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UNRAVELING THE POTENTIAL OF ACC DEAMINASE-PRODUCING MICROBES IN VARIOUS AGRICULTURAL STRESSES: CURRENT STATUS, LIMITATIONS, AND RECOMMENDATIONS

SITI HALIMAH LAREKENG[1*], NGADIMAN[2], YENI KHAIRINA[3],
RUMELLA SIMARMATA[3] AND MARGARETTA CHRISTITA[3]

[1]Faculty of forestry, Hasanuddin University, Jl. Perintis Kemerdekaan KM 10, Makassar 90245, Indonesia
[2]Departement of Agricultural Microbiology, Universitas Gadjah Mada, Jl. Flora, Bulaksumur, Yogyakarta, Indonesia
[3]Research Center for Applied Microbiology, National Research and Innovation Agency, Jl. Raya Jakarta-Bogor Km 46, Cibinong 16911, Indonesia
**Corresponding author's email: sittihalimah@unhas.ac.id*

Abstract

More than 50% of the main crops in the world are lost to agricultural stressors, either biotic or abiotic. It has been demonstrated that using chemical approaches to boost plant yield causes other serious problems, including a decline in soil fertility and significant health problems. While advanced plant biotechnology techniques, like genetic modification, still faces ethical questions, unpredictable environmental risks, challenges in their usability and commercial viability, as well as high labour and costs. Using plant-associated microbes with 1-aminocyclopropane-1-carboxylate deaminase (ACCD) activity can be a solution to speed up plant production upon environmental stresses. They offer stress-protective responses by reducing the production of the plant stress hormone ethylene to a level that is not detrimental to plants. Furthermore, adopting ACCD-producing microbes with additional supporting traits or mixing them with other beneficial microbes in a consortium can be a promising strategy to sustain their effectiveness in practical use. This paper reviews the current research on the role of ACCD-producing microbes in increasing plant productivity under various stresses, along with their limitations and recommendations for field application.

Key words: ACCD-producing microbes, Salinity, Drought, Waterlogging, Pathogen.

Introduction

Due to their immobility, plants are vulnerable to various biotic or abiotic stresses, including phytopathogen or pest attack, heat, drought, waterlogging, salt, cold, nutritional deficiencies, heavy metals, etc. (Maxton *et al.*, 2018; Singh *et al.*, 2022b). Over 50% of the main crops are lost due to those accumulated stressors (Oshunsanya *et al.*, 2019; Singh *et al.*, 2022b). Along with that issue, it has also become difficult to satisfy the food demand because of the continuous growth in the global population (*In Brief to The State of Food Security and Nutrition in the World 2022*, 2022). While the extension of agricultural land to boost plant productivity is almost impossible because of the growth of industrialization, urbanization, degraded lands, and limited water sources (Wang *et al.*, 2022). Soil salinity, drought, and waterlogging are the most problematic abiotic stresses for food and agricultural production; in response to those stresses, ethylene production in the plant increases (Shabbir *et al.*, 2022). The excessive production of ethylene leads to the change in plant physiology and molecular biology, including disturbance in enzyme activity, stomatal closure, and low photosynthetic rate, which slow down the plant's growth and development (Dubois *et al.*, 2018; Kumar *et al.*, 2018). Similar to abiotic stresses, the growth of plants is directly hampered when exposed to biotic stressors. Pathogen and pest attacks could reduce crop yields by 10% to 40%. They are commonly eliminated using agrochemicals resulting in a decline in soil quality and nutrient content, polluting nearby water bodies, and negatively impacting the growth of various beneficial organisms in the soil (Ali & Kim, 2018; Chaudhary *et al.*, 2023).

Nowadays, biotechnological approaches are receiving much attention in response to reducing the use of synthetic fertilizers or pesticides. Those approaches include simple classical breeding of superior plant varieties, genetic engineering, protoplast fusion, *In vitro* selection techniques, etc., (Kumar *et al.*, 2018; Munaweera *et al.*, 2022). Classical breeding offers a cheap and simple method. However, it takes more time to produce hybrids with desirable features. In contrast, other strategies may provide a more effective and rapid result, but the work requires high labour and cost (Table S1). Genetic modification is one common strategy used in plant engineering to make the plant more resistant to environmental stresses. Even though creating transgenic plants is a potential solution, several ethical concerns, environmental risks, field usability, commercial acceptability, and production time constraints limit their use (Rodríguez *et al.*, 2022). Countries cultivating transgenic plants have also been heavily criticized for using large amounts of pesticides and destroying the rainforest to grow even more crops. In addition, there are indications that transgenic plants can cause the extensive spread of pest insects (Bello *et al.*, 2021). Proper integration, reproducible expression, and predictable transmission of the introduced transgene over successive generations are also crucial for harnessing the benefits of this technology in agriculture. Improper management of transgenic plants could result in inactivation, undesired expression, or failure transmission to the successive generation. Plant-associated microbes, such as endophytic and phyllosphere microbes, or rhizobacteria equipped with 1-aminocyclopropane-1-carboxylate deaminase (ACCD) activity, can be a solution to speed up plant production in agricultural stressors under the limitation of the plant genetic manipulation approach.

Supplementary data

Unraveling the potential of ACC deaminase-producing microbes in various agricultural stresses: current status, limitations, and recommendations

Table S1. Biotechnological approach to improving plant productivity in agricultural stresses.

No.	Biotechnology approaches	Description	Merit	Limitation	References
1.	Classical breeding	The development of new lines and varieties by employing natural selection under the strict supervision of preselected animals or plants with desirable traits	No genetic changes or other forms of tampering that could potentially harm people, and the risk to the plant or animal is often very low	1. Producing hybrids combining favorable agronomically important from two species is challenging 2. A random process in which some characteristics emerge while others are lost 3. Relatively slow process	(Ishaku *et al.*, 2020; Xynias *et al.*, 2020)
2.	Marker-assisted breeding approach (MAS.	Marker-assisted breeding selects a plant or animal for presence in breeding early in its development using DNA markers associated with favourable characteristics	Significantly reducing the time required to identify since many crops are only visible when they reach flowering initiation or maturity	1. Expensive, labour-intensive, and uses a large amount of DNA 2. False positives could result from recombination between the marker and the target gene 3. Markers developed are specific and may be untransferable	(Ishaku *et al.*, 2020; Xynias *et al.*, 2020)
3.	Genetic manipulation/ engineering	A technique that entails inserting DNA into an organism's genome.	1. More gene-specific 2. Increasing genetic diversity and producing more variant alleles that could also be crossed over and implanted into other species	1. Pathogens adapt to the new genetic profiles 2. Unexpected negative side effects 3. Genetic engineering can change specific traits, which can create ethically questionable outcomes 4. Copyright technology is costly to use	(Ishaku *et al.*, 2020; Xynias *et al.*, 2020)
4.	Protoplast fusion	The technique of transferring the target gene from the donor plant to the target plant via protoplast fusion	1. Enabling the combining of two genomes and is used in crosses at the interspecific, intergeneric, and intraspecific level 2. Generating new strains with required properties and improving existing strains	1. After the isolation procedure, it tends to produce very few protoplasts 2. It cannot be used to isolate protoplast from meristematic or less vacuolated cells 3. The protoplast becomes extremely sensitive to osmotic stress during and after cell wall digestion	(Navrátilová, 2018; Ishaku *et al.*, 2020)
5.	*In vitro* selection technique (Tissue culture)	The *In vitro* tissue culture approach employs a selective medium containing selective agents to select and improve plants with specific features.	1. Offering the opportunity to regenerate and induce stress tolerance in plants using selective agents such as NaCl, polyethylene glycol or mannitol, etc, 2. Many plants can be produced in a short period, including a plant that propagated using the tissue culture technique	1. It is an expensive technique (well-qualified staff and state-of the-art equipment are required) 2. It must be performed in sterile conditions; otherwise, the whole stock can be contaminated. 3. Propagated plants may be more susceptible to diseases	(Babiye *et al.*, 2020; Ishaku *et al.*, 2020)

ACCD-producing microbes offer stress-protective responses to reduce agricultural stressors that hamper the productivity of plants (Kumar *et al*., 2020). Some may also be coupled with additional plant-growth properties, such as the ability to produce phytohormones, siderophores, and exopolysaccharides, fix nitrogen, or solubilize phosphate and therefore boost plant growth even more (Ferreira *et al*., 2019; Li *et al*., 2022). Furthermore, by metabolizing ACC as the ethylene precursor, ACCD-producing microbes reduce the elevated ethylene to its ideal level under biotic and abiotic stress circumstances (Singh *et al*., 2022). As a result, microbial strains that have ACCD activity are crucial for minimizing the negative impacts of agricultural stresses. This review presents current studies on the activity of ACCD-producing microbes to promote plant productivity under various agricultural challenges. Besides, the limitation and recommendations regarding ACCD-producing microbes' application are also addressed.

An overview of ACCD-producing microbes: Applying plant growth-promoting microbes (PGPM) that enhance plant yield can be one alternative to advance sustainable agriculture. The term "PGPM" refers to a class of helpful microbes, including endophytes, free-living microbes, and those with a symbiotic relationship with plants. They have been proven in several studies to be the most superior and environment-friendly alternative to agrochemicals and other conventional agricultural practices for enhancing plant growth and stress resistance (Gupta & Pandey, 2019; Singh *et al*., 2022a). PGPM mainly support plant growth directly by forming biofilms, producing extracellular polymeric substances (EPS), fixing nitrogen, producing phytohormones and siderophores, and performing ACCD activity, or indirectly through the reduction of a plant pathogen. Thus, the enzyme 1-aminocyclopropane-1-carboxylate deaminase (ACCD) activity is one of the strategies used by PGPM to alleviate agricultural stress.

It has been reported that ACCD-producing microbes could lower down ethylene levels due to biotic or abiotic stress. All higher plants generate ethylene, which is referred to as a gaseous plant hormone (Tadiello *et al*., 2018). Less than 1 $mg \cdot L^{-1}$ of ethylene triggers a variety of reactions in plants, such as the promotion of seed germination, generation of leaf and root primordia, the development of adventitious roots and root hairs, and other impacts on plant growth and development (Singh *et al*., 2015). However, in highly stressful situations, the ethylene level might increase to a harmful level of 25 $g \cdot L^{-1}$, which has adverse effects such as promotion of leaf senescence and epinasty, thereby causing leaves to abscise and lose their chlorophyll pigments (Singh *et al*., 2015). In plants, forming *S*-adenosyl-methionine (SAM) from the substrate methionine and ATP is the first step in ethylene synthesis. Then the enzyme ACC-synthase transforms SAM into ACC. Finally, the generated ACC is oxidized by ACC oxidase to ethylene and other volatile substances, including carbon dioxide and hydrogen cyanide. ACCD-producing microbes reduce ACC levels by using ACC deaminase to cleave ACC into ammonia and α-ketobutyrate. The decrease of ACC in the plant will improve plant growth and decrease stress levels induced by ethylene (Yim *et al*., 2010) Furthermore, α-ketobutyrate and ammonia, due to ACC breakdown, can provide additional sources of carbon and nitrogen for plants and other microbes.

Some studies have reported that *acdS* gene is an important for ACCD expression in several microbes (Gao *et al*., 2020; Glick & Nascimento, 2021). ACCD structural gene (*AcdS*) is present in the genomes of rhizosphere bacteria, symbiotic rhizobia, and bacterial endophytes. Depending on the quantity of substrate, oxygen existence, and product accumulation, *acdS* can be regulated and expressed differently. In *Pseudomonas putida* UW4, for example, the regulation for *acdS* gene expression is made through LRP coupled with CRP and FNR (Fig. 1a) (Shahid *et al*., 2023). There are numerous regulatory elements upstream of *acdS* in that mechanism, such as *acdR* gene, which encodes LRP (leucine-responsive regulatory protein), *acdB* box, which encodes FNR box (fumarate-nitrate regulatory protein), and CRP box, which binds cAMP receptor protein (Ali & Glick, 2021; Bomle *et al*., 2021). When ACC is present, the *acdR* gene expression is promoted to activate the regulatory protein LRP to form LRP-octamer. LRP-octamer will then activate *acdB* for the formation of glycerophosphoryl diester phosphodiesterase. A tripartite regulatory complex is created when LRP binds to glycerophosphoryl diester phosphodiesterase and ACC. AcdS promoter region is then activated when the LRP-ACC-GDP complex binds to FNR box (in a low O_2 environment) or CRP box (in a high O_2 environment) (P2 or P3). Complex LRP-ACC-GDP then activates the *acdS* gene, causing the ACC molecule to break down into α-ketobutyrate and ammonia. Leucine, a branched-chain amino acid produced by the metabolism of α-ketobutyrate, binds to LRP octamer and breaks it apart into inactive dimers, inhibiting the *acdS* gene from being expressed (Bomle *et al*., 2021).

In nitrogen-fixing bacteria like *Rhizobia* and *Mesorhizobium*, the regulation mechanism of *acdS* is different. *NifA2* gene and the σ54 sigma factor control the expression of *acdS* gene in N-fixing bacteria (Moeller *et al*., 2021; Bomle *et al*., 2021). NifA2, a protein encoded by *nifA2*, interacts with RNA polymerase σ54 to promote *acdS* transcription (Fig. 1(b)). In other studies, the expression of *acdS* may be influenced by RNA Polymerase Sigma gene (*RpoS*) (Fig. 1(c)). In proteobacteria, the sigma factor rpoS is a crucial stress regulator in response to particular stress stimuli or the stationary phase of their growth. In a genetically altered strain of *Enterobacter cloacae* CAL2, *rpoS* gene over-expression led to a rise in ACC deaminase levels by 30% (Duca & Glick, 2020; Bomle *et al*., 2021). However, in *Pseudomonas* sp. UW4 was transformed with rpoS; the resultsshowed the opposite effect, where ACCD levels were 20% lower than those by the wild type (Zboralski & Filion, 2020; Bomle *et al*., 2021). Overall, further genetic and biochemical research is still required to fully comprehend the mechanisms governing ACCD regulation and activity in various bacterial species. Understanding the regulation mechanism of the ACCD genes would help maximize the utilization of ACCD bacteria to improve plant growth and development.

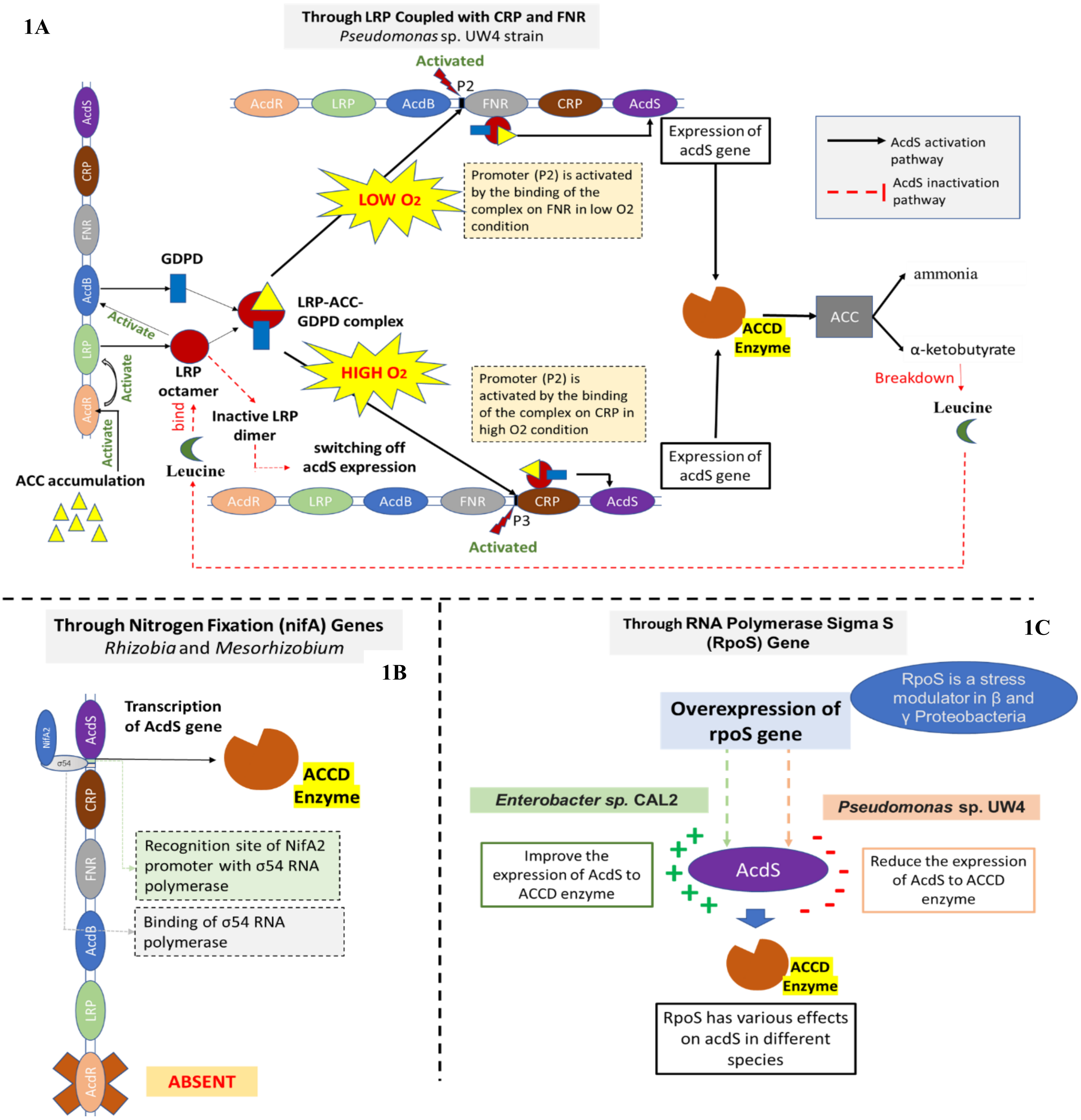

Fig. 1. Mechanism of acdS activation through 1(a) LRP coupled with CRP and FNR; 1(b) Nitrogen fixation (*NifA*) gene; 1(c) RNA polymerase sigma S (*RpoS*) gene. LRP = Leucine Responsive regulatory Protein; FNR = Fumarate nitrate reduction regulatory protein; CRP = Cyclic AMP receptor protein; GPDP = Glycerophosphoryl diester phosphodiesterase.

The role of ACCD-producing microbes in salinity stress: Salinity is a significant abiotic stress and a severe issue for agriculture, because it makes valuable lands less productive. High salinity has harmed plant health by increasing ethylene synthesis in the roots and cells, decreasing nutrients in the soil, increasing negative osmotic water pressure on plants, and disturbing nutrient absorption (Etesami & Noori, 2019). Saline conditions also harm the plant-associated microbiome (Abdul Rahman *et al*., 2021)). Reactive oxygen species (ROS) are produced in salinity stress, limiting the absorption of several micro- and macro-nutrients and resulting in an osmotic and ionic imbalance. Poor farming practices, pesticides, and irrigation with salt water have contributed to the expansion of all damaged areas (Dagar *et al*., 2019). In addition, salinity impacts physiological activities, including respiration, photosynthesis, nitrogen fixation, etc., which lower agricultural yield and plant productivity (Kirova & Kocheva, 2021; Jaiswal *et al*., 2021; Iqbal *et al*., 2020) In dry and semiarid locations, the issue of salinity in the soil is common. It worsens due to inefficient irrigation water use and the excessive use of chemical fertilizers (Pahalvi *et al*., 2021).

Many studies report that plants with ACCD-producing microbes have improved stress tolerance and growth promotion (Gamalero & Glick, 2022). Microbes that produce ACCD have recently emerged as a possible alternative to reduce salinity-induced plant stress (Venugopalan *et al*., 2023; Gupta *et al*., 2022). For instance, it has been discovered that inoculating canola and cucumber with *Pseudomonas putida* UW4 improves plant development in saline soil (Gamalero & Glick, 2022). Several studies have isolated and identified the ACCD-producing endophytic bacteria from the roots of *Theobroma cacao* L., *Solanum tubesorum* L., and *Oryza sativa*. It showed that those bacteria have the potential to promote the growth of soybean (*Glycine max* L.) under saline conditions. Therefore, they can potentially ameliorate the development of salt-stressed soybean (*Glycine max*. L.). Gupta & Pandey (2019) isolated ACCD-producing bacteria such as *Paenibacillus* sp. ACC06 and *Aneurinibacillus aneurinilyticus* ACC02; all enhanced *In vitro* stress resistance in response to NaCl (6%) and drought (-0.73 MPa). Some ACCD-producing microbes that have been isolated and tested on various plants during stress conditions are described in (Table S2).

Some microbes produce osmoprotective substances such as proline and trehalose, quaternary ammonium compounds in the cytoplasm, volatile organic molecules, exopolysaccharides, and ACC deaminase to reduce plant stress in a saline environment (Gowtham *et al*., 2022). Proline is an osmolyte; a bacterium may protect a plant from salinity or oxidative stress by increasing intrinsic proline levels. TSS (total soluble sugars) also functions as an osmoprotectant similar to proline. But, salinity stress can decrease TSS levels in plants. ACCD-producing microbes that can also increase TSS levels will be beneficial in reducing salinity stress in plants (Patel *et al*., 2023). ACC deaminase production by microbes is most likely an essential and efficient mechanism for manipulating the host cells. Therefore, a microbe's action for reducing salinity stress may involve several processes that work together to produce the desired outcome (Fig. 2).

The role of ACCD-producing microbes in drought stress: Water stress is one of the significant abiotic problems, and it is becoming a severe threat food security worldwide. Drought limits crop productivity and affects 1-3% of all lands (Camaille *et al*., 2021). Drought stress reduces photosynthesis, causes hormonal imbalances, and impairs mineral absorption, all of which contribute to lower plant yield (Rivas *et al*., 2016; Sharma, 2017; Batool *et al*., 2022). Plants must use sophisticated and complex mechanisms to survive in unfavorable water-deficit conditions to perceive the stress signal and maximize crop production (Camaille *et al*., 2021). Plant hormones are necessary for controlling responses to many environmental stimuli, including indirect and direct mechanisms. However, according to a recent study, plant hormone activation would be better if the presence of plant associated microbe induces it. Plant growth-promoting bacteria, including soil microbes, is an example of studying the mechanism of plant hormone activation against a stress. Soil microbes can reduce abiotic stress and stimulate plant growth, leading to sustainable agriculture (Vejan *et al*., 2016). Plant growth-promoting microbes use indoleacetic acid, abscisic acid, cytokinins, volatile organic compounds, ACC deaminase, and exopolysaccharides to mitigate the adverse effects of these stresses (Forni *et al*., 2017).

Water stress increases ethylene metabolic pathways, limiting root elongation and development (Fig. 2). The ability of many PGPR to control ethylene formation via the ACC deaminase enzyme is a crucial feature; thus, PGPR acts as an ACC sink (Saleem *et al*., 2018). Reducing ACC concentration in root tissues promotes plant growth by reducing endogenous ethylene formation. Several studies have reported that plant drought tolerance could be improved by lowering the inhibitory effect of ethylene on plant (Glick, 2014; Fadiji *et al*., 2022; Ma *et al*., 2023; Khan *et al*., 2023).

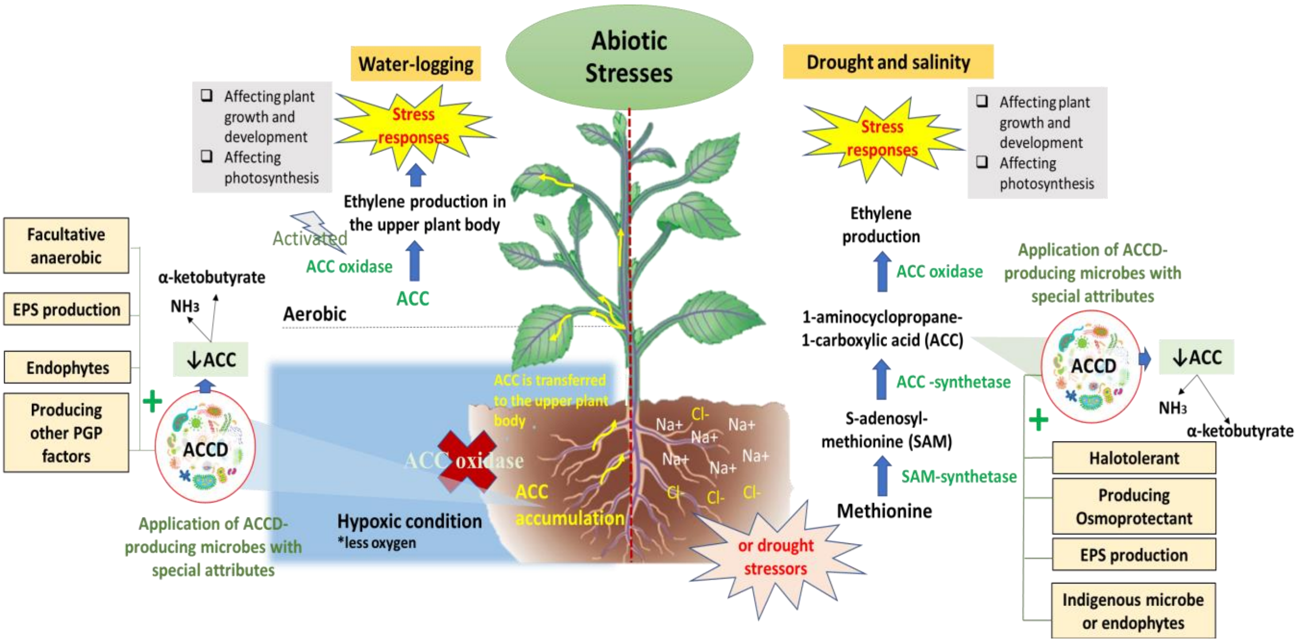

Fig. 2. Plant response in abiotic stresses and application of ACCD-producing microbes with additional potential traits.

Table S2. List of ACCD-producing microbes tested in various plants in stress conditions.

No.	Types of microbes	Microbial strain	PGPF (plant growth promoting factors)	Host plant	Stress type	Plant-growth support under stress	References
1.	**Bacteria**	*Methylobacterium oryzae* strain CBMB20	ACCD	*Oryza sativa* L.	Salt	Enhanced photosynthetic activity, antioxidant activity, and ethylene regulation proteins for reducing salt-induced apoptotic cell death and maintaining growth and development	(Roy Choudhury *et al.*, 2022)
2.		*Myroides* sp. strain JIL321	ACCD activity and IAA production	*Oryza sativa* L.	Salt	Increased chlorophyll content and accumulated osmotic adaptation substances such as proline and soluble sugars	(Wang *et al.*, 2000)
3.		*Stenotrophomonas maltophilia* strain Tetr 2	ACCD activity, IAA production, cell wall degrading enzymes, and antifungal	*Tetragonia tetragonioid*	Salt and pathogen	Stimulated plant root and shoot growth under NaCl conditions	(Egamberdieva *et al.*, 2022)
4.		*Kocuria arsenatis* strain ST19	ACCD activity	*Solanum esculentum* L. cv. Aïcha	Salt	Enhanced the plant growth, germination, biomass, and root and shoot length	(Dif *et al.*, 2021)
5.		*Bacillus paramycoides* strain C08	ACCD activity, IAA production, phosphate solubilization, siderophore production, and ammonia production	*Phaseolus vulgaris*	Salt	Improved chlorophyll concentration, relative water content, photosynthesis rate, and stomatal conductance	(Gupta & Pandey, 2020)
6.		*Serratia plymuthica*	ACCD activity, IAA production, phosphate solubilization, siderophore production, nitrogen fixation, EPS production	*Ziziphus jujuba*	Drought	Enhanced the plant height, root and shoot dry weight, and phosphorus and nitrogen level compared with the control	(Zhang et al., 2020b)
7.		*Achromobacter xylosoxidans*	ACCD activity, IAA production, phosphate solubilization, and potassium solubilization	*Zea mays* (cv. Kenzo-123 Hybrid)	Drought	Enhanced grain yield, photosynthetic rate, stomatal conductance, total chlorophyll, and carotenoid contents in maize	(Danish *et al.*, 2020)
8.		*Bacillus velezensis* strain D3	ACCD activity and EPS production	*Zea mays*	Drought	Enhanced plant physiological parameters such as photosynthesis rate, vapour pressure, stomatal conductance, transpiration rate, and water-use efficiency	(Nadeem *et al.*, 2021)
9.		*Pseudomonas* sp. strain S3	ACCD activity, IAA synthesis, phosphate solubilization, siderophore production, hydrocyanic acid (HCN) and ammonia production, and antagonism against *Rhizoctonia solani*.	*Solanum lycopersicum*	Salt and pathogen	Mitigated salinity stress and exhibited various plant growth-promoting characteristics	(Pandey & Gupta, 2020b)
10.		*Burkholderia* sp.	ACCD activity, phosphate solubilization, and phytase and phosphatase enzymes	*Oryza sativa* and *Glycine max*	Salt	Enhanced root, shoot, leaf, and nodule biomass of the tested plant	(Adhikari & Pandey, 2020)
11.		Consortia of *Aneurinibacillus aneurinilyticus* strain ACC02 and *Paenibacillus* sp. strain ACC06	ACCD activity, IAA production, phosphate solubilization, siderophore production, ammonia production, and Hydrogen cyanide production	*Phaseolus vulgaris*	Salt and drought	Increased fresh weight, dry weight, shoot biomass, and total chlorophyll	(Pandey & Gupta, 2020a)

Table S2. (Cont'd.).

No.	Types of microbes	Microbial strain	PGPF (plant growth promoting factors)	Host plant	Stress type	Plant-growth support under stress	References
12.		*Lysinibacillus fusiformis* strain A11	ACCD activity, IAA production, phosphate solubilization, siderophore production, ammonia production, and antifungal activity	*Triticum aestivum* var. KRL 215	Salt and pathogen	Increased seed germination and fresh and dry weight of root and shoot	(Damodaran *et al.*, 2019)
13.		*Klebsiella* sp. strain 8LJA	ACCD activity, IAA production, siderophore production	*Triticum aestivum* L.	Salt	Increased plant biomass and SOD activity in roots with and without salt stress	(Acuña *et al.*, 2019)
14.		*Bacillus* sp. strains (SR-2-1/1)	ACCD activity, IAA production, and phosphate solubilization	*Solanum tuberosum* L.	Salt	Increased auxin production in the rhizosphere of potato, which in turn regulated enzymatic antioxidant production and absorption of Na^+, K^+, and Ca^{2+}, led to higher tuber in both natural and saline soils	(Tahir *et al.*, 2019)
15.		*Cronobacter sakazakii* strain OF115	ACCD activity, IAA production, phosphate solubilization and ammonia production	*Triticum aestivum* L.	Salt	Improved all morphological and biochemical parameters of plant, including fresh and dry weight, root and shoot length, proline and chlorophyll content	(Afridi *et al.*, 2019)
16.		*Kocuria rhizophila* (14ASP)	ACCD, phosphate solubilization, IAA production, and ammonia production	*Triticum aestivum* L.	Salt	Improved plant growth and enhanced K^+/Na^+ ratio	(Afridi *et al.*, 2019)
17.		*Variovorax paradoxus* strain RAA3	ACCD activity, phosphate solubilization, siderophore production, and nitrogen fixation	*Triticum aestivum* L.	Waterlogging	Improved plant growth and nutrient uptake	(Chandra *et al.*, 2019)
18.		*Rhizobium legominozaroum* bv. R281Phaseoli	ACCD activity, IAA production, and phosphate solubilization	*Brassica napus* L.	Salt	Increased both plant growth and nutrients absorption	(Saghafi *et al.*, 2019)
19.		*Curtobacterium* sp. strain SAK1	ACCD activity, phytohormones production, antioxidants, and ACC deaminase enzyme.	*Glycine max* cv. Pungsannamul	Salt	Enhanced plant growth and produced different phytohormones and antioxidants	(Khan *et al.*, 2019)
20.		*Enterobacter cloacae*	ACCD activity, phosphate solubilization, siderophore production, and nitrogen fixation	*Musa* spp.	Pathogen	Stimulated growth parameters and prevented accelerated senescence	(Macedo-Raygoza *et al.*, 2019)
21.		*Bacillus megaterium* strain NMp082	ACCD activity, IAA production, and nitrogen fixation	*Medicago* spp.	Salt	Enhanced nodulation and plant biomass	(Chinnaswamy *et al.*, 2018)
22.		Consortium *Ochrobactrum pseudogrignonense* strain RJ12, *Pseudomonas* sp.RJ15 and *Bacillus subtilis* RJ46	ACCD activity	*Vigna mungo* L. *and Pisum sativum* L.	Drought	Increased seed germination percentage, root and shoot length, and dry weight.	(Saikia *et al.*, 2018)
23.		*Bacillus subtilis* strain BERA 71	ACCD activity	*Cicer arietinum* cv. Giza 1	Drought	Enhanced plant biomass and photosynthetic pigment and reduced the reactive oxygen species (ROS) level and lipid peroxidation in plants	(Abd-Allah *et al.*, 2018)
24.		*Bacillus licheniformis*	ACCD activity	*Panicum maximum*	Salt and drought	Increased shoot/root length and water content	(Gontia-Mishra *et al.*, 2014)
25.		*Bacillud cereus*	ACCD activity and IAA production	*Carthamus tinctorius*	Salt	increased plant growth and the ascorbate-glutathione redox cycle when compared to non-inoculated controls	(Hemida & Reyad, 2019)

Table S2. (Cont'd.).

No.	Types of microbes	Microbial strain	PGPF (plant growth promoting factors)	Host plant	Stress type	Plant-growth support under stress	References
26.		*Bulkhorderia cepacia*	ACCD activity and EPS production	*Capsicum annuum*	Drought and salt	Increased plant biomass	(Maxton *et al.*, 2018)
27.		*Enterobacter* sp. P23	ACCD activity, IAA production, phosphate solubilization, siderophore production, and HCN production.	*Triticum aestivum* L.	Salt	Increased germination and overall plant growth	(Sarkar *et al.*, 2018)
28.		*Pseudomonas* sp. RJ15	ACCD activity, IAA production, phosphate solubilization, siderophore production, and HCN production.	*Vigna mungo* L. *and Pisum sativum* L.	Drought	Increased activities of ROS scavenging enzymes, cellular osmolytes, chlorophyll and water content, and root recovery intension	(Saikia *et al.*, 2018)
29.		*Streptomyces* sp. strain GMKU 336	ACCD activity	*Oryza sativa* L. cv. KDML105	Salt	Increased salt tolerance of rice plants by reducing ethylene through the action of ACCD and assisting plants to scavenge ROS and balance ion composition and osmosis	(Jaemsaeng *et al.*, 2018)
30.		*Pseudomonas fluorescens* strain DPB15	ACCD activity and IAA production	*Triticum aestivum*	Drought	Promoted shoot and root biomass, plant height, and foliar nutrient levels than untreated plants and protected the plant from the oxidative damage	(Chandra *et al.*, 2018)
31.		*Pseudomonas veronii* strain KJ	ACCD activity	*Sesamum indicum* L.	Waterlogging	Reduced the negative effects of waterlogging on sesame and improved plant growth-promoting properties	(Ali *et al.*, 2018)
32.		*Pseudomonas* sp. strain OFT5	ACCD activity	*Solanum esculentum* L. *cv. Aïcha*	Salt	Enhanced salinity stress tolerance, influenced tomato plant growth, physiological condition, and ionic balance	(Win *et al.*, 2018)
33.		*Enterobacter* sp. strain EN-21	ACCD activity	*Saccharum officinarum* L.	Salt	Increased plant length, dry and fresh biomass, and chlorophyll content	(Kruasuwan & Thamchaipenet, 2018)
34.		*Streptomyces* sp. strain GMKU 336	ACCD activity, phosphate solubilization, and siderophore production	*Vigna radiata* (L.) Wilczek cv. CN72	Waterlogging	Increased root elongation, chlorophyll contents, and plant biomass	(Jaemsaeng *et al.*, 2018)
35.	**Yeast**	*Saccharomyces cerevisae*	ACCD activity	*Triticum aestivum*	Salinity	Reduced the effects of salinity on early seed germination	(Hussein *et al.*, 2022)
36.		*Yarrowia lipolytica*	ACCD activity.	*Triticum aestivum*	Salinity	Enhanced the plumule length and the radicle length	(Hussein *et al.*, 2022)
38.	**Fungal**	*Trichoderma asperellum* T203	ACCD activity, biocontrol	*Brassica napus*	Biotic, pathogen	Promoted root elongation and produced antimicrobial activity	(Viterbo *et al.*, 2010)
39.		*Trichoderma longibrachiatum* TL-6	ACCD activity	*Triticum aestivum*	Salt	Enhanced plant tolerance to salt stress	(Illescas *et al.*, 2021)
40.		*Trichoderma asperelloides*	ACCD activity	*Cucumis sativus*	water	Stimulated root elongation of cucumber	(Illescas *et al.*, 2021)
41.		*Trichoderma asperellum* MAP1	ACCD activity	*Canna indica* L	Waterlogging	Mitigated the adverse effect of water stress on wheat	Rauf *et al.*, 2021)

Several investigations have been conducted, mainly related to the role of ACCD-producing microbes in food crops (Patil *et al*., 2022; Shahid *et al*., 2023; Pandey *et al*., 2023; Choudhury *et al*., 2023). The addition of rhizobacteria *Pseudomonas* spp. containing ACCD to pea (*Pisum sativum* L.) plants have been shown to promote growth during pea disposal, yield production, and maturation in water shortage (Arshad *et al*., 2008). ACCD-producing and salt-tolerant *Streptomyces* can potentially prevent crop loss in tomato plants under drought conditions (Abbasi *et al*., 2020). *Bacillus thuringiensis* demonstrated significant improvements in root hair elongation of wheat plants through auxin and ACCD production, assisting in improved water and nutrient absorption (Sati *et al*., 2022). The activity of ACCD produced by the endophytic bacterial strain *Streptomyces* sp. induces tolerance in rice trough converting an ethylene precursor into ammonia and α-ketobutyrate, thereby lowering ethylene levels in plants. In addition to rhizobacteria, fungi are also microbes that produce ACCD and can positively influence plant growth (Tyśkiewicz *et al*., 2022). ACCD induced by *Trichoderma harzianum* positively affected maize seedling germination and growth (Zhang *et al*., 2020). Silencing the *Tas-AcdS* gene from *T. Asperellum* reduced the ability of canola plants to stimulate root elongation (Viterbo *et al*., 2010).

The role of ACCD-producing microbes in waterlogging stress: Waterlogging, which typically happens several times during the growing season, is one of the biggest obstacles in agriculture, leading to yield lost. The effects of global warmings, such as heavy rainfall and insufficient drainage and irrigation system, are some factors causing waterlogging. The oxygen diffusion into plant cells will be significantly lowered when plants are submerged in water because oxygen diffusion in water is 10,000 times slower than in air (Brazel *et al*., 2023). The roots of the plants immediately get hypoxic due to the soil's excess water and low oxygen level. In these situations, enzyme ACC synthase is generated, substantially increasing the amount of ACC in the roots. Since enzyme ACC oxidase cannot function in the anaerobic conditions of flooded roots, ACC builds up within the roots before being transferred to the shoots, where it is converted to ethylene (Ali & Kim, 2018). The ethylene buildup in plant tissues speeds up ROS production, inhibiting photochemical function. It also degrades macromolecules, ultimately resulting in cell death in the host plant (Fig. 2). Some of ACCD-producing microbes are facultative anaerobes, which may easily survive in environments with low oxygen levels, including in waterlogging (Simarmata *et al*., 2019; Saikia *et al*., 2023). The significant levels of ACC produced by the host plant in waterlogging stress can be utilized by ACC-producing microbes, which results in minimal ethylene synthesis inside plant tissues. According to some studies, ACC-producing microbes application promoted plant productivity in waterlogged conditions while reducing the levels of ethylene by 60–90% (Grichko & Glick, 2001; Ali & Kim, 2018).

The transcriptional control model of acdS gene regulates the activation of ACCD structural gene at lower oxygen levels (Glick *et al*., 2007). It has been shown that different bacterial strains with ACCD activity can effectively protect plants against waterlogging. The damaging effects of waterlogging on *Brassica napus* were mitigated by applying the bacterium *Pseudomonas putida* UW4 (Farwell *et al*., 2007), while the bacteria *Ochrobactrum rhizosphaerae, Serratia ureilytica,* and *Achromobacter xylosoxidans* elevated the impact of waterlogging on *Ocimum sanctum* plant (Barnawal *et al*., 2014). The use of endophytic bacteria *Streptomyces* sp. GMKU has also been reported to improve plant biomass, chlorophyll content, and adventitious roots and reduce the ethylene levels of mung bean under flooding conditions (Jaemsaeng *et al*., 2018). Even though it was initially isolated from the rice plant, it can also colonize mung beans. Endophytic bacteria may survive harsh environmental conditions inside the plant tissue while positively improving the plant host's growth. ACCD-producing microbes capable of synthesizing exopolysaccharides (EPS) could also be potential inoculants. EPS can help the microbes to withstand environmental stress and aggregate the microbes while maintaining stable attachment of microbes on plant surfaces (Naseem *et al*., 2018); Thus, the plant-microbe interaction could be enhanced.

The role of ACCD-producing microbe in biotic stress: Plant growth and development are frequently hampered by bacteria and fungi-causing diseases, which also cause the plant to produce stress ethylene (Fig. 3). The sustained damage of plant infections results from the plant's response to excess levels of ethylene. It was reported that the exogenous ethylene raised the prevalence of fungal infections, whereas the application of ethylene inhibitors lowered the occurrence of fungal infections (Marcos *et al*., 2005; Ha *et al*., 2021; Prusky & Romanazzi, 2023). The application of pesticides, fungicides, and agrochemicals is a common practice to prevent plant diseases caused by phytopathogen, resulting in the degradation of soil quality and decreased available nutrients. ACCD-producing microbes act as biocontrol agents to thwart pathogen attacks. They have proven to defend plants from various diseases, including *Fusarium* wilt, bacterial leaf blight, root rot, and leaf infection.

ACCD-producing microbes have been reported to suppress pathogens by either direct or indirect mechanisms, such as by the production of antimicrobial compounds, lytic enzymes, bacteriocins, and disruption of the pathogen quorum sensing, or by inducing the plant defence system and its signalling pathways, respectively (Saraf *et al*., 2010). The cucumber disease caused by *Pythium ultimum* was lessened by a *P. fluorescens* strain that had been genetically altered with *acdS* gene of *Pseudomonas putida* UW4 (Wang *et al*., 2000). The growth of mycelium of *Fusarium* sp. was highly inhibited by *P. fluorescens* possessing ACCD activity ((Donate-Correa *et al*., 2014). Another study demonstrated that plant disease caused by *Ralstonia solani* and *Ralstonia solanacearum* could be prevented by ACCD-producing bacteria (Rasche *et al*., 2006). In another experiment, ACCD gene was introduced into a biocontrol bacterial strain, *Pseudomonas putida* UW4, to compare the effects of transformed and untransformed bacteria on *Pythium ultimum* that cause disease in cucumbers (Wang *et al*., 2000). The results showed that biocontrol bacteria with transformed ACCD genes were more effective in combatting plant disease and stimulating plant growth. The root and fresh shoot weights were higher in the ACCD-transformed strain. Additionally, the soft rot disease of potato slices caused by the bacterial pathogen *Erwinia carotovora* subsp. *carotovora* was also dramatically reduced by ACCD-transformed strains. In that experiment, the production of

ACCD coupled with biocontrol traits prevents the production of stress ethylene and inhibits phytopathogens from the affected plants. These findings suggest that ACCD-producing microbes are essential in increasing disease resistance. Future study is still needed to fully comprehend the disease resistance capacity.

Challenges in the application of ACCD-producing microbes and recommendations: When growing in the natural environment, plants possess a specific system to adapt to agricultural stressors. However, excessive ethylene synthesis caused by continuing stress environments still decreases plant productivity. Global warming and climate change harm agricultural productivity, facing a continuing risk to food resilience worldwide. ACCD-producing microbes are important for improved stress resistance. Pesticides and synthetic fertilizers, which cause several side effects, are supposed to be substituted in the future by a more environment-friendly approach, such as the utilization of ACCD-producing microbes.

Despite successful experiments in laboratory and greenhouse settings on the application of ACCD-producing microbes, there has been a reluctance to use these microbes on a large field scale. One of the critical problems of applying ACCD-producing microbes as bioinoculants is their lower environmental viability and unstable ACCD activity. Only a few studies have used ACCD-producing microbes for stress reduction in certain crops in field settings (Nadeem *et al*., 2009; Kiani *et al*., 2016). Under laboratory conditions, ACCD-producing microbes can encounter similar environmental stress. However, the laboratory-to-field transfer of bacterial strains results in decreased efficacy and survivability. Thus, it is crucial to isolate ACCD-producing strains that can survive in particular environmental conditions.

Some factors must be considered to apply ACCD-producing microbes in field settings. The first important step is to select appropriate microbial strains with the traits necessary to endure a target environmental stress. The simplest method is to isolate a native strain from the field since they could be adaptable when returned to their natural habitat. Fungi can also potentially be applied because they usually have higher survival rates since they can go through to dormant phase. Fungi may recover from the dormant phase and interact with the host plant when the environment has returned to its ideal state or after receiving a growth stimulus. It is also possible to select prospective ACCD-producing microbes based on additional beneficial features. In high salt and drought environments, microbes with the capacity to produce osmoprotectants, improve water intake, and resist high salinity, could be employed. While in waterlogging stress, ACCD-producing endophytes or facultative anaerobic microbes may assure their effectiveness in low O_2 conditions. EPS production is also one of the important features for ACCD-producing microbes to protect them from various environmental stresses and stabilize their attachment to plants for effective mutual interaction between plants and microbes. For biotic stress, the microbes that have dual functions as biocontrol and stress reliever may be more effective in improving plant fitness. Applying microbial consortia can also be another option since it has been reported that microbial consortia could have more potent activity than single bacteria (Zhang & Zhang, 2022). Single bacteria with excellent performance over a wide range of attributes are pretty uncommon. The combination of mycorrhiza and ACCD-producing bacteria may increase plant stress during drought conditions while simultaneously reviving the soil's water content.

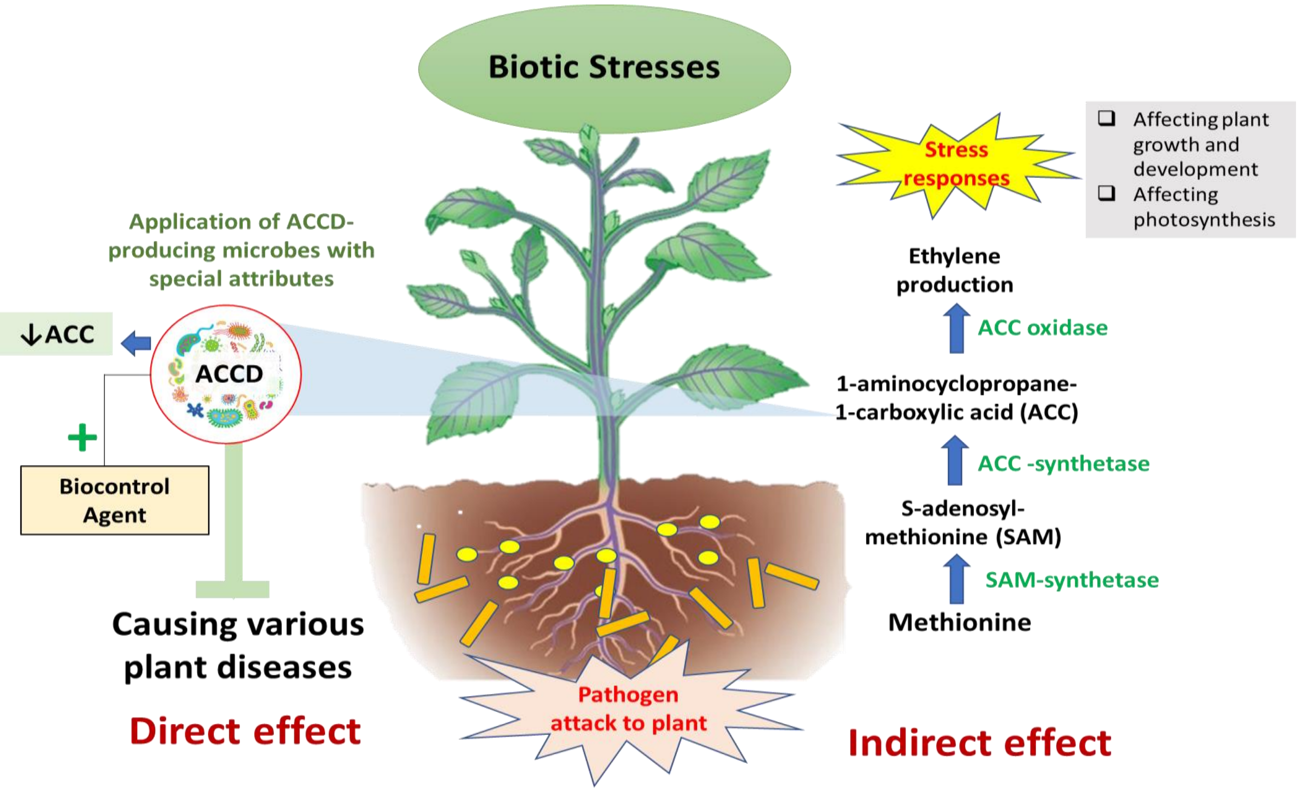

Fig. 3. Plant response in biotic stresses and application of ACCD-producing microbes with additional potential traits.

The next stage considers which microbial production media and carriers will work best for ACCD-producing microbes and the target field. In developed countries, agricultural chemicals are inexpensive, effective, and simple, while microbial inoculants require more labour and are considered unproven technology. Different from less-developed countries, microbial inoculants are considered more appropriate when agricultural chemicals are expensive. Producing microbial biomass with low-cost compounds can be an option to suppress the production cost of bacterial biomass. Crude glycerol, corn flour, soybean meal, dairy sludge, and maize bran residue are industrial wastes or byproducts that can be utilized as inexpensive carbon or nitrogen sources for microbial growth (Lobo *et al.*, 2019). In the case of microbial formulation, it may be common to use liquid carriers, especially for bacteria, because they are easy to multiply in a liquid medium. However, there is a great possibility that other microbes may easily grow and contaminate the liquid carriers and compete with the beneficial bacteria for nutrients. Utilizing pasta or granulated carriers may prevent other microbes from contaminating the carrier rapidly.

Finally, manipulating the soil's properties can potentially promote ACCD activity. It was reported that ACCD activity was more stable in the alkali pH compared to that in the neutral one. ACCD extracted from *Penicillium citrinum* has an optimum degradation of ACC at pH 8.5. These findings are identical to those of Honma *et al.*, (1979) that the activity of ACCD from *Pseudomonas* sp. strain ACP was increased in the alkali pH. However, it is worth noting that manipulating soil conditions should also consider their effect on the soil microbiome.

After passing a series of laboratory-scale assays, the use of ACCD-producing microbes can also be considered on an industrial scale. However, the potential for commercialization faces several challenges. The management of such strains in consistent proportions is a significant challenge. Furthermore, preparing a mixture of bacterial strains is more advantageous than single strain-based formulations because it allows interaction between them. In addition, before commercialization, it requires monitoring and other management practice considerations, further refinement of the final product, confirmation of no toxicological impacts, other formulation considerations for delivery, and registration for regulatory approval (Backer *et al.*, 2018).

Considering the unwillingness of many consumers worldwide to consume genetically modified organisms, it might be beneficial to utilize either organic or genetically modified plant growth-promoting bacteria in the near future. Furthermore, it can promote growth by reducing plant ethylene levels or minimize disease by inducing resistance genes rather than modifying the plant's genetics. Implementing molecular engineering approaches for plants is still challenging because they have wide varieties and breeding materials that must be adapted due to their susceptibility to biotic and abiotic stresses. It is much more sensible to modify the plant growth-promoting bacteria.

Conclusion

The biological approach offers excellent opportunities to use bacteria, fungi, yeast, and other microbial consortia as sustainable plant enhancement agents. Under various agricultural stresses, ACCD-producing microbes can potentially improve plant productivity. Several reports showed successful experiments in laboratory and greenhouse settings on using ACCD-producing microbes. However, knowledge concerning how to employ ACCD-producing microbes on-site effectively is still limited. It is recommended to select appropriate microbial strains for the target stress, investigate the additional supportive traits in potential microbes, formulate effective microbial consortia, and prepare microbial biomass for easy and successful field application. Finally, research about developing ACCD-producing inoculants into commercial biofertilizers is encouraged to overcome several challenges in microbial strain management and pre-commercial preparations.

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