Postprint: The Promoting Effect of HCO3- on Plant Growth, Development and Metabolism

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Abstract

Bicarbonate (HCO3-) is a product of carbonate rock weathering through karst processes, which profoundly influences plant growth and development and the ecological environment of karst regions. Previous research has primarily focused on the negative effects of HCO3- on plant growth and metabolism, such as inhibiting photosynthesis, reducing the activity of key enzymes in carbon and nitrogen metabolism, and disrupting ion balance, while few studies have addressed its positive roles. Based on previous research findings, this paper reviews the promoting effects of HCO3- on plant growth and metabolism. Existing studies demonstrate that HCO3- not only provides short-term carbon and water sources for plants under stress conditions such as drought, promoting stomatal opening and restoring photosynthesis; it also enhances plant carbon and nitrogen metabolism by regulating the activity of key enzymes in carbon and nitrogen metabolism, participating in the regulation of complex physiological processes such as carbon assimilation and nitrogen reduction. Furthermore, HCO3- influences glucose metabolic partitioning, altering the distribution between the glycolytic pathway and the pentose phosphate pathway to enhance plant stress resistance and obtain survival opportunities. These positive roles of HCO3- not only make it a key factor promoting plant physiological metabolism but also serve as a link between photosynthesis and karst processes. Elucidating the positive effects of HCO3- on plant growth and development can provide a theoretical basis for maintaining biodiversity and stability in karst ecosystems and optimizing karst ecosystem functions.

Full Text

Promoting Effect of Bicarbonate on Plant Growth and Metabolism

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Abstract

Bicarbonate (HCO_3^-) is the product of carbonate rock weathering through karst processes, which profoundly influences plant growth, metabolism, and the ecological environment in karst regions. Previous research has predominantly focused on the negative effects of HCO_3^- on plant growth and metabolism, such as inhibiting photosynthesis (Zhang et al., 2019), reducing the activity of key enzymes in carbon and nitrogen metabolism (Gong et al., 2013), and disrupting ion balance (Sun et al., 2020). Few studies have examined its positive effects on plant growth and metabolism. Based on existing research, this paper reviews the promoting effects of HCO_3^- on plant growth and metabolism. Recent studies have shown that under abiotic stresses such as drought, HCO_3^- promotes plant growth and metabolism by providing short-term carbon and water sources (Wu, 2011a; Tang & Lian, 2012), alleviating stomatal closure (Wu, 2011c; Wang et al., 2017), regulating key enzyme activities in carbon and nitrogen metabolism (Wu et al., 2018), and influencing glucose metabolism disproportionation (Yao & Wu, 2021). Moreover, HCO_3^- profoundly affects carbonate rock dissolution and deposition at the "rock-soil" interface, indicating that HCO_3^- serves as a coupling factor connecting photosynthesis and karstification. This review examines the positive roles of HCO_3^- in plant growth and development from the perspectives of carbon source function, stomatal movement, carbon-nitrogen metabolism, and glucose metabolism disproportionation, aiming to provide a theoretical basis for maintaining biodiversity and stability in karst ecosystems and optimizing their functions.

Keywords: bicarbonate, plant, growth, coupling, metabolism

1. Carbon Source Function of HCO_3^-

The ability to utilize HCO_3^- is a key indicator of its role as a carbon source for plants under drought and other stresses. On one hand, extensive carbonate rock areas and intense karst processes promote the formation of karst-adversity conditions—including drought, high bicarbonate concentrations, and high pH—that cause stomatal closure and inhibit photosynthesis. To adapt to these adverse conditions, plants upregulate carbonic anhydrase (CA) activity, which catalyzes the conversion of root-absorbed HCO_3^- into CO_2 and H_2O, thereby opening stomata and replenishing photosynthesis (Wang et al., 2015; Hang et al., 2018). Previous studies have investigated this carbon source function of HCO_3^-. For instance, when exogenous HCO_3^- concentrations of 5, 10, and 15 $mmol \cdot L^{-1}$ were applied, the total photosynthesis of *Orychophragmus violaceus* decreased, yet HCO_3^- utilization capacity increased with concentration, reaching 5.28%, 13.28%, and 17.31%, respectively (Hang & Wu, 2016). Under drought stress, the HCO_3^- utilization capacities of mulberry, paper mulberry, rapeseed, and *O. violaceus* at 10 $mmol \cdot L^{-1}$ were 15%, 30%, 2%, and 37%, respectively, demonstrating that paper mulberry and *O. violaceus* possess higher HCO_3^- utilization abilities (Wu et al., 2018). Using bidirectional carbon isotope labeling, Wu et al. (2012) calculated that under simulated drought and bicarbonate stress, paper mulberry's HCO_3^- utilization share reached as high as 30%, while mulberry's was 0, indicating that HCO_3^- serves as a more significant carbon source for paper mulberry. Rao (2017) reported that under drought stress simulated by 0, 100, and 200 $g \cdot L^{-1}$ PEG, HCO_3^- contributed 6.26%–9.71% to total inorganic carbon assimilation in *Camptotheca acuminata*. As an important carbon source for photosynthesis, HCO_3^- not only improves plant inorganic carbon utilization efficiency but also provides electrons to photosystem II (PSII), alleviating "idling" of photosynthetic apparatus and promoting carbon assimilation (Wu, 2011a; Banerjee et al., 2019). On the other hand, HCO_3^- promotes plant photosynthesis and growth metabolism, facilitating biodiversity formation and exerting important positive regulatory effects on karst processes and habitats (Wu et al., 2018). These findings demonstrate that HCO_3^- is both a crucial carbon source for plants and an important coupling factor linking plant photosynthesis and karstification [Figure 1: see original paper].

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2. Positive Regulatory Effects of HCO_3^- on Other Plant Metabolic Processes

2.1 Stomatal Movement HCO_3^- plays a vital role in regulating stomatal movement [Figure 2: see original paper] (Meyer et al., 2010). Under high HCO_3^- conditions, plants upregulate CA to decompose HCO_3^- into CO_2 and H_2O, which participates in regulating guard cell stomatal movement, compensating for CO_2 supply deficiency caused by stomatal closure and securing survival opportunities (Wu, 2011a; Hang, 2016; Shahsavandi et al., 2020). Research shows that under high HCO_3^- environments, plant S-type anion channels (SLAC1) are activated, promoting Cl^- or NO_3^- efflux from cells while facilitating R-type channels (AtALMT12/QUAC1) to extrude malate (Stefan et al., 2010). Additionally, HCO_3^- is an important signal in the abscisic acid (ABA) pathway, which positively regulates anion channel proteins (OST1) by activating protein kinase (RHC1) expression and inhibiting heat shock protein (HT1) expression, thereby promoting anion efflux and regulating leaf stomatal movement (Meyer et al., 2010).

2.2 Carbon and Nitrogen Metabolism Several studies have reported HCO_3^- involvement in regulating carbon and nitrogen metabolism, primarily through modulating key enzyme activities, organic acid metabolism, and related gene expression [Figure 3: see original paper]. On one hand, HCO_3^- coordinates plant carbon and nitrogen metabolism together with acetyl-CoA carboxylase (ACC) and phosphoenolpyruvate carboxylase (PEPC). Fatty acids are crucial substances involved in tricarboxylic acid cycle and flavonoid A-ring biosynthesis (Yukiko et al., 2004) and regulate ethylene synthesis metabolism (Nikolau et al., 2003b). HCO_3^- influences ACC-catalyzed acetyl-CoA carboxylation, thereby regulating the formation of malonyl-CoA, a fatty acid precursor. On the other hand, HCO_3^- participates in carbon metabolism processes in C_4 and CAM plants together with PEPC. PEPC gene overexpression is considered an evolutionary mechanism for C_4 and CAM plants to adapt to adversity. HCO_3^- is irreversibly catalyzed by PEPC to generate oxaloacetic acid (OAA), which plays a vital role in regulating plant malate metabolism and carbon-nitrogen assimilation. Under NADPH or NADP assistance, OAA is catalyzed by malate dehydrogenase (MDH) to form malate and other organic acids stored in plants to enhance stress resistance (Doubnerová et al., 2011). HCO_3^- also participates in regulating plant organic acid metabolism; $NaHCO_3$ stress can induce GsPEPCs gene overexpression in *Medicago truncatula*, with significant co-expression observed between MDH, pyruvate kinase (PK), and other genes with GsPEPCs (Zhang et al., 2019). Under low $NaHCO_3$ stress, PEPC activity in maize significantly increased with higher organic acid content, whereas PEPC activity and organic acid content substantially decreased when PEPC activity declined (Jia et al., 2020). Drought-induced PEPC overexpression in transgenic rice significantly alleviated drought-induced photosynthesis inhibition (Doubnerov et al., 2011). Furthermore, HCO_3^- participates in regulating plant nitrogen metabolism; HCO_3^- is irreversibly converted to OAA and phosphate (Pi) under PEPC catalysis, with some OAA participating in root nitrogen assimilation to ultimately produce aspartic acid (Asp) for plant metabolic utilization (Zhao, 2019).

2.3 Glucose Metabolism Disproportionation Under drought and other stress conditions, HCO_3^- enhances plant stress resistance by affecting glucose metabolism disproportionation. Plant glucose metabolism primarily includes the Embden-Meyerhof pathway (EMP) and the phosphopentose pathway (PPP). ATP produced through the EMP pathway provides essential energy for driving physiological processes such as plant carbon and nitrogen metabolism, making EMP activity an indicator of photosynthetic productivity (Wu et al., 2018). NAD(P)H generated through the PPP pathway provides reducing power for photosynthesis and nitrogen metabolism, playing a crucial role in plant stress resistance; thus, PPP activity is used to characterize plant adaptability to adversity. Glucose metabolism intensity is commonly represented by the activity of rate-limiting enzymes: phosphofructokinase (PFK) and glucose-6-phosphate dehydrogenase (G6PDH) (Mutuku & Nose, 2012; Zhao et al., 2015). PFK, the rate-limiting enzyme in the EMP pathway, irreversibly catalyzes fructose-6-phosphate to fructose-1,6-bisphosphate, channeling glucose into EMP metabolism to produce ATP; therefore, PFK activity indicates EMP pathway strength. G6PDH, the rate-limiting enzyme in the PPP pathway, irreversibly catalyzes glucose-6-phosphate to 6-phosphogluconate, directing glucose into PPP metabolism to produce NAD(P)H and other reducing coenzymes; thus, G6PDH activity indicates PPP pathway strength (Mutuku and Nose, 2012; Yao & Wu, 2021; Li et al., 2020). Both PFK and G6PDH are important substances for plant stress resistance. Studies show that low-concentration HCO_3^- can simultaneously promote plant EMP and PPP pathways, enhancing stress resistance. Yao & Wu (2021) proposed that under simulated drought stress, 3 $mmol \cdot L^{-1}$ HCO_3^- promoted photosynthesis and glucose metabolism disproportionation in paper mulberry, increasing Rubisco activity, net photosynthetic rate, and both EMP and PPP pathways. In contrast, 9 $mmol \cdot L^{-1}$ HCO_3^- restricted stomatal movement in paper mulberry leaf cells, impairing photosynthesis and glucose metabolism [Figure 4: see original paper]. Wu et al. (2018) used PFK and G6PDH activities to represent plant photosynthetic growth capacity and RuBP regeneration capacity, respectively. Under combined treatment with 10 $mmol \cdot L^{-1}$ $NaHCO_3$ and simulated drought, plant photosynthetic growth capacity showed positive correlation with PFK activity and average daily photosynthetic rate (APN), while RuBP regeneration capacity positively correlated with G6PDH activity and APN, suggesting that plants under stress may preferentially select the PPP pathway to maintain viability.

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3. Summary and Outlook

The promoting effects of HCO_3^- on plant growth, development, and metabolism are manifested in three aspects: (1) Under drought and other stresses, plant roots absorb HCO_3^- and convert it to H_2O and CO_2 via CA to alleviate stomatal limitation and replenish photosynthesis; (2) HCO_3^- influences plant carbon and nitrogen metabolism by regulating key enzymes and organic acid metabolism; (3) HCO_3^- alters plant glucose metabolic pathways, prompting plants to preferentially select the PPP pathway to maintain vitality under stress. These findings demonstrate that HCO_3^- is a coupling factor between karstification and photosynthesis, playing a crucial role in water, carbon, and multi-element cycling in karst ecosystems [Figure 5: see original paper]. Such research provides a theoretical basis for screening biochemical indicators of plant stress resistance, breeding karst-adapted plants, and improving karst ecosystem productivity. Future studies should emphasize the carbon source function of HCO_3^- and further clarify its regulatory role and mechanisms in the water-carbon cycle of carbonate rock-soil-vegetation ecosystems. Additionally, research should strengthen investigations into the coupled metabolic responses to HCO_3^-, such as the coordinated responses of stomatal movement, carbon-nitrogen metabolism, and glucose disproportionation under drought and other stresses. A comprehensive understanding of HCO_3^-'s positive effects on plant growth, development, and metabolism will establish a solid theoretical foundation for increasing biodiversity and promoting sustainable ecological development in karst regions.

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