International Journal of Biotechnology and Microbiology
www.biotechnologyjournals.com
Online ISSN: 2664-7680, Print ISSN: 2664-7672
Received: 31-01-2023, Accepted: 02-03-2023, Published: 17-03-2023
Volume 5, Issue 1, 2023, Page No. 48-52

Carbonic anhydrase and its potential applications in carbon harvesting

Shekhawat VPS
Department of Botany, R.D. and S.H. National College and S.W.A. Science College, Affiliated to University of Mumbai, Bandra (W), Mumbai, Maharashtra, India

Abstract

Carbonic anhydrases (CAs) are very important enzymes for plant growth and development. Conversion of carbon dioxide to bicarbonate catalyzed by these enzymes is central to many crucial processes for plant growth and development including photosynthesis. In recent years, burgeoning carbon emissions and climate change are posing serious threat to mankind and sustaining life on the earth. Since carbonic anhydrases are the key players in enhancing carbon fixation by the process of photosynthesis, a number of investigations have been put forth highlighting its potential applications in carbon sequestration. This enzyme is affected by a number of factors determining the enzyme synthesis and overall efficiency of this enzyme. Use of genetic and protein engineering has been suggested for improving carbonic anhydrase-based systems for carbon sequestration. The current review is aimed at presenting various aspects of carbonic anhydrase pertaining to its use in mitigation of atmospheric carbon. The review highlights some crucial factors affecting this enzyme and emerging technologies for the use of carbonic anhydrase to address environmental challenges.

Keywords: Carbonic anhydrase, carbon emission, carbon fixation, biomimetic techniques, carbon sequestration

Introduction

In recent decades, indiscriminative anthropogenic activities have resulted in continuous increment in carbon dioxide in the atmosphere that is considered a major factor for rise in global mean temperatures. The continuously increasing levels of atmospheric carbon dioxide (CO_2) have become a global concern that needs urgent attention worldwide. Consequently these concerns are driving research into mechanisms that can harvest carbon effectively or can mitigate impact of increasing carbon dioxide on climate change. Worldwide research policies and exploration are inclining towards development of technologies that can provide effective ways to harvest the excess carbon dioxide and can balance the CO_2 emission due to anthropogenic activities. Plants are naturally endowed with an adorable mechanism, the photosynthesis which is the most efficient way for harvesting carbon from atmosphere and sequester it into fixed forms of carbon. Hence, plants play the most crucial role in mitigating increasing atmospheric carbon through their ability to fix atmospheric CO_2 during the process of photosynthesis. Therefore, the photosynthesis is one of the most important processes enabling plants to play a very crucial role in the global carbon cycle. At the core of the photosynthetic process, lies the key enzyme carbonic anhydrase (CA), which facilitates the carbon fixation by plants and also enhances soil carbon storage. Carbonic anhydrase catalyzes the reversible hydration of CO_2 to bicarbonate (HCO_{3-}) and protons (H^+) (Supuran, 2016) [1] in following manner:

$$CO_2 + H_2O \leftrightharpoons HCO_3 + H^+$$

The enzyme Carbonic anhydrase is ubiquitous across all sort of biological forms. This extraordinary enzyme has evolved to catalyze diverse processes in general and processes in photosynthetic organisms in particular. Considering multifaceted roles of carbonic anhydrase in physiological processes of plants, a significant research all over the world has been carried out in recent decades to explore its diverse applications. A precise understanding of various roles of carbonic anhydrase is very crucial for unravelling the intricacies of plant carbon metabolism. Such exploration should help in developing strategies to enhance carbon sequestration and crop productivity to address some important challenges posed by climate change (Hines *et al*., 2021) [2].

The current review is aimed to synthesize the current knowledge on some of the important aspects clarifying the pivotal role of carbonic anhydrase in plant carbon fixation and consequently harvesting of atmospheric carbon by the plants. This review will explore carbonic anhydrase for its biochemical properties, physiological functions, and potential applications in improving plant performance. By examining the interplay between CA activity and plant carbon dynamics, this reviews makes an attempt to highlight opportunities for leveraging carbonic anhydrase enzyme in agricultural and environmental strategies aimed at mitigating the impacts of rising atmospheric CO_2 levels.

Carbonic anhydrase: A key player in physiological processes

Several different classes of carbonic anhydrase (CAs) have been described. These classes differing in their structure, localization, and physiological functions have been regarded as α-, β-, γ-, δ-, ζ-, η-, θ-, and ι-CAs (Supuran, 2016 [1]; DiMario *et al*., 2017 [3]). The hydration of CO_2 to bicarbonate (HCO_{3-}) catalyzed by Carbonic anhydrase is essential for the efficient uptake and utilization of inorganic carbon (Ci) by in the process of photosynthesis (DiMario *et al*., 2017 [3]). The carbonic anhydrase becomes even more important in aquatic environments where the CO_2 diffusion is relatively slow as compared to the terrestrial environments (Badger and Price, 2003) [4]. Overall efficiency of photosynthesis in plants mainly depends on efficient supply of carbon di oxide (CO_2) for its fixation by carboxylation enzyme like ribulose-1,5-bisphosphate carboxylase (RUBISCO) (DiMario *et al*., 2017) [3] and phophoenol pyruvate carboxylase (PEP Case). The supply of CO_2 to these carboxylating enzymes are mainly decided by efficiency of Carbonic anhydrase. The efficient conversion of CO_2 to HCO^{3-} by carbonic anhydrase ensures a adequate supply of the substrate HCO^{3-} which is the primary source of inorganic carbon for RuBisCO (Moroney *et al*., 2011) [5]. Due to low concentration of CO_2 in aquatic habitats several aquatic phototrophs like cyanobacteria, algae, and some aquatic vascular plants have evolved carbon concentration mechanisms (CCMs) to ensure adequate supply of inorganic carbon to carboxylation enzyme RuBisCO. Carbonic anhydrase is shown to play a central role in such carbon carbon concentration mechanisms (CCMs) in plants growing in such aquatic habitats (Badger, 2003 [6]; Poschenrieder *et al*., 2018 [7]). The role of carbonic anydrase is not confined only to photosynthesis. This extra ordinary enzyme plays a significant role in various physiological processes like pH regulation, ion transport, and plant defence responses (Floryszak-Wieczorek and Arasimowicz-Jelonek, 2017) [8]. Similarly, Carbonic anhydrase is also involved in other important processes such as respiration, and stomatal movement in plants (Floryszak-Wieczorek and Arasimowicz-Jelonek, 2017 [8]; Polishchuk, 2021 [9]). The importance of carbonic anhydrase in different stress responses in plants has also been put forward. Its role in abiotic stress conditions like drought, salinity, heavy metal toxicity, and pathogen attacks etc is very well known (Polishchuk, 2021) [9]. Carbonic anhydrase expression studies and activity under stress conditions clearly indicate participation of this enzyme various adaptation strategies of plants (Rudenko *et al*., 2020) [10]. Considering all the exploration put forward on physiological roles of carbonic anhydrase, this enzyme can be regarded as one of the most important enzymes for plant growth and development. Besides being involved in efficient uptake of inorganic carbon this enzyme also participates in several crucial processes of plants, therefore role of carbonic anhydrase in of paramount importance in plant growth, development and consequently biomass production efficiency of a plant. (Hu *et al*., 2015 [11]; Dąbrowska-Bronk *et al*., 2016 [12]).

Role of carbonic anhydrase in carbon fixation

The process of photosynthesis is a concerted action of several enzymes where Carbonic anhydrase works in close coordination with other key photosynthetic enzymes, for the essential fixation of carbon dioxide. At several occasions, the suitable spatial organization of Carbonic anhydrase is ensured by plant systems to facilitate the efficient transfer of HCO_3^- to RuBisCO, enhancing the overall carbon fixation rate (Badger and Price, 2003 [4]). In cyanobacteria and green algae, Carbonic anhydrase has been reported to be physically associated with the carboxysome or pyrenoid, specialized microcompartments that enclose RuBisCO (Rae *et al*., 2013) [13]. The high photorespiration specially in C3 plants can also be mitigated via effective intervention of carbonic anhydrase as it maintains a high concentration of CO_2 in the close proximity the carboxylase enzymes. Consequently, the carboxylation rates are enhanced and the oxygenation reaction (photorespiration) responsible for carbon loss is reduced (Adler *et al*., 2022) [14]. The studies have been put forward to explain impact of carbonic anhydrase on carbon assimilation rates. The manipulation in the expression level of carbonic anhydarse had a significant effect on the photosynthetic capacity and consequently on the growth of plants. The over expression the carbonic anhydrase for increasing the CO_2 assimilation rate is still a unclear and contradictory aspect and needs more explorations. The reduction in carbonic anhydrase resulted in seedling survival in Arabidopsis (Ferreira *et al*., 2008) [15]. The impact of carbonic anhydrase activity on the carbon assimilation rates in photosynthesis may be attributed to several aspects. Carbonic anhydrase can increase the rate of CO_2 diffusion across cell membranes, and hence enhances the supply of CO_2 to RuBisCO for photosynthesis. Likewise carbonic anhydrase activity in low atmospheric CO_2 concentration is enhanced to ensure adequate supply of carbon for carboxylation reactions (Sage and Coleman, 2001) [16]. The product of carbonic anhydrase reaction i.e. carbonic acid is a key product for several other biosynthetic processes in cells therefore it affects overall growth of plants also. The biochemical or molecular inhibition of carbonic anhydrase activity has been reported to affect the rate of plant lipid biosynthesis (Hoang and Chapman, 2002) [17].

Carbonic anhydrase: carbon harvesting

The industrial emissions are pegged at their peak in recent decades and have a major share in CO_2 emissions impacting climate change. The mitigation strategies of climate change can be utilized for industrial emissions that often discuss the CO_2 Capture Utilization and Storage (CCUS). The CCUS is a fundamental strategy for mitigation of climate change and using carbon harvesting capabilities of CA for the conversion of CO_2 to bicarbonates can be an effective way forward (Maciel *et al*.,2022) [18]. Use of carbonic anhydrase in CCUS can enhance the possibilities of achieving the carbon harvesting goals in many ways. Plants are the naturally equipped with photosynthesis which is efficient in sequestering CO_2. Carbonic anhydrase is a key enzyme in plant CO_2 fixation methods that works in concert with ribulose 1,5-bisphosphate carboxylase (Rubisco) in C3 plants and was discovered as a component of chloroplast by Neish, (1939) [19]. In C4 and CAM plants, carbonic anhydrase is known to deliver carbon dioxide to phosphoenolpyruvate carboxylase (Tiwari *et al*., 2005) [20]. A portion of the fixed carbon is used for plant growth and development, while the rest enters the soil carbon pool through plant litter and root exudates (Lal, 2004) [21]. Moroney and Ynalvez, 2007 [22], demonstrated the crucial role of carbonic anhydrase for the accumulation of CO_2 in *Chlamydomonas reinhardtii.* Depending on the CO_2 concentrating mechanism (CCM), carbonic anhydrase can be found at different locations in the cell such as thylakoids of *Chlamydomonas reinhardtii*, pyrenoids of *Pheodactylum tricorutum* and mesophyll cells of C4 plants (DiMario *et al*., 2017) [3]. There is a significant share of carbon in the plant biomass (above ground and belowground) like stem, leaves, rhizomes, roots and other woody tissues (Jansson *et al*., 2010) [23]. An increase in the carbon dioxide diffusion and fixation by carbonic anhydrase can improve the rates of photosynthesis (Momayyezi *et al*., 2020) [24] that improve plant growth as well as increase its biomass with increasing carbon flux deposited in the soil (Hoang and Chapman, 2002) [17]. While low CO_2 environments can increase expression of anhydrase as well activity (Fukuzawa *et al*., 1990) [25]., increased concentrations of HCO_3^-in the plant environment can improve the carbon accumulation and assimilation processes like photosynthesis that promote carbon harvesting and sequestration (Dąbrowska-Bronk *et al*., 2016) [12]. Improved sequestration and accumulation of soil organic carbon (SOC) can avoid decomposition and soil erosion (Sarfraz *et al*., 2019) [26]. Moreover, expression of this enzyme can get upregulated in conditions of stress like light, temperature, drought etc that suggest a significant role of the enzyme in plant survival and fitness (Kaul *et al*., 2011 [27]; Pal and Borthakur, 2014 [28]; Rudenko *et al*., 2017 [29]). Fatty acid and amino acid production are a few other metabolic processes utilizing the interconversion capabilities (CO_2 and HCO_3^-) of carbonic anhydrase (Hoang and Chapman, 2002) [17]. Salama *et al*., (2006) [30] found low level of Rubisco in the plants grown with low zinc concentrations. Nathan and Ammini (2019) [31] elucidated the role of bacterial carbonic anhydrase in the rhizosphere of mangrove plants. The carbonic anhydrase isoforms may be explored from strained but resilient natural habitats that exhibit both efficiency and resistance to environmental conditions. These enzymes provide an opportunity to utilize the natural systems for the quest of climate change mitigation. Biocatalytic performance of CA can be enhanced using methods of genetic and protein engineering, and other biotechnological tools (Di Fiore *et al*.,2015) [32]. Utilization of carbonic anhydrase in bio-mimicking based technologies like use of immobilized carbonic anhydrase for CO_2 can also be an effective strategy to sequester carbon in industrial setup for reducing the emissions to a significant extent.

Table 1: Factors influencing the activity of Carbonic anhydrase in plant systems (Kaiser, 1987 [33]; Ignatova *et al*., 2001 [34]; Demir *et al*., 2009 [35]; Lazova *et al*., 2012 [36]; Rudenko *et al*., 2015 [37]; Rudenko *et al*., 2017 [29]; Sauze *et al*., 2018 [38]; Rudenko *et al*., 2020 [10]; Hines *et al*., 2021 [2]; Rudenko *et al*., 2022 [39]).

Factor and its Influence on Carbonic Anhydrase Activity	Changes in Carbonic Anhydrase Activity	Actual Influence on Mechanism of Action of Enzyme	Plant System used for the Study
▪ **pH** Strongly affects enzyme activity, particularly at acidic or alkaline conditions.	Activity increases at neutral to slightly alkaline pH (e.g., 7.4–8.5), decreases at extremes.	Changes catalytic efficiency by altering protonation states of active site residues and zinc-bound water molecule.	Arabidopsis thaliana, Tobacco
▪ **CO_2 Concentration** Higher CO_2 concentrations generally increase CA activity.	Increases activity under low CO_2, decreases under high CO_2 levels.	Enhances the enzyme's ability to convert CO_2 to bicarbonate (HCO_3^-).	Arabidopsis thaliana, Tobacco
▪ **Zinc Availability** Zinc is essential as a cofactor for CA activity.	Activity decreases significantly in zinc-deficient conditions.	Zinc ion stabilizes the hydroxide ion in the active site, critical for catalysis.	Tobacco
▪ **Light Intensity** Increased light intensity upregulates CA gene expression.	Enhances CA activity in chloroplasts and thylakoids during higher light conditions.	Likely linked to the role of CA in photosynthesis-related carbon fixation and electron transport.	Arabidopsis thaliana, Pea
▪ **Temperature** Optimal activity at moderate temperatures (20–40°C); extremes inhibit activity.	Activity peaks at optimal temperatures and declines at low or high temperatures.	Affects the enzyme's structural stability and the rate of catalytic conversion of CO_2 and HCO_3^-.	Potato, Spinach
▪ **Drought Stress** Drought reduces CA activity in leaves.	Decreases CA activity, particularly in photosynthetic tissues.	Likely reduces the supply of CO_2 to RuBisCO and affects pH buffering, impairing photosynthesis.	Pea, Barley
▪ **Salinity Stress** Salinity has a dual effect—short-term increase followed by long-term decrease in CA activity.	Initial increase in CA hydratase activity followed by suppression in prolonged salt stress.	Impacts ion balance and osmotic stress, indirectly inhibiting CA's role in CO_2 hydration and bicarbonate formation.	Pea
▪ **CA Inhibitors** Lipophilic inhibitors like ethoxyzolamide and water-soluble inhibitors like acetazolamide significantly reduce activity.	Strong inhibition—up to 60% reduction in activity in protoplasts.	Block the active site by binding zinc ion or disrupting proton transfer, impairing the enzyme's catalytic efficiency.	Pea, Tobacco
▪ **Gene Knockout or Suppression** Decreases CA activity depending on the isoform targeted.	Reduced activity in mutants or transgenic plants with suppressed CA gene expression.	Reduces overall catalytic capacity and affects CO_2 fixation efficiency and downstream photosynthetic reactions.	Tobacco

Factors influencing the activity of carbonic anhydrase

Carbonic anhydrase activity in plants is modulated by several important factors like pH, presence of zinc, photon flux and carbon dioxide content available (McConnell *et al*., 2007 [40]; Salama *et al*., 2006) [30]. *In vitro* studies have demonstrated inhibition of carbonic anhydrase activity by nitrites, nitrates, chlorides, mercury, magnesium, iodides among many others (Tiwari *et al*., 2005) [20]. The cellular location and regulation of Carbonic anhydrase in different cellular compartments is also very significant in plant carbon metabolism. This has immense strategic significance for genetic engineering and biotechnological applications aimed at enhancing carbon fixation and sequestration. Various factors important for carbonic anhydrase functioning are presented in table (1)

Emerging technologies for using carbonic anhydrase for carbon harvesting

Reducing carbon emission and use of carbon neutral processes are two major focus areas to achieve carbon neutral and environmentally sustainable industrial processes. Recently biomemtic approach-based technologies and industrial applications of carbonic anhydrase are emerging that involves immobilization of CA for carbon harvesting (Maciel *et al*., 2022) [32]. Carbonic anhydrase (CA) based membranes with efficient enzymatic activities are extensively reviewed for carbon capture and storage (CCS) (Zhang *et al*., 2022) [41]. Migliardini *et al*., (2014) [42] immobilized carbonic anhydrase from thermophilic bacteria Sulfurihydrogenibium yellowstonense using polyurethane (PU) foam. This immobilized enzyme exhibited efficient conversion of CO2 into bicarbonates. In this bioreactor-based setup enzyme was catalytically active and showed a long-term stability. In an another important study, the fastest known CA from *Sulfurihydrogenibium azorense* (SazCA) was fused with a silica-condensing peptide (R5). The fusion protein named as R5-SazCA; which was more efficient than the original form of enzyme and could be reused efficiently up to 10 cycles exhibiting its value for applications in carbon (Hsieh *et al*., 2021**)** [43]. Immobilization of microalgae cells for utilizing carbonic anhydrase for carbon harvesting has also been explored. Freshwater Chlorella was immobilized as algal beads (sodium alginate-calcium chloride) by Kassim *et al.*, (2019) [44]. They found that the entrapment of algae produces higher CA activity suggesting this could be further utilised for extended biomimetic CO2 capture systems. Hence immobilization of carbonic anhydrase can be effectively used to develop technologies to harvest atmospheric carbon very effectively to achieve carbon neutrality in industrial processes.

Conclusion

Carbonic anhydrase enzymes have a very critical and significant role in enhancing carbon fixation and thereby carbon sequestration by the plants. Besides photosynthesis this enzyme enhances several physiological processes in plants. A better understanding of this enzyme can significantly contribute to strategies aimed at mitigating climate change through improved carbon harvesting and soil carbon storage. Use of immobilization and innovative biomimetic methods utilizing carbonic anhydrase properties can be a significant step towards achieving carbon neutrality in industrial processes.

References

1. Supuran CT. Structure and function of carbonic anhydrases. Biochemical Journal,2016:473(14):2023-2032
2. Hines KM, Chaudhari V, Edgeworth KN, Owens TG, Hanson MR. Absence of carbonic anhydrase in chloroplasts affects C3 plant development but not photosynthesis. Proceedings of the National Academy of Sciences,2021:118 (33):e2107425118.
3. DiMario RJ, Machingura MC, Waldrop GL, Moroney JV. The many types of carbonic anhydrases in photosynthetic organisms. Plant Science,2017:268:11-17.
4. Badger MR, Price GD. CO2 concentrating mechanisms in cyanobacteria: molecular components, their diversity and evolution. Journal of Experimental Botany,2003:54(383):609-622.
5. Moroney JV, Ma Y, Frey WD, Fusilier KA, Pham TT, Simms, TA, *et al*. The carbonic anhydrase isoforms of Chlamydomonas reinhardtii: intracellular location, expression, and physiological roles. Photosynthesis Research,2011:109(1-3):133-149.
6. Badger MR. The roles of carbonic anhydrases in photosynthetic CO2 concentrating mechanisms. Photosynthesis Research,2003:77(2-3):83-94.
7. Poschenrieder C, Fernández J, Rubio L, Pérez L, Terés J, Barceló J. Transport and use of bicarbonate in plants: Current knowledge and challenges ahead. International Journal of Molecular Sciences,2018:19(5):1352.
8. Floryszak-Wieczorek J, Arasimowicz-Jelonek M. The multifunctional face of plant carbosnic anhydrase. Plant Physiology and Biochemistry,2017:112:362-368.
9. Polishchuk OV. Stress-related changes in the expression and activity of plant carbonic anhydrases. Planta,2021:253(2):58.
10. Rudenko NN, Fedorchuk TP, Terentyev, VV, Dymova, OV, Naydov, IA, Golovko TK, Borisova-Mubarakshina MM, Ivanov BN. The role of carbonic anhydrase α-CA4 in the adaptive reactions of photosynthetic apparatus: the study with α-CA4 knockout plants. Protoplasma,2020:257:489-499
11. Hu H, Rappel WJ, Occhipinti R, Ries A, Böhmer M, You L, Xiao C, Engineer CB, Boron WF, Schroeder JI. Distinct Cellular Locations of Carbonic Anhydrases Mediate Carbon Dioxide Control of Stomatal Movements. Plant Physiol. 2015:169(2):1168-78.
12. Dąbrowska-Bronk J, Komar DN, Rusaczonek A, Kozłowska-Makulska A, Szymańska R, Kruk J. β-carbonic anhydrases and carbonic ions uptake positively influence Arabidopsis photosynthesis, oxidative stress tolerance and growth in light dependent manner. Journal of Plant Physiology,2016:203:44-54.
13. Rae BD, Long BM, Badger MR, Price GD. Functions, compositions, and evolution of the two types of carboxysomes: polyhedral microcompartments that facilitate CO2 fixation in cyanobacteria and some proteobacteria. *Microbiology and Molecular Biology Reviews*,2013:77(3):357-379.
14. Adler L, Díaz-Ramos A, Mao Y, Pukacz KR, Fei C, McCormick AJ, New horizons for building pyrenoid-based CO_2-concentrating mechanisms in plants to improve yields, Plant Physiology,2022:190 (3):1609–1627,
15. Ferreira FJ, Guo C, Coleman JR. Reduction of plastid-localized carbonic anhydrase activity results in reduced Arabidopsis seedling survivorship. Plant Physiology,2008:147(2):585-594.
16. Sage RF, Coleman JR. Effects of low atmospheric CO (2) on plants: more than a thing of the past. Trends Plant Sci,2002:6(1):18-24
17. Hoang CV, Chapman KD. Regulation of carbonic anhydrase gene expression in cotyledons of cotton (Gossypium hirsutum L.) seedlings during post-germinative growth. Plant Mol Biol,2002:49:449–458
18. Maciel DOA, Christakopoulos P, Rova U, Antonopoulou I. Carbonic anhydrase to boost CO2 sequestration: Improving carbon capture utilization and storage (CCUS). Chemosphere,2022:299:134419.
19. Neish AC. Studies on chloroplasts: Their chemical composition and the distribution of certain metabolites between the chloroplasts and the remainder of the leaf. Biochem J. 1939:33(3):300-308.
20. Tiwari A, Kumar P, Singh S, Ansari SA. Carbonic anhydrase in relation to higher plants. Photosynthetica,2005:43:1–11.
21. Lal R. Soil carbon sequestration impacts on global climate change and food security. Science,2004:304:1623-1627.

22. Moroney JV, Ynalvez RA. Proposed carbon dioxide concentrating mechanism in Chlamydomonas reinhardtii. Eukaryot Cell. 2007:6(8):1251-1259.
23. Jansson C, Wullschleger SD, Kalluri UC, Tuskan GA. Phytosequestration: Carbon Biosequestration by Plants and the Prospects of Genetic Engineering, BioScience,2010:60:685–696
24. Momayyezi M, McKown AD, Bell SCS, Guy RD. Emerging roles for carbonic anhydrase in mesophyll conductance and photosynthesis. The Plant Journal,2020:101(4):831-844.
25. Fukuzawa H, Fujiwara S, Yamamoto Y, Dionisio-Sese ML, Miyachi S. cDNA cloning, sequence, and expression of carbonic anhydrase in Chlamydomonas reinhardtii: Regulation by environmental CO2 concentration. Proceedings of the National Academy of Sciences,1990:87(11):4383-4387.
26. Sarfraz R, Hussain A, Sabir A, Fekih IB, Ditta A, Xing S. Role of biochar and plant growth promoting rhizobacteria to enhance soil carbon sequestration—A review. Environmental Monitoring and Assessment,2019:191(4):251.
27. Kaul T, Reddy PS, Mahanty S, Thirulogachandar V, Reddy RA, Sopory SK, Reddy MK. Biochemical and molecular characterization of stress-induced β-carbonic anhydrase from a C4 plant, Pennisetum glaucum. Journal of Plant Physiology,2011:168(6):601-610.
28. Pal A, Borthakur D. Tissue-specific differential expression of two β-carbonic anhydrases in *Leucaena leucocephala* under abiotic stress conditions. Journal of Applied Biotechnology,2014:2(2):43-64.
29. Rudenko NN, Vetoshkina DV, Fedorchuk TP, Ivanov BN. Effect of light intensity under different photoperiods on expression level of carbonic anhydrase genes of the α- and β-families in Arabidopsis thaliana leaves. Biochemistry (Moscow),2017:82(9):1025–1035.
30. Salama ZA, El-Fouly MM, Lazova G, Popova LP. Carboxylating enzymes and carbonic anhydrase functions were suppressed by zinc deficiency in maize and chickpea plants. Acta Physiol Plant,2006:28:445–451
31. Nathan VK, Ammini P. Carbon Dioxide Sequestering Ability of Bacterial Carbonic Anhydrase in a Mangrove Soil Microcosm and Its Bio-mineralization Properties. *Water Air Soil Pollut,* 2019, 230,192
32. Di Fiore A, Alterio V, Monti SM, De Simone G, D'Ambrosio K. Thermostable Carbonic Anhydrases in Biotechnological Applications. International Journal of Molecular Sciences,2015:16(7):15456-15480.
33. Kaiser WM. Effects of water deficit on photosynthetic capacity. Physiologia Plantarum,1987:71(1):142–149.
34. Ignatova LK, Moskvin OV, Ivanov BN. Effects of carbonic anhydrase inhibitors on proton exchange and photosynthesis in pea protoplasts. Russian Journal of Plant Physiology,2001:48(4):467–472.
35. Demir N, Nadaroglu H, Demir Y. Carbonic anhydrase from potato (Solanum tuberosum) roots and leaves. *Asian Journal of Chemistry,*2009:*21*(7):5104–5116.
36. Lazova G, Ignatova L, Baydanova V. Drought and salinity stress: Changes in hydratase and dehydratase activities of thylakoid-associated carbonic anhydrase in pea seedlings. International Journal of Plant Sciences,2012:173(1): 7–15.
37. Rudenko NN, Ignatova L, Zhurikova E, Borisova-Mubarakshina M, Ivanov B. Carbonic anhydrases in photosynthesizing cells of c3 higher plants. Metabolites,2015:80(6):674–687.
38. Sauze J, Jones SP, Wingate L, Wohl S, Ogée J. The role of soil pH on soil carbonic anhydrase activity. Biogeosciences,2018:15(2):597–612.
39. Rudenko NN, Permyakova NV, Ignatova LK, Nadeeva EM, Zagorskaya AA, Deineko EV, Ivanov BN. The Role of Carbonic Anhydrase αCA4 in Photosynthetic Reactions in *Arabidopsis thaliana* Studied, Using the Cas9 and T-DNA Induced Mutations in Its Gene. Plants (Basel),2022:29:11(23):3303.
40. McConnell IL, Badger MR, Wydrzynski T, Hillier WA. quantitative assessment of the carbonic anhydrase activity in photosystem II. Biochim Biophys Acta,2007:1767(6):639-647.
41. Zhang Y, Zhu J, Hou J, Yi S, Van der Bruggen B, Zhang Y. Carbonic anhydrase membranes for carbon capture and storage. Journal of Membrane Science Letters,2022:2:100031.
42. Migliardini F, De Luca V, Carginale V, Rossi M, Corbo P, Supuran CT, Capasso C. Biomimetic CO2 capture using a highly thermostable bacterial α-carbonic anhydrase immobilized on a polyurethane foam. Journal of enzyme inhibition and medicinal chemistry,2019:29(1):146-50.
43. Hsieh CJ, Cheng JC, Hu CJ, Yu CY. Entrapment of the Fastest Known Carbonic Anhydrase with Biomimetic Silica and Its Application for CO_2 Sequestration. Polymers,2021:13(15):2452.
44. Kassim MA, Adnan MM, Tan KM, Bakar MHA, Lalung J, Mohamed MS. Carbonic anhydrase (CA) activity by Chlorella sp. in immobilised matrix under carbon dioxide rich cultivation condition. Materials Science and Engineering, 716:012-015