

Combined Role of ACC Deaminase Producing Bacteria and Biochar on Cereals Productivity under Drought

Subhan Danish^{1,2} and Muhammad Zafar-ul-Hye^{1,*}

¹Department of Soil Science, Faculty of Agricultural Sciences and Technology, Bahauddin Zakariya University, Multan, 60800, Pakistan

²Soil and Water Testing Laboratory, PakArab Fertilizer Limited, Plantsite, Multan, 60800, Pakistan

*Corresponding Author: Muhammad Zafar-ul-Hye. Email: zafarulhyegondal@yahoo.com

Received: 02 September 2019; Accepted: 18 November 2019

Abstract: Most of the cereal crops are widely cultivated to fulfil the humans food requirements. Under changing climate scenario, the intensity of drought stress is continuously increasing that is adversely affecting the growth and yield of cereal crops. Although the cereals can tolerate moderate drought to some extent, but mostly they are susceptible to severe drought stress. Higher biosynthesis of ethylene under drought stress has been reported. Many scientists observed that inoculation of 1-aminocyclopropane-1-carboxylate (ACC) deaminase producing plant growth promoting rhizobacteria (PGPR) is an efficacious tool to overcome this problem. These PGPR secrete ACC deaminase which cleavage the ACC into the compounds, other than ethylene. Furthermore, secretion of growth hormones also play imperative role in enhancing the growth of the cereals under limited availability of water. In addition, the use of biochar has also been recognized as another effective amendment to grant resistance against drought. Biochar application improves the soil physiochemical attributes i.e., porosity, nutrients retention and water holding capacity which decrease the loss of water and increase its bioavailability. In recent era, the idea of co-application of ACC deaminase producing PGPR and biochar is becoming popular which might be more efficient to use water under drought stress. The aim of current review is to combine the facts and understanding of this novel idea to grant maximum resistance to crops against drought stress. Some scientists have observed significant improvement in yield of cereal crops by combined use of ACC deaminase producing PGPR and biochar. However, more research is suggested for deep understanding of complex synergistic mechanism of ACC deaminase activity in combination with biochar.

Keywords: ACC deaminase; biochar; cereals; drought; ethylene; PGPR; yield

1 Introduction

Most of the crops demand ideal environment conditions for their good growth and development. But due to their static nature, plants have to face different adverse climatic conditions i.e., cold, heat, drought, salinity, flooding etc. [1]. Elevation in CO₂ level in air due to continuously varying climatic conditions has intensified the situation for the cultivation of crops in agriculture [2]. It is expected that the temperature of earth would be enhanced 2°C till the end of 21st century, as compared era of 1850-1900 AD [3]. Elevation in earth temperature by increasing CO₂ level is playing a vital role in enhancement of drought area [4]. Drought stress is a worldwide common problem, especially in arid and semi-arid areas. The vulnerability of water scarcity is elevating with each passing year [5]. The intensity of drought might be more in the coming future as well due to its direct link with global climate change [1]. It is predicted that demand for irrigation



water for the cultivation of plants would increase by 10% until the 2050 AD [6]. Because of water competition among industrial, domestic and agricultural users, it is also not possible to expand the irrigated cultivatable land [7]. On the other hand, the area under irrigation production systems is expected to decline resulting in reduction of food production [7]. In this review, the facts related drought, ethylene synthesis, combined and sole application of ACC deaminase producing PGPR and biochar will be focused. The aim of current review is to understand and uncover the efficacy perspectives of combined use of ACC deaminase producing PGPR and biochar regarding mitigation of drought in cereals.

2 Adverse Effects of Drought on Plants

Limited accessibility of water, i.e., drought, induced negatively affects the plant growth and yield (Tab. 2). Drought affects several biochemical and physiological functions in plants i.e, decrease in water potential, loss of turgor, disturbance in protein structure and stomatal closure [8]. A significant amount of salts becomes accumulated in the upper layers of soil under limited water supply which causes osmotic stress and ion toxicity to the plant roots [9]. Reduction of stomatal conductance is the first response of plants which is regulated by roots via sending signals through abscisic acid [10]. In this way, CO₂ diffusion in leaves is reduced under drought as a result of poor conductance of mesophyll. Such conditions impair the photosynthesis [11]. It also causes a considerable decrease in crop yield [12,13]. Some of the studies showing the effect of drought on cereal yield are listed in Tab. 1. Additionally, the drought stress also develops an imbalance between amount of Reactive Oxygen Species (ROS) and antioxidant defenses that induce an oxidative stress. The ROS are important for intracellular signaling yet their higher concentration can induce adverse effects at different organization i.e., chloroplasts [14]. The ROS have the capacity to initiate lipid peroxidation and degrade proteins, lipids and nucleic acids [15]. Mechanism of retardation of lipid peroxidation consists of free radical scavenging enzymes such as catalase, peroxidase and superoxide dismutase [16]. A number of enzymatic and nonenzymatic antioxidants are present in chloroplasts that serve to prevent ROS accumulation [17].

Table 1: Yield losses in cereals due to drought stress

Crop	Stress	Yield Losses (%)	References
Wheat	40% of soil water reduction	20.6%	[18]
	Drought, the SPEI (Standardized Precipitation Evapotranspiration Index) denoting extreme dry (0.05 quantile)	4.4%	[19]
	-40% water deficit	20.4%	[20]
	50% field capacity	50%	[21]
Rice	30% field capacity	68%	[21]
	Drying, soils dried beyond -20 kPa	22.6%	[22]
	Drought, water stress (-40% water deficit)	> 50%	[20]
Maize	Meta-analysis of drought under field conditions (40% water reduction)	39.3%	[18]
	50% irrigation	30-48%	[23]
	Progressive drought (PD)	41.6-46.6%	[24]

Table 2: Adverse effects of drought on cereals

Crop	Adverse effect of drought	References
Wheat	Decrease 1000 grains weight, decrease chlorophyll	[25]
Wheat	Increase electrolyte leakage, decrease growth and gas exchange attributes	[26]
Wheat	Decrease biological, grains yield	[21]
Wheat	Decrease grain numbers	[27]
Wheat	Malfunction and irreversible abortion of male and female reproductive organs	[28-30]
Wheat	Over production of reactive oxygen species	[31]
Rice	Grain filling	[32]
Rice	Affects the activity of the enzymes for starch synthesis	[33]
	Poor imbibition, germination and seedling establishment	[34]
Maize	Reduced the plumule and radicle growth	[35]
	Reduction in shoot elongation is more than root elongation	[36]
All crops	Reduced CO ₂ diffusion	[37]

2.1 Drought and Stress Ethylene

Drought stress leads to higher ethylene production in plants, which has a detrimental effect on plant growth (Tab. 3). Ethylene acts as signalling agent for biotic and abiotic stress [38]. It also plays an imperative role in connection with plant responses under oxygen deficiency i.e., induction of gene expression linked with leaf senescence, formation of aerenchyma, glycolysis and fermentation. Accumulation of the ethylene precursor ACC in roots is transported via the transpiration stream to aerial part of the plant. Here, presence of O₂ allows it to be changed into ethylene, triggering petiole epinasty [39]. Drought stress stimulates the methionine through the intermediates S-adenosyl methionine (SAM) and the cyclic amino acid 1-aminocyclopropane-1-carboxylic acid (ACC). The enzyme converting methionine to SAM is SAM synthetase, ACC synthase converts SAM to ACC, and ACC is oxidized to ethylene by ACC oxidase. Higher levels of ethylene adversely affect the growth and yield attributes of plants [40]. Therefore, reduction in stress ethylene has become an efficacious approach to enhance crops yield in stress conditions. Recently, soil microbiologists have proved that the use/inoculation of plant growth-promoting rhizobacteria (PGPR) improved the crops productivity under variable environmental stresses [41].

Table 3: Threshold and stress generating levels of ethylene

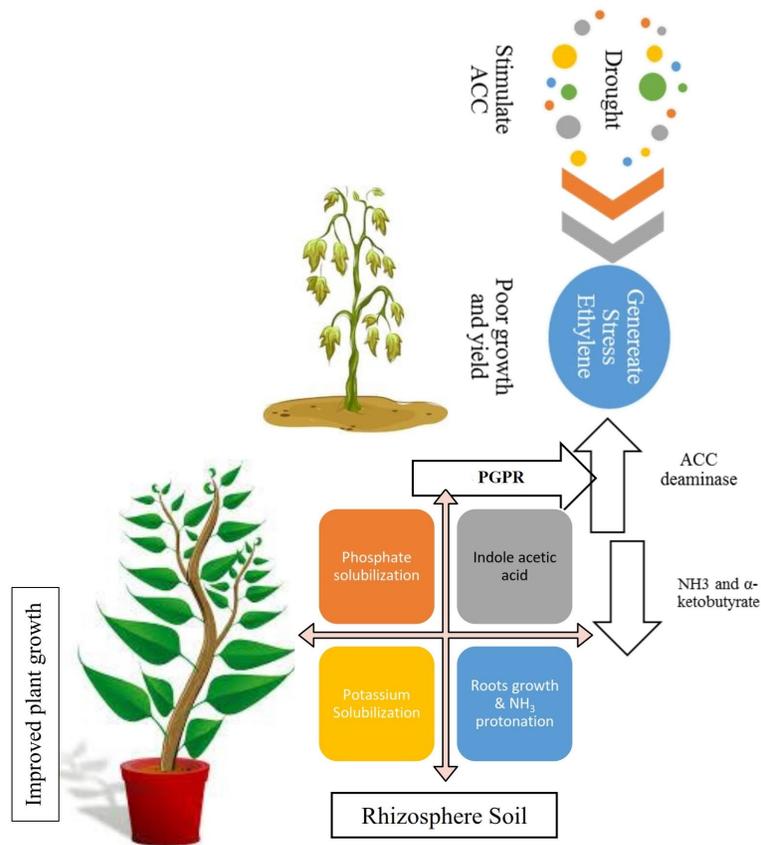
Crop	Normal Ethylene level	Stress Ethylene level due to drought	Negative effect/Stress induction	Reference
	0.3–0.6 nl.g ⁻¹ .h ⁻¹	37 nl.g ⁻¹ .h ⁻¹	9% fresh weight loss	[42]
Wheat	-	approx. 36 nl g ⁻¹ fresh weight (initial 24h)	8% fresh weight loss (water potential about –2.3 megapascals)	[43]
Arabidopsis	-	approx. 2.4 nl g ⁻¹ fresh weight h ⁻¹	Fe generated stress	[44]
Wheat	approx. 0.1 nl.g ¹ fresh weight h ⁻¹	approx. 0.39 nl.g ¹ fresh weight h ⁻¹	–0.08 MPa water potential mild drought	[45]
Wheat	approx. 10 nmol g ⁻¹ fresh weight h ⁻¹	approx. 15 nmol g ⁻¹ fresh weight h ⁻¹	20mg ml ⁻¹ NaCl generated stress	[46]

3 ACC Deaminase Producing PGPR

Rhizosphere is a area wher millions of PGPR's make a complex community. They affect the yield of crops positively [47,48]. The PGPR improve crops yield by a wide range of mechanisms i.e., inorganic nutrients (P, Zn, K) solubilization, synthesis of phytohormones, decreasing stress ethylene (Fig. 1) and stimulating the root growth [49]. Under drought stress, the PGPR that contains 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase activity can improve the plant growth by changing ethylene concentrations in plants (Tab. 4). Thats why, such PGPR can be termed as “stress modulators” [26,50]. Several authors have reported the utilization of ACC- deaminase producing PGPR for ameliorating drought stress in crops i.e., chickpea [51], wheat [21] and *Lavandula dentata* [52].

Table 4: ACC deaminase producing PGPR mitigate drought stress in cereals

Crop	Study	ACC deaminase PGPR	Stress	References
Wheat	Hydroponic	<i>Leclercia adecarboxylata</i> , <i>Bacillus amyloliquefaciens</i> , <i>Agrobacterium fabrum</i> , <i>Pseudomonas aeruginosa</i>	PEG 6000 induced Drought	[21]
	Pot	<i>Leclercia adecarboxylata</i> , <i>Bacillus amyloliquefaciens</i> , <i>Agrobacterium fabrum</i> , <i>Pseudomonas aeruginosa</i>	WHC maintained Drought	[26]
	Field	<i>Bacillus amyloliquefaciens</i> , <i>Agrobacterium fabrum</i>	Drought generated by skipping irrigations	[53]
	Glasshouse pot	<i>Variovorax paradoxus</i> RAA3; <i>Pseudomonas</i> spp. DPC12, DPB13, DPB15, DPB16; <i>Achromobacter</i> spp. PSA7, PSB8; and <i>Ochrobactrum anthropi</i> DPC9. Enterobacter	WHC maintained Drought	[54]
	Field	<i>Enterobacter mori</i> (KF747680), <i>E. asburiae</i> (KF747681) and <i>E.</i> <i>ludwigii</i> (KF747683), <i>Enterobacter cloacae</i> , <i>Achromobacter xylosoxidans</i> ,	Non-limiting water condition, medium drought and severe drought	[55]
	Hydroponic	<i>Leclercia adecarboxylata</i> , <i>Pseudomonas aeruginosa</i>	PEG 6000 induced Drought	[56]
Maize	Field Study	BN-5 and MD-23 (PGPR not identified)	vegetative and tasseling stages ~50% field capacity (FC) induced drought	[57]
	Pot experiment	<i>B. megaterium</i> strain HX-2	PEG 6000 induced Drought	[58]
Rice	Lab Experiment	IS 4–7, AP 3–7, CS 10–12, and IS 8–9	Polyethylene glycol (PEG) 8000 induced drought	[59]

**Figure 1:** ACC deaminase producing PGPR promote plant growth under drought stress

Some of the important reported studies are listed in Tab. 4. In maize, leaf ethylene changes are not linked with decrease in elongation under limited availability of water [60] suggesting that ethylene may play a role in leaf growth inhibition and ACC may be one component of long distance root-sourced signals under drought [61]. A report in wheat showed that after 2 days under drought-stress, plants treated with an ethylene inhibitor (1-MCP) closed their stomata, suggesting chemical but not hydraulic signals controlled stomatal closure [62]. In rice, waterlogging induced adventitious root formation mediated by ethylene also appeared to facilitate aerenchyma formation [63].

4 Biochar

On the other hand, activated biochar (BC) is a potential nutrient-rich organic amendment. Its potential benefits include the minimum emission of greenhouse gas (GHG), contaminants adsorption, enhancement of soil nutrients availability as well as crop productivity in cultivatable soils [64,65]. Depending upon plant and soil processes, the cultivatable land acts as a sink and source for carbon (C) [66,67]. An increase in carbon dioxide (CO₂) emissions by addition of fertilizers can be partially offset by increased in photosynthetic rate, that are not limited due to deficiency of nutrients. As BC can give an exceptional solution for such potential problems of nutrients, it has become the centre of attention for the farmers and scientists [68].

Sequestration of C, especially in arable land, is an important route to lessen the climatic changes. In cultivatable soils, reserves of organic carbon (OC) are limited. Biochar mixing in such soils can be an efficacious approach for improvement of SOC. It increases recalcitrant C in bulk amount which is resistant against decomposition, thus, it decreases the GHG emissions [60,64,69]. As BC is stable and has capability to improve soil carbon for hundred years thus, modified water holding capacity (WHC). Nutrient holding can be maintained by its application for a long period of time [70].

4.1 Production and Potential Soil Benefits

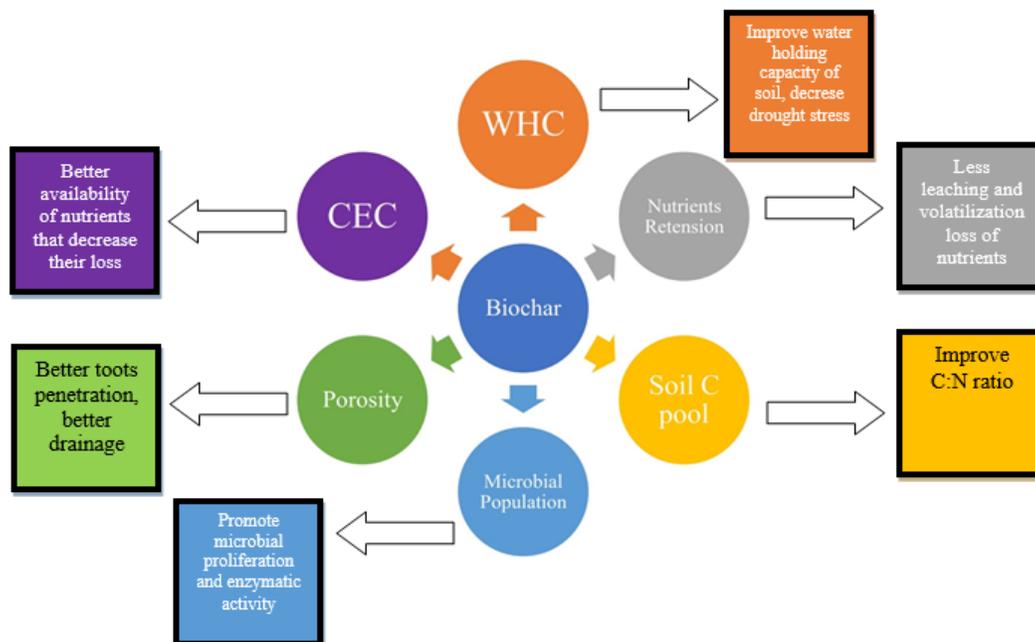


Figure 2: Biochar potential benefits when it is applied in soil

Biochar is manufactured via pyrolysis under low or no supply of O₂ and high temperature [71]. In complete or partial absence of O₂, thermal disintegration of waste-biomass can be changed to yield.

Besides CO₂, combustible gases (CO, H₂, CH₄), tarry-vapors, volatile-oils and C-rich residue are referred as char [70]. It is considered to contain biomass-derived char projected specifically for addition in soil. Both biochar and char in general are mainly composed of stable aromatic forms of organic C compared to C in a pyrolysis feedstock which cannot readily be returned in the air as CO₂ even under favorable biological and environmental conditions [70]. The physiochemical properties of BC depend on the nature of waste material used and temperature of the pyrolysis [72,73]. Biochar application enhances soil pH, WHC, pore-spaces and organic C that facilitate the soil aggregation (Fig. 2) while decreases tensile strength and soil bulk density (BD) [74–76].

Low density and high porosity of BC comparative to soils usually aid in holding air and water. In that way the BD of soil is decreased [77]. Low BD and higher WHC of soil stimulate the growth of root and improve microbial activities in soil [78–79]. Some of important reported studies are listed in Tab. 5.

Table 5: Drought stress alleviation by application of various rate of biochar in cereals

Crop	Experimental condition	Application rate	References
Wheat	Pot study	0, 0.75 and 1.5%	[21]
Wheat	Field study	0, 1.5%	[53]
Maize	Pot experiment	0, 5, 10 and 20 t/ha	[80]
Rice	Pot experiment	2.5% (w/w)	[81]
Maize	Field study	0, 1, 2 and 5%	[82]
Maize	Field study	0, 12 t ha ⁻¹	[83]
Maize	Pot experiment	0 and 5%	[84]
Wheat	Pot experiment	0 and 5%	[85]
Maize	Greenhouse study	0, 1.5 and 3 % (w/w)	[86]
Wheat	Field study	0, 12 t ha ⁻¹	[87]
pseudo-cereal <i>Chenopodium quinoa</i>	Greenhouse study	0, 100 and 200 t ha ⁻¹	[88]

5 Combined Use of Biochar and ACC Deaminase Producing PGPR

Nowadays, scientists are focusing to improve the potential benefits of both PGPR and biochar. In that context, a significant improvement has been documented by many scientists [21,53]. In general, a large amount of carbon in biochar becomes unavailable for the microbes [89]. Solid evidence is available regarding potential benefits of biochar in the improvement of soil microbial biomass and activities [90–92]. For example, microbial growth and activities are significantly improved when C of biochar becomes available in soil after burning of trees [93]. In biochar-amended soils, sorption and succeeding inactivation of growth inhibiting matter by BC, control the abundance of soil biota [94]. It also strongly affects the soil microbial abundance and community as observed terra preta soils of Amazon that are rich in biochar [95–97]. Changes in microbial community and their activities in response to biochar addition, influence the nutrient cycles, crop growth, and soil organic matter decomposition [97].

Biochar enhanced the proliferation of some bacterial families i.e., Bradyrhizobiaceae and Thermomonosporaceae (8%), Streptosporangineae and Hyphomicrobiaceae (6% and 14%), either by progressing their abundance or decreasing the scale of loss. However, it suppressed the proliferation of Micromonosporaceae and Streptomycetaceae (–7% to –11%) [98]. Of these, Hyphomicrobiaceae and Bradyrhizobiaceae are linked with N cycling (NO₃ to N₂ denitrification), including 454 genera or species. Thus, PGPR involved in NH₄⁺ to nitrite (NO₂⁻) are low in abundant. Biochar also improved the growth of such PGPR that are capable of decreasing the N₂O flux [98]. Moreover, its application enhanced P solubilizing PGPR and improved C fluctuations by inspiring the proliferation of microbial families which has capability to decompose recalcitrant C [98].

6 Conclusion and Future Directions

Drought adversely affects the yield of cereal crops by disturbing different biochemical and physiological functions (conductance of stomata, photosynthetic rate, transpiration rate, dry weight of root and shoot, harvest index and root system) in plants. Over and imbalance production of multifunctional phytohormone, i.e., higher biosynthesis of ethylene under drought also restricts the growth of plants and causes senescence at seedling stage. Inoculation of ACC deaminase producing PGPR is well established and effective technique to mitigate drought stress in cereal crops. Such PGPR has potential to improve root growth by decreasing ethylene and secretion of growth hormones. Similarly, addition of biochar also has potential to alleviate drought stress in cereal crops. Biochar not only improves soil water holding capacity (WHC) but also improves other soil properties i.e., porosity, nutrients retention, soil C pool and microbial activity. So far, the positive effects of ACC deaminase producing PGPR and biochar have been observed by some scientists. However, more detailed experimentations are yet required to understand the complex synergistic mechanism of ACC deaminase activity with biochar to minimize the drought-induced stress in cereals.

Conflicts of Interest: The authors declare no conflicts of interests.

References

1. Sapre, S., Gontia-Mishra, I., Tiwari, S. (2019). ACC deaminase-producing bacteria: a key player in alleviating abiotic stresses in plants. *Plant Growth Promoting Rhizobacteria for Agricultural Sustainability*, pp. 267–291. Springer Singapore, Singapore.
2. Peters, G. P., Marland, G., Le Quéré, C., Boden, T., Canadell, J. G. et al. (2012). Rapid growth in CO₂ emissions after the 2008-2009 global financial crisis. *Nature Climate Change*, 2, 2–4.
3. Zandalinas, S. I., Mittler, R., Balfagón, D., Arbona, V., Gómez-Cadenas, A. (2018). Plant adaptations to the combination of drought and high temperatures. *Physiologia Plantarum*, 162(1), 2–12.
4. Mir, R. R., Zaman-Allah, M., Sreenivasulu, N., Trethowan, R., Varshney, R. K. (2012). Integrated genomics, physiology and breeding approaches for improving drought tolerance in crops. *Theoretical and Applied Genetics*, 125(4), 625–645.
5. Wilhite, D. (2000). *Drought: a global assessment*. D. A. Wilhite (Ed.), *drought as a natural hazard*, pp. 3–18. Routledge, London.
6. Wada, Y., Wisser, D., Eisner, S., Flörke, M., Gerten, D. et al. (2013). Multimodel projections and uncertainties of irrigation water demand under climate change. *Geophysical Research Letters*, 40, 4626–4632.
7. Alexandratos, N., Bruinsma, J. (2012). *World Agriculture Towards 2030/2050: the 2012 Revision*. ESA Working Paper. FAO.
8. Kaushal, M., Wani, S. P. (2016). Plant-growth-promoting rhizobacteria: drought stress alleviators to ameliorate crop production in drylands. *Annals of Microbiology*, 66, 35–42.
9. Bagheri, A. (2009). Effects of drought stress on chlorophyll, proline and rates of photosynthesis and respiration and activity of superoxide dismutase and peroxidase in millet (*Panicum milenaceum* L.). *National Conference on Water Scarcity and Drought Management in Agriculture*, 16.
10. Nezhadahmadi, A., Prodhon, Z. H., Faruq, G. (2014). Drought tolerance in wheat. *Cercet Agron Mold*, 4, 133–140.
11. Flexas, J., Ribas-Carbó, M., Diaz-Espejo, A., Galmés, J., Medrano, H. (2008). Mesophyll conductance to CO₂: current knowledge and future prospects. *Plant, Cell & Environment*, 31, 602–621.
12. Farooq, M., Hussain, M., Siddique, K. H. M. (2014). Drought stress in wheat during flowering and grain-filling periods. *Critical Reviews in Plant Sciences*, 33, 331–349.
13. Hussain, M., Farooq, S., Hasan, W., Ul-Allah, S., Tanveer, M. et al. (2018). Drought stress in sunflower: physiological effects and its management through breeding and agronomic alternatives. *Agricultural Water Management*, 201, 152–167.
14. Smirnov, N. (1993). The role of Reactive Oxygen in the response of plants to water deficit and desiccation. *New Phytologist*, 125, 27–30.

15. Hendry, G. A. (2005). Oxygen free radical process and seed longevity. *Seed Science Research*, 3, 141–147.
16. Fridovich, Lu., Rao, S. (2000). Oxygen radicals, hydrogen peroxide and oxygen toxicity. *Free Radical in Biology*, 1, 239–277.
17. Srivalli, B., Chinnusami, V., Renu, K. C. (2003). Antioxidant defense in response to abiotic stresses in plants. *Journal of Plant Biology*, 30, 121–139.
18. Daryanto, S., Wang, L., Jacinthe, P. A. (2016). Global synthesis of drought effects on maize and wheat production. *PLoS One*, 11, e0156362. Vidoz, M. L., Loreti, E., Mensuali, A., Alpi, A., Perata, P. (2010). Hormonal interplay during adventitious root formation in flooded tomato plants. *Plant Journal*, 63, 551–562.
19. Matiu, M., Ankerst, D. P., Menzel, A. (2017). Interactions between temperature and drought in global and regional crop yield variability during 1961–2014. *PLoS One*, 12, e0178339.
20. Daryanto, S., Wang, L., Jacinthe, P. A. (2017). Global synthesis of drought effects on cereal, legume, tuber and root crops production: a review. *Agricultural Water Management*, 179, 18–33.
21. Danish, S., Zafar-ul-Hye, M., Hussain, M., Shaaban, M., Núñez-delgado, A. (2019). Rhizobacteria with ACC-deaminase activity improve nutrient uptake, Chlorophyll contents and early seedling growth of wheat under PEG- induced osmotic stress. *International Journal of Agriculture and Biology*, 21, 1212–1220.
22. Carrijo, D. R., Lundy, M. E., Linqvist, B. A. (2017). Rice yields and water use under alternate wetting and drying irrigation: a meta-analysis. *Field Crops Research*, 203, 173–180.
23. Zhao, J., Xue, Q., Jessup, K. E., Hao, B., Hou, X. et al. (2018). Yield and water use of drought-tolerant maize hybrids in a semiarid environment. *Field Crops Research*, 216, 1–9.
24. Na, M., Fu, C., Yushu, Z., Ruipeng, J., Shujie, Z. et al. (2018). Differential responses of maize yield to drought at vegetative and reproductive stages. *Plant, Soil and Environment*, 64, 260–267.
25. Beltrano, J., Ronco, M. G., Montaldi, E. R. (1999). Drought stress syndrome in wheat is provoked by ethylene evolution imbalance and reversed by rewatering, aminoethoxyvinylglycine, or sodium benzoate. *Journal of Plant Growth Regulation*, 18, 59–64.
26. Danish, S., Zafar-ul-Hye, M. (2019). Co-application of ACC-deaminase producing PGPR and timber-waste biochar improves pigments formation, growth and yield of wheat under drought stress. *Scientific Reports*, 9, 5999.
27. Dong, B., Zheng, X., Liu, H., Able, J. A., Yang, H. et al. (2017). Effects of drought stress on pollen sterility, grain yield, abscisic acid and protective enzymes in two winter wheat cultivars. *Frontiers in Plant Science*, 8, 1008.
28. Lalonde, S., Beebe, D. U., Saini, H. S. (1997). Early signs of disruption of wheat anther development associated with the induction of male sterility by meiotic-stage water deficit. *Sexual Plant Reproduction*, 10, 40–48.
29. Dolferus, R., Ji, X., Richards, R. A. (2011). Abiotic stress and control of grain number in cereals. *Plant Science*, 181, 331–341.
30. Onyemaobi, I., Liu, H., Siddique, K. H. M., Yan, G. (2017). Both male and female malfunction contributes to yield reduction under water stress during meiosis in bread wheat. *Frontiers in Plant Science*, 7.
31. Cechin, I., Cardoso, G. S., de Fátima Fumis, T., Corniani, N. (2015). Nitric oxide reduces oxidative damage induced by water stress in sunflower plants. *Bragantia*, 74, 200–206.
32. Yin, C. C., Zhao, H., Ma, B., Chen, S. Y., Zhang, J. S. (2017). Diverse roles of ethylene in regulating agronomic traits in rice. *Frontiers in Plant Science*, 8, 1676.
33. Naik, P. K., Mohapatra, P. K. (2000). Ethylene inhibitors enhanced sucrose synthase activity and promoted grain filling of basal rice kernels. *Australian Journal of Plant Physiology*, 27, 997–1008.
34. Achakzai, A. K. K. (2009). Effect of water stress on imbibition, germination and seedling growth of maize cultivars. *Sarhad Journal of Agriculture*, 25, 165–172.
35. Gharoobi, B., Ghorbani, M., Nezhad, M. G. (2012). Effects of different levels of osmotic potential on germination percentage and germination rate of barley, corn and canola. *Iranian Journal of Plant Physiology*, 2, 413–417.
36. Khodarahmpour, Z. (2011). Effect of drought stress induced by polyethylene glycol (PEG) on germination indices in corn (*Zea mays* L.) hybrids. *African Journal of Biotechnology*, 10, 18222–18227.
37. Wilkinson, S., Davies, W. J. (2010). Drought, ozone, ABA and ethylene: new insights from cell to plant to

- community. *Plant, Cell & Environment*, 33, 510–525.
38. Iqbal, N., Nazar, R., Syeed, S., Masood, A., Khan, N. A. (2011). Exogenously-sourced ethylene increases stomatal conductance, photosynthesis, and growth under optimal and deficient nitrogen fertilization in mustard. *Journal of Experimental Botany*, 62, 4955–4963.
 39. Vidoz, M. L., Loreti, E., Mensuali, A., Alpi, A., Perata, P. (2010). Hormonal interplay during adventitious root formation in flooded tomato plants. *Plant Journal*, 63, 551–562.
 40. Müller, R., Stummann, B. M. (2003). *Ethylene. Encyclopedia of Rose Science*. Elsevier Science Publishers.
 41. Bharti, N., Pandey, S. S., Barnawal, D., Patel, V. K., Kalra, A. (2016). Plant growth promoting rhizobacteria *Dietzia natronolimnaea* modulates the expression of stress responsive genes providing protection of wheat from salinity stress. *Scientific Reports*, 6, 34768.
 42. Apelbaum, A., Yang, S. F. (1981). Biosynthesis of stress ethylene induced by water deficit. *Plant Physiology*, 68, 594–596.
 43. Narayana, I., Lalonde, S., Saini, H. S. (1991). Water-stress-induced ethylene production in wheat: a fact or artifact? *Plant Physiology*, 96, 406–410.
 44. Li, G., Xu, W., Kronzucker, H. J., Shi, W. (2015). Ethylene is critical to the maintenance of primary root growth and Fe homeostasis under Fe stress in *Arabidopsis*. *Journal of Experimental Botany*, 66, 2041–2054.
 45. Valluru, R., Davies, W. J., Reynolds, M. P., Dodd, I. C. (2016). Foliar abscisic acid-to-ethylene accumulation and response regulate shoot growth sensitivity to mild drought in wheat. *Frontiers in Plant Science*, 7, 461.
 46. Zhang, S., Gan, Y., Xu, B. (2019). Mechanisms of the IAA and ACC-deaminase producing strain of *Trichoderma longibrachiatum* T6 in enhancing wheat seedling tolerance to NaCl stress. *BMC Plant Biology*, 19, 22.
 47. Berg, G. (2009). Plant-microbe interactions promoting plant growth and health: perspectives for controlled use of microorganisms in agriculture. *Applied Microbiology and Biotechnology*, 84, 11–18.
 48. Schmidt, R., Köberl, M., Mostafa, A., Ramadan, E. M., Monschein, M. et al. (2014). Effects of bacterial inoculants on the indigenous microbiome and secondary metabolites of chamomile plants. *Frontiers in Microbiology*, 5, 64.
 49. Gontia-Mishra, I., Sapre, S., Kachare, S., Tiwari, S. (2017). Molecular diversity of 1-aminocyclopropane-1-carboxylate (ACC) deaminase producing PGPR from wheat (*Triticum aestivum* L.) rhizosphere. *Plant Soil*, 414, 213–227.
 50. Kang, B. G., Kim, W. T., Yun, H. S., Chang, S. C. (2010). Use of plant growth-promoting rhizobacteria to control stress responses of plant roots. *Plant Biotechnology Reports*, 4, 179–183.
 51. Tiwari, S., Lata, C., Chauhan, P. S., Nautiyal, C. S. (2016). *Pseudomonas putida* attunes morphophysiological, biochemical and molecular responses in *Cicer arietinum* L. during drought stress and recovery. *Plant Physiology and Biochemistry*, 99, 108–117.
 52. Armada, E., Probanza, A., Roldán, A., Azcón, R. (2016). Native plant growth promoting bacteria *Bacillus thuringiensis* and mixed or individual mycorrhizal species improved drought tolerance and oxidative metabolism in *Lavandula dentata* plants. *Journal of Plant Physiology*, 192, 1–12.
 53. Zafar-ul-Hye, M., Danish, S., Abbas, M., Ahmad, M., Munir, T. M. (2019). ACC deaminase producing PGPR *Bacillus amyloliquefaciens* and *agrobacterium fabrum* along with biochar improve wheat productivity under drought stress. *Agronomy*, 9, 343.
 54. Chandra, D., Srivastava, R., Gupta, V. V. S. R., Franco, C. M. M., Sharma, A. K. (2019). Evaluation of ACC-deaminase-producing rhizobacteria to alleviate water-stress impacts in wheat (*Triticum aestivum* L.) plants. *Canadian Journal of Microbiology*, 65, 387–403.
 55. Zhang, G., Sun, Y., Sheng, H., Li, H., Liu, X. (2018). Effects of the inoculations using bacteria producing ACC deaminase on ethylene metabolism and growth of wheat grown under different soil water contents. *Plant Physiology*, 125, 178–184.
 56. Danish, S., Zafar-ul-Hye, M., Hussain, S., Riaz, M., Qayyum, M. F. (2020). Mitigation of drought stress in maize through inoculation with drought tolerant ACC deaminase containing PGPR under axenic conditions. *Pakistan Journal of Botany*, 52(1), 1–12.
 57. Tahir, M., Khalid, U., Khan, M. B., Shahid, M., Ahmad, I. et al. (2019). Auxin and 1-Aminocyclopropane-1-carboxylate deaminase activity exhibiting rhizobacteria improved maize quality and productivity under drought

- conditions. *International Journal of Agriculture and Biology*, 21, 943–954.
58. Li, H., Zhao, Y., Jiang, X., Li, H., Zhao, Y. et al. (2019). Seed soaking with *Bacillus* sp. strain HX-2 alleviates negative effects of drought stress on maize seedlings. *Chilean Journal of Agricultural Research*, 79, 396–404.
 59. Cruz, J. A., Bautista, J. M. R., Ordonio, R. L., Paterno, E. S. (2018). Enhancement of rice seedling growth with rhizobacteria inoculation in response to polyethylene glycol (PEG)-induced drought. *Mindanao Journal of Science and Technology*, 16(1).
 60. Liu, H. Y., Yu, X., Cui, D. Y., Sun, M. H., Sun, W. N. et al. (2007). The role of water channel proteins and nitric oxide signaling in rice seed germination. *Cell Research*, 17, 638–649.
 61. Schachtman, D. P., Goodger, J. Q. D. (2008). Chemical root to shoot signaling under drought. *Trends in Plant Science*, 13(6), 281–287.
 62. Sharipova, G. V., Veselov, D. S., Kudoyarova, G. R., Timergalin, M. D., Wilkinson, S. (2012). Effect of ethylene perception inhibitor on growth, water relations, and abscisic acid content in wheat plants under water deficit. *Russian Journal of Plant Physiology*, 59, 573–580.
 63. Justin, S., Armstrong, W. (1991). Evidence for the involvement of ethene in aerenchyma formation in adventitious roots of rice (*Oryza sativa* L.). *New Phytologist*, 118, 49–62.
 64. Lehmann, J., Gaunt, J., Rondon, M. (2006). Bio-char sequestration in terrestrial ecosystems-a review. *Mitigation and Adaptation Strategies for Global Change*, 11, 395–419.
 65. Spokas, K. A. (2010). Review of the stability of biochar in soils: predictability of O:C molar ratios. *Carbon Management*, 1, 289–303.
 66. IPCC (2007). *Climate change 2007: the physical science basis*. Cambridge University Press, Cambridge.
 67. Stavi, I., Lal, R. (2013). Agroforestry and biochar to offset climate change: a review. *Agronomy for Sustainable Development*, 33, 81–96.
 68. Pratt, K., Moran, D. (2010). Evaluating the cost-effectiveness of global biochar mitigation potential. *Biomass and Bioenergy*, 34, 1149–1158.
 69. Spokas, K. A., Koskinen, W. C., Baker, J. M., Reicosky, D. C. (2009). Impacts of woodchip biochar additions on greenhouse gas production and sorption/degradation of two herbicides in a Minnesota soil. *Chemosphere*, 77, 574–581.
 70. Sohi, S. P., Krull, E., Bol, R. (2010). A review of biochar and its use and function in soil. *Advances in Agronomy*, 105, 47–82.
 71. Laird, D. A., Brown, R. C., Amonette, J. E., Lehmann, J. (2009). Review of the pyrolysis platform for coproducing bio-oil and biochar. *Biofuels, Bioproducts and Biorefining*, 3, 547–562.
 72. Glaser, B., Lehmann, J., Zech, W. (2002). Ameliorating physical and chemical properties of highly weathered soils in the tropics with charcoal-a review. *Biology and Fertility of Soils*, 35, 219–230.
 73. Navia, R., Crowley, D. E. (2010). Closing the loop on organic waste management: biochar for agricultural land application and climate change mitigation. *Waste Management & Research*, 28, 479–480.
 74. Abel, S., Peters, A., Trinks, S., Schonsky, H., Facklam, M. et al. (2013). Impact of biochar and hydrochar addition on water retention and water repellency of sandy soil. *Geoderma*, 202–203, 183–191.
 75. Cao, X., Ma, L., Gao, B., Harris, W. (2009). Dairy-manure derived biochar effectively sorbs lead and atrazine. *Environmental Science & Technology*, 43, 3285–3291.
 76. Liu, C., Wang, H., Tang, X., Guan, Z., Reid, B. J. et al. (2016). Biochar increased water holding capacity but accelerated organic carbon leaching from a sloping farmland soil in China. *Environmental Science and Pollution Research*, 23, 995–1006.
 77. Downie, A., Crosky, A., Munroe, P., Crosky, A., Munroe, P. (2012). Physical properties of biochar. In: Lehmann, J., Joseph, S. (Eds.), *Biochar for Environmental Management: Science and Technology*, pp. 13–32. Routledge, Earthscan, London.
 78. Major, J., Lehmann, J., Rondon, M., Goodale, C. (2010). Fate of soil-applied black carbon: downward migration, leaching and soil respiration. *Global Change Biology*, 16, 1366–1379.
 79. Zhang, A., Cui, L., Pan, G., Li, L., Hussain, Q. et al. (2010). Effect of biochar amendment on yield and methane and nitrous oxide emissions from a rice paddy from Tai Lake plain, China. *Agriculture, Ecosystems &*

Environment, 139, 469–475.

80. Shashi, M., Mannan, M., Islam, M., Rahman, M. (2018). Impact of rice husk biochar on growth, water relations and yield of maize (*Zea mays* L.) under drought condition. *Agriculturists*, 16, 93–101.
81. Nguyen, B. T., Trinh, N. N., Le, C. M. T., Nguyen, T. T., Tran, T. V. et al. (2018). The interactive effects of biochar and cow manure on rice growth and selected properties of salt-affected soil. *Archives of Agronomy and Soil Science*, 64, 1744–1758.
82. Kim, H. S., Kim, K. R., Yang, J. E., Ok, Y. S., Owens, G. et al. (2016). Effect of biochar on reclaimed tidal land soil properties and maize (*Zea mays* L.) response. *Chemosphere*, 142, 153–159.
83. Lashari, M. S., Ye, Y., Ji, H., Li, L., Kibue, G. W. et al. (2015). Biochar-manure compost in conjunction with pyrolytic solution alleviated salt stress and improved leaf bioactivity of maize in a saline soil from central China: a 2-year field experiment. *Journal of the Science of Food and Agriculture*, 95, 1321–1327.
84. Akhtar, S. S., Andersen, M. N., Naveed, M., Zahir, Z. A., Liu, F. (2015a). Interactive effect of biochar and plant growth-promoting bacterial endophytes on ameliorating salinity stress in maize. *Functional Plant Biology*, 42, 770–781.
85. Akhtar, S. S., Andersen, M. N., Liu, F. (2015b). Residual effects of biochar on improving growth, physiology and yield of wheat under salt stress. *Agricultural Water Management*, 158, 61–68.
86. Haider, G., Koyro, H. W., Azam, F., Steffens, D., Müller, C. et al. (2015). Biochar but not humic acid product amendment affected maize yields via improving plant-soil moisture relations. *Plant Soil*, 395, 141–157.
87. Lashari, M. S., Liu, Y., Li, L., Pan, W., Fu, J. et al. (2013). Effects of amendment of biochar-manure compost in conjunction with pyrolytic solution on soil quality and wheat yield of a salt-stressed cropland from Central China Great Plain. *Field Crop Research*, 144, 113–118.
88. Kamman, C. I., Linsel, S., Göbbling, J. W., Koyro, H. W. (2011). Influence of biochar on drought tolerance of *Chenopodium quinoa* willd and on soil-plant relations. *Plant Soil*, 345, 195–210.
89. Thies, J., Rillig, M. C. (2009). Characteristics of biochar: biological properties. *Biochar for Environmental Management: Science and Technology*. Earthscan, London.
90. Joseph, S., Anwar, H. M., Storer, P., Blackwell, P., Chia, C. et al. (2015). Effects of enriched biochars containing magnetic iron nanoparticles on mycorrhizal colonisation, plant growth, nutrient uptake and soil quality improvement. *Pedosphere*, 25, 749–760.
91. O'Neill, B., Grossman, J., Tsai, M. T., Gomes, J. E., Lehmann, J. et al. (2009). Bacterial community composition in Brazilian Anthrosols and adjacent soils characterized using culturing and molecular identification. *Microbial Ecology*, 58, 23–35.
92. Rondon, M. A., Lehmann, J., Ramirez, J., Hurtado, M. (2007). Biological nitrogen fixation by common beans (*Phaseolus vulgaris* L.) increases with bio-char additions. *Biology and Fertility of Soils*, 43, 699–708.
93. Kolb, S. E., Fermanich, K. J., Dornbush, M. E. (2009). Effect of charcoal quantity on microbial biomass and activity in temperate soils. *Soil Science Society of America Journal*, 73, 1173–1181.
94. Lehmann, J., Rillig, M. C., Thies, J., Masiello, C. A., Hockaday, W. C. et al. (2011). Biochar effects on soil biota-A review. *Soil Biology and Biochemistry*, 43, 1812–1836.
95. Grossman, J. M., O'Neill, B. E., Tsai, S. M., Liang, B., Neves, E. et al. (2010). Amazonian anthrosols support similar microbial communities that differ distinctly from those extant in adjacent, unmodified soils of the same mineralogy. *Microbial Ecology*, 60, 192–205.
96. Kim, J. S., Sparovek, G., Longo, R. M., De Melo, W. J., Crowley, D. (2007). Bacterial diversity of terra preta and pristine forest soil from the Western Amazon. *Soil Biology and Biochemistry*, 39, 648–690.
97. Liang, B., Lehmann, J., Sohi, S. P., Thies, J. E., O'Neill, B. et al. (2010). Black carbon affects the cycling of non-black carbon in soil. *Organic Geochemistry*, 41, 206–213.
98. Anderson, C. R., Condon, L. M., Clough, T. J., Fiers, M., Stewart, A. et al. (2011). Biochar induced soil microbial community change: implications for biogeochemical cycling of carbon, nitrogen and phosphorus. *Pedobiologia (Jena)*, 54, 309–320.