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Title- Phytohormones: Biosynthesis, function and regulation

V.K. Patel [1*], DR. V.M. Chaudhari [2]
[1,2] P.S.G.V.P.M'S A.S.C. College,Shahada Dist-Nandurbar,Maharashtra,India.
[1*]Corresponding Author: vasimpatelmicro@gmail.com

ABSTRACT: Changes in climate have an impact on plants' morphological, physiological, biological, and biochemical conditions. Biochemical changes, protein regulation, molecular processes, post-translational modification, and signal transduction are all examples of how plants react to abiotic stress. The roles, synthesis, and effects of phytohormones are fascinating. It's interesting to note that in recent decades, there has been a lot of interest in using phytohormones to lessen the effects of abiotic stress. By promoting seed germination, seedling growth, leaf photosynthesis, root growth, and antioxidant enzymes while decreasing the buildup of reactive oxygen species, malonaldehyde, and electrolyte leakage, phytohormones might enhance resistance to abiotic stressors. Plant growth and development are regulated by phytohormones, which can be essential to a plant's ability to adapt and survive under various stressors. Plant growth-promoting bacteria (PGPB) also produce several of these phytohormones, including cytokinin, gibberellin, salicylic acid, auxin, and ethylene. Numerous microorganisms create and release hormones that aid plants in absorbing nutrients including N, P, and Fe. Utilising these bacteria exogenously aids plants in resolving nutritional deficiencies caused by abiotic stressors. Given the function of hormones and the ability of microbes to produce hormones, we suggest using both hormones and microbes as a possible crop stress control technique.

Key words- phytohormones, bacteria, IAA, cytokinin.

INTRODUCTION

An increase in agricultural output is imperative given the recent changes in the worldwide environment and the rise in global population. To meet the needs of the world's expanding population, agricultural output by the middle of the century is expected to be 70% higher than it is now [1]. Furthermore, variations in the climate have a major impact on horticultural crop productivity. Numerous biotic and abiotic stressors are significant variables that restrict the productivity and production of agriculture [2]. Through the coordination of distinct signal transduction pathways, phytohormones play a crucial role during abiotic stressors [3,4]. Additionally, they participate in the regulation of various external and internal stimuli, which leads to significant modifications in plant development [5]. Hitherto, the role of phytohormones as signaling molecules in abiotic stress resistance has been studied in horticultural plant [6,7].

Abiotic stressors such as salt, heat, drought, and nutrient deficiency challenges all affect crop yield and quality, which results in crop losses [8]. There is evidence of a broad spectrum of stress reactions in plants, such as a decrease in the yield of the photosynthetic machinery, leaf water potential, membrane integrity, photosynthetic pigments, and plant development [9]. Numerous phytohormones, such as auxin, ethylene, gibberellin, cytokinin, jasmonic acid, salicylic acid, and brassinosteroids, govern the physiological functions of plants. It's interesting to note that a variety of phytohormones, such as cytokinin, gibberellin, salicylic acid, auxin, and ethylene, can also be synthesised or broken down by PGPBs [10,11]. Furthermore, plants can make use of the phytohormone-degrading activity found in numerous soil bacteria to maintain optimally efficient levels of different phytohormones [12].

Adding pure hormones to plants in a lab setting and recording the impact of these hormones on the growth and development of the plants forms a large portion of the present knowledge base regarding the precise mechanism of action of different phytohormones. It is challenging to determine the precise amount of a phytohormone that has been supplied to a plant and its target tissue(s), whether the phytohormone is added as a pure chemical or as a phytohormone synthesised by a PGPB. Furthermore, the production or breakdown of additional phytohormones in a plant's tissues may be influenced by the quantity and activity of a specific phytohormone. It is also sometimes impossible to link a plant's physiological reaction to a PGPB to a single phytohormone because most PGPB can synthesise many phytohormones or alter their quantities. It is recommended to generate phytohormone-minus or overproducing mutants of a specific PGPB strain and examine the effects of these mutant strains on plant growth and development in comparison to the wild-type strain in order to comprehend the role that phytohormone plays in encouraging plant growth.

INDOLE ACETIC ACID

Indole-3-acetic acid (IAA) is the most abundant naturally occurring auxin phytohormone and plays a critical role in plant growth, development and responses against a broad range of biotic and abiotic stresses [13,14,15]. Numerous processes, such as the synthesis of cytokinin, gibberellin, indole-3-acetic acid (IAA), and ACC deaminase, as well as nitrogen fixation, phosphorous solubilisation, and siderophore chelation of iron in soil, allow PGPB to have a favourable impact on plants [16]. Many tryptophan-dependent and tryptophan-independent IAA biosynthesis routes have been proposed for plant-associated bacteria [17]. The environmental circumstances that bacteria frequently encounter include tryptophan content, pH, temperature, and supplies of carbon and nitrogen,

among other variables. These abiotic parameters have the ability to alter IAA biosynthesis [18]. Auxin is essential for plant growth and stress resistance since it increases plant growth at low concentrations [19]. The most common and vital auxin for plants is indole-3-acetic acid, or IAA. Moreover, IAA might greatly enhance root exudation, which would boost PGPR root colonisation and enhance the inoculation result [20]. It has been observed that bacteria and fungi, as well as plants, create IAA [21]. Additionally, IAA plays a crucial part in the interaction between bacteria and plants and can function as a reciprocal signalling molecule by influencing the expression of several bacteria's genes [22].

Auxin produced by PGPB is historically thought to be the main method by which the bacteria promote plant development. Furthermore, although there are multiple auxins that have biological action, indoleacetic acid (IAA) is the subject of the majority of scholarly publications; as a result, the terms auxin and IAA are commonly used interchangeably. IAA stimulates many different aspects of plant growth, such as the growth of roots and shoots, cell division, bacterial colonisation of roots, vascular tissue differentiation, and protection against pathogens, elongation of stems and roots, and loosening of root cell walls[23,24,25, ,26].Different plant tissues react best to different IAA concentrations; the concentration needed to stimulate shoots maximally is approximately 100,000 times higher than the concentration needed to stimulate root growth maximally. Approximately 75% of the total IAA in a plant is usually found in its conjugated (and inactive) state, which is how the IAA is most frequently found in plants.Significantly, it was discovered that a high proportion (~80–90%) of characterised PGPB synthesise IAA, indicating that IAA is an essential part of the mechanism(s) by which these bacteria support plant growth and development. Furthermore, at least five distinct metabolic pathways for the production of IAA are identified in different bacterial strains, according to a combination of biochemical and genetic research [27]. Furthermore, it has been demonstrated that many characterised PGPB include multiple IAA biosynthesis routes, and these pathways frequently cross over (overlap) with one another [28]. This suggests that IAA is critical to these PGPB's ability to function, that is, to promote plant development. The existence of several IAA biosynthetic pathways may be explained by the fact that harmful mutations in one pathway won't interfere with the operation of the other biosynthetic pathway or pathways, maintaining the PGPB strain's ability to promote plant growth and development. This is pertinent to agriculture since the use of biostimulants based on PGPB that produces auxin, such IAA, usually has positive impacts on the growth and development of plants. In fact, the production of IAA has been reported in various genera of PGPB including *Acetobacter, Acinetobacter,Azospirillum, Arthrobacter, Azotobacter, Bacillus, Bradyrhizobium, Burkholderia, Herbaspirillum, Klebsiella, Mesorhizobium, Paenibacillus, Pantoea, Pseudomonas, Rhizobium, Rhodococcus,Serratia, Strenotophomonas, Streptomyces,* and *Rouxiella* [29,30].

Enhancing the solubilising capacities of elements like phosphate is another way via which the creation of IAA in PGPB promotes the absorption of inorganic phosphate by plants, especially in soils with solubilisation issues [31]. This is another significant function of IAA production. It has been linked to positive effects on the nitrogen utilisation efficiency (NUE) and IAA generation in three diazotrophic strains of the genus *Klebsiella* in barley and chickpea plants. This finding was mainly reached by comparing two strains that produced IAA with one that did not, and by noting that the strains that produced IAA encouraged root growth in both plant species far more than the strain that did not synthesise IAA. As was already noted, IAA is one of the most widely distributed and researched hormones in a variety of plant crops, most notably those that yield grains, fruits, and vegetables [32]. IAA, however, also plays important roles in the control of growth and development in woody, aromatic, and medicinal plants [33]. In the latter instance, when injected into these seedlings, the auxin-line metabolite-producing bacterium *Pantoea agglomerans* improved root architecture and boosted root emergence in two woody species, including *Pyrus communis* L (pear) and hazelnut. Additionally, in comparison to actin genes that served as reference controls, some auxin response genes, including as PcARF6, PcARF7, and PcARF8, were overexpressed [34].

PATHWAYS OF IAA PRODUCTION

THE INDOLE-3-PYRUVIC ACID PATHWAY

IAA can be produced by both bacteria and plants through the indole-3-pyruvic acid (IPA) pathway.An aminotransferase first deaminate L-tryptophan to IPA. IPA is subsequently changed into indole-3-acetylaldehyde (IAAld) by a decarboxylase enzyme, which is then oxidised to IAA by an enzyme called an aldehyde dehydrogenase, mutase, or oxidase [35,36]. Numerous plant-associated bacteria have been found to include aromatic amino acid aminotransferases [37,38]. A bacterium may have numerous isoforms of the enzyme, each of which is frequently able to use multiple substrate amino acids, including all three aromatic amino acids and aspartate [37]. This raises the possibility that these enzymes have a role in metabolic pathways other than IAA production [39].

THE INDOLE-3-ACETAMIDE PATHWAY

Although it also occurs in phytosymbiotic bacteria, the indole-3-acetamide (IAM) route has primarily been studied in phytopathogenic bacteria [40]. IAA is created by this mechanism in a two-step reaction from a precursor tryptophan. Tryptophan 2-monooxygenase is the first enzyme, and it transforms tryptophan into the IAM intermediate. An IAM-specific hydrolase/amidase, which hydrolyzes IAM to IAA, catalyses the second step [35]. Based on the chemical identification of the IAM intermediate, the formation of IAA after feeding the bacterial cells with IAM, and/or the incorporation of radioactive carbon from tryptophan into IAM and IAA, this route is present in several bacteria [41].

THE INDOLE-ACETALDOXIME/INDOLE-3-ACETONITRILE PATHWAY

In contrast to plants, bacteria have not undergone as much research on the IAOx/IAN route for IAA production. The transformation of tryptophan into indole-3-acetaldoxime is the initial step in this process. An oxidoreductase, which has not yet been found in bacteria, is most likely the microorganism enzyme in charge of this reaction. According to research done on plants, cytochrome

p450 oxidoreductases catalyse this phase [42,43]. This theory is founded on these findings. An indoleacetaldoxime dehydratase transforms the intermediate indole-3-acetaldoxime into indole-3-acetonitrile in the second step. Numerous bacteria have been shown to have the aldoxime dehydratase enzyme, which is encoded by the oxd genes. However, phenylacetaldoxime has been used as the substrate to characterise the majority of their enzymatic activities. Since phenylacetaldoxime and indoleacetaldoxime have a similar structure, it is possible that enzymes annotated as phenylacetaldoxime dehydratases can also convert the indole-type substrate. Experimental enzyme assays must be performed using both of these arylaldoxime substrates to reveal the substrate specificity of these enzymes. The indole-3-acetonitrile intermediate is consequently converted to IAA by a nitrilase enzyme in a single step or by a nitrile hydratase and an amidase in a two-step process [44].

REGULATION OF AUXIN

Auxins are well-known growth and development regulators that are of great interest because of their versatility in controlling trade-offs with suppression of defence. Indole-3-acetic acid (IAA) is the primary bioactive form, and its distribution, concentration, and production are all strictly controlled [45,13]. Auxin response transcription factors regulate signalling in different tissues (ARFs). Because class A ARFs and the majority of Aux/IAA proteins can interact with several transcription factors from different pathways as well as with one another, ARFs can serve as important hubs for co-expression [46]. Auxin biosynthesis and transport regulate DELLA protein abundance, indicating a complicated relationship between auxins and gibberellins. DELLA proteins interact with ARFs and target them for destruction. Auxins interact with other growth-promoting hormones through cross-talk, although their interactions with cytokinins and strigolactones during immunity are less well understood [47]. Through ARF-binding auxin-response elements in their promoters, auxins are known to enhance expression of the brassinosteroid receptor, BRI1, and brassinosteroid-responsive genes. Additionally, BIN2 is essential for enhancing auxin signalling through phosphorylating ARF7 and ARF19, two AUXIN RESPONSE FACTORS. Auxin signalling is decreased during immunological responses when BIN2 is dephosphorylated. MAMP-triggered immunity inhibits auxin signalling and plant growth, and exogenous SA treatment causes the stabilisation of Aux-IAA protein, which attenuates auxin responses by negatively regulating auxin signalling. In the meantime, SA biosynthesis and SA signalling can be inhibited by activating auxin signalling [48]. Furthermore, it has been demonstrated that Arabidopsis plants with auxin signalling defects or those treated with the auxin transport inhibitor TIBA (2,3,5-triiodobenzoic acid) are more vulnerable to the necrotrophic fungus *Plectosphaerella cucumerina*[49]. Auxin signalling changes can make a person more susceptible to infection, which explains why some diseases produce auxins or alter host auxin signalling to become more virulent. Auxins are produced by bacterial and fungal pathogens, such as. *P syringae* and *Leptosphaeria maculans*, in order to facilitate infection [50, 51]. While exogenous administration of indole-3-acetic acid increases expression of virulence components, such as type III secretion system effectors and enzymes involved in cell wall breakdown, mutations in the bacterial auxin biosynthesis pathway may impact pathogen proliferation [50,52]. Moreover, pathogens use effectors to target the auxin pathway. For example, *Phytophthora parasitica's* PENETRATION SPECIFIC EFFECTOR 1 (PSE1) lowers auxin accumulation near the root apex.This modifies the distribution of PIN-FORMED auxin efflux carriers, PIN4 and PIN7, which suppresses immunological responses and increases the plant's susceptibility to disease. Furthermore, a number of distinct rice RNA viruses control auxin levels by focussing on elements of the auxin signalling system, which promotes infection and produces dwarf phenotypes [53,54,55].

Table 1: Microbes involved in IAA production

Organisms	Pathway	Reference
Bradyrhizobium japonicum E109		56
Variovorax boronicumulans CGMCC 4969	Indole-3-Acetonitrile	57
Astraeus odoratus, Gyrodon suthepensis, Phlebopus portentosus, Pisolithus albus, Pisolithus orientalis ,Scleroderma suthepense.	Indole-3-pyruvic acid	
Arthrobacter pascens ZZ21	Indole-3-acetamide (IAM), Indole-3-pyruvic acid (IPyA)	59
Agrobacterium sp. NA11001, Phyllobacterium sp. C65, Bacillus sp. CS14, and *Rhizobium sp. V3E1*.		60
Coniochaeta sp. and *Cladosporium sp.*		61
Burkholderia pyrrocinia JK-SH007	Indole-3-acetamide	
B. cereus SEM-15		62
Aspergillus ustus		64
Curvularia lunata, Pholiota multicingulata, Trichoderma atroviride, T. harzianum and *Schizophyllum commune.*		65

Cladosporium, Colletotrichum, Cylindrocarpon, Fusarium, Hypoxylon, Leptosphaerulina and Trichoderma		66
Enterobacter hormaechei CIP 103441T, Bacillus aryabhattai B8W22T		67
Klebsiella aerogenes KE-1		68
Penicillium commune EP-5		69
Nigrospora oryzae (MH071153), Alternaria alternata (MH071155),		70
Aspergillus niger and *Penicillum glabrum*		71
(CMU-A109) Colletotrichum fructicola		72
Astraeus odoratus, Gyrodon suthepensis, Phlebopus portentosus, Pisolithus albus, Pisolithus orientalis and *Sclero-derma suthepense.*		
Cyanodermella asteris.		73
Pseudarthrobacter sp. NIBRBAC000502770,		74
Bacillus pumilus 98F, Burkholderia cenocepacia 127F, Burkholderia sp. 12F and *Pseudomonas fuorescens 27F*		75
Pseudomonas sp. UW4		76
C. tropicalis	Indole-3-pyruvate pathway	77
Caballeronia glathei DSM50014		78
Sordariomycetidae sp. CJAN1179		79
Bacillus siamensis		80
Rhodosporidiobolus fuvialis DMKU-CP293		81
Staphylococcus aureus ,Micrococcus luteus, Micrococcus roseus, Bacillus cereus,Bacillus subtilis, Pseudomonas aeruginosa		82
B. subtilis DR2 (KP455653)		83
E. xiangfangensis BWH6, E.asburiae STY10.		84
Chlorella vulgaris Beijerinck		85

CYTOKININ

Adenine and cytokinins (CKs) share a structural resemblance. Zeatin, which was initially identified from Zea mays (corn) in the 1950s, is the most prevalent type of cytokinin in plants [86]. Plant cell division, or cytokinesis, can be aided by cytokinins[87]. Apart from cytokinins produced by plants, a number of bacteria, including phytopathogens and PGPB, are also capable of synthesising cytokinins such as isopentenyladenine, zeatin, and zeatin riboside. Only a small percentage of soil bacteria synthesise cytokinin, and it appears that phytopathogens synthesise cytokinins at a significantly higher level than PGPB, according to biochemical and DNA sequence data [88]. Plant cells of many different kinds are impacted by cytokinins. They have the ability to regulate a variety of processes including cell division, seed germination, apical dominance, root elongation, xylem and chloroplast differentiation, transition to the reproductive growth phase, flower and fruit development, leaf senescence, nutritional signalling, and plant–pathogen interactions [89,90]. Cytokinins stimulate plant cell division, which prevents plant senescence. When plants grow naturally, shoots form more often than roots because of a higher cytokinin to auxin ratio. In a recent study, transgenic *Solanum* plants—which include potatoes, tomatoes, and eggplants—that overexpressed isopentenyltransferase (IPT) in their roots were used to assess the effects of cytokinins . The CKs biosynthesis route involves the enzyme IPT. The study's findings demonstrated that overexpressing IPT in tomato plants delayed defoliation and raised plant chlorophyll concentrations after 18 days, all while raising CK levels in leaves. According to the authors, these effects are caused by CKs that communicate with shoots and roots over great distances by using the xylem as a signalling channel [91]. Recently assessed the CK production in 46 *Methylobacterium* strains of bacteria [92]. Remarkably, the majority of these strains generated large amounts of CKs, including trans-Zeatin (tZ), the most active type. The strains were also able to create indoleacetic acid (IAA) from L-tryptophan, and the scientists stated that the only method to promote cytokinin production was to include carbon, which was produced from reduced methanol, in the bacterial medium. As different bacterial methylotrophs have been widely identified as growth-promoting agents, including under stressful conditions, in rice, sugar cane, mustard, potato, radish, peach, and groundnut, it will be crucial to determine in the future what impact strains with high levels of cytokinin production have on the bacterial interaction with plants [93]. It has also been revealed that Pseudomonas and other genera manufacture CKs [94]. In this study, the authors discovered that when the bacterium was used to inoculate the plant roots, the cytokinin-producing strain *Pseudomonas fluorescens* G20–18 increased tomato plant growth and increased its tolerance to drought

stress. In comparison to non-infected plants, inoculated plants exhibited a rise in some plant characteristics, including increased levels of stomatal closure and chlorophyll and abscisic acid (ABA) in their leaves. There was a notable rise in the activity of various antioxidant enzymes as well as an increase in the activity of certain enzymes involved in the metabolism of carbohydrates. Higher concentrations of secondary metabolites, such as phenols, flavonoids, and anthocyanins, were linked to this. Crucially, when plants were treated with the two mutant strains of G20–18 (CNT1 and CNT2) that were faulty in cytokinin production, several plant parameters did not manifestly differ from those of plants treated with the wild-type strain. However, the genes that react to plant drought stress had less regulation in these treated plants (particularly in the case of CNT1). The study's overall findings suggest that CKs generated by bacteria can increase crops' tolerance to stress and overall robustness.

Micrococcus luteus		95
Arthrobacter sp., *Bacillus* sp., *Azospirillum* sp.		96
Bacillus subtilis		97

GIBBERELLIN

There are approximately 126 known gibberellins, which belong to the broad family of related tetracyclic diterpenoid chemicals. Only four of this family's members seem to be biologically active, though. GA1, GA3, GA4, and GA7 are the gibberellins that are biologically active. The most prevalent form of this phytohormone is gibberellin GA3, which is marketed in pure form. The production or breakdown of the active gibberellins may involve the other (non-active) gibberellins[98]. Gibberellins, both purified and synthesised using PGPB, have the ability to boost fruit and leaf senescence, change the dormancy of germination seeds, and accelerate plant stem development[99,100]. Gibberellin tends to primarily stimulate shoot growth, however it can also stimulate root growth at lower concentrations[101]. Plant-associated bacteria that are both beneficial and pathogenic, like PGPB, produce gibberellin (GA) through the GA operon, which is made up of the core genes cyp112, cyp114, and cyp117 (which are cytochrome P450 (CYP) monooxygenases), fd (ferredoxin), sdr (short-chain dehydrogenase/reductase), ggps (geranylgeranyl diphosphate synthase), cps and ks (two diterpene synthases/cyclases). Both processes are significant in the interaction with host leguminous plants since the GA operon has been studied in the group of alphaproteobacterial rhizobia, which can also fix nitrogen[102]. In reality, it has been proposed that the genetic pathways underlying GA production in bacteria, plants, and fungus are converging. For instance, genes with comparable activities regulate the production of GA in fungus belonging to the genera *Aspergillus*, *Cladosporium*, *Neurospora*, *Fusarium*, *Penicillium*, and *Phoma*, among others[98]. GA often comes in two varieties: molecules with 20 carbon atoms and molecules with 19 carbon atoms that incorporate a lactone ring[103]. Notably, only four GAs have biological activity, as was previously reported[104]. Accordingly, Soybean (*Glycine max*) nodules express a *Bradyrhizobium diazoefficiens* GA three-oxidase enzyme, which is involved in the final step of the synthesis of the bioactive GA4 by hydroxylating a non-active GA9[105]. This enzyme was also linked to an increase in the size of the nodules. There were more tiny nodules and fewer large nodules in a knockout mutant of the GA operon. According to these authors, the regulation of nodule size brought about by the generation of an active GA4 might be a result of the plant and its bacterial host's metabolism co-evolving over time, with both parties benefiting from nodule formation. Since GAs control plant growth, their own regulation needs to be carefully coordinated in response to various environmental stressors. For instance, in drought or cold stress situations, post-transcriptional alterations that boost the activity of the enzyme maize GA 20 oxidase—which is involved in the production of active GA—determine the distribution of GA in maize plants[106].

Aspergillus fumigatus		107
Azospirillum lipoferum		108
Phoma glomerata, Penicillium sp.		109

SALICYLIC ACID

Two biosynthetic routes converted cinnamic acid (CA) into SA during the 1960s. One route uses a side chain of CA that is decarboxylated to yield benzoic acid, which is then 2-hydroxylated to synthesise SA in crops including rice and tobacco [110,111]. It did, however, speculate that there may be some other enzymes in this route that are currently unknown. The second mechanism for the biosynthesis of SA involves CA. After undergoing 2-hydroxylation, o-coumaric acid is produced. This acid is then decarboxylated to produce SA. This process is catalysed by the enzyme trans-cinnamate-4-hydroxylate [112,113]. Pea seedlings were used in the initial research on this pathway [114].

Plants treated with PGPB frequently develop long-lasting, broad-spectrum systemic resistance to a variety of phytopathogenic bacteria and fungi [115] . Plant defences are primed by this induced systemic resistance (ISR) prior to their contact with phytopathogens, making plants more resilient to pathogen attack in the future. Increases in the lignification of plant cells and the development of enzymes like peroxidase, catalase, and superoxide dismutase that reduce the amount of reactive oxygen species (ROS) are frequently linked to the ISR. ISR induction is commonly linked to the signalling pathways of ethylene and jasmonic acid. Furthermore, phytopathogens themselves can frequently trigger a defence mechanism in plants known as systemic acquired resistance (SAR), which involves the induction of a set of genes related to plant pathogenesis (PR) that encode proteins with antipathogen activity (like enzymes that break down fungal cell walls and antibiotics) [116]. Salicylic acid (SA) signalling is typically linked to the induction of SAR. Apart from its association with SAR, salicylic acid has also been discovered to play a role in the alleviation of multiple abiotic stresses experienced by plants, such as extreme heat or cold, elevated salt concentrations, metal-induced inhibition, low oxygen and ozone levels, the existence of harmful organic compounds, UV radiation, and drought. An

improvement in indicators including CO2 absorption, transpiration, stomatal conductance, water use efficiency, and carboxylation efficiency when SA was administered to tomato leaves that were under water stress, indicating a beneficial plant response. Two of the previously identified positive effects—gas exchange and the efficiency of CO2 uptake and carboxylation—improved tomato fruit output [117]. After two fruitful years of monitoring the tomato fruit output, it was evident that SA was essential to this process. Similar results have been reported with wheat plants (*Triticum aestivum* L.) grown hydroponically. The application of SA topically to plants experiencing water stress resulted in enhanced plant growth and the advancement of stress tolerance [118]. Salicylic acid can promote protein synthesis, nutrition transfer, ion absorption, blooming, and stomata movement in plants. By binding to specific amino acids like proline and arginine, salicylic acid can help plants withstand a variety of environmental challenges [119]. Salicylic acid is a defence hormone because of its part in abiotic stress reduction as well as SAR. In one study, PGPB by itself had a much greater ameliorative effect when salicylic acid was added to chickpea plants under extreme salt stress [120]. Salicylic acid seemed to work in concert with PGPB-encoded pathways in this study as well as others [121, 122]. Co-inoculated white bean plants with two PGPB strains (*Bacillus subtilis* and *Pseudomonas putida*) and SA, resulting in increased plant development under drought stress conditions relative to plants that were not treated with SA [123]. The co-application of SA with the aforementioned endophytic bacteria also increased other parameters like relative water content, proline synthesis, nitrogen content, and chlorophyll content. Four cowpea genotypes were treated with a similar approach of co-applying SA and a PGPB (*Bradyrhizobium* sp. strain W100)[124]. Three plant genotypes that got this co-application and were under water stress showed favourable effects from the addition of SA, according to these authors' findings. A few characteristics were increased, including proline synthesis and leaf water potential, in addition to other antioxidant actions.In plants exposed to various forms of stress, other researchers have also documented beneficial effects on plant growth with the administration of SA and other chemicals, such as potassium silicate (silicon), melatonin (MT), or the disaccharide trehalose. In the first instance, it was found that silicon and SA were crucial in helping tomato plants withstand the harmful effects of the Gram-negative bacterium *Ralstonia solanacearum* [125]. In contrast, co-application of MT and SA enhanced the growth of wheat plants that were exposed to salt stress. The co-application of MT and SA significantly enhanced the functions of plants, including the accumulation of osmoprotectants, transpiration rate, net photosynthetic rate, photosynthetic pigment content, and photochemical reactions of photosynthesis [126]. It is commonly known that trehalose, a disaccharide produced by a variety of PGPB species, is crucial for microbial and plant resistance to biotic factors like bacterial pathogens as well as heat, drought, salt, and cold stress [127,128,129]. In this instance, the detrimental effects of drought stress on sweet basil plants were lessened by the application of trehalose and SA. The plants responded positively by improving their production of osmolytes (glycine and glycine betaine), some antioxidant enzymes (superoxide dismutase, peroxidase, and catalase), as well as their general growth under drought stress conditions [130].

Achromobacter xylosoxidans, Bacillus pumilus		131
Serratia marcescens		132

ETHYLENE

Gaseous phytohormone ethylene is widely present and exhibits a broad spectrum of biological activity at concentrations that are approximately 10,000 times greater. Ripe fruit usually has higher levels of ethylene, while much lower levels are linked to early vegetative development, germination of seeds, tissue differentiation, establishment of root and shoot primordia, branching and elongation of roots, lateral bud development, growth of pollen tubes, flowering initiation, synthesis of anthocyanins, flower opening and senescence, synthesis of volatile organic compounds, senescence of leaves and fruits, formation of Rhizobia nodules, mycorrhizae-plant interaction, and the way plants react to different biotic and abiotic stressors[133,134]. According to new theories, ethylene controls growth responses through a variety of signalling channels, including auxins and abscisic acid (ABA), which can inhibit roots' capacity to pierce the soil, especially in compacted soils [135]. S-Adenosyl methionine (SAM), the precursor of ET and the starting point for the underlying mechanism facilitating ET production, is typically synthesised in high concentrations in a variety of crops and fruit trees. Methylthioadenosine (MTA), which is then recycled to L-methionine, and 1-aminocyclopropane-1-carboxylic acid (ACC) synthase catalyse the initial chain reaction that converts SAM to ACC. L-methionine levels don't alter even during the height of ethylene production because of this recycling. Moreover, the ET biosynthesis pathway is affected by ACC synthase enzyme, which is extremely labile and tends to limit biosynthesis rate and rises proportionally as that of ethylene levels in tissues, flowers, and fruits [136].

ACC usually conjugates and transforms into inactive forms in plant tissues during times when there is an excess of this chemical present. This is particularly significant since, according to some recent research, ACC alone, rather than just ethylene, may have some signalling function that was previously thought to be related to ethylene [137]. Alpha-ketobutyrate and ammonia can be produced by the enzyme ACC deaminase, which is present in several PGPB [138,139]. A model that explains how ACC deaminase functions in plant growth promotion involves IAA from a PGPB being absorbed by a plant and, in conjunction with endogenous plant IAA, promoting growth and, at the same time, facilitating the transcription of plant ACC synthase, which raises the level of ethylene and inhibits plant growth [140,141]. The ACC deaminase containing PGPB absorbs most of the increased ACC that results from IAA stimulating ACC synthase transcription, cleaves it, and deactivates it. Therefore, the PGPB's activity lowers ACC levels, which in turn lowers plant ethylene levels. This allows IAA to keep promoting plant growth without causing an inhibitory increase in ACC.The activity of ACC deaminase is one of the primary methods that PGPB uses to promote plant growth and development because of its important role in controlling plant ethylene levels, particularly during times of both biotic and abiotic stress [142]. The study, in which they identified and isolated bacterial strains from the rhizosphere, endosphere, and phyllosphere of plants that live in Antarctica, serves as evidence for this [143]. 77 microorganisms in this study produced ACC deaminase and were cold tolerant.

The most studied taxa as bioinoculants in cold-stressful agriculture, *Pseudomonas, Serratia*, and *Staphylococcus*, were among the isolates classified as "cold-tolerant and hyper-ACC-degrading bacteria." Numerous environmental stressors, including soil salinity and drought, have already been discussed in relation to plants. But the cultivation of plants like rice, which are usually grown in soggy soils, can also result in stress and raise ethylene levels. Because of this, the application of ACC deaminase-producing bacteria, such as *Methylophaga* sp. AR-ACC3 and *Paenibacillus* sp. ANR-ACC3, is effective in relieving the stress caused by submergence in rice plants. It even exhibits growth stimulation in parameters like seedling vigour, root and shoot length, and total chlorophyll concentration [144]. Although PGPB have a variety of strategies for fostering plant growth, not much research has been done to examine the relationships between them. The relationship between the production of ACC deaminase and the solubilisation of phosphate in PGPB, such as *Bacillus, Burkholderia, Pseudomonas*, and *Variovorax* [145]. Through the stimulation of phosphorus uptake from rock phosphate, Burkholderia sp. strain 12F, which expresses ACC deaminase, was able to boost chickpea nodulation and development, according to plant studies.In addition to other metabolites produced by the plant, the ACC, the precursor of ethylene, is released from plant tissues under stress, including roots in the rhizosphere [146]. This can then function as a chemoattractant for rhizobacteria [147]. Nevertheless, since microbial cell cytoplasm contains ACC deaminase, ACC can enter bacteria that carry ACC deaminase by exopolysaccharides, chelators, peptides/chaperones, hormones, or concentration gradient variations [138]. The equilibrium between the ACC found in plant tissues, the rhizosphere ecology, and the bacteria that produce ACC deaminase would be preserved by this last mechanism. Furthermore, additional ACC deaminase-producing microbes, such as fungi and archaea, may find this attraction and transport mechanism to be significant [148]. In one study, the overexpression of acdS genes in PGPB *Pseudomonas* sp. UW4 was examined. This resulted in an increase in the bacterial capacity to colonise the rhizosphere and promote wheat plant growth. The study's authors came to the conclusion that ACC, which the plant produced and expelled, can be an extremely potent chemoattractant for microbial strains that exhibit significant ACC deaminase activity[149]. For controlling the number of cells in the rhizosphere of ACC-producing bacteria, other mechanisms including quorum sensing (QS) might also be crucial. The study involved the construction and testing of QS-deletion mutants of *Serratia fonticola* strain GS2, serves as evidence for this[150]. These strains demonstrated that QS functions can affect PGPB's growth-promoting properties. The synthesis of IAA, biofilm formation, and ACC deaminase are a few of the processes impacted in the QS mutants. Finding the finest candidates to include in bioinoculants—which can also be referred to as biostimulants, biofertilizers, or biofungicides due to the variety of roles that ACC deaminase activity exhibits—requires searching and screening for PGPB that produces ACC deaminase. Because of this, identifying genes (like acdS) and ACC deaminase activities in PGPB has been the focus of a large number of research projects and publications in the literature. Early studies, looked at the existence of acdS genes and the ACC deaminase activity of these genes in over 200 strains that were isolated from the Canadian Prairies. Techniques such as PCR amplification, Southern hybridization and phylogenetic analysis revealed the existence of these genetic elements in various previously uncharacterized strains, most of which were nitrogen-fixing Rhizobia [65].

In a more recent study, extensively screened the acdS genes in strains of ACC deaminase linked to maize and other plant species, primarily those in the Poaceae family [151]. In order to accomplish this, the authors created particular primers for the amplification of acdS genes and the measurement of the amount of mRNA encoding this enzyme present in various soil communities among acdS+ bacteria belonging to the same plant species. The findings demonstrated the widespread presence of acdS genes and gene transcripts in Poaceae rhizospheres. These findings indicate that these genes are often associated with the ability of rhizosphere bacteria to support plant growth and their propensity to survive in various types of agroecosystems.A beneficial evolutionary relationship could exist between these Poaceae species and their rhizosphere microorganisms exhibiting ACC deaminase activity.

ABSCISIC ACID

Early in the 1960s, researchers discovered that abscisic acid was a phytohormone that broke seed dormancy [152]. Subsequent research has revealed that it may play a part in plant development and stress adaptation [153,154]. For instance, ABA has a role in a plant's ability to adjust to external stressors, regulate water levels in the plant body through stomatal opening and shutting, and mature and dormant seeds. When there is a water shortage, ABA is biosynthesised in the roots and transported to the leaves through the xylem, increasing the concentration in the leaves. An increase in ABA signals the guard cells to begin a signalling cascade that controls the turgor of the guard cells [155,156]. The manufacture and redistribution of ABA result in stomatal closure and a decrease in transpiration rate during the abiotic stress response, which limits cell development [157]. The roles that ABA plays in plant-water connections are well known [158]. Hormone-responsive transcription factors are up-regulated by ABA, and phosphatases and kinases in ABA signalling are involved in mediating quick reactions to a variety of abiotic stressors [159].

Carotenoids are the source of the ABA biosynthesis pathway [160]. Stress stimuli quickly cause the enzyme 9-cis-epoxy carotenoid di-oxygenase (NCED) to catalyse the production of ABA from β-carotene oxidative cleavage. Zeaxanthin epoxidase generates trans-violaxanthin, which is then transformed into neoxanthin, a 15-C molecule. Subsequently, xanthoxin is converted to abscisic aldehyde, which is oxidised to produce ABA. Certain plant species exposed to abiotic stressors have been found to employ an alternative pathway for ABA synthesis, which involves the β-glucosidase homologs from ABA-GE biosynthesising the compound[161,162].

Furthermore, in plants exposed to abiotic stressors, ABA interacts with other PHs to modulate physiological responses in addition to mediating them through its own signalling [163]. It is important to note that ABA activates and mobilises a variety of biochemical defences, including the strengthening of cuticular waxes, the biosynthesis of proline, antioxidants, ROS detoxifying enzymes, heat shock proteins, and unsaturated fatty acids. These defences help plants partially fend off the negative effects of abiotic stress [164,165].

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