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Comprehensive protection of tomato photosystem under cold stress by *Streptomyces* sp. TOR3209

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Abstract: The plant growth-promoting rhizobacterium *Streptomyces* sp. TOR3209 induces plant tolerance in a wide range of stress conditions. However, the protection of photosystem under cold stress has not been fully understood. Here we reported that the photochemistry activity of photosystem II (PSII) was increased in tomato plants receiving TOR3209 treatment, including the maximum quantum efficiency of PSII photochemistry (*Fv*/*Fm*), PSII operating efficiency (ΦPSII), PSII maximum efficiency (*Fv*'/*Fm*'), and non-photochemical quenching (NPQ). Microscopic study revealed that the integrity of chloroplast structure was greatly improved by TOR3209, which was damaged at low temperature. Moreover, TOR3209 treatment resulted in good protection on leaf stomatal and guard cell size. In response to TOR3209 treatment, the intercellular CO_2 concentration (*Ci*) and stomatal limitation values (*Ls*) were decreased while the mesophyll conductance (g_m) and chloroplast CO_2 concentration (*Cc*) were increased. The carotenoid content in TOR3209-treated tomato was accumulated at a higher level, which was involved in photoprotection and biosynthesis of abscisic acid (ABA), as well as the increased amounts of ABA in the leaves were subsequently verified in the plants treated with TOR3209. These results demonstrated that TOR3209 treatment comprehensively protected tomato photosynthesis at low temperatures.

Keywords: chlorophyll *a* fluorescence; chloroplast ultrastructure; low temperature; photosystem II efficiency; *Streptomyces*

Low temperature (LT) is regarded as a major abiotic stress that affects plant growth and crop productivity throughout the world (Zhu et al. 2010). Cold extreme weather is more common in high-latitude regions, such as North America, Europe, and northeastern Asia. There are 3.70 million ha of vegetable facility areas in China, 80% of the world's facility horticulture area, while plants grown in greenhouses, especially suffer LT during winter and winter-spring seasons in northern China. As a worldwide important vegetable crop, tomato (*Solanum lycopersicum* L.) is a thermophilic plant that is sensitive to LT stress and extensively cultivated in northern China (Ré et al. 2017; Zhang et al. 2020). Tomato

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plants grown at LT undergo many morphological, biochemical, physical and chemical processes, which consequently pose a great threat to the growth and development of the plants (Theocharis et al. 2012). Numerous studies have shown that plant photosynthesis is sensitive to LT. The photosynthesis capacity and efficiency are decreased owing to the decreased photosynthetic pigments, chlorophyll fluorescence and damaged chloroplast development (Major et al. 2010). The primary injury site in the photosynthesis system caused by cold stress is photosystem II (PSII) (Sharkey, Zhang 2010). Furthermore, LT leads to unconvertible damage to chloroplast development by altering chlorophyll antenna complexes or the thylakoid structures (Sveshnikov et al. 2006). Plasmalemma disruption leads to destructive damage of the inner section, including grana lamella, stroma lamella, and chloroplast thylakoid (Liu et al. 2012; Zhang et al. 2016). Chlorophyll (Chl) *a* fluorescence has been used as a rapid and accurate detection marker to study photosynthetic function, especially PSII (Dong et al. 2019).

Plants have evolved several mechanisms to protect the photosynthetic apparatus against photoinhibition, such as pigment production, abscisic acid (ABA) biosynthesis and antioxidant system. The radiant energy absorbed by chlorophylls is converted into steady chemical energy via photochemical processes which are coupled with reactive oxygen species (ROS) formation. However, production of excessive ROS under LT usually forms an oxidative stress, causing oxidative damage to membranous organ structures, especially PSII (Liu et al. 2015). The improved efficiency of the antioxidant system facilitates diminishing the deleterious effects of ROS. Carotenoids are crucial photosynthetic pigments that act as antioxidants against photooxidative stress and redox intermediates of PSII. Biosynthesis of carotenoids has been widely used to assess the plant growth affected by abiotic stress (Hugh et al. 2002; Zhang et al. 2012). Plant hormone ABA protects the photosynthetic apparatus against photoinhibition by enhancing the xanthophyll cycle and inducing an antioxidative defence (Han et al. 2020).

Plant growth-promoting rhizobacteria (PGPR) possess a prominent biological trait that regulates stress tolerance in a wide range of plants (Zhu et al. 2010). PGPR activates a set of mechanisms in plants to increase the resistance against biotic and abiotic stresses, including nutrient uptake facilitation and stimulating the production of phytohormones (Bhattacharyya, Jha 2012). *Pseudomonas fluorescens* strains induce a subnetwork specific to *Arabidopsis thaliana* roots enriched for genes participating in RNA regulation, protein degradation, and hormonal metabolism. Simultaneously, *P. fluorescens* GM30 induces the expression of genes related to photosynthesis and phytohormone metabolism (Weston et al. 2012). *A. thaliana* plants inoculated with *Azospirillum brasilense* show increased photosynthesis efficiency, biosynthesis of photoprotective pigments, and ABA production level (Bashan et al. 2006; Cohen et al. 2008).

Streptomyces sp. TOR3209 has been verified to be a PGPR for various plants (Hu et al. 2012; Hu et al. 2020). It plays an important role in protecting the growth of tomato plants under LT conditions (Ma et al. 2023). However, the LT protective mechanism of TOR3209 has largely remained elusive. To further analyse the mechanisms of tomato induced by TOR3209, detailed data on the physiological characteristics were investigated in this study. The changes of photosynthesis characteristics in carotenoids, chlorophyll fluorescence, and chloroplast ultrastructure were studied in tomato plants receiving TOR3209 treatment at LT. Our research fully manifested the role of TOR3209 for enhancing the PSII efficiency in tomato seedlings under cold stress.

MATERIAL AND METHODS

Plant cultivation. *Solanum lycopersicum* cultivar 'Chaoyan 219' (Tianjin Chaoyan Seed Technology Co., Ltd.), sensitive to cold stress, was used in this study. The seeds were surface sterilised by immersing in 70% (v/v) ethanol for 5 min, washed four times with deionised water, and then germinated in a 48-well nursery tray with plant soil mixture (peat : perlite : vermiculite, 1 : 1 : 1). After germination, the seedlings were placed in the greenhouse (16 h light/8 h dark, 25 °C). Plants were watered every two days. Thirty days after grown at green house, the seedlings were transplanted into pots (7 cm × 7 cm × 5 cm) with 100 g of the mixture of black soil (the basic physicochemical properties as following: pH 7.29, organic matter 18.17 g/kg, total nitrogen 1.09 g/kg, total phosphorus 0.91 g/kg and total potassium 19.47 g/kg) and vermiculite (1 : 1.5, v/v) at 25 °C, among these plants, twenty-five seedlings were irrigated with *Streptomyces* sp. TOR3209 at a dose of 10^7 CFU/g as previ-

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ously described (Hu et al. 2020). Fifteen days later, twenty-five seedlings with no inoculation were cultivated at 25 °C (day/night). Fifty seedlings were cultivated at 5 °C (day/night), which was designed as grown at LT, and the twenty-five seedlings were inoculated with *Streptomyces* sp. TOR3209 were included. The growing phenotype was scored at 1, 3, 6 and 10 days post LT treatment. Plant leaf length, width, and height were measured at 6 days post LT treatment by using five plants per treatment.

Quantitative assay of carotenoids and ABA biosynthesis. The carotenoids were extracted from 200 mg of fresh three samples from the second fully expanded top leaf at 1, 3, 6 and 10 days post LT treatment. The samples were fully ground in a mortar with a mixture of ethanol, acetone, and water in the proportion of 4.5 : 4.5 : 1 (v/v/v). After 25 mL of 96% ethanol was added, the samples were placed in the dark for 48 hours. Then the supernatant was used for absorption analysis at 649 nm, 665 nm, and 470 nm by using a UV-VIS spectrophotometer (UV 3200S, MAPADA, China). The contents of carotenoids in every extraction were calculated following standard equations (Wellburn, Lichtenthaler 1984). The experiment was repeated three times on three independent cultivated plants.

ABA was measured from tomato leaves according to the protocol of Wang et al. (2016a). Briefly, 1.0 g of fresh leaves was homogenised in liquid nitrogen and extracted in 5 mL of extraction buffer (methanol : formic acid : water = 15 : 1 : 4) for 24 h at –20 °C. After centrifuging at 10 000 × g for 15 min, ABA in the supernatant was quantified by light chromatography (LC)/tandem mass spectrometry (MS/MS) on an HPLC (Rigol L3000, Rigol Technologies, Beijing, China).

Assay of chlorophyll *a* fluorescence parameters. According to the manufacturer's instructions, the chlorophyll *a* fluorescence parameters were detected on the second top fully expanded leaf by a LI-6400 portable system (Li-Cor Inc., Lincoln, NE, USA). At 1, 3, 6 and 10 days post LT treatment, the plants were adapted to the dark for 30 min from 9 a.m. to 11 a.m. local time. The minimum chlorophyll *a* fluorescence (*Fo*) was measured at 0.1 μmol/m^2/s in a 2 × 3 cm^2 opaque leaf chamber. Maximum chlorophyll *a* fluorescence (*Fm*) and the relative PSII electron transport rate (ETR) were recorded with an 8-s saturating pulse of 3 000 μmol/m^2/s (Alsadon et al. 2013). The maximum quantum efficiency of PSII photochemistry (*Fv*/*Fm*), PSII operating efficiency (ΦPSII), PSII maximum efficiency (*Fv*'/*Fm*'), maximum chlorophyll fluorescence in the light-adapted state (*Fm*'), and photochemical quenching coefficient (*qP*) were recorded with a 3-s saturating pulse. Non-photochemical quenching (*NPQ*) was calculated from the approximation formulas of Baker (2008):

$$\text{NPQ} = Fm/Fm' - 1 \quad (1)$$

Each parameter was tested on three plants from each treatment.

The chloroplast CO_2 concentration (*Cc*) and mesophyll conductance (g_m) of chloroplast carboxylation sites were obtained through variable electron transfer rates. Based on the measured gas exchange indicators, stomatal limitation values (*Ls*) were calculated as follows:

$$Ls = 1 - Ci/Ca \quad (2)$$

where: *Ci* – intercellular CO_2 concentration; *Ca* – atmosphere CO_2 concentration.

Each parameter was tested on three plants from each treatment.

Observation of chloroplast ultrastructure. The top second fully expanded leaves of three treatments were collected at 6 days post LT treatment, and three plants were stochastically selected from each treatment. The leaf sections were cut in 2 mm × 1 mm and immediately fixed in 4% (w/v) glutaraldehyde in 0.1 M phosphate buffer (pH 7.2) for 2 h, thoroughly postfixed in 1% (w/v) osmium tetroxide for 1 h and washed in 0.1 M potassium phosphate buffer (pH 7.2) for 1 h, dehydrated in an alcohol series from 30% to 100% (v/v) with 10% interval, and embedded in Epon 812 (Liu et al. 2012). Electron microscopy observations of chloroplast ultrastructure and photographs were performed with H-7650 and AMT600 systems (Hitachi, Tokyo, Japan).

Leaf stomatal density and guard cell size. The leaves selected for measuring photosynthetic parameters were also used to measure stomatal density, length, width, and pore width (Xu, Zhou 2008). The thin film was peeled off from the leaf surface with fine-point tweezers. Microscopic examination of stomata was performed under a photomicroscope system (ZEISS Primo Star, Germany) with a magnification of 40×, and ImageJ version 1.53 software (National Institutes of Health, USA) was used

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to analyse stomatal aperture. The measurement was conducted on ten randomly selected stomata from each treatment.

Statistical analysis. Analysis of variance (ANOVA) was carried out for the experimental data. The significant difference analysis was calculated and performed with SPSS version 22.0 software. Duncan's multiple range test at the 5% level was used to analyse the statistically significant differences between the three treatments.

RESULTS

***Streptomyces* sp. TOR3209 protects tomato leaves from cold damage.** *Streptomyces* sp. TOR3209 showed a significant growth-promoting effect on *S. lycopersicum* cv. 'Chaoyan 219'. At 6 days post LT treatment, the heights and leaf sizes of inoculated plants were significantly larger than those of uninoculated ones at either 25 °C or 5 °C, and increased the heights and leaf sizes by 39.14% and 56.74% compared with the plants grown at 5 °C ($P < 0.05$) (Figure 1). The growth of TOR3209-inoculated plants exposed to 5 °C treatment showed no difference from those grown at 25 °C. In contrast, the uninoculated plants were wilted at 5 °C, and the wilt was not found in the TOR3209-inoculated plants (Figure 1). This demonstrated that *Streptomyces* sp. TOR3209 had the ability to protect the cold damage of tomato leaves.

Tomato chlorophyll fluorescence parameters are recovered by TOR3209 in cold stress. To determine whether TOR3209 treatment causes any effect on photosystem, eight parameters, *Fo*, *Fm*, *Fv*/*Fm*, Φ_{PSII}, *Fv*'/*Fm*', ETR, *qP*, and NPQ, were studied on the plants grown at 5 °C. The *Fo* value was increased in the plants exposed to cold stress in comparison to the plants grown at 25 °C. TOR3209 treatment resulted in a significant reduction of *Fo* value at every time point by 3.62–22.58% in the plants exposed to cold stress. The values of the left seven parameters were reduced in the plants exposed to cold stress. TOR3209 treatment resulted in significant increase of the seven parameters, compared with the plants grown at 5 °C, inoculated of TOR3209 enhanced *Fm* (by 22.25–58.25%), *Fv*/*Fm* (by 2.57–10.10%), Φ_{PSII} (by 25.16–77.89%), *Fv*'/*Fm*' (by 10.49–20.63%), ETR (by 18.00–81.16%), *qP* (by 22.13–50.47%), and NPQ (by 17.25–70.59%) in the plants exposed to cold stress (Figure 2). There-

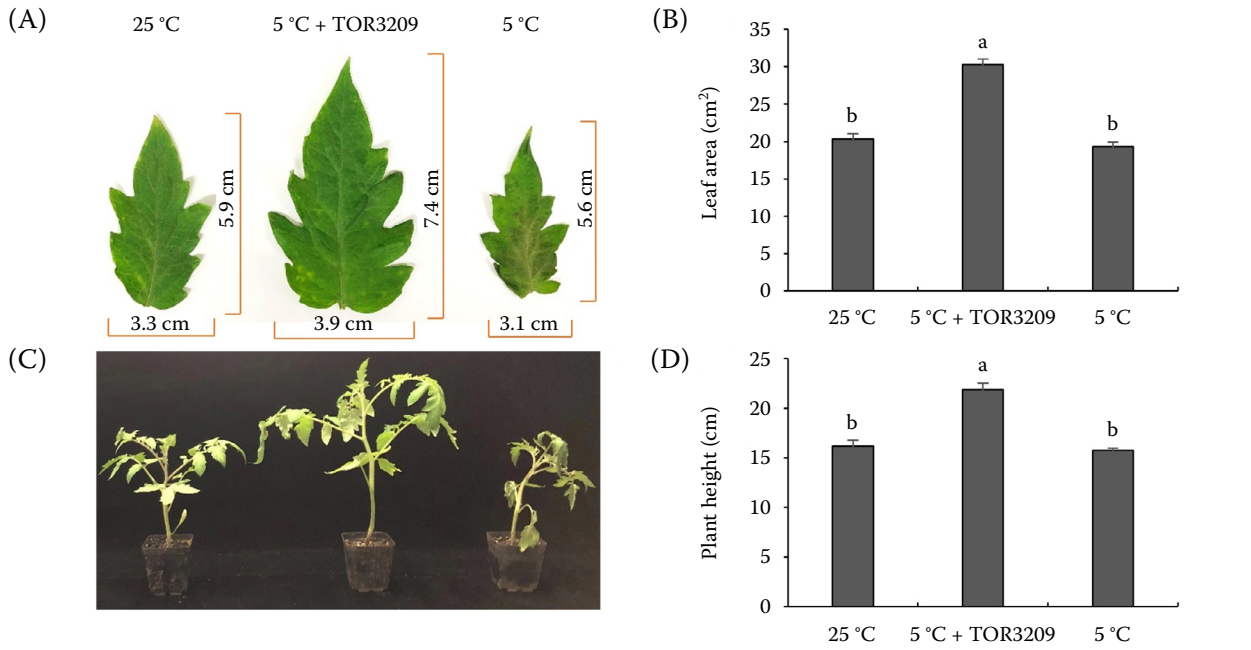

Figure 1. Effects of TOR3209 inoculation on the growth of tomato seedlings at 6 days post low temperature treatment
(A) Leaf morphology of tomato plants in different treatments, (B) leaf areas of tomato seedlings in different treatments, (C) seedling morphology in different treatments, (D) plant heights of seedlings in different treatments
Bars indicate SD
[a,b]different lowercase letters above the bars indicate significant differences between means of leaf areas or plant heights ($n = 5$, $P < 0.05$) based on one-way ANOVA analyses with Duncan's multiple range test

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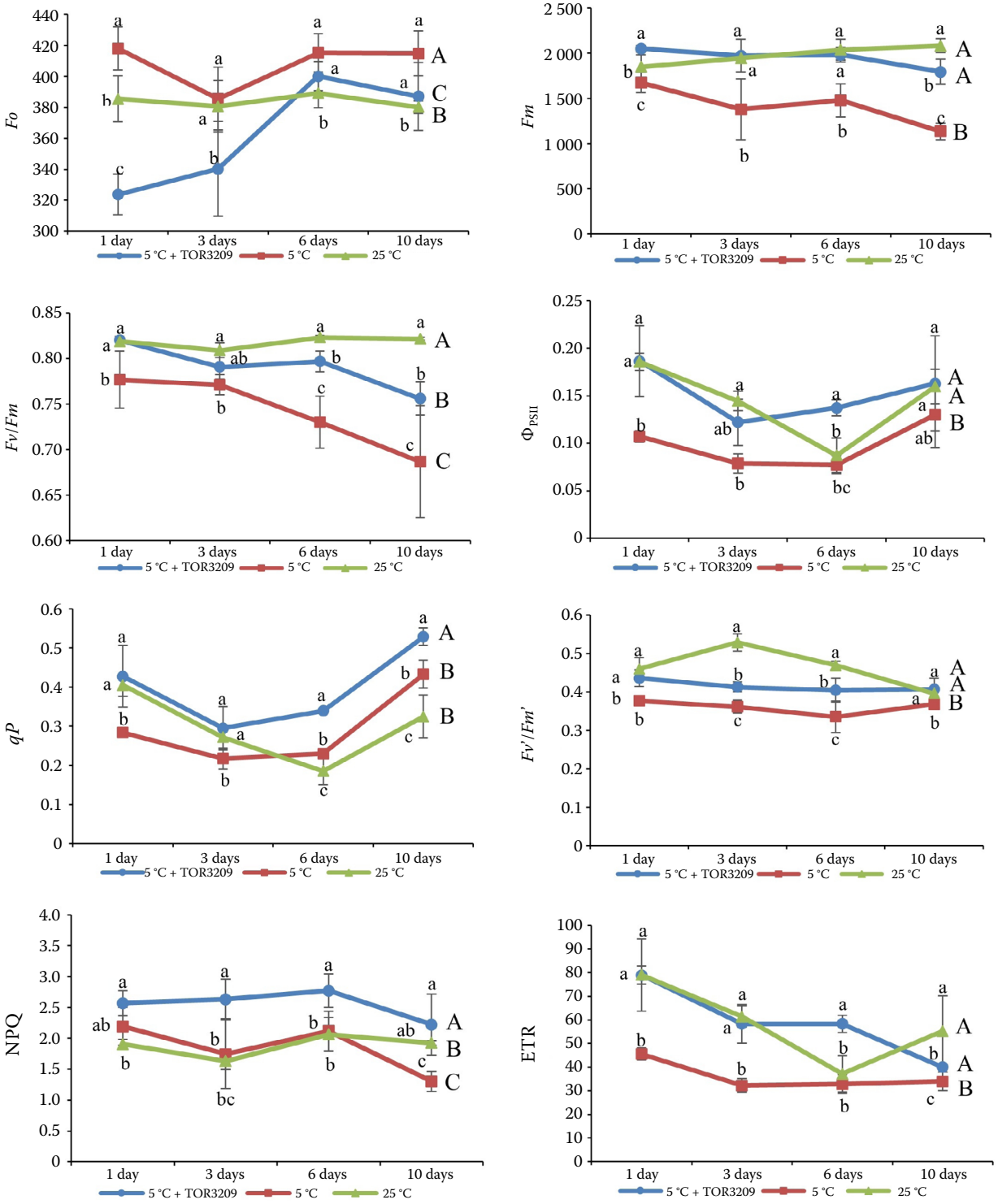

Figure 2. Effects of TOR3209 on chlorophyll fluorescence parameters

Data represents the mean value results from triplicate experiments ± SD

Fo – minimum chlorophyll *a* fluorescence; *Fm* – maximum chlorophyll *a* fluorescence; *Fv*/*Fm* – maximum quantum efficiency of PSII photochemistry; Φ_{PSII} – PSII operating efficiency; *qP* – photochemical quenching coefficient; *Fv'*/*Fm'* – PSII maximum efficiency; NPQ – non-photochemical quenching; ETR – relative PSII electron transport rate

[a,b,c]different lowercase letters at every time point indicate significant differences between treatments ($P < 0.05$); [A,B,C]different uppercase letters indicate the significant difference among groups ($P < 0.05$)

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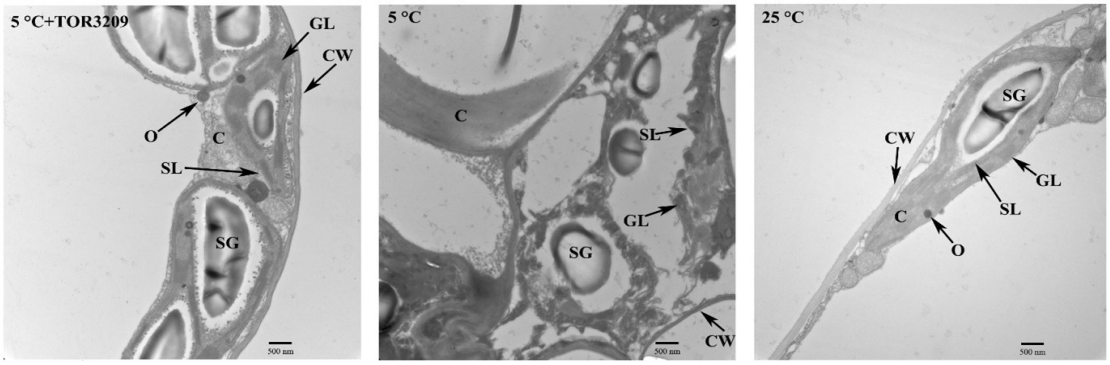

Figure 3. Chloroplast ultrastructure in tomato leaf at 6 days post low temperature treatment
Pictures were observed in the top second fully expanded leaves at 6 days post low temperature treatment (bars = 500 nm)
C – chloroplasts; CW – cell wall; SL – stroma lamellae; GL – grana lamellae; SG – starch grains.; O – osmophilic granules

fore, the chlorophyll fluorescence parameters of tomato were recovered in TOR3209-inoculated plants under cold stress.

Observation of chloroplast ultrastructure. The transmission electron microscopy (TEM) image of the tomato leaves illustrated the effect of TOR3209 inoculation under LT stress (Figure 3). In the plants grown at 25 °C, the chloroplasts exhibited an organised shape, regular grana lamellae and stroma lamellae. Moreover, the starch grains were lined close to the cell membrane. Under LT conditions, the chloroplasts showed many visible changes, as well as cell disorganisation. The LT stress caused severe destruction to the chloroplast ultrastructure and induced much swelling. The chloroplast was decreased in the strength of swelling in TOR3209-inoculated plants, and the starch content was increased (Figure 3).

Effects of TOR3209 inoculation on leaf stomatal parameters. The g_m value was reduced in plants under LT stress. At 1 day post-grown at 5 °C, the g_m value was reduced to 0.00694, showing a significant reduction ($P < 0.05$). At 3, 6, and 10 days post LT treatment, g_m value was reduced to an extremely low level ($P < 0.05$), decreased by 90.72%, 89.09%, 94.50% and 99.25% respectively. The g_m values were increased in plants receiving TOR3209 treatment at 1, 3, 6, and 10 days post LT treatment. Similar to the g_m value, the *Cc* value was decreased to a lower level as the time duration of cold treatment, and the TOR3209 treatment improved the value to a higher level. The *Ci* and *Ls* values of the tomato plant were increased with the duration of cold stress. TOR3209 treatment led to a reduction under cold stress conditions, decreased *Ci* by 16.62–28.15%, *Ls* by 5.76–29.85%, respectively (Figure 4).

Leaf stomatal density and guard cell size were increased in response to TOR3209 inoculation. Tomato stomata consist of two specialised guard cells, which modulate their turgor to regulate the pore aperture. Exposure to cold stress led to increased stomatal density but reduced guard cell size. The stomatal structure in tomato leaves was protected by TOR3209 when grown at 5 °C (Figure 5). At 6 days post-growth at 5 °C, the stomatal density in cold stress was 196.56 pores/mm^2. In contrast, the stomatal density in the plants receiving TOR3209 inoculation was 178.67 pores/mm^2. This implied that the number of stomata was reduced in the plants receiving TOR3209 treatment. Stomatal density was also negatively correlated with stomatal length under cold stress conditions. The length and width of stomata and pore width all declined under cold stress, which were all significantly improved in TOR3209-treated plants ($P < 0.05$).

Carotenoid and ABA biosynthesis affected by TOR3209 treatment. To discover the hormones signalling mediated by TOR3209 inoculation, the carotenoid and ABA biosynthesis were quantified in tomato plants. The content of carotenoids in tomato plants was reduced in plants exposed to 5 °C compared to the plants grown at 25 °C. The content of carotenoids was increased to a higher level by 2.99–61.94% in TOR3209-inoculated plants exposed to 5 °C; no significant difference was observed between these two treatments on the 6th and 10th days. For ABA biosynthesis, the content was increased in tomato plants exposed to 5 °C compared to those grown at 25 °C. The application of TOR3209 led to an increased content of ABA of 7.13%–19.71% in plants exposed to 5 °C (Figure 6).

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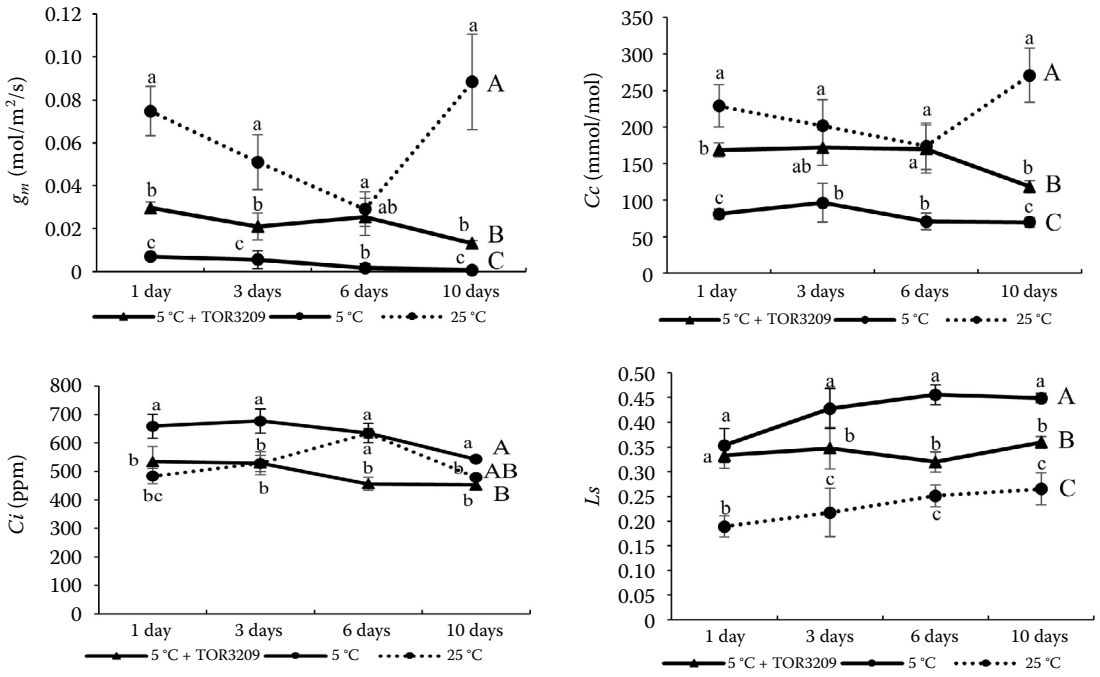

Figure 4. Leaf stomatal parameters affected by TOR3209 under cold stress

Parameters were assayed at 1, 3, 6, and 10 days post low temperature treatment; data represent the mean value results from triplicate experiments ± SD; g_m – mesophyll conductance; *Cc* – chloroplast CO_2 concentration; *Ci* – intercellular CO_2 concentration; *Ls* – stomatal limitation value; ^{a,b,c}different lowercase letters at every time point indicate significant differences between treatments ($P < 0.05$); ^{A,B,C}different uppercase letters indicate the significant difference among groups ($P < 0.05$)

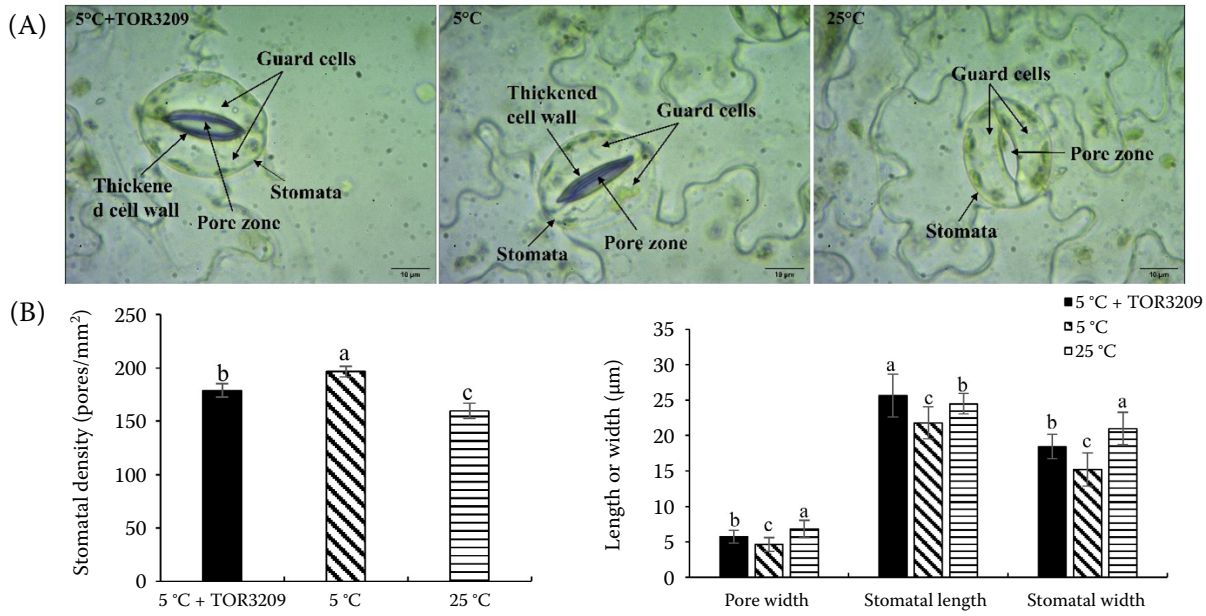

Figure 5. Effects of TOR3209 inoculation on stomatal density and structure of tomato plants at low temperature

(A) Microscopic structure of stomata, (B) quantification of stomatal pore width, stomatal density, length, and width affected by TOR3209

Arrows indicate the guard cell and pore zone with changed morphology; error bars indicate SD ($n = 10$)

^{a,b,c}different lowercase letters indicate significant differences between means of stomata in the treatments ($n = 5$, $P < 0.05$) based on one-way ANOVA analyses with Duncan's multiple range test

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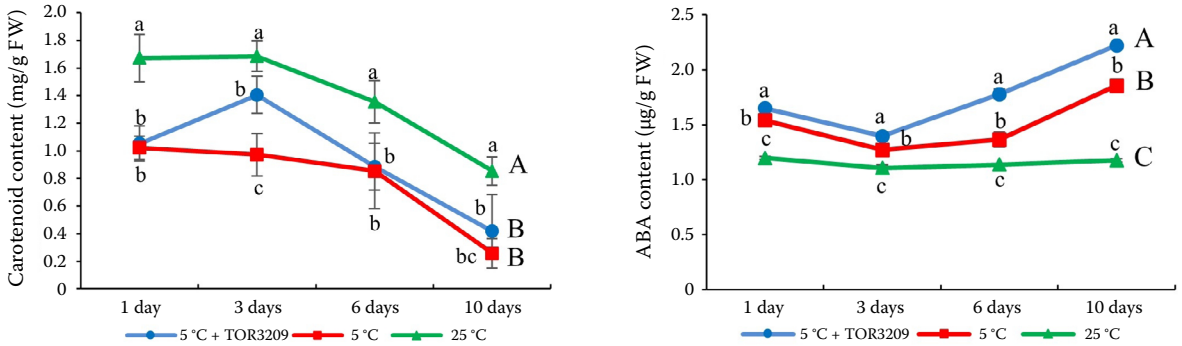

Figure 6. Carotenoid and ABA biosynthesis in tomato plants inoculated with TOR3209

Each assay was conducted at 1, 3, 6, and 10 days post low temperature treatment; each bar represents the mean value results from triplicate experiments ± SD

FW – fresh weight; ABA – abscisic acid; ^{a,b,c}different lowercase letters at every time point indicate significant differences between treatments ($P < 0.05$); ^{A,B,C}different uppercase letters indicate the significant difference among groups ($P < 0.05$)

DISCUSSION

LT stress severely impacts photochemical and biochemical reactions of plants, such as photosynthesis, photosynthetic pigments, and plant hormones, which leads to stress-induced perturbations (Ritonga, Chen 2020). Among these damages caused by LT, PSII is particularly sensitive because the absorbed radiant energy is far beyond utilisation, which usually generates ROS, harming the photosynthetic systems or apparatus (Zhang et al. 2008). It has been found that PGPR can alleviate plant cold damage (Yang et al. 2016; Elhindi et al. 2017) by inhibiting the peroxidation level of membrane lipid, altering endogenous hormone accumulation, and enhancing antioxidant enzyme activities (Chandrasekaran et al. 2019). Our previous comparative transcriptome work reported that the PGPR strain *Streptomyces* sp. TOR3209 induces up-regulation of photosynthesis-associated genes in tomato plants under LT stress (Ma et al. 2023). The present study presented detailed data to show the improvement of photosynthesis parameters and apparatus. It was concluded that TOR3209 comprehensively protected the PSII of tomato. This highlighted that photosynthesis is one of the important mechanisms utilised by TOR3209 to improve tomato cold tolerance.

Photosynthetic efficiency of PSII is closely related to adaptive response to abiotic stress, which was revealed by detecting the photochemical reactions (Weng et al. 2011). TOR3209 inoculation enhanced PSII photochemical efficiency because the ChlF (chlorophyll *a* fluorescence) parameters *Fm*, *Fv*/*Fm*, Φ_{PSII}, *Fv*'/*Fm*', ETR, *qP*, and NPQ were increased. Those parameters were mutually corroborated to suggest that the TOR3209-inoculated plants showed enhanced PSII photosynthetic capacity. For example, the wilted leaves of the plants grown at 5 °C may also be characterised by the decline of PSII activity, as reflected by a drastic decrease in *Fv*/*Fm*, the enhanced Φ_{PSII} in 5 °C + TOR3209 plants was due to a higher efficiency of *Fv*/*Fm*, this is consistent with previously observed in other studies (Wang et al. 2016b). Simultaneously, the NPQ parameter indicates excess energy dissipation of PSII, mainly reflecting thermal energy from the light-harvesting complex of PSII (LHCII) dissipated by the zeaxanthin quencher (Bielczynski et al. 2017; Moustakas et al. 2020). The increased NPQ suggested that the dissipation of the excess excitation energy was enhanced in the TOR3209-inoculated plants, as well as the prevention of ROS production, causing PSII damage. Previously, it has been reported that increases in NPQ are usually accompanied by decreases in ETR, and these changes are closely related to a lower rate of electron transport at the level of PSII (de Andrade et al. 2015). The results in our present study did not coincide with the report of de Andrade et al. (2015), since NPQ and ETR were both increased in TOR3209-inoculated plants, implying that TOR3209 could activate the reaction centre of PSII by driving electron transport (Baker 2008). The *Fo* value is increased when the chloroplast thylakoid is destroyed. Therefore, *Fo* acts as a marker of malfunction in the PSII reaction centre and decreased efficiency of the photochemical reaction centre. The decreased *Fo* values in TOR3209-treated plants demonstrated the protection of the chloroplast thylakoid structure.

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Carotenoids are tetraterpene pigments found in all photosynthetic organs (Dong et al. 2007). They are recognised as essential components to reduce the damage of photoinhibition (Sun et al. 2013). According to our results, the concentration of carotenoids was significantly decreased in tomato plants under LT, demonstrating that LT stress caused a severe effect on carotenoid biosynthesis. The concentration of carotenoids was increased in the plants inoculated with TOR3209, albeit a statistical difference was found only at 3 days post cold treatment. Carotenoids participate in regulating the membrane organisation to promote chloroplast development (Dong et al. 2007). Cell disorganisation and plasmalemma disruption were found in plants with LT stress. In contrast, no plasmalemma disruption was found in TOR3209-inoculated plants. The TOR3209 inoculation may protect the grana thylakoids and chloroplast envelope by increased accumulation of carotenoid, which was consistent with the reports that a larger carotenoid pool contributes to plant growth under cold conditions (Abdel Latef, He 2011).

Photosynthesis limitation results from both stomatal and non-stomatal effects. A greater stomatal size facilitates CO_2 diffusion into the leaf because its conductance is proportional to the square of the effective radius of the stomatal pore. The present study found that leaf stomatal size was decreased in plants exposed to cold stress, which is consistent with the results of Liu et al. (2017), while it was increased significantly by TOR3209 inoculation. Coinciding with the decreased photosynthetic parameters *Ci* and *Ls* (Figure 4), it was estimated that strain TOR3209 treatment resulted in a change in the stomatal opening degree under LT stress. The increased g_m and *Cc* indicated that TOR3209 treatment could increase the diffusion of CO_2, and thereby enhance photosynthesis, because g_m and *Cc* showed a coupling interaction between CO_2 entry for photosynthesis and transpiration.

Stomatal opening is controlled by plastoquinone redox state in response to light, with an increased stomatal opening corresponding to a more reduced redox state (Busch 2014; Glowacka et al. 2018). The plant's photosynthesis is involved in a regulatory process of chloroplast redox. The enhanced photosynthetic capacity caused by TOR3209 was associated with an increased accumulation of photosynthetic carotenoids, regulating the chloroplast redox (Hajiboland et al. 2010; Wu, Zou 2010; Abdel Latef, He 2014).

CONCLUSION

Conclusively, *Streptomyces* sp. TOR3209 induced an increased LT resistance of tomato plants via complex physiological processes. Based on the assays of accumulation of ABA and carotenoids, PSII photochemical efficiency, and stomatal opening, it was suggested that TOR3209 had the ability to comprehensively protect tomato PSII.

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