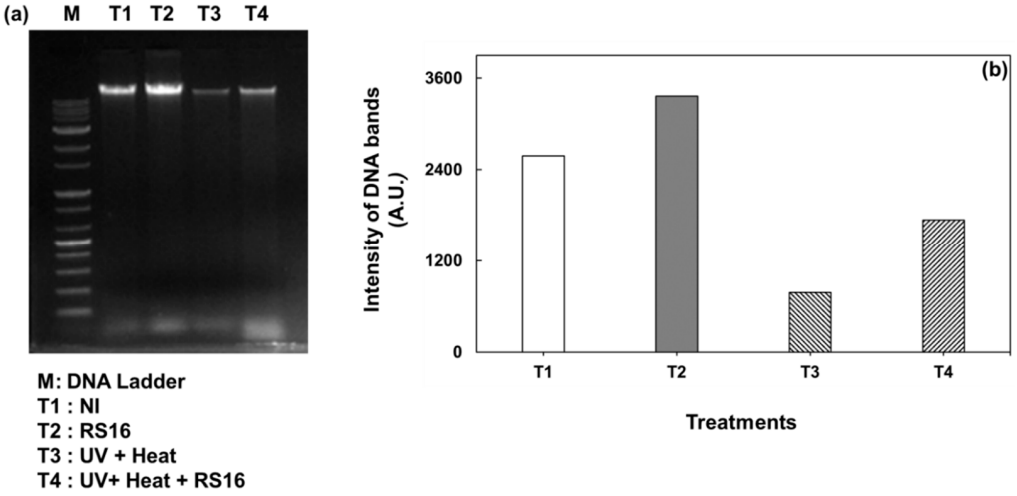

Figure 3. DNA-laddering (**a**) and band intensity (**b**) of rice genomic DNA inoculated with *B. linens* RS16 and imposed with combined UV-B radiation and heat stresses for 5 days.

4. Conclusions

The combined UV-B radiation and heat stresses have shown severe effects on physiological and biochemical aspects of rice plants. The combined stress treatment has resulted in enhanced ethylene emissions, leading to a decrease in plant biomass and also an acceleration in leaf necrosis during the prolonged exposure period. The combination of ionizing radiation and high temperature have also shown DNA damage that can be attributed to the induction of apoptosis and senescence. The resultant decrease in stress ethylene emissions through the ACC deaminase activity of *B. linens* RS16 was able to enhance plant biomass. Additionally, the increase in plant biomass can be attributed to the efficient functioning of the photosynthetic machinery through the bacterial inoculation and restriction of DNA damage, leading to the delayed senescence of rice plants. Hence, this study puts forward a novel paradigm in utilizing ACC deaminase-producing bacterial inoculants to enhance the tolerance of rice plants under combined UV-B radiation and heat stresses.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/su131810013/s1, Figure S1: Relative spectral distributions of the fluorescent lamps (a) and UV-B lamps (b) of the growth chamber; and Figure S2: Photograph of rice plants imposed with combined UV-B radiation and heat stresses for 3 (a), 4 (b), and 5 (c) days.

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Conflicts of Interest: The authors declare no conflict of interest.

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