

Impact of bicarbonate on organic acid exudation, silicon uptake and utilization in maize roots

Jing Wei¹ · Mohamed Aboueldahab^{2,3} · Yanyou Wu²  · Deke Xing¹ · Jing Wang¹ · Qian Zhang¹ · Weixu Wang¹

Received: 14 March 2025 / Revised: 7 April 2025 / Accepted: 24 April 2025 / Published online: 25 May 2025

© The Author(s), under exclusive licence to Science Press and Institute of Geochemistry, CAS and Springer-Verlag GmbH Germany, part of Springer Nature 2025

Abstract Global climate change has made carbon neutrality a crucial goal. The karst environment, with high bicarbonate content, challenges plant growth and carbon sequestration. Bicarbonate has both negative and positive effects on plants, and selecting suitable crops to effectively leverage the positive effects of bicarbonates is vital for karst agriculture. This study aimed to investigate how different bicarbonate concentrations affect organic acid exudation from maize roots. It also explored the impact on silicon uptake, growth, photosynthesis and cellular metabolic energy in two maize varieties (Jingke 968 and Tiannuo 182) and compared their adaptability to bicarbonate environments. The experiment was conducted in a greenhouse. Maize seedlings were cultured with Hoagland's nutrient solution containing different concentrations of NaHCO_3 (0, 5 and 10 mM). After 21 days, various indices were measured. The results show that malic and citric acids were key organic acids in maize's response to bicarbonate stress. Jingke 968, under bicarbonate stress, exhibits reduced photosynthesis and growth, with less energy for silicon uptake and lower carbon storage in phytoliths. Tiannuo 182 adapts better to a 5 mM bicarbonate

environment. It also exudes more organic acids, improving its adaptation to high bicarbonate (10 mM) conditions and enhancing carbon sequestration. Tiannuo 182 is more suitable for karst regions with complex bicarbonate environments as it can allocate more energy to growth and silicon absorption. The differential response of maize varieties to bicarbonate stress provides scientific support for variety selection and zoning in karst cultivation areas.

Keywords Maize · Bicarbonate · Organic acids · Silicon uptake · Phytolith · Carbon sink

1 Introduction

Global climate change is one of our most widely discussed issues, and addressing global warming represents a universal challenge. Achieving carbon neutrality is a key solution to this problem. Karst landscapes are extensively distributed in China, and karst carbon sinks play a significant role in helping the country reach its carbon neutrality goals. However, the karst environment in southwest China is characterized by exposed bedrock, rock leakage, poor soil quality, high pH, high bicarbonate content and elevated calcium and magnesium levels, which present significant challenges to the growth and development of local plants as well as their carbon sequestration potential (Liu et al. 2020b; Wu and Wu 2022; Yang et al. 2022). Among these challenges, bicarbonates, as alkaline salts, significantly negatively impact plant physiological processes, having detrimental effects on plant growth and development and the ecological environment in karst regions.

Bicarbonate negatively impacts plant growth and metabolism. Elevated levels of bicarbonate can induce stomatal closure (Kolla et al. 2007). The accumulation of bicarbonate

✉ Yanyou Wu
wuyanyou@mail.gyig.ac.cn

✉ Deke Xing
xingdeke@ujs.edu.cn

¹ Key Laboratory of Modern Agricultural Equipment and Technology, Ministry of Education, School of Agricultural Engineering, Jiangsu University, Zhenjiang 212013, China

² State Key Laboratory of Environmental Geochemistry, Institute of Geochemistry, Chinese Academy of Sciences, Guiyang 550081, China

³ University of Chinese Academy of Sciences, Beijing 100049, China

within chloroplasts disrupts the electron transfer chain, leading to reduced ATP and NADPH production, which are crucial for the Calvin cycle. This, in turn, results in decreased carbon fixation and an overall inhibition of photosynthesis (Poschenrieder et al. 2018). High bicarbonate concentrations also negatively affect nitrogen assimilation and carbon fixation enzymes, such as nitrate reductase and phosphoenolpyruvate carboxylase. The decreased activity of these enzymes disrupts normal carbon-nitrogen metabolism, impacting protein synthesis and the production of other essential organic compounds (Bie et al. 2004; Burbulis et al. 2017; Poschenrieder et al. 2018). Furthermore, high bicarbonate levels disturb plants' uptake and distribution of vital ions. For example, bicarbonate interferes with the absorption of iron, zinc and other micronutrients, mainly because of the formation of insoluble complexes with these metal ions in the soil solution, reducing their availability to plant roots. High bicarbonate concentrations can interfere with nutrient absorption, leading to nutrient deficiencies and imbalances, further weakening the plant's ability to sequester carbon (Custic et al. 2008).

However, recently, studies have increasingly explored the positive effects of bicarbonate on plants. During drought or other stress conditions, bicarbonate serves as an alternative carbon source for plants. On the one hand, plant roots can absorb bicarbonate and transport it to the leaves; on the other, it helps maintain plant cell water-holding capacity, providing a short-term water source. This process promotes stomatal opening, facilitating gas exchange and restoring photosynthesis (Li et al. 2023). Bicarbonate also regulates key enzymes in carbon-nitrogen metabolism. It enhances Calvin cycle enzymes, promotes carbon assimilation and increases nitrogen reduction enzymes like glutamine synthetase, aiding inorganic nitrogen conversion to organic nitrogen compounds in plants (Xia and Wu 2022). Furthermore, bicarbonate influences glucose metabolism in plants. Altering the distribution between glycolysis and the pentose phosphate pathway boosts plant antioxidant capacity and stress resistance (Yao and Wu 2021). Plants treated with appropriate bicarbonate levels showed increased antioxidant enzymes and osmolyte accumulation under stress, enabling better environmental adaptation (Burbulis et al. 2022; Yao and Wu 2021).

Therefore, in the agricultural ecosystems of karst areas, an urgent issue to be addressed is the selection of appropriate crops to effectively leverage the positive effects of bicarbonates in response to the challenges posed by carbonate environments, thereby enhancing crop yield and carbon sequestration potential.

Plants can resist environmental stresses by modulating the exudation of organic acids from their roots (Panchal et al. 2021). Carbon fixed through photosynthesis is the primary source of organic acids exuded by plants, and the organic

acids released by the roots are the primary dynamic source of soil organic acids, representing one of the most active carbon pools in the soil and acting as a regulatory carbon sink (Zhou et al. 2023). In karst soil environments, the increased organic acids released by plant roots directly affect the formation and flow of carbon sinks (Zhao and Wu 2011). Additionally, organic acids exuded by the roots can influence soil properties, pH and other dynamic changes, profoundly affecting nutrient availability and microbial activity in the soil, thus indirectly impacting the plant's carbon sequestration capacity (Chen et al. 2021; Panchal et al. 2022). The exudation of organic acids by plant roots can increase the availability of poorly soluble nutrients in the soil rhizosphere through acidification, chelation, ion exchange and reduction, thereby enhancing nutrient uptake and promoting plant growth (Widodo et al. 2010; Liao et al. 2006; Ohta and Hiura 2016). Low-molecular-weight organic acids, such as oxalic acid, can form complexes with aluminum and silicate ester compounds containing SiO_2 , thus increasing the solubility of Al and Si in water (Sokolova et al. 2018). Therefore, the exudation of organic acids by plant roots plays a crucial role in both silicon absorption and utilization and in enhancing ecosystems' carbon sequestration potential.

Phytoliths, also referred to as plant phytoliths, are created when higher plants uptake soluble SiO_2 from the soil via their roots during growth. The absorbed SiO_2 is subsequently transported through the plant's vascular system to organs such as stems and leaves where it precipitates between and within plant cells, forming amorphous SiO_2 particles (Ma and Yamaji 2006). Phytoliths are silicon-impregnated cells and tissues. During their development, phytoliths encapsulate approximately 0.1% to 6% of organic carbon, known as phytolith-occluded carbon (PhytOC) or phytolith carbon (Sun et al. 2017; Parr and Sullivan 2011; Rajendiran et al. 2012). The stability of the phytolith carbon is closely linked to the phytoliths' stability. Phytoliths exhibit high-temperature resistance and resistance to degradation, enabling them to be stored in soil for extended periods. Compared to other carbon forms, they are more stable and, post-plant death, can enter the soil and remain sequestered for long durations, not engaging in the atmospheric carbon cycle for an extended period. This attribute confers significant carbon sequestration potential on them (Li et al. 2013; Huang et al. 2014; Yang et al. 2020).

Research has indicated that the foliar application of silica solutions can enhance lignin accumulation in rapeseed stems, promoting lignification, improving mechanical strength and increasing resistance to lodging (Hu et al. 2022). Silica also stimulates root growth in rice, boosting root vitality and enhancing the plant's capacity to absorb water and nutrients. It causes leaves to grow more upright, improving light capture and increasing photosynthetic efficiency. Furthermore, it can reduce transpiration and

enhance drought resistance (Gao et al. 2004; Chen et al. 2011; Wang et al. 2019). In plants, silica acts as a substitute for carbon in growth and metabolism and enhances growth efficiency and stress resistance through various mechanisms (Tuna et al. 2008; Habibi 2014; Sourì et al. 2021).

Maize is a crop with high light efficiency and a significant capacity for carbon sequestration, making it suitable for cultivation in karst regions (Shinano et al. 2004). Additionally, maize is a silicon-loving plant with a substantial requirement for silicon, leading to a considerable accumulation of phytoliths and the occlusion of organic carbon (Gao et al. 2004). This crop exhibits a high tolerance to drought and cold, adapts well to poor soil conditions and possesses commendable environmental adaptability (Asai and Soisouvanh 2017; Liu et al. 2021). Research into phytoliths has predominantly concentrated on their morphological traits and archeological significance. For example, plant fossils serve as valuable tools for deducing historical water availability, as the ratio of long to short cells in phytoliths tends to rise with increased water availability (Esteban et al. 2018; D'Agostini et al. 2023).

Plants obtain energy via photosynthesis, which can be converted into photosynthetic and internal energy. Photosynthetic energy is characterized by the net photosynthetic rate, whereas internal energy pertains to the energy stored within the plant's electrical components (including resistance, inductance and capacitance), referred to as metabolic energy. Both photosynthetic and internal energy collectively contribute to plant growth, resilience against adversity, ion uptake and other metabolic processes (Duan et al. 2022). According to the law of conservation of energy, the energy required by plants to withstand stress in various environments is the sum of photosynthetic and metabolic energy minus the energy expended on the plant's growth and the energy needed for metabolic processes such as ion uptake (Chen et al. 2022). Consequently, the distribution of energy a plant acquires through photosynthesis among growth, stress resistance and ion uptake (including silicon uptake) will dictate the plant's carbon sink capacity and ability to adapt to stress.

This study holds significant implications for enhancing our understanding of carbon sequestration mechanisms in maize under bicarbonate stress, particularly in karst regions. By elucidating the role of organic acid exudation, photosynthesis, silicon accumulation and energy allocation in maize's response to high bicarbonate environments, the research contributes to selecting varieties and optimizing maize cultivation practices for both food security and carbon sink enhancement. The findings also provide valuable insights into the potential for utilizing maize as a carbon sink in karst agricultural ecosystems, supporting sustainable agricultural development and climate change mitigation strategies.

2 Materials and methods

The experiment was conducted in the greenhouse at Jiangsu University from July to September 2022 and June to July 2023. The experimental materials included two maize varieties: Jingke 968 and Tiannuo 182. Seeds of both varieties were sown in a 50-cell seedling tray, and after the seedlings emerged, uniform seedlings were selected and transplanted into pots filled with perlite, with three plants per pot. The plants were then cultured with Hoagland's nutrient solution, with the pH adjusted to 8.0 ± 0.2 . The nutrient solution was supplemented with NaHCO_3 at concentrations of (0, 5 and 10 mM). Each treatment group contained five seedlings, and each treatment was repeated five times. The nutrient solution was replaced every 2 days to meet the plants' nutritional needs. After 21 days of treatment, various indices were measured.

2.1 Sample collection and measurement

2.1.1 Measurement of root organic acid exudation, total silicon, phytoliths and phytolith-occluded carbon content (PhyTOC)

Following treatment, maize plants were harvested, and the samples were separated into three components: roots, stems and leaves. The samples were initially rinsed with tap water and subsequently washed thrice with distilled water. They were then blanched at 110°C for 15 min and dried at 65°C until a constant weight was achieved. Post-drying, the maize roots, stems and leaves were ground and sieved through a 0.27-mm mesh. Subsequently, the organic acids within the maize root tissue, as well as the total silicon, phytoliths and phytolith-occluded carbon in the roots, stems and leaves, were extracted and analyzed (Zhao and Wu 2014, 2018; Liu et al. 2020a).

2.1.2 Measurement of photosynthetic indices and plant height

Between 8:30 a.m. and 11:30 a.m., five plants were randomly selected from each treatment. The fourth or fifth fully expanded leaves of plants exhibiting consistent growth were selected for measurement. The net photosynthetic rate (P_N , $\mu\text{mol m}^{-2} \text{s}^{-1}$), stomatal conductance (g_s , $\text{mmol m}^{-2} \text{s}^{-1}$) and transpiration rate (E , $\text{mmol m}^{-2} \text{s}^{-1}$) were recorded using a portable Li-6400XT Photosynthesis Measurement System (LI-COR, Lincoln, NE, USA). Furthermore, the instantaneous water use efficiency (WUE_i , $\mu\text{mol mmol}^{-1}$) was calculated. The measurements

were conducted in quintuplicate at each treatment level. The WUE_i calculation formula is as follows:

$$\text{WUE}_i = \frac{P_N}{E} \quad (1)$$

During the tests, the daily photosynthetic photon flux density (PPFD) ranged from 56.79 to 1508.81 mmol m⁻² s⁻¹, with air temperature maintained at 31.44 ± 1.25 °C and CO₂ concentration at 413.44 ± 11.39 μmol·mol⁻¹.

2.1.3 Measurement and calculation of cell metabolic energy

A homemade parallel plate capacitor sensor connected to an LCR meter was used to measure the plant electrophysiological signals, including inductance (L), capacitance (C) and resistance (R) with the clamping force (F) by applying a test voltage of 1.5 V and a frequency of 3 kHz. The cell metabolic energy (ΔG_B) was then calculated (Chen et al. 2022). A model of the variation in electrophysiological parameters of the plant leaf with clamping force was constructed to obtain the parameters of the model, as detailed below:

Capacitance (C):

$$C = y_0 + k_0 F \quad (2)$$

Resistance (R):

$$R = y_1 + k_1 e^{-b_1 F} \quad (3)$$

Impedance (Z):

$$Z = y_2 + k_2 e^{-b_2 F} \quad (4)$$

Here:

y_0 , y_1 and y_2 are constants representing the initial values of capacitance, resistance and impedance, respectively.

k_0 , k_1 and k_2 are constant, representing the sensitivity of each parameter to the clamping force.

b_1 and b_2 are constants controlling the exponential decay of resistance and impedance with increasing clamping force.

Using the above model parameters, the specific effective thickness (d) of the plant leaf can be calculated as follows:

$$d = \sqrt{\frac{U^2 k_0}{2}} \quad (5)$$

U is the applied test voltage (1.5 V, as mentioned), and k_0 is the constant associated with the capacitance force relationship.

According to the method proposed by Duan et al. (2022), the cell metabolic energy based on Z (ΔG_Z) and R (ΔG_R) of plant leaves was calculated:

$$\Delta G_R = \frac{\ln k_1 - \ln y_1}{b_1} \times d \quad (6)$$

$$\Delta G_Z = \frac{\ln k_2 - \ln y_2}{b_2} \times d \quad (7)$$

Here, k_1 , y_1 , b_1 and k_2 , y_2 , b_2 are constants obtained from fitting experimental data to exponential models (Eqs. 3 and 4). The term d (specific effective thickness) accounts for leaf structural properties (Eq. 5).

The cell metabolic energy (ΔG_B) was defined as the average between the cell metabolic energies based on the Z (ΔG_Z) and R (ΔG_R) of plant leaves.

$$\Delta G_B = (\Delta G_Z + \Delta G_R) / 2 \quad (8)$$

2.2 Statistical analysis

Data are presented as the mean ± standard error from five independent replicates. The data presented above were analyzed using one-way analysis of variance (ANOVA), followed by Duncan post hoc testing at a significance level of $P \leq 0.05$.

3 Results

3.1 Organic acid distribution in root tissues of two maize varieties under HCO₃⁻ treatment

Malic acid (MA) is the most significant organic acid exuded by the roots of Jingke 968 and Tiannuo 182. In the roots of Jingke 968, the oxalic acid (OA) exudation was notably higher under 5 mM HCO₃⁻ treatment compared to the control. Conversely, the exudation of citric acid (CA), MA and succinic acid (SA) was significantly lower under 5 mM and 10 mM HCO₃⁻ treatments than the control. For Tiannuo 182, the exudation of CA, MA and SA was notably higher under 10 mM HCO₃⁻ treatment compared to the control. Compared to Jingke 968, Tiannuo 182 exhibited significantly higher levels of CA, MA, and SA under both 5 mM and 10 mM HCO₃⁻ treatments (Fig. 1).

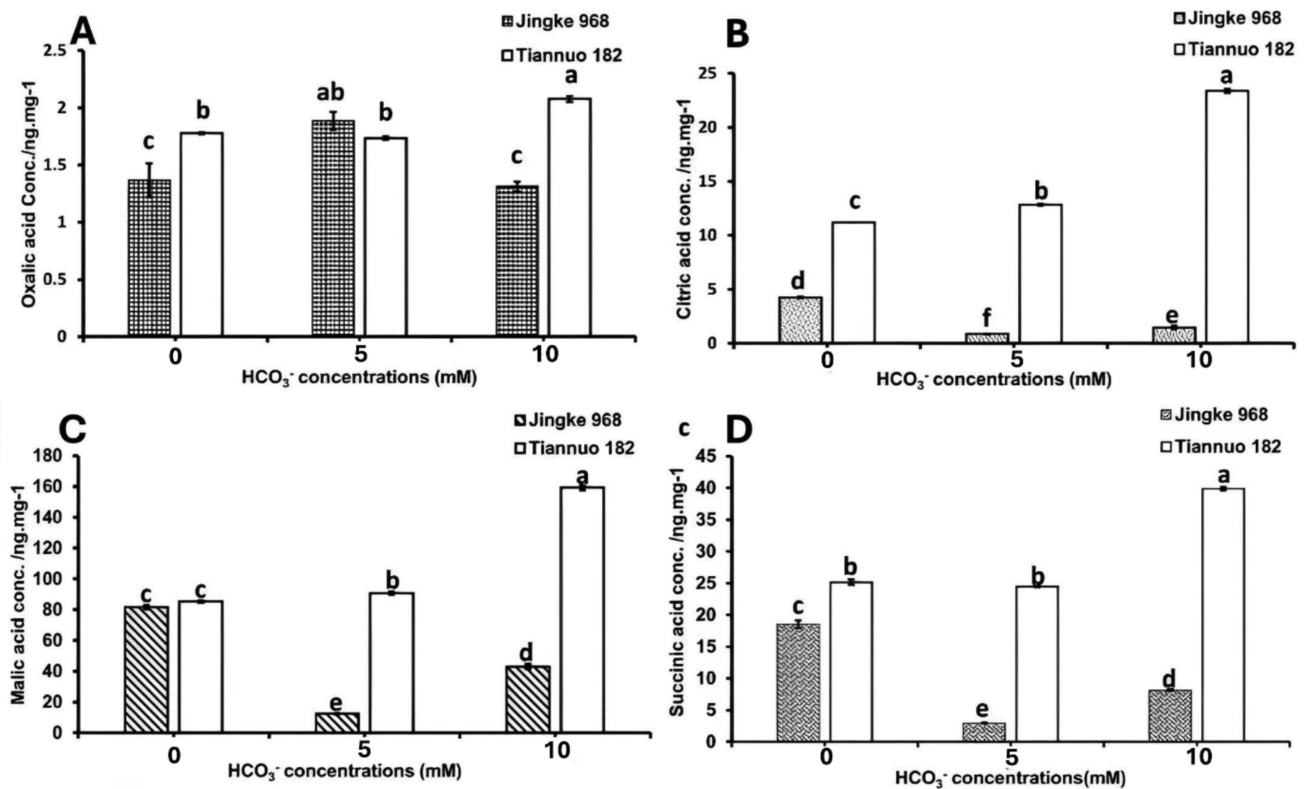


Fig. 1 The content of organic acids in Jingke 968 and Tiannuo 182 under different treatments. Note: OA, CA, MA and SA denote oxalic acid, citric acid, malic acid and succinic acid, respectively; According to one-way ANOVA, mean $\pm$ standard error marked with the same letter indicates no significant difference at the 0.05 level, the same as below

3.2 Distribution characteristics of total silica, phytoliths and phytolith-occluded carbon in two maize varieties under HCO_3^- treatments

The total silica and phytolith contents in Jingke 968 were significantly lower than the control under 5 mM and 10 mM HCO_3^- treatments. The PhytOC was considerably higher than the control under 5 mM and 10 mM HCO_3^- treatments. In Tiannuo 182, the phytoliths and

phytolith-occluded carbon contents were significantly higher than those of the control under 5 mM HCO_3^- treatment. The phytolith-occluded carbon content in Tiannuo 182 was significantly higher than that in Jingke 968 under 5 mM HCO_3^- treatment (Fig. 2).

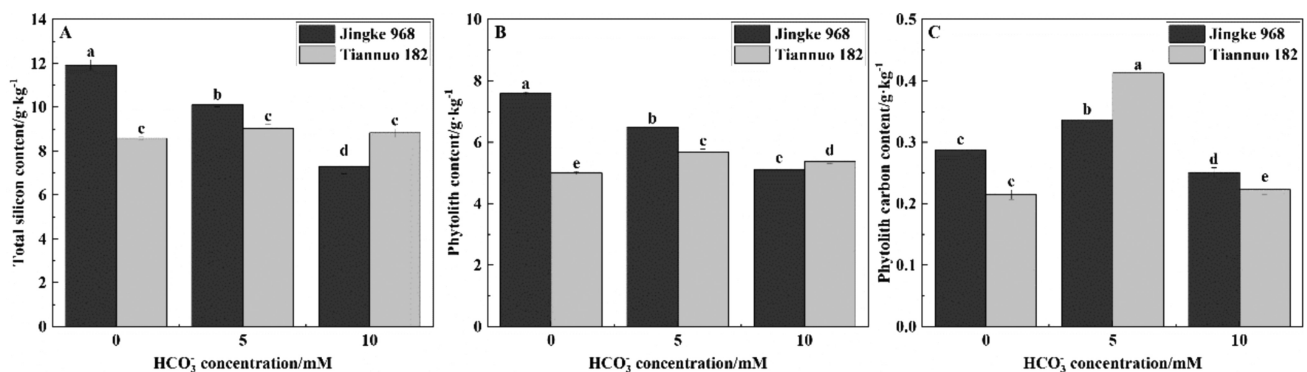


Fig. 2 Total silicon A, phytolith B and PhytOC C contents of Jingke 968 and Tiannuo 182 under different treatments

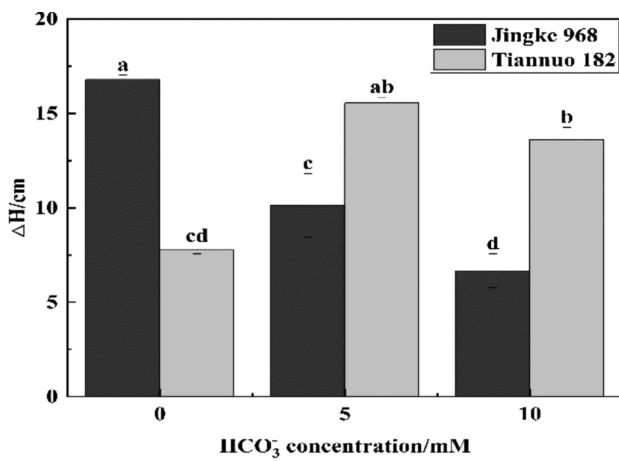


Fig. 3 Plant height increment of Jingke 968 and Tiannuo 182 under different treatments

3.3 Effect of HCO₃⁻ treatments on plant height increments of the two maize varieties

As the HCO₃⁻ concentration increased, the plant height increment of Jingke 968 was significantly lower than the control. In contrast, the plant height increment of Tiannuo 182 was considerably higher than the control. Under 5 mM and 10 mM HCO₃⁻ treatments, the plant height increment of Tiannuo 182 was significantly higher than that of Jingke 968 (Fig. 3).

3.4 Effect of HCO₃⁻ treatments on the photosynthetic parameters of the two maize varieties

Under treatment with 10 mM HCO₃⁻, the P_N and g_s values of Jingke 968 were significantly lower than those of the control. However, no significant difference was observed between the 5 mM HCO₃⁻ treatment and the control. For Tiannuo 182, the P_N value did not significantly differ from the control under 5 mM and 10 mM treatments. However, the g_s value exhibited a significant reduction under 10 mM HCO₃⁻ treatment compared to the control. The WUE_i value was significantly higher under the 10 mM HCO₃⁻ therapy than in the control (Fig. 4).

3.5 Effect of HCO₃⁻ treatments on ΔG_B of the two maize varieties

The ΔG_B of Jingke 968 was significantly higher under the 10 mM HCO₃⁻ treatment than in the control. In contrast, for Tiannuo 182, the ΔG_B was significantly lower under both 5 mM and 10 mM HCO₃⁻ treatments compared to the control. Furthermore, the ΔG_B of Tiannuo 182 was significantly higher than that of Jingke 968 under the control and 5 mM HCO₃⁻ treatments (Table 1).

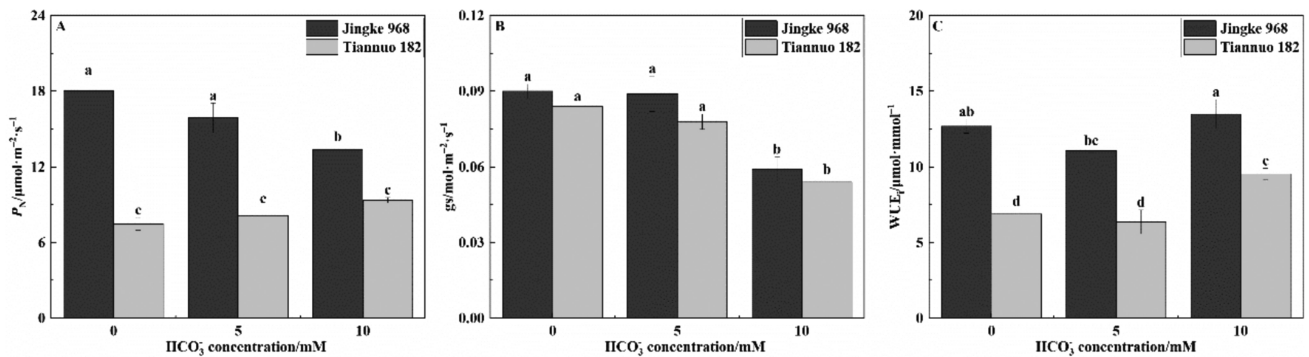


Fig. 4 Net photosynthetic rate (P_N , $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) **A**, stomatal conductance (g_s , $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) **B** and instantaneous water use efficiency (WUE_i , $\mu\text{mol}\cdot\text{mmol}^{-1}$) **C** of Jingke 968 and Tiannuo 182 under different treatments

Table 1 ΔG_B of Jingke 968 and Tiannuo 182 under different treatments

Parameters	Plant species	HCO ₃ ⁻ concentrations (mM)		
		0	5	10
ΔG _B	Jingke 968	1196.57 ± 112.699 ^d	799.12 ± 189.141 ^d	2299.29 ± 25.854 ^c
	Tiannuo 182	8299.79 ± 575.206 ^a	7086.77 ± 342.319 ^b	1553.78 ± 31.519 ^{cd}

Representations with the same letter following the mean ± standard error in the same indicator data do not differ significantly at the 0.05 level

4 Discussion

4.1 Influence of root exudation of organic acids on maize's adaptability to bicarbonates

Bicarbonate is a product of the weathering of carbonate rocks through karst dissolution processes. Previous research has primarily focused on the adverse effects of HCO_3^- on plant growth and metabolism, such as inhibiting photosynthesis, reducing the activity of key enzymes in carbon and nitrogen metabolism and disrupting ionic balance, while little attention has been paid to its positive effects (Bie et al. 2004; Kolla et al. 2007; Burbulis et al. 2017; Poschenrieder et al. 2018). However, existing research indicates that HCO_3^- not only provides plants with a short-term carbon source and water source under drought and other stress conditions but also regulates the activity of key enzymes in carbon and nitrogen metabolism. Additionally, HCO_3^- enhances plants' stress resistance and survival potential by affecting glucose metabolism dismutation and altering the distribution of glycolysis and the pentose phosphate pathway (Yao and Wu 2021; Xia and Wu 2022).

Bicarbonate can induce a massive exudation of organic acids from plant roots, an adaptive response to environmental changes (Alhendawi et al. 1997). Plant organic acids are mainly produced during glycolysis and the tricarboxylic acid (TCA) cycle. These organic acids primarily originate from carbon fixed during photosynthesis and, in turn, affect the plant's photosynthesis and other physiological processes (Adeleke et al. 2017).

In this study, the effects of two maize varieties on the organic acids exuded by the root system under bicarbonate stimulation differed. The main type of organic acids exuded by the root systems of the two maize varieties was malic acid (MA). Bicarbonate significantly reduced the exudation of MA by Jingke 968, while the exudation of MA by Tiannuo 182 increased with increased bicarbonate concentration. Tiannuo 182 roots exude organic acids such as MA and CA. These organic acids can, on the one hand, reduce the soil pH by reacting with bicarbonates, alleviating the high-pH stress caused by excessive bicarbonates (Augagneur et al. 2007; Sagerwanshi et al. 2021), and, on the other hand, regulate the ion balance in response to alkaline stress (Li et al. 2022). Moreover, they can chelate with metal ions, increasing the availability of essential nutrients for plants. This process promotes plant growth and improves its adaptability to bicarbonate-rich environments (Nian et al. 2002).

4.2 Negative impact of bicarbonates on coupling of metabolic energy, organic acid exudation and silicon uptake in Jingke 968

In this study, we observed that both photosynthesis (growth) and silicon (phytolith) content in Jingke 968 decline with increasing bicarbonate concentration, suggesting that, overall, bicarbonates exert a negative effect on Jingke 968 despite any counterbalancing impacts of positive and negative actions. Under bicarbonate stress, Jingke 968 demonstrated reduced photosynthesis and exhibited heightened sensitivity to high bicarbonate concentrations. It maintains a relatively high WUE_i by decreasing stomatal conductance (g_s), thus preventing bicarbonate absorption at high concentrations (D'Agostini et al. 2023; Li et al. 2023). Concurrently, the reduction in photosynthesis also results in fewer photosynthetic products being allocated towards resistance against bicarbonate and the creation of phytoliths (Rajendiran et al. 2012).

Despite Jingke 968 exhibiting higher photosynthesis rates than Tiannuo 182, its metabolic energy is notably low. This suggests that Jingke 968 allocates a considerable portion of its photosynthetic energy to mitigate the adverse effects of bicarbonates, leaving less energy available for growth and silicon uptake. Furthermore, bicarbonates significantly diminish the exudation of primary organic acids (MA, CA, SA) by Jingke 968's root system, thereby reducing the absorption and accumulation of silicon and, consequently, lowering the silicon content. In summary, Jingke 968 showcases the detrimental effects of bicarbonates on the interplay among photosynthesis, metabolic energy, organic acid exudation and silicon uptake, as depicted in Fig. 5A.

4.3 Positive impact of bicarbonates on coupling of metabolic energy, organic acid exudation and silicon uptake in Tiannuo 182

In this study, the metabolic energy of Tiannuo 182 under 5 mM bicarbonate treatment exhibited only a slight decrease compared to the control. This suggests that it allocates less metabolic energy to counteract the adverse effects of bicarbonate and instead channels a significant amount of energy towards growth and silicon absorption, thereby maximizing the positive impact of bicarbonate. The carbon sequestration capacity and adaptability to bicarbonate environments are dictated by the plant's net photosynthetic rate and metabolic energy as well as the distribution of these energies across growth, resistance to bicarbonate stress, exudation of organic acids and other metabolic processes (including silicon uptake) (Chen et al. 2022; Duan et al. 2022). Consequently, it is suggested that a 5 mM HCO_3^- environment is the most adaptable, effectively enhancing both the growth and carbon sequestration of Tiannuo 182.

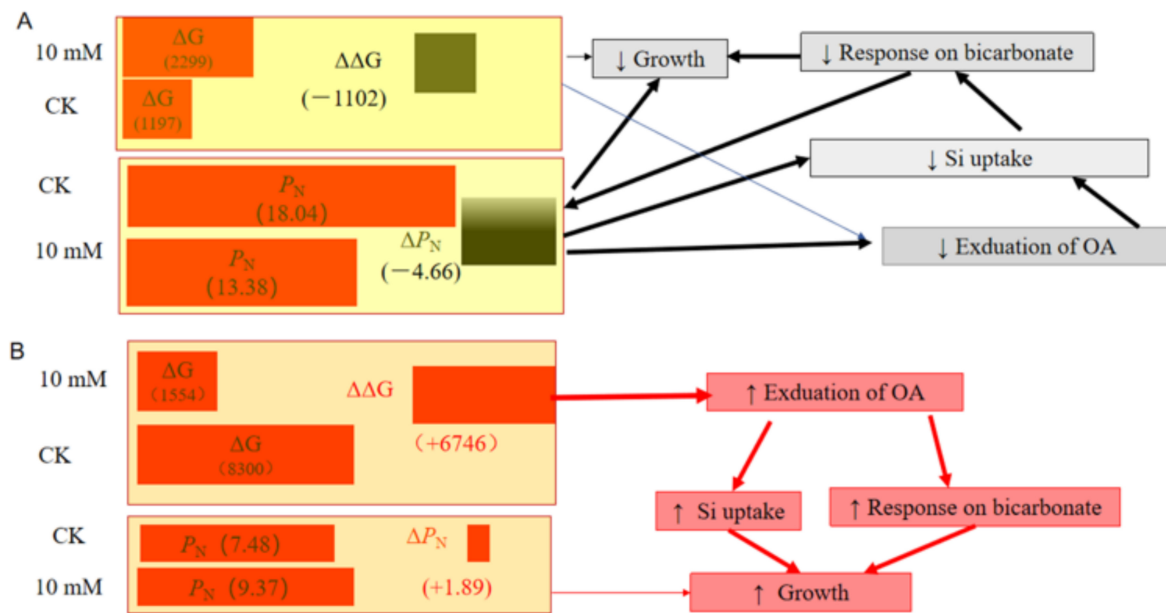


Fig. 5 The response mechanism of Jingke 968 **A** and Tiannuo182 **B** to bicarbonates. Note: $\Delta\Delta G$ is the difference in metabolic energy between the CK treatment and the 10 mM bicarbonate treatment, with a red background indicating a positive value, meaning an increase, and a black background indicating a negative value, meaning a decrease. ΔP_N is the difference in P_N between the 10 mM bicarbonate treatment and the CK treatment, with a red background indicating a positive value, meaning an increase, and a black background indicating a negative value, meaning a decrease. Numbers in parentheses represent the value of this parameter, thick arrows represent primary effects, and thin arrows represent secondary effects; $\downarrow$ represents a decrease, $\uparrow$ represents an increase

Conversely, when treated with 10 mM bicarbonate, the metabolic energy of Tiannuo 182 decreases significantly, yet photosynthesis remains unchanged. Concurrently, the organic acids exuded by the root system, primarily malic acid (MA) and citric acid (CA), increase substantially. This could be attributed to bicarbonate's promotion of organic acid exudation, which, on the one hand, lowers soil pH, thereby mitigating the adverse effects of excessive bicarbonate on photosynthesis and growth. On the other hand, it counteracts bicarbonates' negative impact on reducing plant roots' silicon uptake.

Despite variations in bicarbonate concentration, photosynthesis and the content of silicon (phytoliths) in Tiannuo 182 remain constant. In contrast, high concentrations of bicarbonate promote plant growth. However, as bicarbonate concentration increases, there is a rise in the exudation of primary organic acids [malic acid (MA) and citric acid (CA); by Tiannuo 182's roots, accompanied by a reduction in metabolic energy. This indicates that bicarbonate has a beneficial effect on Tiannuo 182, offsetting negative impacts. The exudation of organic acids is contingent upon the consumption of metabolic energy. In summary, Tiannuo 182 showcases the positive effects of bicarbonates on the interplay among photosynthesis, metabolic energy, organic acid exudation and silicon uptake, as depicted in Fig. 5B.

5 Conclusion

Selecting the appropriate maize variety for karst regions with complex bicarbonate environments is essential. In such environments, Jingke 968 and Tiannuo 182 exhibit contrasting responses to bicarbonate stress. Under bicarbonate stress, Jingke 968 experiences inhibited photosynthesis and slowed growth. The variety allocates more energy to stress resistance, decreasing silicon absorption and utilization. Consequently, organic carbon storage in phytoliths is reduced. In contrast, Tiannuo 182 adapts better to a 5 mM bicarbonate environment. It allocates more energy to growth and silicon absorption, increasing organic carbon storage in phytoliths. Additionally, Tiannuo 182 exudes more organic acids in response to high bicarbonate levels, enhancing its ability to adapt to high bicarbonate stress. This increases the carbon sequestration capacity of plants in such environments. In comparison, Jingke 968 demonstrates the detrimental effects of bicarbonates on photosynthesis, metabolic energy, organic acid exudation and silicon uptake. Tiannuo 182, however, shows positive effects, highlighting its suitability for karst regions with complex bicarbonate environments.

Acknowledgements We thank the foundations of the National Natural Science Foundation of China (No. U1612441-2) and Support Plan Projects of Science and Technology Department of Guizhou Province [No. (2021)YB453].

Authors contributions Project construction, Y.W.; research design, Y.W., D.X., and J.W.; plant material cultivation and acquisition of original data, J.W. and Q.Z.; data analysis, J.W., Q.Z. and D.X.; writing, J.W., D.X. and Y.W.; D.X., M.Q. and W.W. revised the manuscript. M.A. writing and review All authors have read and agreed to the published version of the manuscript.

Funding Funding was provided by National Natural Science Foundation of China, U1612441-2, Yanyou Wu, Support Plan Projects of Science and Technology Department of Guizhou Province, (2021) YB453, Yanyou Wu

Data availability The data that support the findings of this study are available from the corresponding author upon reasonable request.

Declarations

Conflict of interest The authors declare no conflict of interest.

References

- Adeleke R, Nwangburuka C, Oboirien B (2017) Origins, roles and fate of organic acids in soils: a review. *S Afr N J Bot* 108:393–406. <https://doi.org/10.1016/j.sajb.2016.09.002>
- Alhendawi RA, Römhild V, Kirkby EA, Marschner H (1997) Influence of increasing bicarbonate concentrations on plant growth, organic acid accumulation in roots and iron uptake by barley, sorghum, and maize. *J Plant Nutr* 20(12):1731–1753. <https://doi.org/10.1080/01904169709365371>
- Asai H, Soisouvanh P (2017) Yield performance of upland rice, maize and Job's tears in a rainfed upland ecosystem in mountainous Laos. *Jpn Agric Res Q JARQ* 51(4):309–318. <https://doi.org/10.6090/jarq.51.309>
- Augagneur Y, Ritt JF, Linares DM, Remize F, Tourdot-Maréchal R, Garmyn D, Guzzo J (2007) Dual effect of organic acids as a function of external pH in *Oenococcus oeni*. *Arch Microbiol* 188(2):147–157. <https://doi.org/10.1007/s00203-007-0230-0>
- Bie ZL, Ito T, Shinohara Y (2004) Effects of sodium sulfate and sodium bicarbonate on the growth, gas exchange and mineral composition of lettuce. *Sci Hortic* 99(3–4):215–224. [https://doi.org/10.1016/S0304-4238\(03\)00106-7](https://doi.org/10.1016/S0304-4238(03)00106-7)
- Burbulis N, Vainorienė R, Blinstrubienė A, Jonytienė V, Liakas V (2017) Effect of potassium bicarbonate on photosynthetic parameters of *Setaria viridis* under drought conditions. *Zemdirb-Agric* 104(1):79–84. <https://doi.org/10.13080/z-a.2017.104.011>
- Burbulis N, Blinstrubienė A, Baltušnikienė A, Deveikytė J (2022) Foliar spraying with potassium bicarbonate reduces the negative impact of drought stress on sweet basil (*Ocimum basilicum* L.). *Plants* 11(13):1716. <https://doi.org/10.3390/plants11131716>
- Chen W, Yao XQ, Cai KZ, Chen JN (2011) Silicon alleviates drought stress of rice plants by improving plant water status, photosynthesis and mineral nutrient absorption. *Biol Trace Elem Res* 142(1):67–76. <https://doi.org/10.1007/s12011-010-8742-x>
- Chen LY, Fang K, Wei B, Qin SQ, Feng XH, Hu TY, Ji CJ, Yang YH (2021) Soil carbon persistence governed by plant input and mineral protection at regional and global scales. *Ecol Lett* 24(5):1018–1028. <https://doi.org/10.1111/ele.13723>
- Chen T, Wu YY, Xing DK, Duan RR (2022) Effects of NaHSO_3 on cellular metabolic energy, photosynthesis and growth of *Iris pseudacorus* L. *Horticulturae* 8(2):185. <https://doi.org/10.3390/horticulturae8020185>
- Custic MH, Gluhic D, Coga L, Petek M, Goscak I (2008) Vine plant chlorosis on unstructured calcareous soils and leaf Ca, Mg and K content. *Cereal Res Commun* 36(3):439–442. <https://doi.org/10.1007/s12011-010-8742-x>
- D'Agostini F, Ruiz-Pérez J, Madella M, Vadez V, Kholova J, Lancelotti C (2023) Phytoliths as indicators of plant water availability: the case of millets cultivation in the Indus Valley civilization. *Rev Palaeobot Palynol* 309:104783. <https://doi.org/10.1016/j.revpa.2022.104783>
- Duan RR, Xing DK, Chen T, Wu Y (2022) Effects of different inorganic nitrogen sources of *Iris pseudacorus* and *Iris Japonica* on energy distribution, nitrogen, and phosphorus removal. *HortScience* 57(6):698–707. <https://doi.org/10.21273/HORTSCI116510-22>
- Esteban I, Marean CW, Fisher EC, Karkanas P, Cabanes D, Albert RM (2018) Phytoliths as an indicator of early modern humans plant gathering strategies, fire fuel and site occupation intensity during the Middle Stone Age at Pinnacle Point 5–6 (south coast, South Africa). *PLoS ONE* 13(6):e0198558. <https://doi.org/10.1371/journal.pone.0198558>
- Gao XP, Zou CQ, Wang LJ, Zhang FS (2004) Silicon improves water use efficiency in maize plants. *J Plant Nutr* 27(8):1457–1470. <https://doi.org/10.1081/pln-200025865>
- Habibi G (2014) Silicon supplementation improves drought tolerance in canola plants. *Russ J Plant Physiol* 61(6):784–791. <https://doi.org/10.1134/S1021443714060077>
- Hu Y, Javed HH, Asghar MA, Peng X, Brestic M, Skalický M, Ghafoor AZ, Cheema HN, Zhang FF, Wu YC (2022) Enhancement of lodging resistance and lignin content by application of organic carbon and silicon fertilization in *Brassica napus* L. *Front Plant Sci* 13:807048. <https://doi.org/10.3389/fpls.2022.807048>
- Huang ZT, Li YF, Jiang PK, Chang SX, Song ZL, Liu J, Zhou GM (2014) Long-term intensive management increased carbon occluded in phytolith (PhytOC) in bamboo forest soils. *Sci Rep* 4:3602. <https://doi.org/10.1038/srep03602>
- Kolla VA, Vavasseur A, Raghavendra AS (2007) Hydrogen peroxide production is an early event during bicarbonate induced stomatal closure in abaxial epidermis of *Arabidopsis*. *Planta* 225(6):1421–1429. <https://doi.org/10.1007/s00425-006-0450-6>
- Li ZM, Song ZL, Parr JF, Wang HL (2013) Occluded C in rice phytoliths: Implications to biogeochemical carbon sequestration. *Plant Soil* 370(1):615–623. <https://doi.org/10.1007/s11104-013-1661-9>
- Li JW, Liu JH, Wang JY, Guo LC, Wang CL, Ren CZ (2022) Effects of salt and alkali stresses on ion balance and organic acid content in oats. *Acta Bot Boreali-Occident Sin* 42(10):1700–1710. <https://doi.org/10.7606/j.issn.1000-4025.2022.10.1700>
- Li HT, Lv JM, Su Y, Wu YY (2023) Appropriate sodium bicarbonate concentration enhances the intracellular water metabolism, nutrient transport and photosynthesis capacities of *Coix lacryma-jobi* L. *Agronomy* 13(7):1790. <https://doi.org/10.3390/agronomy13071790>
- Liao H, Wan HY, Shaff J, Wang XR, Yan XL, Kochian LV (2006) Phosphorus and aluminum interactions in soybean in relation to aluminum tolerance. Exudation of specific organic acids from different regions of the intact root system. *Plant Physiol* 141(2):674–684
- Liu LN, Song ZL, Yu CX, Yu GH, Ellam RM, Liu HY, Singh BP, Wang HL (2020a) Silicon effects on biomass carbon and phytolith-occluded carbon in grasslands under high-salinity conditions. *Front Plant Sci* 11:657. <https://doi.org/10.3389/fpls.2020.00657>
- Liu Y, Liu C, Rubinato M, Guo K, Zhou J, Cui M (2020b) An assessment of soil's nutrient deficiencies and their influence on the restoration of degraded karst vegetation in southwest China. *Forests* 11(8):797. <https://doi.org/10.3390/f11080797>

- Liu YE, Hou P, Huang GR, Zhong XL, Li HR, Zhao JR, Li SK, Mei XR (2021) Maize grain yield and water use efficiency in relation to climatic factors and plant population in northern China. *J Integr Agric* 20(12):3135–3169. [https://doi.org/10.1016/S2095-3119\(20\)63428-1](https://doi.org/10.1016/S2095-3119(20)63428-1)
- Ma JF, Yamaji N (2006) Silicon uptake and accumulation in higher plants. *Trends Plant Sci* 11(8):392–397. <https://doi.org/10.1016/j.tplants.2006.06.007>
- Nian H, Yang ZM, Ahn SJ, Cheng ZJ, Matsumoto H (2002) A comparative study on the aluminium- and copper-induced organic acid exudation from wheat roots. *Physiol Plant* 116(3):328–335. <https://doi.org/10.1034/j.1399-3054.2002.1160307.x>
- Ohta T, Hiura T (2016) Root exudation of low-molecular-mass-organic acids by six tree species alters the dynamics of calcium and magnesium in soil. *Can J Soil Sci* 96(2):199–206. <https://doi.org/10.1139/cjss-2015-0063>
- Panchal P, Miller AJ, Giri J (2021) Organic acids: Versatile stress-response roles in plants. *J Exp Bot* 72(11):4038–4052. <https://doi.org/10.1093/jxb/erab019>
- Panchal P, Preece C, Peñuelas J, Giri J (2022) Soil carbon sequestration by root exudates. *Trends Plant Sci* 27(8):749–757. <https://doi.org/10.1016/j.tplants.2022.04.009>
- Parr JF, Sullivan LA (2011) Phytolith occluded carbon and silica variability in wheat cultivars. *Plant Soil* 342(1):165–171. <https://doi.org/10.1007/s11104-010-0680-z>
- Poschenrieder C, Fernández JA, Rubio L, Pérez L, Terés J, Barceló J (2018) Transport and use of bicarbonate in plants: current knowledge and challenges ahead. *Int J Mol Sci* 19(5):1352. <https://doi.org/10.3390/ijms19051352>
- Rajendiran S, Coumar MV, Kundu S, Ajay DML, Rao AS (2012) Role of phytolith occluded carbon of crop plants for enhancing soil carbon sequestration in agro-ecosystems. *Curr Sci* 103(8):911–920
- Sagervanshi A, Naem A, Kaiser H, Pitann B, Mühling KH (2021) Early growth reduction in *Vicia faba* L. under alkali salt stress is mainly caused by excess bicarbonate and related to citrate and malate over accumulation. *Environ Exp Bot* 192:104636. <https://doi.org/10.1016/j.envexpbot.2021.104636>
- Shinano T, Taigen Z, Yamamura T, Meng Y, Lu W, Tan H (2004) Production of maize in the karst mountain area of southwest China. *Trop Agric* 81(4):204–210
- Sokolova TA, Tolpeshta II, Lysak LV, Zavgorodnyaya YA, Chalova TS, Karpukhin MM, Izosimova YG (2018) Biological characteristics and concentrations of extractable Fe, Al, and Si compounds in spruce rhizosphere in podzolic soil. *Eurasian Soil Sci* 51(11):1317–1325. <https://doi.org/10.1134/s106422931811008x>
- Souri Z, Khanna K, Karimi N, Ahmad P (2021) Silicon and plants: Current knowledge and future prospects. *J Plant Growth Regul* 40(3):906–925. <https://doi.org/10.1007/s00344-020-10172-7>
- Sun X, Liu Q, Zhao GM, Chen X, Tang TT, Xiang YY (2017) Comparison of phytolith-occluded carbon in 51 main cultivated rice (*Oryza sativa*) cultivars of China. *RSC Adv* 7(86):54726–54733. <https://doi.org/10.1039/C7RA10685H>
- Tuna AL, Kaya C, Higgs D, Murillo-Amador B, Aydemir S, Girgin AR (2008) Silicon improves salinity tolerance in wheat plants. *Environ Exp Bot* 62(1):10–16. <https://doi.org/10.1016/j.envexpbot.2007.06.006>
- Wang YW, Zhang BB, Jiang DX, Chen GX (2019) Silicon improves photosynthetic performance by optimizing thylakoid membrane protein components in rice under drought stress. *Environ Exp Bot* 158:117–124. <https://doi.org/10.1016/j.envexpbot.2018.11.022>
- Widodo B, Broadley MR, Rose T, Frei M, Pariasca-Tanaka J, Yoshihashi T, Thomson M, Hammond JP, Aprile A, Close TJ, Ismail AM, Wissuwa M (2010) Response to zinc deficiency of two rice lines with contrasting tolerance is determined by root growth maintenance and organic acid exudation rates, and not by zinc-transporter activity. *New Phytol* 186(2):400–414. <https://doi.org/10.1111/j.1469-8137.2009.03177.x>
- Wu YY, Wu YS (2022) The increase in the karstification–photosynthesis coupled carbon sink and its implication for carbon neutrality. *Agronomy* 12(9):2147. <https://doi.org/10.3390/agronomy12092147>
- Xia AT, Wu YY (2022) Joint interactions of carbon and nitrogen metabolism dominated by bicarbonate and nitrogen in *Orychophragmus violaceus* and *Brassica napus* under simulated karst habitats. *BMC Plant Biol* 22(1):264. <https://doi.org/10.1186/s12870-022-03646-1>
- Yang SL, Hao Q, Wang HL, Van Zwieten L, Yu CX, Liu TZ, Yang XM, Zhang XD, Song ZL (2020) A review of carbon isotopes of phytoliths: Implications for phytolith-occluded carbon sources. *J Soils Sediments* 20(4):1811–1823. <https://doi.org/10.1007/s11368-019-02548-4>
- Yang W, Min Z, Yang MX, Yan J (2022) Exploration of the implementation of carbon neutralization in the field of natural resources under the background of sustainable development-an overview. *Int J Environ Res Public Health* 19(21):14109. <https://doi.org/10.3390/ijerph192114109>
- Yao K, Wu YY (2021) Rhizospheric bicarbonate improves glucose metabolism and stress tolerance of *Broussonetia papyrifera* L. seedlings under simulated drought stress. *Russ J Plant Physiol* 68(1):126–135. <https://doi.org/10.1134/S1021443721010209>
- Zhao K, Wu YY (2011) Influence of root-secreted organic acid on plant and soil carbon sequestration in Karst ecosystem. *Carsologica Sin* 30(4):466–471
- Zhao K, Wu YY (2014) Rhizosphere calcareous soil P-extraction at the expense of organic carbon from root-exuded organic acids induced by phosphorus deficiency in several plant species. *Soil Sci Plant Nutr* 60(5):640–650. <https://doi.org/10.1080/00380768.2014.934191>
- Zhao K, Wu YY (2018) Effect of Zn deficiency and excessive bicarbonate on the allocation and exudation of organic acids in two Moraceae plants. *Acta Geochim* 37(1):125–133. <https://doi.org/10.1007/s11631-017-0174-2>
- Zhou S, Lin JJ, Wang P, Zhu P, Zhu B (2023) Resistant soil organic carbon is more vulnerable to priming by root exudate fractions than relatively active soil organic carbon. *Plant Soil* 488(1):71–82. <https://doi.org/10.1007/s11104-021-05288-y>

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.