Integrated application of bacterial carbonate precipitation and silicon nanoparticles enhances productivity, physiological attributes, and antioxidant defenses of wheat (*Triticum aestivum* L.) under semi-arid conditions

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The use of calcium carbonate-precipitating bacteria (CCPB) has become a well-established ground-improvement technique. However, the effect of the interaction of CCPB with nanoparticles (NPs) on plant performance is still meager. In this study, we aimed at evaluating the role of CCPB and/or silicon NPs (Si-NPs) on the growth, physio-biochemical traits, and antioxidative defense of wheat (*Triticum aestivum* L.) under semi-arid environmental conditions. A 2-year pot experiment was carried out to determine the improvement of the sandy soil inoculated with CCPB and the foliar application of Si-NPs on wheat plants. We tested the following treatments: spraying plants with 1.0 or 1.5 mM Si-NPs (control = 0 mM Si-NPs), soil inoculated with *Bacillus licheniforms* (MA16), *Bacillus megaterium* (MA27), or *Bacillus subtilis* (MA34), and the interaction of individual *Bacillus* species with Si-NPs. Our results showed that soil inoculation with any of the three isolated CCPB and/or foliar application of Si-NPs at the rates of 1.0 or 1.5 mM significantly improved (*p* ≤ 0.05) the physiological and biochemical attributes as well as the enzymatic antioxidant activities of wheat plants.
Therefore, the combined treatments of CCPB + Si-NPs were more effective in enhancing physio-biochemical characteristics and enzymatic antioxidant activities than the individual treatments of CCPB or Si-NPs, thus achieving the best performance in the treatment of MA34 + 1.5 mM Si-NPs. Our results demonstrated that the co-application of CCPB and Si-NPs, particularly MA34 + 1.5 mM Si-NPs, considerably activated the antioxidant defense system to mitigate the adverse effects of oxidative stress, thus increasing tolerance and enhancing the production of wheat plants in sandy soils under semi-arid environmental conditions.

KEYWORDS
antioxidant system, Bacillus, reactive oxygen species, sandy soil, silicon, wheat production

Introduction

Wheat (Triticum aestivum L.), belonging to the Poaceae family, is the most important cereal crop globally due to its higher content of protein, carbohydrates, vitamins, and calories than other cereal crops (Elrys et al., 2020). It is cultivated in rain-fed and irrigated areas in tropical and subtropical regions. Additionally, it is grown on approximately 200 million hectares globally, yielding about 700 Tg (10^12 g) year^{-1} (FAOSTAT, 2020). Therefore, the global need for wheat is increasing, predominantly in developing nations with limited croplands and resources, including Egypt, which poses challenges in producing the quantities of wheat required to meet this growing demand. For instance, wheat covers around 1.40 million hectares in Egypt, producing 9.0 Tg of grain in 2019, approximately 34.5% of annual consumption (FAOSTAT, 2020).

Consequently, it is imperative to maximize wheat production, especially in soils with poor physicochemical and biological properties, such as sandy soils, which cover about 90% of the Egyptian soils (Merwad and Abdel-Fattah, 2015). Furthermore, under Egypt’s semi-arid climatic conditions, these soils provide significant prospects for agricultural expansion. Promising techniques for increasing productivity in such soils include effective agricultural bio-systems that consider the biochemical diversity of agricultural systems, their ability to reduce the negative influences of low soil fertility, and water-retaining capacity in sandy soils. However, the use of calcium carbonate (CaCO_3) precipitating bacteria (CCPB) and silicon (Si) nanoparticles (Si-NPs) are innovative and effective technologies that improve the productivity of crops under semi-arid environmental conditions (Chaparro-Acuña et al., 2018; Desoky et al., 2021).

The precipitation of CaCO_3 is a process in which microorganisms, mainly bacteria, provide adequate substrates, creating CaCO_3 crystals (Chaparro-Acuña et al., 2018). The Bacillus group is non-pathogenic and tolerant of extreme conditions, with high concentrations of urease enzyme (Achal et al., 2015); therefore, it can potentially be used as CCPB. Urease hydrolyzes urea in soils to carbonate (CO_3^{2-}) and ammonium (NH_4^+). The produced NH_4^+ raises the pH of the solution, causing the reaction to form CaCO_3 on the bacterial cell surface whenever there is sufficient calcium (Ca^{2+}) and CO_3^{2-} ion content in the solution (Chaparro-Acuña et al., 2018). The resulting CaCO_3 can coat surfaces and bind various particles together (Seifan et al., 2020). CCPB is a practical approach to enhance soil quality (Chaparro-Acuña et al., 2018) and increase sand stabilization and soil hardness while decreasing soil porosity in sandy soils (Whiffin et al., 2007). Similarly, the induction of CCPB binds sand grains and enhances soil stiffness and strength (DeJong et al., 2010; Mortensen et al., 2011).

Due to its favorable physic-mechanical activities, Si alleviates the adverse effects of water shortage and improves plant performance (Rady et al., 2019; Desoky et al., 2020). Nano-materials have emerged as a promising solution to various technological and environmental problems in several disciplines (Ansari and Husain, 2012). Compared with bulk Si, Si-NPs have a larger surface area with higher surface reactivity and solubility (Qados and Moftah, 2015). Specifically, particle size is a crucial factor influencing particle adhesion, absorption, and transportation in plant cells (Wang et al., 2009). Furthermore, NPs interact with plant cells by aiding the movement of numerous compounds that control plant metabolism and various physiological processes (Giraldo et al., 2014; Desoky et al., 2021).

However, knowledge of the effect and interaction of CCPB and Si-NPs on the performance of wheat plants cultivated in sandy soils under semi-arid environmental conditions is limited. Therefore, this study investigated the mechanism of inoculating sandy soil with CCPB and foliar application of Si-NPs to plants in influencing the physio-biochemical characteristics, performance, and antioxidative defenses of wheat grown under semi-arid environmental conditions. We hypothesized that inoculating soil with CCPB or foliar spraying with Si-NPs would improve wheat performance and defense against erosion.
in sandy soils under semi-arid environmental conditions. However, the co-addition of CCS and Si-NPs would be more effective than single additions.

**Materials and methods**

**Isolation and identification of calcium carbonate-precipitating bacteria**

Calcium carbonate-precipitating bacterial isolates were isolated from the calcareous soil of the Mariout sector, Alexandria, Egypt. The soil sample was suspended in a sterilized saline solution (0.85% NaCl), and serial dilutions were carried out up to $10^{-6}$. Each dilution was plated on a medium containing 2.12 g NaHCO$_3$, 3.0 g nutrient broth (Lab M Limited, Lancashire, UK), 20.0 g urea, 10.0 g NH$_4$Cl, 30.0 mM CaCl$_2$, 20.0 g agar L$^{-1}$, and pH 8.5. The plates were then incubated at 28°C for 7 d. After isolation, all colonies were individually plated on CaCO$_3$ precipitation medium supplemented with five concentrations of CaCO$_3$ (10.0%, 15.0%, 20.0%, 25.0%, and 30.0%). Individual colonies that are found to be positive were selected based on their crystal formation visibility and purification by streaking on CaCO$_3$ precipitation media without CaCl$_2$.

The selected colonies were assessed under a stereomicroscope and primarily identified using Bergey’s manual of systematic bacteriology morphological and biochemical tests (Vos et al., 2009; Guinebretière et al., 2013). Further identification was performed by matrix-assisted laser desorption/ionization-time of flight (MALDI-TOF) mass spectrometry (MS) (Bruker Daltonics, Bremen, Germany) according to Schumaker et al. (2012) and Sauget et al. (2017). The manufacturers suggested score values of 2.30–3.00, 2.00–2.30, and 1.70–2.00 as highly probable species identification, secure genus identification and probable species identification, and probable genus identification, respectively.

**Optimization of calcium carbonate-precipitating bacterial isolates**

**Effect of pH on bacterial growth**

The chosen isolates were inoculated into 10 ml nutrient broth tubes with different pH levels ranging from 1 to 14. The pH was adjusted using 1 N NaOH and 1 N HCl. The turbidity of each isolate was adjusted to the 0.5% McFarland standard, and the tubes were incubated for 24 h at 37°C. The growth was next assessed using a spectrophotometer (UV-2101/3101 PC; Shimadzu Corporation, Analytical Instruments Division, Kyoto, Japan) at an optical density of (OD)$_{600}$ nm, and the results were compared with a bacterial blank suspension. Results were determined after 30 min, 1 h, 2 h, 4 h, 8 h, 24 h, and 32 h of inoculation.

**Effect of temperature on bacterial growth**

The selected bacterial isolates were briefly inoculated into 10 ml nutrient broth tubes, and the turbidity of each isolate was adjusted to the 0.5% McFarland standard. The tubes were incubated at 0, 10, 20, 30, 40, 50, and 60°C for 24 h. The growth was next assessed using a spectrophotometer (Shimadzu Corporation) at OD$_{600}$ nm, and the results were compared with a bacterial blank suspension.

**Production of urease**

In assaying the urease activity, urea agar media (UAM) containing 15.0 g, 20.0 g, 1.0 g, 1.0 g, 5.0 g, 2.0 g, and 0.012 g of agar, urea, dextrose, pancreatic digest gelatin, sodium chloride, monosodium phosphate, and phenol red, respectively, were used. The medium pH was adjusted to a pH of 6.8 (Hammes et al., 2003; Chahal et al., 2011). Each candidate strain’s cell suspension (10$^6$ cells mL$^{-1}$) was inoculated on UAM. The plates were incubated for 24–48 h at 28°C, and the color change from yellow to pink was determined. Urease activity was measured as the concentration of the produced ammonium ions (NH$_4^+$) as described by Tavares et al. (2021).

**Calcium carbonate precipitation ability**

All isolates were cultivated aerobically in 500 ml Erlemeyer flasks with 100 ml of liquid CaCO$_3$ precipitation medium. Flasks were incubated at 28°C for 3 d for CaCO$_3$ precipitation and collection. The uninoculated liquid CaCO$_3$ precipitation medium served as the control. After incubation, the entire culture was centrifuged for 1 min at 10,000 × g. The pellet was resuspended in a 50 ml TE buffer, which contained CaCO$_3$ and bacterial cells (10 mM Tris, 1 mM EDTA at pH 8.5).

To digest the bacterial cell wall, lysozyme was added to the cell suspension at a final rate of 1 mg mL$^{-1}$, and the tubes were incubated at 37°C for 1 h. Notably, centrifugation was used to remove the cell debris, and sterile distilled water (pH 8.5) was used to wash the pellet before being air-dried at 37°C for 24 h. The pellet was weighed to calculate the number of carbonate crystals precipitated by the various isolates.

**Experimental layout**

A 2-year pot trial was performed in 2019/2020 and 2020/2021 using an open greenhouse at the Botany Department, Faculty of Agriculture, Zagazig University, Zagazig, Egypt. The average daily temperature was 17.7°C ± 2.0°C (15.3°C to 20.1°C), and the average daily relative humidity was 48.2 ± 4.3% (45.4%–51.0%). Wheat (Triticum aestivum L., cv. Misr 2) grains were obtained from the Agronomy Research Institute of the Agriculture Research Centre, Giza, Egypt. Before sowing, the grains were surface-sterilized for 5 min with 1%
(v/v) sodium hypochlorite, washed several times with distilled water, and finally, air-dried for 1 h. Additionally, 10 kg of sandy soil was filled into plastic pots with inner diameters of 35 cm and depths of 30 cm. The physicochemical attributes of the tested soil, were measured (Page et al., 1982; Klute and Dirksen, 1986), and are illustrated in Supplementary Table 1.

A total of 240 pots were used in this study with the following investigated treatments: control, spraying plants with 1.00 or 1.50 mM Si-NPs; soil inoculated with Bacillus licheniforms (MA16), Bacillus megaterium (MA27), Bacillus subtilis (MA34), MA16 + 1.00 or 1.50 mM Si-NPs, MA27 + 1.00 or 1.50 mM Si-NPs, and MA34 + 1.00 or 1.50 mM Si-NPs. The recommended dose of inorganic nitrogen (N) as ammonium sulfate (205 g N kg⁻¹ fertilizer) was added to all pots in three equal splits at a rate of 100 mg N kg⁻¹ soil. The first split was added before the first irrigation, while the second and third doses were added 40 and 70 days after the first split.

Before sowing, phosphorus (P) and potassium (K) were applied to all experimental treatments at the recommended rates. Phosphorus was added as ordinary superphosphate at 15 mg P kg⁻¹ soil, and K was applied as potassium sulfate at 40 mg K kg⁻¹ soil. All pots were rotated (moved from one location to another) every 2 d to ensure equal light distribution and sunlight intensity to all plants. Notably, ten homogeneous grains were sown in each pot, leaving only five uniform seedlings in each pot after germination.

Foliar application of silicon nanoparticles

Nano-Si dioxide was employed at 99.5% purity, 20–30 nm, and a surface area of 180–600 m² g⁻¹. A pressurized spray bottle was used to apply foliar sprays of 1 and 1.5 mM Si-NPs. In total, 0.1% of tween 20 was used as a surfactant (Desoky et al., 2021).

Growth characteristics and yield determination

Wheat plants were harvested during each growing season to measure the growth attributes, physiology and biochemistry, and antioxidant defense system components after 65 days of planting. The leaf area (cm²) and plant height (cm) were determined. In measuring the dry weight (DW), samples were dried at 70°C until a constant weight was reached. During harvesting, the 1000 grain weight (g), the number of grains spike⁻¹, and DW of grains plant⁻¹ (g) were determined.

Determination of physio-chemical constituents

The acetone extraction method was used to determine the contents of photosynthetic pigments—carotenoids and total chlorophylls (Arnon, 1949). Absorbance readings at 663 nm, 645 nm, and 480 nm were taken using a spectrophotometer (Shimadzu Corporation) to compute pigment content in mg g⁻¹ leaf fresh weight. In upper fully expanded leaf tissue (second fully expanded leaf), chlorophyll fluorescence parameters using a PAM chlorophyll fluorimeter, the conductance of stomata (gs), net photosynthesis rate (Pn),

### Table 1: Isolation and screening of calcium carbonate precipitating bacteria (CCPB).

| Isolate | CaCO₃ concentration (%) |
|---------|-------------------------|
|         | 10 | 15 | 20 | 25 | 30 |
| MA1     | +  | –  | –  | –  | –  |
| MA2     | +  | –  | –  | –  | –  |
| MA3     | +  | +  | +  | +  | –  |
| MA4     | +  | +  | –  | –  | –  |
| MA5     | +  | +  | –  | –  | –  |
| MA6     | +  | +  | –  | –  | –  |
| MA7     | +  | +  | –  | –  | –  |
| MA8     | +  | +  | –  | –  | –  |
| MA9     | +  | +  | –  | –  | –  |
| MA10    | +  | –  | –  | –  | –  |
| MA11    | +  | –  | –  | –  | –  |
| MA12    | +  | +  | –  | –  | –  |
| MA13    | +  | +  | –  | –  | –  |
| MA14    | +  | +  | –  | –  | –  |
| MA15    | +  | +  | –  | –  | –  |
| MA16    | +  | +  | +  | +  | +  |
| MA17    | +  | –  | –  | –  | –  |
| MA18    | +  | +  | –  | –  | –  |
| MA19    | +  | –  | –  | –  | –  |
| MA20    | +  | +  | –  | –  | –  |
| MA21    | +  | +  | –  | –  | –  |
| MA22    | +  | +  | –  | –  | –  |
| MA23    | +  | +  | –  | –  | –  |
| MA24    | +  | +  | –  | –  | –  |
| MA25    | +  | +  | –  | –  | –  |
| MA26    | +  | –  | –  | –  | –  |
| MA27    | +  | +  | +  | +  | +  |
| MA28    | +  | +  | –  | –  | –  |
| MA29    | +  | –  | –  | –  | –  |
| MA30    | +  | –  | –  | –  | –  |
| MA31    | +  | +  | –  | –  | –  |
| MA32    | +  | +  | –  | –  | –  |
| MA33    | +  | +  | –  | –  | –  |
| MA34    | +  | +  | +  | +  | +  |

CaCO₃, calcium carbonate. (+) growth, (−) no growth. (MA) bacterial isolate code.
and transpiration (Tr) rate were measured (Li et al., 2007). The formulas of Maxwell and Johnson (2000) were used to compute the maximum PS II \( F_v/F_m \) quantum yield as follows:

\[
F_v/F_m = (F_m - F_0)/F_m.
\]

Where, \( F_v \); variable fluorescence, \( F_m \); maximum light-adaptive fluorescence, and \( F_0 \); minimum-adaptive fluorescence.

Photochemical quenching (qP) and non-photochemical quenching (NPQ) were determined as described by Han et al. (2022) and Ruban and Wilson (2021), respectively. Barrs and Weatherley’s (1962) method was used to measure the relative water content (RWC). We also determined the membrane stability index (MSI) based on the method reported by Rady (2011). The total inorganic ions that leached from the leaves (electrolyte leakage, EL) and malondialdehyde (MDA) contents were estimated according to the methods used previously (Heath and Packer, 1968; Sullivan and Ross, 1979). The leaf contents of superoxide oxide radical (\( O_2^- \); at A580 \( g^{-1} \) FW) and hydrogen peroxide (\( H_2O_2 \); \( \mu \)mol \( g^{-1} \) FW) were assessed following the procedures of Mukherjee and Choudhuri (1983) and Kubis (2008), respectively. Proline (Pro) accumulation in leaves and total soluble sugar (TSS) content were also determined (Bates et al., 1973; Irigoyen et al., 1992). Additionally, glycine betaine (GB; Grieve and Grattan, 1983), and \( \alpha \)-tocopherol (\( \alpha \)-TOC; Ching and Mohamed, 2001) were calculated.

**Determination of enzymatic and non-enzymatic antioxidant compounds and activity**

The contents (mol \( g^{-1} \) fresh weight) of ascorbate (AsA) and reduced glutathione (GSH) were assessed according to the methods of Griffith (1980) and Kampfenkel et al. (1995), respectively. Enzyme concentrations were extracted according to Vitória et al. (2001). The catalase (CAT) enzyme concentration was measured spectrophotometrically according
TABLE 2 Effect of soil application with calcium carbonate precipitating bacteria (CCPB), *Bacillus licheniforms* (MA16), *Bacillus megaterium* (MA27), and *Bacillus subtilis* (MA34), and follar application with silicon nanoparticles (Si-NPs) on growth and yield components of wheat plants (cv. Misr 2).

| Treatment          | Plant height (cm) | Shoot DW (g) | Leaf area (cm²) | Number of grains spike⁻¹ | 1000 grain weight (g) | Grain yield plant⁻¹ (g) |
|--------------------|-------------------|--------------|-----------------|--------------------------|-----------------------|-------------------------|
| **First season**   |                   |              |                 |                          |                       |                         |
| Control            | 60.1 ± 2.3i       | 3.39 ± 0.11i | 19.2 ± 0.9i     | 20.1 ± 1.1k              | 36.8 ± 2.1i           | 3.54 ± 0.15j            |
| 1.0 mM Si-NPs      | 66.7 ± 2.5h       | 3.54 ± 0.12k | 21.7 ± 1.1g     | 25.1 ± 1.6j              | 37.6 ± 2.2i           | 5.49 ± 0.21i            |
| 1.5 mM Si-NPs      | 69.2 ± 2.8g       | 3.71 ± 0.14j | 22.9 ± 1.3f     | 28.0 ± 1.8i              | 39.6 ± 2.3h           | 6.17 ± 0.23h            |
| MA16               | 75.4 ± 3.2e       | 4.16 ± 0.17h | 25.6 ± 1.2d     | 31.7 ± 2.3g              | 43.8 ± 2.1f           | 7.14 ± 0.25f            |
| MA27               | 73.8 ± 3.7f       | 3.97 ± 0.13i | 24.6 ± 1.5e     | 29.5 ± 2.4h              | 42.1 ± 2.6g           | 6.67 ± 0.19g            |
| MA34               | 77.6 ± 3.4d       | 4.44 ± 0.21g | 25.7 ± 1.6d     | 34.2 ± 2.1f              | 45.9 ± 2.8e           | 7.42 ± 0.26f            |
| MA16 + 1.0 mM Si-NPs | 79.3 ± 3.4c       | 4.87 ± 0.22e | 26.7 ± 1.8c     | 38.1 ± 2.6d              | 48.9 ± 2.4cd          | 8.72 ± 0.28d            |
| MA16 + 1.5 mM Si-NPs | 81.2 ± 3.9b       | 5.81 ± 0.25b | 28.4 ± 1.7a     | 41.0 ± 1.9ab             | 51.8 ± 2.3a           | 9.85 ± 0.33ab           |
| MA27 + 1.0 mM Si-NPs | 78.3 ± 2.9d       | 4.63 ± 0.18f | 26.3 ± 1.4c     | 36.5 ± 1.8e              | 47.8 ± 3.1d           | 8.30 ± 0.37e            |
| MA27 + 1.5 mM Si-NPs | 79.9 ± 2.8c       | 5.56 ± 0.23c | 27.6 ± 1.6b     | 39.7 ± 2.2bc             | 50.4 ± 3.2b           | 9.59 ± 0.35b            |
| MA34 + 1.0 mM Si-NPs | 79.6 ± 3.5c       | 5.27 ± 0.31d | 27.4 ± 1.9b     | 39.2 ± 2.3cd             | 49.9 ± 3.1bc          | 9.14 ± 0.38e            |
| MA34 + 1.5 mM Si-NPs | 83.0 ± 3.2a       | 6.07 ± 0.33a | 28.9 ± 2.1a     | 42.3 ± 2.4a              | 52.8 ± 3.4a           | 9.69 ± 0.34a            |
| **Second season**  |                   |              |                 |                          |                       |                         |
| Control            | 62.2 ± 1.9l       | 3.51 ± 0.13l | 20.6 ± 1.2i     | 19.2 ± 1.2i              | 37.3 ± 1.6j           | 3.60 ± 0.11h            |
| 1.0 mM Si-NPs      | 67.8 ± 2.8h       | 3.66 ± 0.15k | 22.1 ± 1.3h     | 24.3 ± 1.3j              | 38.3 ± 1.8j           | 5.58 ± 0.19g            |
| 1.5 mM Si-NPs      | 70.3 ± 2.9g       | 3.83 ± 0.12j | 23.2 ± 1.5g     | 27.3 ± 1.1g              | 40.4 ± 1.9i           | 6.33 ± 0.21f            |
| MA16               | 76.8 ± 2.7e       | 4.36 ± 0.17h | 26.1 ± 1.3e     | 30.9 ± 2.1f              | 44.6 ± 2.1g           | 7.40 ± 0.31d            |
| MA27               | 75.1 ± 3.2f       | 4.17 ± 0.16i | 25.1 ± 1.8f     | 28.4 ± 1.3g              | 42.8 ± 2.3h           | 6.89 ± 0.35e            |
| MA34               | 79.1 ± 3.5d       | 4.64 ± 0.19g | 26.2 ± 1.9e     | 34.2 ± 1.9e              | 47.2 ± 2.2f           | 7.64 ± 0.36d            |
| MA16 + 1.0 mM Si-NPs | 80.7 ± 3.4c       | 5.04 ± 0.25e | 27.1 ± 2.1d     | 37.4 ± 2.4cd             | 49.7 ± 2.5de          | 8.91 ± 0.35c            |
| MA16 + 1.5 mM Si-NPs | 82.6 ± 3.6b       | 5.97 ± 0.24b | 28.8 ± 2.2b     | 40.3 ± 2.6b              | 52.7 ± 2.6b           | 10.1 ± 0.39a            |
| MA27 + 1.0 mM Si-NPs | 79.7 ± 3.5d       | 4.80 ± 0.21f | 26.7 ± 2.3d     | 35.8 ± 1.6d              | 48.7 ± 2.7e           | 8.59 ± 0.28d            |
| MA27 + 1.5 mM Si-NPs | 81.2 ± 4.1c       | 5.73 ± 0.23c | 28.1 ± 2.5c     | 39.0 ± 2.1bc             | 51.8 ± 2.6c           | 9.84 ± 0.29ab           |
| MA34 + 1.0 mM Si-NPs | 81.1 ± 3.8c       | 5.47 ± 0.26d | 27.9 ± 2.3c     | 38.6 ± 2.9bc             | 50.7 ± 2.3cd          | 9.41 ± 0.34b            |
| MA34 + 1.5 mM Si-NPs | 84.4 ± 3.6a       | 6.27 ± 0.28a | 29.4 ± 2.9a     | 41.5 ± 2.8a              | 55.6 ± 3.1a           | 10.3 ± 0.36a            |

Data are means ± SE. Within columns, values followed by different letters are significantly (p < 0.05) different according to Tukey's HSD test. DW, dry weight.
In total, 140 isolates were successfully isolated from calcareous soil on CCPB medium. Additionally, 34 isolates coded MA1–MA34 were grown on the CCPB plates supplemented with 10% of CaCO$_3$, 26 isolates were grown on the CCPB plates supplemented with 15% of CaCO$_3$, and 11 isolates survived at 20% of CaCO$_3$. On the other hand, only four isolates grew on CCPB medium supplemented with 25% CaCO$_3$. Only three isolates (MA16, MA27, and MA34) precipitated 30% CaCO$_3$ (Table 1), and only these three isolates were selected for the experiments described below. Furthermore, the screened isolates were all gram-negative, aerobic, motile, and non-spore-forming bacilli. According to Bergey's manual of systematic bacteriology morphological and biochemical tests, the obtained results showed that MA16, MA27, and MA34 isolates were similar to the *Bacillus* species.

They were identified as *B. licheniforms* MA16, *B. megaterium* MA27, and *B. subtilis* MA34. These three *Bacillus* spp. were further identified by MALDI–TOF mass spectrometry, as recommended by Biswas and Rolain (2013). Our results showed that they were 99% similar to the numerous *Bacillus* spp. According to the MALDI–TOF, score values were 2.332, 2.361, and 2.318. The local bacterial isolates *B. licheniforms* MA16, *B. megaterium* MA27, and *B. subtilis* MA34 were similar to *B. licheniforms* DSM30243$^T$, *B. megaterium* DSM76$^T$, and *B. subtilis* sp. subtilis DSM10$^T$, respectively (Supplementary Table 2). *Bacillus subtilis* MA34 grew better when treated with a higher concentration of CaCO$_3$, thus inducing the best growth (Table 1).

Furthermore, the selected CCPB (MA16, MA27, and MA34) showed rapid growth and the highest turbidity at pH 8, indicating that these isolates are moderate alkaliphiles (Figure 1A). MA34 showed more growth at optimum pH with a turbidity of $1.5 \times 10^6$ with a relative increase of 20% and 40% over MA27 and MA16, respectively. Conversely, the optimum temperature for the best growth of CCPB isolates was in the range of 30–40°C, with a preference for 37°C (Figure 1B). Similarly, the MA34 isolate had the best performance at 37°C.

According to the precipitation mass per cell, *B. subtilis* MA34 was the most efficient strain in inducing CaCO$_3$ precipitation. *B. subtilis* MA34 had the highest growth rate of $7.8 \times 10^6$. They precipitated the highest value of CaCO$_3$, i.e., 990 ppm, with a relative increase of 25% and 57% for *B. megaterium* MA27 and *B. licheniforms* MA16, respectively (Figure 2).

Furthermore, the urease activity was recorded in all strains and expressed as the amount of NH$_4^+$ produced. *B. subtilis* MA34 produced 775 ppm of NH$_4^+$ compared to 510 ppm and 325 ppm in *B. megaterium* MA27 and *B. licheniforms* MA16, respectively. Therefore, our findings showed that the mass of CaCO$_3$ precipitation was directly and positively correlated with urease activity (Figure 2).

### Effects of calcium carbonate-precipitating bacteria and silicon nanoparticles on wheat growth and production

The soil inoculated with the three isolated CCPB (MA16, MA27, and MA34) and/or foliar application of wheat plants with Si-NPs at 1.0 and 1.5 mM significantly increased the plant height, leaf area, shoot DW, the 1000 grain weight, and the number of grains spike$^{-1}$ compared to control (Table 2). In addition, the combined treatments (CCPB + Si-NPs) were more effective than the individual applications (CCPB or Si-NPs) in improving the above attributes. Notably, MA34 + 1.5 mM Si-NPs was the best treatment, increasing plant height by 38.1% and 35.6%, shoot DW by 79% and 78.6%, leaf area by 50.5% and 42.7%, number of grains spike$^{-1}$ by 110% and 116%, the 1000 grain weight by 43.4% and 49.1%, and plant grain yield by 173% and 186% in both seasons, respectively (Table 2).
Effect of calcium carbonate-precipitating bacteria and silicon nanoparticles on gas exchange parameters and photosynthetic pigments in wheat plants

Compared with the control, the soil inoculated with the three isolated CCPB (MA16, MA27, and MA34) and/or foliar application of wheat plants with Si-NPs at 1 and 1.5 mM impacted significant increases in the chlorophylls, carotenoids, \( Pn \), \( Tr \), and \( gs \) and photosynthetic efficiency (quantum yield of PSII; FPSII, \( qP \) and efficiency of PSII; \( Fv/Fm \)) except for the NPQ, which was significantly reduced (Tables 3, 4). The combined addition of CCPB and Si-NPs was more effective than individual applications in improving these parameters. Additionally, MA34 + 1.5 mM Si-NPs showed the best treatment by increasing the total chlorophylls (61.2% and 63.5%), total carotenoids (18.3% and 23.3%), \( Pn \) (60.1% and 61.4%), \( Tr \) (55.6% and 52.8%), \( gs \) (69.9% and 62.1%), FPSII (118% and 124%), \( qP \) (49.5% and 50.4%), and \( Fv/Fm \) (64.1% and 57%); however, decreased NPQ by 48.9% and 49.7% in both seasons, respectively (Tables 3, 4).

**Effect of calcium carbonate-precipitating bacteria and silicon nanoparticles on oxidative stress biomarkers and cell membranes in wheat plants**

Applying three isolated bacteria and/or Si-NPs at different rates considerably increased the RWC and MSI but reduced EL, MDA, \( O_2^- \), and \( H_2O_2 \) in wheat plants compared with the control (Tables 4, 5). Furthermore, the co-addition of CCPB and Si-NPs was more effective than the individual application.

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**TABLE 3** Effect of soil application with calcium carbonate precipitating bacteria (CCPB), *Bacillus licheniforms* (MA16), *Bacillus megaterium* (MA27), and *Bacillus subtilis* (MA34), and foliar application with silicon nanoparticles (Si-NPs) on photosynthetic pigments and gas exchange of wheat plants (cv. Misr 2).

| Treatment | Total chlorophylls (mg g\(^{-1}\) FW) | Total carotenoids (mg g\(^{-1}\) FW) | Net photosynthetic rate; \( Pn \) (\( \mu \) mol CO\(_2\) m\(^{-2}\) s\(^{-1}\)) | Transpiration rate; \( Tr \) (mMol H\(_2O\) m\(^{-2}\) s\(^{-1}\)) | Stomatal conductance; \( gs \) (mMol H\(_2O\) m\(^{-2}\) s\(^{-1}\)) |
|-----------|--------------------------------------|--------------------------------------|-----------------------------------------------|-----------------------------------------------|-----------------------------------------------|
| Control   | 1.55 ± 0.07f                         | 0.763 ± 0.03g                        | 7.18 ± 0.32f                                   | 4.13 ± 0.16j                                   | 0.343 ± 0.01j                                  |
| 1.0 mM Si-NPs | 1.66 ± 0.06k                       | 0.786 ± 0.02f                        | 8.62 ± 0.33k                                   | 4.58 ± 0.15i                                   | 0.386 ± 0.02i                                  |
| 1.5 mM Si-NPs | 1.76 ± 0.08i                        | 0.796 ± 0.04f                        | 8.80 ± 0.35j                                   | 4.72 ± 0.21h                                   | 0.410 ± 0.02h                                  |
| MA16       | 1.86 ± 0.09h                         | 0.816 ± 0.05e                        | 9.28 ± 0.41h                                   | 5.31 ± 0.11f                                   | 0.460 ± 0.03f                                  |
| MA27       | 1.82 ± 0.11i                         | 0.810 ± 0.06e                        | 9.15 ± 0.45i                                   | 5.16 ± 0.19g                                   | 0.433 ± 0.02g                                  |
| MA34       | 1.94 ± 0.09g                         | 0.836 ± 0.05d                        | 9.54 ± 0.49g                                   | 5.48 ± 0.22e                                   | 0.476 ± 0.03e                                  |
| MA16 + 1.0 mM Si-NPs | 2.11 ± 0.12e                    | 0.853 ± 0.04c                        | 10.0 ± 0.49e                                   | 5.94 ± 0.23d                                   | 0.506 ± 0.03d                                  |
| MA16 + 1.5 mM Si-NPs | 2.43 ± 0.15b                    | 0.890 ± 0.06b                        | 11.2 ± 0.61b                                   | 6.25 ± 0.28b                                   | 0.573 ± 0.04a                                  |
| MA27 + 1.0 mM Si-NPs | 1.98 ± 0.09f                    | 0.836 ± 0.08d                        | 9.91 ± 0.52f                                   | 5.88 ± 0.21d                                   | 0.493 ± 0.03d                                  |
| MA27 + 1.5 mM Si-NPs | 2.35 ± 0.13c                    | 0.886 ± 0.06b                        | 11.0 ± 0.73c                                   | 6.12 ± 0.32c                                   | 0.553 ± 0.04b                                  |
| MA34 + 1.0 mM Si-NPs | 2.25 ± 0.14d                    | 0.863 ± 0.07c                        | 10.6 ± 0.62d                                   | 6.07 ± 0.33c                                   | 0.526 ± 0.03c                                  |
| MA34 + 1.5 mM Si-NPs | 2.50 ± 0.16a                    | 0.903 ± 0.09a                        | 11.5 ± 0.66a                                   | 6.43 ± 0.35a                                   | 0.583 ± 0.02a                                  |

**First season**

**Second season**

Data are means ± SE. Within columns, values followed by different letters are significantly (\( P < 0.05 \)) different according to Tukey’s HSD test.
Notably, MA34 + 1.5 mM Si-NPs were more effective than other treatments, increasing RWC by 27.8% and 28.1% and MSI by 37.8% and 38.1%, and decreasing El by 42.7% and 45.2%, MDA by 67.6% and 73.5%, O$_{2}^{-}$ by 65% and 72.5%, and H$_{2}$O$_{2}$ by 71.3% and 77% in both seasons, respectively (Tables 4, 5).

**Effect of calcium carbonate-precipitating bacteria and silicon nanoparticles on non-enzymatic antioxidant compounds in wheat plants**

Compared with the control, the addition of CCPB and/or Si-NPs significantly increased osmoprotectants (Pro, TSS, and GB), α-TOC, AsA, and GSH (Table 6). The treatments of CCPB + Si-NPs were more effective than individual applications (CCPB or Si-NPs). MA34 + 1.5 mM Si-NPs was the best treatment, as it increased Pro (39.3% and 38.6%), TSS (114% and 115%), GB (48.5% and 49.9%), α-TOC (76.9% and 80.5%), AsA (94.2% and 93.5%), and GSH (157% and 147%) during the two seasons, respectively (Table 6).

### Table 4 Effect of soil application with calcium carbonate precipitating bacteria (CCPB), Bacillus licheniformis (MA16), Bacillus megaterium (MA27), and Bacillus subtilis (MA34), and foliar application with silicon nanoparticles (Si-NPs) on chlorophyll fluorescence parameters, RWC and MSI of wheat plants (cv. Misr 2).

| Treatment                  | FPSII    | qP       | NPQ     | Fv/Fm (%) | RWC (%) | MSI (%) |
|----------------------------|----------|----------|---------|-----------|---------|---------|
| **First season**           |          |          |         |           |         |         |
| Control                    | 0.420 ± 0.021 | 6.10 ± 0.12k | 1.20 ± 0.09a | 0.546 ± 0.03h | 60.4 ± 2.2i | 40.7 ± 1.2k |
| 1.0 mM Si-NPs              | 0.533 ± 0.04b | 7.20 ± 0.21l | 0.990 ± 0.08b | 0.616 ± 0.02g | 64.8 ± 2.3h | 43.3 ± 1.5j |
| 1.5 mM Si-NPs              | 0.586 ± 0.03g | 7.48 ± 0.22i | 0.956 ± 0.08bc | 0.640 ± 0.04g | 66.73 ± 1g | 44.4 ± 1.4i |
| MA16                       | 0.756 ± 0.05e | 8.16 ± 0.23g | 0.903 ± 0.07de | 0.706 ± 0.05ef | 70.4 ± 3.3e | 47.9 ± 2.1g |
| MA27                       | 0.710 ± 0.05f | 7.86 ± 0.25h | 0.930 ± 0.09cd | 0.693 ± 0.04f | 68.9 ± 3.5f | 46.7 ± 2.6f |
| MA34                       | 0.783 ± 0.06de | 8.46 ± 0.28f | 0.863 ± 0.04ef | 0.746 ± 0.05e | 71.7 ± 3.6d | 49.5 ± 2.5f |
| MA16 + 1.0 mM Si-NPs       | 0.830 ± 0.06c | 8.78 ± 0.23d | 0.810 ± 0.05gh | 0.823 ± 0.06cd | 73.6 ± 3.3c | 52.1 ± 2.9c |
| MA16 + 1.5 mM Si-NPs       | 0.893 ± 0.08b | 9.01 ± 0.22ab | 0.710 ± 0.03j | 0.833 ± 0.04ab | 76.5 ± 3.5b | 55.0 ± 1.9b |
| MA27 + 1.0 mM Si-NPs       | 0.796 ± 0.06d | 8.66 ± 0.24e | 0.836 ± 0.04fg | 0.790 ± 0.05d | 72.5 ± 2.9c | 50.5 ± 2.8c |
| MA27 + 1.5 mM Si-NPs       | 0.863 ± 0.07b | 8.94 ± 0.28bc | 0.746 ± 0.02j | 0.860 ± 0.03abc | 75.8 ± 3.4b | 54.4 ± 2.9b |
| MA34 + 1.0 mM Si-NPs       | 0.850 ± 0.08c | 8.84 ± 0.26cd | 0.786 ± 0.03ki | 0.846 ± 0.06bc | 74.2 ± 3.6c | 53.5 ± 2.3c |
| MA34 + 1.5 mM Si-NPs       | 0.916 ± 0.07a | 9.12 ± 0.31a | 0.613 ± 0.02k | 0.896 ± 0.04a | 77.2 ± 3.8a | 56.1 ± 2.5a |
| **Second season**          |          |          |         |           |         |         |
| Control                    | 0.443 ± 0.02g | 6.30 ± 0.14g | 1.30 ± 0.08a | 0.596 ± 0.02f | 61.0 ± 3.2k | 41.1 ± 2.4j |
| 1.0 mM Si-NPs              | 0.560 ± 0.03f | 7.43 ± 0.16f | 1.05 ± 0.07b | 0.666 ± 0.03e | 65.3 ± 3.1j | 43.8 ± 2.5i |
| 1.5 mM Si-NPs              | 0.616 ± 0.04f | 7.68 ± 0.19f | 1.00 ± 0.06c | 0.696 ± 0.04e | 67.5 ± 3.6i | 45.0 ± 2.9h |
| MA16                       | 0.790 ± 0.04de | 8.55 ± 0.22e | 0.943 ± 0.07de | 0.756 ± 0.05d | 71.5 ± 3.8g | 48.5 ± 2.6g |
| MA27                       | 0.746 ± 0.06e | 8.23 ± 0.28e | 0.986 ± 0.08cd | 0.753 ± 0.05d | 70.1 ± 3.4h | 47.6 ± 3.2g |
| MA34                       | 0.820 ± 0.07cd | 8.76 ± 0.26d | 0.913 ± 0.06ef | 0.796 ± 0.04cd | 72.2 ± 3.9g | 50.2 ± 2.5f |
| MA16 + 1.0 mM Si-NPs       | 0.890 ± 0.08b | 9.16 ± 0.32bc | 0.860 ± 0.05gh | 0.883 ± 0.06b | 74.5 ± 4.2d | 52.9 ± 2.9d |
| MA16 + 1.5 mM Si-NPs       | 0.930 ± 0.09ab | 9.44 ± 0.35ab | 0.760 ± 0.03j | 0.923 ± 0.07ab | 77.3 ± 3.9b | 55.7 ± 2.8b |
| MA27 + 1.0 mM Si-NPs       | 0.863 ± 0.08bc | 9.11 ± 0.34c | 0.886 ± 0.04fg | 0.830 ± 0.07c | 73.4 ± 3.6f | 51.4 ± 3.1e |
| MA27 + 1.5 mM Si-NPs       | 0.910 ± 0.08b | 9.30 ± 0.36ab | 0.786 ± 0.04j | 0.906 ± 0.08ab | 76.1 ± 3.8a | 55.4 ± 2.5c |
| MA34 + 1.0 mM Si-NPs       | 0.896 ± 0.06b | 9.20 ± 0.33abc | 0.826 ± 0.03hi | 0.896 ± 0.06ab | 75.2 ± 3.7c | 54.4 ± 2.3c |
| MA34 + 1.5 mM Si-NPs       | 0.996 ± 0.08a | 9.48 ± 0.32a | 0.653 ± 0.02k | 0.936 ± 0.09a | 78.2 ± 3.5a | 56.8 ± 2.9a |

Data are means ± SE. Within columns, values followed by different letters are significantly (P < 0.05) different according to Tukey’s HSD test. RWC, relative water content; MSI, membrane stability index; PSII, photosystem II; FPSII, the quantum yield of PSII; qP, photochemical quenching; NPQ, non-photochemical quenching; Fv/Fm, the efficiency of PSII.
TABLE 5 Effect of soil application with calcium carbonate precipitating bacteria (CCPB), Bacillus licheniforms (MA16), Bacillus megaterium (MA27), and Bacillus subtilis (MA34), and foliar application with silicon nanoparticles (Si-NPs) on oxidative stress of wheat plants (cv. Misr 2).

| Treatment                  | EL (%)      | MDA (μ mol g⁻¹ FW) | O₂⁻ (AS80 g⁻¹ FW) | H₂O₂ (μ mol g⁻¹ FW) |
|----------------------------|-------------|--------------------|-------------------|---------------------|
| Control                    | 12.4 ± 0.41a| 4.26 ± 0.11a       | 0.580 ± 0.03a     | 5.20 ± 0.14a        |
| 1.0 mM Si-NPs              | 10.4 ± 0.32b| 3.18 ± 0.16b       | 0.456 ± 0.02b     | 4.55 ± 0.16b        |
| 1.5 mM Si-NPs              | 9.93 ± 0.52c| 2.91 ± 0.12b       | 0.410 ± 0.01c     | 4.26 ± 0.12c        |
| MA16                      | 8.72 ± 0.65d| 2.45 ± 0.13cd      | 0.376 ± 0.01d     | 3.58 ± 0.11d        |
| MA27                      | 9.19 ± 0.32e| 2.56 ± 0.14c       | 0.393 ± 0.01cd    | 3.77 ± 0.14d        |
| MA34                      | 8.11 ± 0.48f| 2.36 ± 0.13cd      | 0.346 ± 0.02e     | 3.23 ± 0.16e        |
| MA16 + 1.0 mM Si-NPs       | 7.84 ± 0.36gh| 1.96 ± 0.11e       | 0.303 ± 0.01f     | 2.82 ± 0.14f        |
| MA16 + 1.5 mM Si-NPs       | 7.44 ± 0.48f| 1.45 ± 0.12f       | 0.236 ± 0.01h     | 1.77 ± 0.08h        |
| MA27 + 1.0 mM Si-NPs       | 7.95 ± 0.48fg| 2.18 ± 0.16de     | 0.323 ± 0.02ef    | 3.08 ± 0.11e        |
| MA27 + 1.5 mM Si-NPs       | 7.62 ± 0.49hi| 1.56 ± 0.15f      | 0.270 ± 0.01g     | 2.02 ± 0.06h        |
| MA34 + 1.0 mM Si-NPs       | 7.73 ± 0.43ghi| 1.40 ± 0.14f     | 0.273 ± 0.01g     | 2.47 ± 0.07g        |
| MA34 + 1.5 mM Si-NPs       | 7.10 ± 0.51j| 1.38 ± 0.13f       | 0.203 ± 0.01i     | 1.49 ± 0.06j        |

Table 5: First season

Data are means ± SE. Within columns, values followed by different letters are significantly (P < 0.05) different according to Tukey’s HSD test. EL, electrolyte leakage; MDA, malondialdehyde; O₂⁻, superoxide anion radical; H₂O₂, hydrogen peroxide.

(123% and 115%), and GR (57% and 56.7%) in both seasons, respectively (Table 7).

Discussion

Calcium carbonate precipitation is a type of bio-mineralization that frequently occurs in bacteria (Boquet et al., 1973). It can be accomplished through biologically controlled or induced mineralization mechanisms (Mann, 1995). However, CCPB consists mainly of induced mineralization (Zamarreño et al., 2009). Globally, several bacterial species participate in mineral carbonate precipitation in various conditions such as soils, oceans, saline lakes, and freshwaters. Mineralization induced by microbial metabolic activities raises the alkalinity of the medium, thus facilitating CaCO₃ precipitation (Castanier et al., 1999). The most common metabolic activity is urea hydrolysis, predominantly found in many microorganisms, majorly catalyzed by urease enzymes (Mobley and Hausinger, 1989). Urea hydrolysis using the microbial urease enzyme produces CO₃²⁻ and ammonia (NH₃), which raises soil pH and CO₂ content which reacts with Ca²⁺ and precipitates it as CaCO₃ (De Muynck et al., 2010).

Calcium carbonate-precipitating bacterial inoculation in sandy soil is one of the significant determinants of soil fertility, resulting in improved plant growth and productivity. It boosts the productivity of sandy soil by enhancing its biological activity, available nutrient content, and soil quality (Chaparro-Acuña et al., 2018; Elrys et al., 2018). These benefits of CCPB contributed to the high growth and yield of wheat when combined with Si-NPs foliar application (Table 2). This high performance was attributed to the improved chlorophyll fluorescence parameters and photosynthetic pigments of a wheat leaf affected by Si-NPs or CCPB treatments, principally the integrative CCPB + Si-NPs treatment. In addition, photosynthetic leaf pigments such as chlorophylls and carotenoids exhibited crucial roles in plant photosynthesis by capturing solar energy to fix carbon dioxide (CO₂) (Table 3). The chlorophyll fluorescence proportion depends on the amount of solar energy absorbed...
The measurements of the photosynthetic pigments and chlorophyll fluorescence in this study serve as indicators of plant health. Therefore, supplying plants with CCPB + Si-NPs preserves the leaf pigments and chlorophyll fluorescence content, which is positively correlated with wheat yields. Additionally, maintaining the efficiency of the antioxidant system components and PSII function (Tables 6, 7) contributed to wheat performance, coupled with the beneficial effects of CCPB and/or Si-NPs. Furthermore, preserving the antioxidant system components in CCPB and/or Si-NPs treatments aided cell membrane stabilization in terms of low EL and MDA in plants (Table 5).

Moreover, CCPB and/or Si-NPs (especially the integrative CCPB + Si-NPs treatment) supplied to plants led to better yield and growth, which is attributed to the enhanced translocation of the photosynthetic assimilates from leaf to spike. This result is linked to the ability of plants to improve the antioxidant defense

### Tables

#### Table 6  Effect of soil application with calcium carbonate precipitating bacteria (CCPB), *Bacillus licheniforms* (MA16), *Bacillus megaterium* (MA27), and *Bacillus subtilis* (MA34), and foliar application with silicon nanoparticles (Si-NPs) on osmoprotectants contents (free Pro and TSS), α–TOC, AsA, GSH and glycine betaine of wheat plants (cv. Msr2).

| Treatments               | Free pro (µ mol g⁻¹ DW) | TSS (mg g⁻¹ DW) | α–TOC (µ mol g⁻¹ DW) | AsA (µ mol g⁻¹ FW) | GSH (µ mol g⁻¹ FW) | GB (µ g g⁻¹ DW) |
|--------------------------|------------------------|----------------|---------------------|--------------------|-------------------|-----------------|
| **First season**         |                        |                |                     |                    |                   |                 |
| Control                  | 25.9 ± 2.1h            | 16.1 ± 1.1k    | 1.78 ± 0.08k        | 1.56 ± 0.06i       | 1.12 ± 0.07i      | 40.6 ± 2.2k     |
| 1.0 mM Si-NPs            | 27.8 ± 2.2g            | 18.5 ± 1.3j    | 2.04 ± 0.11i        | 1.99 ± 0.08h       | 1.66 ± 0.06k      | 44.6 ± 2.3j     |
| 1.5 mM Si-NPs            | 29.1 ± 2.6f            | 19.1 ± 1.5j    | 2.26 ± 0.12h        | 2.24 ± 0.11g       | 1.72 ± 0.04j      | 45.5 ± 2.2i     |
| MA16                     | 32.2 ± 2.3d            | 22.5 ± 1.6h    | 2.51 ± 0.13g        | 2.44 ± 0.12e       | 1.86 ± 0.06h      | 48.6 ± 2.5g     |
| MA27                     | 31.1 ± 2.8e            | 21.1 ± 2.1i    | 2.43 ± 0.14g        | 2.36 ± 0.13f       | 1.77 ± 0.07i      | 46.6 ± 2.6h     |
| MA34                     | 32.9 ± 2.6c            | 24.4 ± 2.3g    | 2.57 ± 0.11f        | 2.48 ± 0.14e       | 1.92 ± 0.03g      | 49.9 ± 2.5f     |
| MA16 + 1.0 mM Si-NPs     | 34.1 ± 2.9b            | 28.9 ± 2.6e    | 2.82 ± 0.15d        | 2.70 ± 0.17cd      | 2.35 ± 0.11e      | 55.7 ± 2.9d     |
| MA16 + 1.5 mM Si-NPs     | 35.5 ± 3.1a            | 33.1 ± 2.8b    | 3.02 ± 0.13h        | 2.97 ± 0.19a       | 2.80 ± 0.12b      | 59.6 ± 2.8b     |
| MA27 + 1.0 mM Si-NPs     | 33.4 ± 3.2c            | 26.6 ± 2.9f    | 2.72 ± 0.13e        | 2.64 ± 0.16d       | 2.13 ± 0.11f      | 53.1 ± 2.4e     |
| MA27 + 1.5 mM Si-NPs     | 34.5 ± 3.3b            | 31.4 ± 2.6c    | 2.96 ± 0.15bc       | 2.87 ± 0.18b       | 2.63 ± 0.13c      | 57.8 ± 2.8c     |
| MA34 + 1.0 mM Si-NPs     | 34.4 ± 2.5b            | 30.2 ± 2.8d    | 2.92 ± 0.14cd       | 2.76 ± 0.17c       | 2.45 ± 0.14d      | 57.7 ± 2.7c     |
| MA34 + 1.5 mM Si-NPs     | 36.1 ± 2.7a            | 34.6 ± 2.4a    | 3.15 ± 0.18a        | 3.03 ± 0.16a       | 2.88 ± 0.15a      | 60.3 ± 2.3a     |
| **Second season**        |                        |                |                     |                    |                   |                 |
| Control                  | 26.4 ± 2.2h            | 16.3 ± 1.3k    | 1.85 ± 0.09i        | 1.71 ± 0.08i       | 1.25 ± 0.06h      | 41.7 ± 1.9k     |
| 1.0 mM Si-NPs            | 28.3 ± 2.3g            | 18.8 ± 1.8j    | 2.17 ± 0.12h        | 2.19 ± 0.11h       | 1.77 ± 0.05g      | 45.7 ± 1.8j     |
| 1.5 mM Si-NPs            | 29.5 ± 2.5f            | 19.5 ± 1.6j    | 2.38 ± 0.14g        | 2.50 ± 0.15g       | 1.94 ± 0.07f      | 46.6 ± 2.3i     |
| MA16                     | 32.9 ± 2.8d            | 22.9 ± 1.9h    | 2.68 ± 0.16f        | 2.75 ± 0.17ef      | 2.10 ± 0.11ef     | 49.7 ± 2.5g     |
| MA27                     | 31.9 ± 2.6d            | 21.5 ± 1.8i    | 2.62 ± 0.12f        | 2.56 ± 0.15g       | 1.95 ± 0.12f      | 48.1 ± 2.9h     |
| MA34                     | 33.6 ± 2.9cd           | 24.8 ± 2.2g    | 2.71 ± 0.14f        | 2.82 ± 0.17de      | 2.14 ± 0.14e      | 51.2 ± 2.8f     |
| MA16 + 1.0 mM Si-NPs     | 34.7 ± 2.4b            | 29.4 ± 1.9e    | 2.97 ± 0.15d        | 2.98 ± 0.18dcd     | 2.58 ± 0.12cd     | 57.4 ± 3.1d     |
| MA16 + 1.5 mM Si-NPs     | 36.1 ± 2.8a            | 33.9 ± 2.6b    | 3.26 ± 0.16ab       | 3.27 ± 0.21a       | 3.09 ± 0.16a      | 61.3 ± 3.2b     |
| MA27 + 1.0 mM Si-NPs     | 33.9 ± 2.6c            | 27.1 ± 2.7f    | 2.89 ± 0.14e        | 2.87 ± 0.16dce     | 2.43 ± 0.18d      | 54.8 ± 3.5e     |
| MA27 + 1.5 mM Si-NPs     | 35.2 ± 3.1b            | 31.8 ± 2.6c    | 3.14 ± 0.19bc       | 3.06 ± 0.22b       | 2.76 ± 0.13b      | 59.5 ± 3.3c     |
| MA34 + 1.0 mM Si-NPs     | 34.9 ± 2.9b            | 30.8 ± 2.4d    | 3.05 ± 0.18cd       | 3.04 ± 0.23bc      | 2.64 ± 0.15bc     | 59.4 ± 3.2c     |
| MA34 + 1.5 mM Si-NPs     | 36.6 ± 2.5a            | 35.1 ± 2.9a    | 3.34 ± 0.13a        | 3.31 ± 0.24a       | 3.09 ± 0.22a      | 62.1 ± 3.3a     |

Data are means ± SE. Within columns, values followed by different letters are significantly (P > 0.05) different according to Tukey’s HSD test. Pro, proline; DW, dry weight; TSS, total soluble sugars; α–TOC, α-tocopherol; AsA, ascorbate; GSH, glutathione; GB, glycine betaine.
system components (Tables 6, 7). Therefore, this enhanced plant's performance in cell expansions and meristematic activities due to the retention of a sufficient quantity of water under sandy soil conditions causing increased contents of osmoprotectants such as TSS, Pro, and GB (Table 6).

In addition, the application of CCPB and/or Si-NPs induced a rise in wheat growth and production (Table 2), correlated with increased photosynthetic efficiency, chlorophyll biosynthesis, and gas exchange (Tables 3, 4). There was also a decrease in H$_2$O$_2$ and O$_2^-$ accumulations. Furthermore, after treating the plants with CCPB and/or Si-NPs, the efficiency of photosynthesis is boosted by increasing the ameliorative influences on chlorophyll fluorescence attributes (e.g., exc, PSI, qP, and Fv/Fm) while reducing the NPQ. Therefore, we revealed that the photosynthetic efficiency elevation in this study largely depends on the protected functioning of the photosynthetic light reaction, which functionally concurred with the enzymes PSI and PSI.

Silicon and/or CCPB application reduced H$_2$O$_2$ and O$_2^-$ accumulation, MDA (a lipid peroxidation marker), and EL in the plants grown in sandy soil (Table 5). In addition, plants provided with CCPB and/or Si-NPs significantly reduced the membrane MDA and EL, improving membrane integrity attributed to the positive influence of the treatments on antioxidant system component maintenance (Table 7) and low peroxidation rates (Table 5). Plants treated with CCPB and/or Si-NPs significantly increased antioxidant enzyme activity with the AsA and GSH contents, shielding them from high H$_2$O$_2$ and O$_2^-$ (Gong et al., 2003; Desoky et al., 2019). Therefore, this mechanism decreases toxic hydroxyl radical (OH$^-$) formation (Singh and Prasad, 2014).

The accumulation of AsA and GSH initiated by CCPB and/or Si-NPs protects wheat plants from ROS-stimulated

**Table 7** Effect of soil application with calcium carbonate precipitating bacteria (CCPB), *Bacillus licheniformis* (MA16), *Bacillus megaterium* (MA27), and *Bacillus subtilis* (MA34), and foliar application with silicon nanoparticles (Si-NPs) on antioxidant enzymes of wheat plants (cv. Misr 2).

| Treatment                        | CAT  | POX  | APX  | SOD  | GR   |
|----------------------------------|------|------|------|------|------|
| **First season**                 |      |      |      |      |      |
| Control                          | 60.7 ± 2.6k | 0.560 ± 0.03h | 55.5 ± 2.5k | 3.21 ± 0.11k | 32.1 ± 1.5f |
| 1.0 mM Si-NPs                    | 62.7 ± 2.8j | 0.880 ± 0.04g | 57.7 ± 2.6j | 4.26 ± 0.13j | 42.6 ± 1.5f |
| 1.5 mM Si-NPs                    | 63.7 ± 3.0i | 1.01 ± 0.06f | 58.4 ± 2.4i | 4.66 ± 0.15i | 43.1 ± 1.6f |
| MA16                             | 65.8 ± 3.1g | 1.09 ± 0.05ef | 59.7 ± 2.7g | 5.94 ± 0.16g | 44.2 ± 1.7e |
| MA27                             | 64.7 ± 3.4h | 1.06 ± 0.07ef | 59.1 ± 2.3h | 5.58 ± 0.17h | 43.2 ± 1.6f |
| MA34                             | 66.4 ± 3.3f | 1.66 ± 0.06e | 60.3 ± 2.9f | 6.07 ± 0.13f | 44.9 ± 1.8de |
| MA16 + 1.0 mM Si-NPs             | 68.2 ± 3.6d | 1.42 ± 0.07cd | 61.7 ± 2.7e | 6.63 ± 0.19d | 46.6 ± 1.6c |
| MA16 + 1.5 mM Si-NPs             | 70.7 ± 3.5b | 1.53 ± 0.08ab | 64.8 ± 2.6b | 7.04 ± 0.21b | 49.6 ± 2.2a |
| MA27 + 1.0 mM Si-NPs             | 67.3 ± 3.7d | 1.33 ± 0.07d | 61.4 ± 2.8e | 6.27 ± 0.17e | 45.8 ± 2.7cd |
| MA27 + 1.5 mM Si-NPs             | 69.9 ± 3.8c | 1.49 ± 0.06abc | 63.5 ± 2.7c | 6.87 ± 0.13c | 48.6 ± 2.6b |
| MA34 + 1.0 mM Si-NPs             | 69.5 ± 3.6c | 1.45 ± 0.03bc | 62.6 ± 2.3d | 6.80 ± 0.18c | 47.7 ± 2.7b |
| MA34 + 1.5 mM Si-NPs             | 71.6 ± 3.4a | 1.60 ± 0.07a | 65.9 ± 2.9a | 7.18 ± 0.21a | 50.4 ± 2.9a |
| **Second season**                |      |      |      |      |      |
| Control                          | 61.6 ± 2.5i | 0.590 ± 0.02f | 56.1 ± 1.9h | 3.37 ± 0.12e | 32.6 ± 1.6f |
| 1.0 mM Si-NPs                    | 63.6 ± 2.8h | 0.910 ± 0.05e | 58.5 ± 2.4g | 4.51 ± 0.14d | 43.4 ± 1.3e |
| 1.5 mM Si-NPs                    | 64.5 ± 2.6g | 1.15 ± 0.06d | 59.2 ± 2.4g | 4.84 ± 0.15d | 43.9 ± 1.8e |
| MA16                             | 66.9 ± 3.7e | 1.22 ± 0.08d | 60.4 ± 3.2f | 6.27 ± 0.16bc | 45.1 ± 1.8de |
| MA27                             | 65.7 ± 3.6f | 1.15 ± 0.09d | 60.3 ± 3.4f | 6.10 ± 0.17c | 44.1 ± 2.2e |
| MA34                             | 67.4 ± 3.8e | 1.26 ± 0.07cd | 61.2 ± 3.5e | 6.46 ± 0.19bc | 45.7 ± 2.6cde |
| MA16 + 1.0 mM Si-NPs             | 68.7 ± 3.6d | 1.57 ± 0.06ab | 62.1 ± 3.5d | 6.99 ± 0.18a | 48.4 ± 2.4abc |
| MA16 + 1.5 mM Si-NPs             | 70.3 ± 3.8c | 1.69 ± 0.07a | 65.6 ± 3.6b | 7.11 ± 0.22a | 50.7 ± 2.9a |
| MA27 + 1.0 mM Si-NPs             | 68.4 ± 3.5d | 1.44 ± 0.09bc | 62.1 ± 3.7d | 6.52 ± 0.21b | 47.7 ± 2.7bcd |
| MA27 + 1.5 mM Si-NPs             | 70.7 ± 3.8bc | 1.66 ± 0.07a | 64.1 ± 3.4c | 7.08 ± 0.25a | 49.9 ± 2.6ab |
| MA34 + 1.0 mM Si-NPs             | 71.3 ± 3.7b | 1.60 ± 0.4ab | 63.5 ± 2.9c | 7.04 ± 0.26a | 49.3 ± 2.5ab |
| MA34 + 1.5 mM Si-NPs             | 72.2 ± 2.9a | 1.73 ± 0.09a | 66.6 ± 2.8a | 7.27 ± 0.28a | 51.1 ± 2.9a |

Data are means ± SE. Within columns, values followed by different letters are significantly (*P < 0.05*) different according to Tukey’s HSD test. CAT, catalase; POX, peroxidase; APX, ascorbate peroxidase; SOD, superoxide dismutase; GR, glutathione reductase.
injuries. Additionally, CCPB and/or Si-NPs-induced upregulation of the ROS scavenging pathway components such as AsA, GR, APX, and GSH which improves plant tolerance mechanisms against oxidative damage. For example, wheat plants treated with CCPB and/or Si-NPs decreased ROS accumulation (H₂O₂ and O₂·−) (Table 5) and increased protection of the photosynthetic pathways (Tables 3, 4), contributing to improved growth and yield productivity (Table 2). H₂O₂, a byproduct of O₂·− elimination by the activity of SOD, degrades in the ascorbate-glutathione cycle and cytoplasm by APX and CAT, respectively (Feierabend, 2005). Furthermore, the APX enzyme is critical in scavenging H₂O₂ in the chloroplasts and cytosol, averting H₂O₂ diffusion into other organelles that could potentially cause damage. Furthermore, the optimal operation of the AsA-GSH cycle pathway when plants were provided with CCPB and/or Si-NPs (Tables 6, 7) effectively preserved GSH and AsA components, reducing the oxidative stress (H₂O₂ and O₂·−; Table 5). Therefore, the increased non-enzymatic and enzymatic antioxidant activity is linked to improved plant health (Elrys et al., 2020; El-Saadony et al., 2021).

Our study treated wheat plants with CCPB and/or Si-NPs, causing the accumulated osmoprotectants (e.g., TSS, GB, Pro, and α-TOC) to raise the RWC, MSI, and water content of plants in sandy soil (Table 4). We also reported limited Pro accumulation, as pro-synthesizing enzymes were upregulated, whereas the catabolizing enzymes were downregulated (Table 6). This result was due to increased antioxidant system components, GB, and TSS. Additionally, Pro was incorporated into proteins (Ahmad, 2010). Si-NPs increased TSS and GB accumulation, maintaining balanced plant water (Ahanger et al., 2014).

Conclusively, wheat plants treated with CCPB and/or Si-NPs developed some potential mechanisms in sandy soils. These include increased accumulation of osmoprotectant compounds that provide a mechanism for water loss reduction in leaves and boost their water content to maintain healthy metabolic processes and membrane stability under sandy soil conditions. Additionally, increased antioxidant activity (enzymatic and non-enzymatic) provides a potential mechanism for strengthening the antioxidant defense system and increasing plant resistance. These mechanisms, combined with others, resulted in plant leaves remaining green, delayed senescence, and enhanced photosynthesis efficiency and chlorophyll content to maintain healthy plants. Therefore, these improvements in antioxidant defense components help limit oxidative damage.

Data availability statement

The original contributions presented in this study are included in the article/Supplementary material, further inquiries can be directed to the corresponding authors.

Author contributions

E-SD, SA, KE-T, and ME-S conceived and designed the research. MR, SA, KE-T, and ME-S supervised the study. E-SD, MR, MN, NM, and AE performed open greenhouse experiments. E-SD, MR, and MN performed the microscopic experiments. E-SD, SA, KE-T, and ME-S analyzed the data. AE, AM, SA, and KE-T assisted with experiments and/or data evaluation. E-SD, SA, KE-T, and ME-S wrote the manuscript. All authors critically revised the manuscript and approved the final version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpls.2022.947949/full#supplementary-material
Improvement of drought tolerance in five different cultivars of Vicia faba by pretreatment using licorice root extract (LRE) as an organic antioxidant defenses, antioxidant gene expression, and salt tolerance in Pisum. Environ. Sci. Pollut. Res. improves wheat production and defenses under salt stress conditions. Ecotoxicol. J. Agric. Food Chem. edible tropical plants. Afr. J. Biotechnol. by different bacterial strains. 126, 9ñ23. doi: 10.1016/S0037-0738(99)00028-7 Nature 246, 527ñ529. doi: 10.1038/246527a0 calcite (calcium carbonate) crystals by soil bacteria is a general phenomenon. J. Am. J. Agric. Sci. 18:605ñ612. doi: 10.5424/sjar/2020182-16122 Rice 91, 39ñ42. doi: 10.1002/(SICI)1097-1347(199805)92:3<205::AID-AERES92>3.0.CO;2-8 Environ. Sci. Pollut. Res. 13, 400ñ408. doi: 10.1038/jnmat3890 J. Agric. Food Chem. 56, 575ñ588. doi: 10.1080/03650340903164231 Physiol. Plant 129, 822ñ829. doi: 10.1016/j.jplph.2007.02.005 J. Agric. Food Chem. 125, 189ñ198. doi: 10.1021/jf990500935 Physiol. Plant 51, 659ñ668. doi: 10.1093/jxb/51.345.659 Water Res. 15446/acag.v67n2.66109. doi: 10.1007/s11976-006-0345-7. doi: 10.1007/bf02374789 Griffin, O. W. (1980). Determination of glutathione and glutathione disulfide using glutathione reductase and 2-xylylpyridine. Anal. Biochem. 106, 207ñ212. doi: 10.1006/abio.1980.0004 Guinebretière, M. H., Auger, S., Galleron, N., Contez, M., De Sarrau, B., De Buyser, M. L., et al. (2013). Bacillus caffeticola sp. nov. is a novel thermotolerant species of the Bacillus cereus group occasionally associated with food poisoning. Int. J. Syst. Evol. Microbiol. 63, 51ñ60. doi: 10.1099/ijs.0.058267-0 Han, J., Gu, L., Warren, J. M., Guha, A., Mclennan, D. A., Zhang, W., et al. (2012). The roles of photosynthetic and non-photosynthetic quenching in regulating photosynthesis depend on the phases of fluctuating light conditions. Tree Physiol. 42, 848ñ861. doi: 10.1093/tree/tpb133 Hammes, F., Boon, N., De Villiers, J., Verstraete, W., and Siciliano, S. D. (2003). Strain-speciﬁc ureolytic microbial calcium carbonate precipitation. Appl. Environ. Microbiol. 69, 4901ñ4909. doi: 10.1128/aem.69.8.4901-4909-2003 Heath, R. L., and Packer, L. (1968). Photoperoxidation in isolated chloroplasts. I. Kinetics and stoichiometry of fatty acid peroxidation. Arch. Biochem. Biophys. 129, 185ñ199. doi: 10.1016/0003-9861(68)90654-1 Irigoyen, J., Emerich, D., and Sánchez-Díaz, M. (1992). Water stress induced changes in concentrations of proline and total soluble sugars in nodulated alfalfa (Medicago sativa) plants. Physiol. Plant 84, 55ñ60. doi: 10.1111/j.1399-3054.1992.tb08764.x Kampenholt, K., Vanmontagu, M., and Inze, D. (1995). Extraction and determination of ascorbate and dehydroascorbate from plant tissue. Anal. Biochem. 225, 165ñ170. doi: 10.1016/0003-9861(89)90318-2 Khatie, A., and Dikken, C. (1991). ‘‘Transgenic plants: a potential tool for the protection of the environment and human health’’. In: ‘‘The Use of Biotechnology in Agriculture’’, F. O. Chan, H. W. Ko, and S. C. Lo (eds.). Ellis Horwood Limited, Chichester, UK. Khatie, A., and Dikken, C. (1992). ‘‘Transgenic plants: a potential tool for the protection of the environment and human health’’. In: ‘‘The Use of Biotechnology in Agriculture’’, F. O. Chan, H. W. Ko, and S. C. Lo (eds.). Ellis Horwood Limited, Chichester, UK. Khatie, A., and Dikken, C. (1992). ‘‘Transgenic plants: a potential tool for the protection of the environment and human health’’. In: ‘‘The Use of Biotechnology in Agriculture’’, F. O. Chan, H. W. Ko, and S. C. Lo (eds.). Ellis Horwood Limited, Chichester, UK. Khatie, A., and Dikken, C. (1992). ‘‘Transgenic plants: a potential tool for the protection of the environment and human health’’. In: ‘‘The Use of Biotechnology in Agriculture’’, F. O. Chan, H. W. Ko, and S. C. Lo (eds.). Ellis Horwood Limited, Chichester, UK. Khatie, A., and Dikken, C. (1992). ‘‘Transgenic plants: a potential tool for the protection of the environment and human health’’. In: ‘‘The Use of Biotechnology in Agriculture’’, F. O. Chan, H. W. Ko, and S. C. Lo (eds.). Ellis Horwood Limited, Chichester, UK. Khatie, A., and Dikken, C. (1992). ‘‘Transgenic plants: a potential tool for the protection of the environment and human health’’. In: ‘‘The Use of Biotechnology in Agriculture’’, F. O. Chan, H. W. Ko, and S. C. Lo (eds.). Ellis Horwood Limited, Chichester, UK. Khatie, A., and Dikken, C. (1992). ‘‘Transgenic plants: a potential tool for the protection of the environment and human health’’. In: ‘‘The Use of Biotechnology in Agriculture’’, F. O. Chan, H. W. Ko, and S. C. Lo (eds.). Ellis Horwood Limited, Chichester, UK. Khatie, A., and Dikken, C. (1992). ‘‘Transgenic plants: a potential tool for the protection of the environment and human health’’. In: ‘‘The Use of Biotechnology in Agriculture’’, F. O. Chan, H. W. Ko, and S. C. Lo (eds.). Ellis Horwood Limited, Chichester, UK.
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