Vol. 19 (Supplementary Issue 3A), September 2025, ISSN 0973-8916 (Print)., 2230-7303 (Online)
10.5530/ctbp.2025.3s.4

Growth promotion and response of staple crops to inoculation with *Azospirillum:* A review

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Abstract

Azospirillum, a genus of plant growth-promoting rhizobacteria, has garnered increasing attention for its pivotal role in sustainable agriculture. It has the capability to increase yield in many crops of agronomic importance especially staple crops by various mechanisms. This review explores the diverse potential of *Azospirillum* spp. in farming, examining how different crops respond to these bacteria. A key focus of this review is *Azospirillum* 's ability to convert atmospheric nitrogen into bioavailable nitrogen for plant which boosts soil nutrients and helps plants grow better. Besides nitrogen fixation, the paper discusses many other benefits linked to *Azospirillum* spp., such as phytohormones production for plant growth promotion, enhancing plant stress tolerance, and ultimately helping farming stay sustainable and strong. This review thoroughly investigates the effect of *Azospirillum* inoculation on staple crops including wheat, maize, rice and sugarcane. It explores the complex relationships these crops have developed with *Azospirillum* spp., uncovering numerous advantages of these interactions.

Keywords: *Azospirillum,* plant growth-promoting rhizobacteria, staple crops, rhizobacteria

Introduction

The agricultural sector holds pivotal significance in enhancing food accessibility and attaining food security. Agriculture is a high-risk sector, with outcomes predominantly influenced by environmental conditions (1). Crops are frequently subjected to variety of stressors, including drought conditions, pathogenic microbial infections, cultivation in saline soils, or exposure to soils contaminated with hydrocarbons, heavy metals, pesticides, radioactive substances, or perchlorates(2). The rapid growth in the global population necessitates enhanced agricultural output and the advancement of food quality to meet fundamental requirements. Despite consensus regarding the anticipated surge in global food demand in forthcoming decades, uncertainties persist regarding agriculture's ability to meet this demand through expanded food production (3).

Conventional agricultural methods, encompassing the use of chemical fertilizers and pesticides, serve to safeguard plants from pathogens, consequently enhancing yield, but the chemical constituents within these agricultural substances pose significant environmental hazards, leading to pollution of soil, air, and water resources (1,3).

Current situation demands for a sustainable and organic approach to boost agricultural production. Employing plant growth promoting microorganisms (PGPM) that promote plant growth is among the most promising approaches to tackle the crisis (4). These microbes play a vital role in organic matter decomposition, contributing to the production of humus and significantly impacting soil quality and structure. Their involvement extends to preserving biological equilibrium, facilitating nutrient recycling between soil and roots. Additionally, they mitigate surface erosion losses, and also regulate soil pH, maintain mineral and nutrient balance, and enhance soil fertility (5).

The utilization of PGPM belonging mainly to the genera like *Pseudomonas*, *Agrobacterium* or *Azospirillum* showcases

Vol. 19 (Supplementary Issue 3A), September 2025, ISSN 0973-8916 (Print)., 2230-7303 (Online)
10.5530/ctbp.2025.3s.4

significant potential in enhancing plant growth and performance across various species(6). For instance, *Acinetobacter sp. RG30* and *Pseudomonas putida GN04* exhibit remarkable effects on Corn (*Zea mays)*, demonstrating increased tolerance to copper, elevated chlorophyll content, and heightened copper concentration in tissues (7), Similarly, *Agrobacterium sp. 10C2* influences *Phaseolus vulgaris* positively by stimulating nodule formation, boosting plant biomass, and enriching the content of phosphorus, polyphenols, and flavonoids in grains, alongside inducing changes in the microbial community structure (8).

Azospirillum, recognized as a key genus among PGPR, exhibits the capability to inhabit the roots of numerous plant species, thereby fostering their growth through different pathways including synthesis of metabolites like plant hormones, its utility as biofertilizers, its capacity to enhance plant stress tolerance against salinity and water stress. Staple crops, such as rice, wheat, maize, and millets, form the cornerstone of global food security(9). However, their productivity is often limited by various biotic and abiotic stresses, declining soil fertility, and excessive use of chemical fertilizers. Integrating *Azospirillum* inoculation offers a sustainable alternative to address these challenges while supporting environmentally friendly farming practices (10, 11).

In this review, we had described the role of *Azospirillum* in plant growth promotion by production of phytohormones, biological nitrogen fixation, biological control agent and mitigation of different types of stress along with a comprehensive overview of the effects of *Azospirillum* on different staple crops.

Biology of *Azospirillum*

Microorganisms classified under the genus *Azospirillum* are free-living plant growth-promoting bacteria. They help in the development of various plant species, including those with significant agronomic and ecological value(12). *Azospirillum* has multiple mode of action. The prevailing hypothesis regarding the mode of action of *Azospirillum* is its role in promoting plant growth by production of phytohormones, biological nitrogen fixation, biological control agent and mitigation of different types of stress (13). *Azospirillum* has been shown to enhance the agricultural productivity of staple crops such as wheat, maize, rice, and sugarcane. Additionally, it has been applied successfully to chili peppers, various fruit tree species, and cacti (14).

Each *Azospirillum* strain displays a unique genomic configuration characterized by a variable count of plasmids, typically ranging from one to six. Members of the *Azospirillum* genus showcase notable genome size variations, exemplified by *A. irakense* which has genome of 4800 kb, *A. lipoferum* has 9600 kb and *A. brasilense* has approximately 7000 kb(6). It is noteworthy that mega plasmids emerge as a distinctive genetic hallmark, some of which exhibit linear conformations. The widespread presence of these mega plasmids represents a prominent and enduring characteristic, constituting one of the principal genomic attributes historically documented within the *Azospirillum* genus. The count of mega plasmid replicons exhibits species-specific disparities, typically spanning from 7 to 8, and, in some instances, expanding to encompass up to 10 such genetic entities. These plasmids exhibit consistent presence in *Azospirillum* strains, existing as solitary copies within individual cells (12).Beyond the plasmid, the occurrence of Mini chromosomes has been duly recorded, for instance, the genome of *A. brasilense* has multiple chromosomes having replicons of 600 kb, 1000 kb, and 1700 kb in size, with the presence of additional 2500 kb chromosome(9).

Azospirillum role in plant growth promotion

Production of Phytohormones

Flora necessitates luminosity, aqueous sustenance, oxygenation, minerals, and assorted nutrients to facilitate their physiological expansion and maturation. In addition to these basic needs, they also rely on specific organic compounds known as phytohormones to start, regulate, and control their growth processes (15). Phytohormones,

Vol. 19 (Supplementary Issue 3A), September 2025, ISSN 0973-8916 (Print)., 2230-7303 (Online)
10.5530/ctbp.2025.3s.4

or plant hormones, are endogenously occurring organic compounds found in trace amounts, exerting their effects locally or remotely on the plant. Demonstrating varied chemical properties and unique structural configurations, these chemical mediators influence holistic plant growth and development via diverse biochemical pathways (16). These growth modulators coordinate the plant's responses simultaneously according to biotic and abiotic stressors. These phytohormones induce alterations in the metabolism as well as morphology of the plant, resulting in enhanced mineral and water uptake, thereby fostering the development of larger and healthier plants(17).

Azospirillum spp. are widely known for their ability to produce various phytohormones like Indole-3-acetic acid, Gibberellins, abscisic acid, Polyamines, Cytokinins and Ethylene(18). Various phytohormones and growth regulators such as putrescine, spermine, spermidine, and cadaverine, were found in the culture supernatant of different strains of *Azospirillum* (19). Most strains of *Azospirillum,* when subjected to fermentation for inoculant preparation, demonstrate the capacity to biosynthesize a spectrum of growth regulators at concentrations sufficient to instigate morphological and physiological changes in emerging seed tissues (20).

The mechanisms by which *Azospirillum* promotes plant growth through the production of phytohormones, are diverse and multifaceted (21); like IAA in *Azosperillium* is known to be biosynthesised by three mechanisms which are related to tryptophan metabolism (Fig. 1); namely, formation via indole-3-pyruvic acid (IPyA) and indole-3-acetaldehyde; tryptophan conversion to indole-3-acetaldoxyme and indole-3-acetonitrile (IAN); and via indole-3-acetamide formation. The exclusion of tryptophan from the *Azosperillium* culture significantly reduces indole-3-acetic acid production by the microbial population in the culture (22,23). Conversely, supplementation with exogenous tryptophan enhance the biosynthesis. Gibberellins are synthesized by the terpenoid pathway(20,24). Table 1 shows different phytohormones produced by

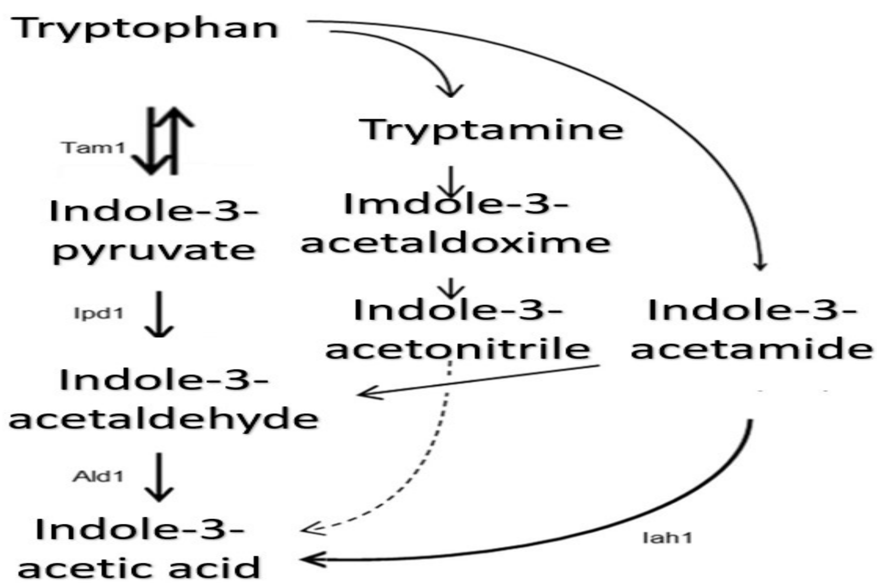

Fig. 1: Biosynthesis of Indole-3-acetic acid in *Azospirillum* by tryptophan metabolism - formation via indole-3-pyruvic acid (IPyA) and indole-3-acetaldehyde; tryptophan conversion to indole-3-acetaldoxyme and indole-3-acetonitrile (IAN) and via indole-3-acetamide formation(25).

Vol. 19 (Supplementary Issue 3A), September 2025, ISSN 0973-8916 (Print)., 2230-7303 (Online)
10.5530/ctbp.2025.3s.4

Azospirillum species along with their effect on growth and development of plants.

Nitrogen fixation

Nitrogen is regarded as the limiting factor for plant growth and development despite it is present abundantly in atmosphere. Nitrogen holds a prominent position within the plant metabolic framework, as it is integrally involved in crucial physiological processes, particularly those associated with protein synthesis(41). Therefore, nitrogen application is essential to enhance crop production. Nitrogen exerts a dual influence by not only increasing the crop yield but by enhancing the quality of food. Increment in the rate of nitrogen cause increment in photosynthetic processes, area of leaf and net assimilation rate (42). Many crops are incapable to utilize the freely available nitrogen present in the atmosphere and necessitates synthetic nitrogen fertilizers which contributes in global warming and various types of pollutions in the atmosphere (43). Nitrogen fixing bacteria has a crucial role in the conversion of atmospheric nitrogen into bioavailable form used by plants(44). *Azospirillum* spp. stands out as a highly proficient nitrogen fixation agent in agricultural field, particularly under optimal conditions for biological nitrogen fixation(45). Around 18 percent nitrogen of the plants are derived by biological nitrogen fixation(46). Numerous investigations on *Azospirillum* inoculation consistently underscore nitrogen fixation as the primary mechanism by which *Azospirillum* favours plant growth, either in a free-living state or in symbiotic association with plants(41,43). Around 50 percent, of the nitrogen content in crops such as sugarcane, paspalum notatum and panicum maximum, could be sourced from symbiotic nitrogen-fixing microorganisms, mainly *Azospirillum* (45,47).

In *Azospirillum,* enzyme nitrogenase mediates nitrogen fixation(48). Nitrogenase facilitates the reduction of atmospheric nitrogen (N_2) to ammonia (NH_3). Ammonia is then released in the rhizosphere, where plants can directly use it or can be converted to ammonium (NH_4^+) and nitrate (NO_3^-) ions by the action of other soil microorganisms(44). This natural process enhances the plant's nitrogen availability, promoting growth while reducing the dependence on synthetic nitrogen fertilizers. Reaction takes place under anaerobic or microaerophilic conditions (49).

$$\mathbf{N_2+8H^++8e^-+16ATP \rightarrow 2NH_3+H_2+16ADP+16Pi}$$

After analysing the huge data collected over many years about how *Azospirillum* helps plants grow by fixing nitrogen, it turns out that this bacterium is really crucial for boosting plant growth. Even in situations where *Azospirillum's* nitrogen-fixing role is not huge, the cumulative effect of nitrogen provided by this process, coupled with other mechanisms works together to help plants thrive (47).

Biological control agent

In order to augment food grain production and productivity in tandem with the escalating annual population growth there arises a necessity for the application of elevated doses of pest control agents. While this approach yields expeditious outcomes, its indiscriminate application, coupled with the persistent nature of these chemicals in the soil, engenders a decline in soil productivity (50). Simultaneously, it leads to water body pollution, posing hazards to both human health and the surrounding environment. Hence, there is a high need to shift from chemical method to biological method of pest control (51).

Azospirillum belongs to a bacterial cohort utilized not only as biological fertilizers but also as integral constituents in pesticide formulations. The integration of *Azospirillum* proves instrumental in mitigating reliance on excessive synthetic chemical compounds, manifesting as biofertilizers for plant nutrient provision and bioprotectants for soil-borne pathogen control (52). Various mechanisms employed by *Azospirillum* to mitigate pathogenic damage have been elucidated like encompassing environmental competition, pathogen displacement, suppression of seed

Vol. 19 (Supplementary Issue 3A), September 2025, ISSN 0973-8916 (Print)., 2230-7303 (Online)
10.5530/ctbp.2025.3s.4

Table 1: Different phytohormones produced by *Azospirillum* species along with their use in plant growth and development

phytohormones	Species producing the particular phytohormone	Effect of hormone on plant	Evidence	References
Auxin (specifically IAA)	*Azospirillum brasilense* *Azospirillum lipoferum* *Azospirillum amazonense* *Azospirillum halo praeferens* *Azospirillum irakense*	Phytohormones within this category escalate the xylem and root development, regulate processes associated with vegetative growth, tropism, flowering, and fruiting in plants. Furthermore, they exert influence on photosynthesis, pigment synthesis, the biosynthesis of diverse metabolites, and confer resistance against biotic stress factors.	• IAA is produced by majority of *Azospirillum* strains *in vitro*. • In numerous instances, mutants exhibiting reduced IAA synthesis were found to be less efficacious when juxtaposed with their wild-type parental strains. • In the plants inoculated with different strains, elevated level of IAA was observed. • Mutants characterized by an overproduction of IAA demonstrated a more potent influence on the plant.	(26,27,28,29)
Gibberellins(GA)	*Azospirillum lipoferum* *Azospirillum brasilense*	GAs stimulates cellular division and elongation processes and plays a crucial role in breaking dormancy. Within the seed embryo, GAs serve as signalling molecules, inducing the synthesis of the enzyme alpha-amylase	• *In vitro Azospirillum* spp. metabolize and synthesize GAs. • The introduction of *Azospirillum* strains exhibiting GA production capabilities to gibberellic acid (GA)-deficient mutant dwarf rice results in the reversal of the dwarf phenotype.	(28,29,30,31)

Vol. 19 (Supplementary Issue 3A), September 2025, ISSN 0973-8916 (Print)., 2230-7303 (Online)
10.5530/ctbp.2025.3s.4

		in the aleurone cells, thereby initiating starch hydrolysis. The resultant glucose serves as an energy source for the seed embryo. GAs also contributes to elevated transcription levels of the gene responsible for coding the alpha-amylase enzyme, thereby promoting the synthesis of this enzymatic catalyst.		
Cytokinins	*Azospirillum amazonense* *Azospirillum halo praeferens*	Cytokinins participate in cellular enlargement and division processes, as well as the morphogenesis of shoots and roots, while also influencing senescence.	*In vitro Azospirillum* produce cytokinins.	(28,29,32,33)
Abscisicacid (ABA)	*Azospirillum lipoferum*	ABA plays a crucial role in mediating responses to environmental stresses.	• This compound was identified *in vitro* across various strains. • The interplay between gibberellic acid (GA) and abscisic acid (ABA) contributes to the alleviation of water stress in plants.	(28,29,34,35)
Ethylene	*A.brasilense*	Ethylene participates in	In the culture filtrate of *A. brasilense*	(28,29,36,37,38)

Vol. 19 (Supplementary Issue 3A), September 2025, ISSN 0973-8916 (Print)., 2230-7303 (Online)
10.5530/ctbp.2025.3s.4

		breaking dormancy of the seeds. Its primary impact lies in the induction of senescence in the plant.	Ethylene was found	
Polyamines	*A. brasilense*	Polyamines are synthesized by pathways which are highly regulated in the cells and regulate the growth. They are important compound for reproductive events like pollen development and fertilization.	• *Invitro. T*hese compounds werefound. • Applications of cadaverine mitigatedosmotic stress in the rice.	(28,29,39,40)

germination in parasitic weeds(53), overall augmentation of plant resistance to pathogen infections, and potential inhibition of fungal growth through synthesis of microbial bioactive substances with toxic properties (54).

The colonization of plant roots by *Azospirillum* facilitates the biosynthesis of amino acids, organic acids, sugars, and various aromatic compounds. These bioactive metabolites serve as protective agents, imparting resistance to plants against root pathogens(55). Siderophore production is another strategy used by *Azospirillum* to inhibit the growth of pathogenic microorganism(56). Siderophores produced by *Azospirillum* bind tightly to iron, make it soluble and available for bacteria. The siderophores iron complex is transported back into the *Azosperillium* and is utilized for various metabolic processes. This reduces the availability of iron for other harmful pathogenic microorganisms. Since pathogens cannot compete for the iron sequestered by *Azospirillum 's*siderophores, their growth is inhibited(53,57). *Azospirillum* triggers induced Systemic Resistance in plants which primes the plant's immune system, enhancing its capacity to mount rapid and robust responses against subsequent pathogen challenges. Induced Systemic Resistance fortifies the plant's defence mechanisms systemically, providing broad-spectrum protection against diverse pathogens(58). Together, all these mechanisms make *Azospirillum* an effective biological control agent, enhancing plant growth, boosting resistance to disease, and improving overall plant health (59).

Mitigation of stresses

Plant stress is a state wherein the plant undergoes suboptimal or impoverished conditions, adversely impacting factors such as plant growth, crop productivity, reproductive capability or even leading to plant death if the stress surpass the tolerance limit of the plant (60). A prevalent rationale for the impact of *Azospirillum* on plant growth involves the mitigation of environmental stressors by the bacteria hence facilitating the

Vol. 19 (Supplementary Issue 3A), September 2025, ISSN 0973-8916 (Print)., 2230-7303 (Online)
10.5530/ctbp.2025.3s.4

plant a more conducive growth environment within an otherwise constraining setting (61). In certain instances, inoculation facilitates plant growth in soils that conventionally impose growth limitations (62). Environmental stressors are of various kind, which include stress due to drought (63), salinity (64), heavy metals and toxicity of other substances like humic substances (65).

Salinity emerges as a paramount environmental stressor, exerting harmful and deleterious effects on crop yield and quality globally (66). Around 20% of arable lands worldwide faces the challenges posed by salt stress and the salt-affected regions are continuously expanding, mainly due to shortage of irrigation water resources(67). Salt stress majorly affect the development and growth of plant (68). It heightened intracellular osmotic pressure, leading to the potentially toxic accrual of sodium. Analogous to other abiotic stressors, salt stress exerts multifaceted adverse effects on plant physiology, encompassing nutritional and hormonal imbalances, ion toxicity, oxidative and osmotic stress, and an elevated susceptibility to diseases (69). In similar manner, water stress also emerges as a major environmental stressor exerting substantial influence on global agricultural output, particularly in arid and semi-arid areas. Vegetation encounters water stress either due to limiting water supply at the root level or heightened transpiration rates (64). The root-cause of water stress lies in the deficiency of water, commonly known as drought conditions (70). Water which comprises around 80 to 90% of the biomass of herbaceous plants, serves as the pivotal molecular entity in all plant physiological processes, functioning as the primary medium for metabolite and nutrient transport (71). Drought causes reductions in plant water potential and turgor which hinder the seamless execution of standard physiological functions especially the photosynthetic capacity of the plant. The growth of the plant and their productivity are acutely diminished if the stress is prolonged (72).

Azospirillum species are known to play a key role in enhancing plant growth under salinity stress conditions through several physiological, biochemical, and molecular responses that promote plant growth (73). Studies indicated that prevalent agricultural *Azospirillum* strains demonstrated resilience to elevated salinity levels, reaching up to 2%. The salt tolerance spectrum among species exhibited an ascending gradient from *A. amazonense* (minimal) to *A. halopraeferans* (maximal), with the latter displaying tolerance exceeding 3% NaCl, equivalent to seawater salinity (74). Plants produce ethylene, a stress harmone under salt stress condition which inhibits the plant growth (75). *Azospirillum* produces 1-aminocyclopropane-1-carboxylate deaminase which inhibits the production of ethylene by breaking down its precursor and maintaining growth and development(71). Salinity even disturbs the water potential between soil and roots making it difficult for plants to absorb water. *Azospirillm* by promoting the accumulation of osmo-protectant like proline and glycine betaine helps in maintaining cellular turgor and enable roots to absorb water (76). *Azospirillum* inhibits the production of reactive oxygen species allowing plants to better cope with other stress (74).

Inoculating the plant with *Azospirillum* under the conditions of water stress improves the growth of plant (as shown in Figure 2) (77). Various phytohormones produced by *Azospirillum,* specifically auxins, promote root growth. Increased root area allows plants to improve water uptake capacity(78). Exopolysaccharides produced by *Azospirillum* improves soil structure and water retention around the roots (79). Under water stress condition, Azospirillum alter the expression of stress related genes which control various biochemical and physiological pathways that helps plant to deal with stressful conditions (80).

Part A in Figure 2 exhibits the mechanism adopted by the plants in response to drought stress. Drought stress affect the

Vol. 19 (Supplementary Issue 3A), September 2025, ISSN 0973-8916 (Print)., 2230-7303 (Online)
10.5530/ctbp.2025.3s.4

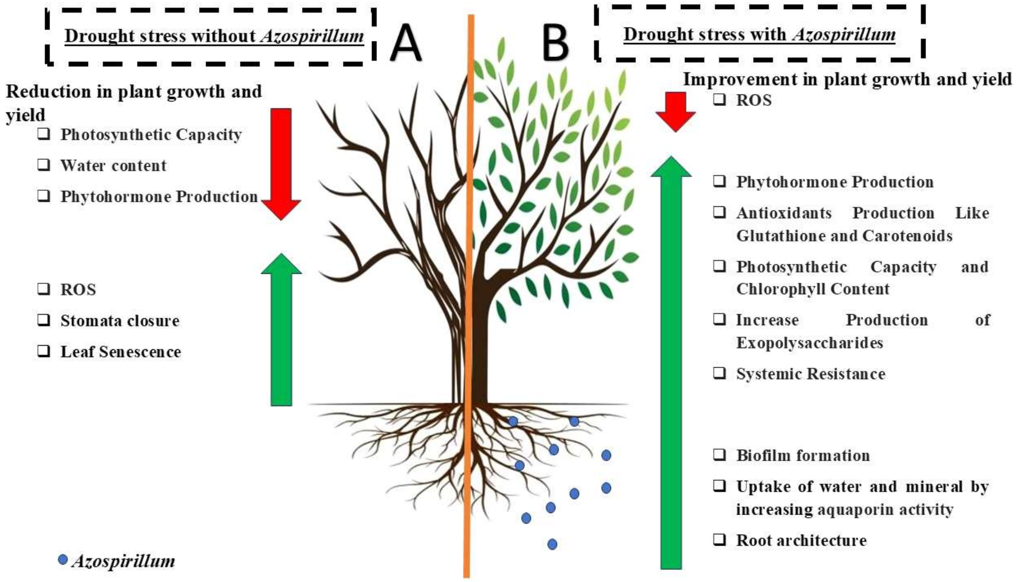

Fig. 2: Comparison of the effects of drought stress with and without *Azospirillum in plants*

plant physiologically and biologically. In stress condition, stomata closure takes place to reduce the water loss through transpiration (Fig. 2, part A). Phytohormone imbalance takes place followed by Reactive oxygen species (ROS) accumulation that causes oxidative stress and inhibit various metabolic pathway like protein synthesis. Root system development gets reduced which reduces the water content. Evapotranspiration (ET) decreases, and leaf senescence takes place, which reduce the yield of the crop. The role of *Azospirillum* in mitigating drought stress can be visualized in Figure 2, part B.*Azospirillum* producesphytohormones like auxin which promotes the development of longer and denser root system. This increases the surface area for the absorption of nutrient and water even from the deeper layers of soil where there are high chances of moisture availability during drought condition. *Azospirillum* influences expression of aquaporin gene in roots of the plant. Proteins of these gene act as water channels, which facilitate efficient movement of water across the membrane of the cells. Exopolysaccharides (EPS) is also secreted by *Azospirillum,* whichis a sticky biofilm that surrounds the root hairs and helps in retaining moisture around the roots and reduce loss of water by evaporation. *Azospirillum* also produces certain antioxidant enzymes like glutathione and carotenoids, which decrease ROS and reduce oxidative stress.

Metal and metalloid ions constitute intrinsic components of Earth's different layer. Nonetheless, high concentrations of these elements can also induce toxicity in various life forms inhabiting the ecosystem, including microorganisms, flora, fauna, and human beings(81). Beyond their inherent occurrence in the environmental matrix, anthropogenic activities have significantly contributed to the release of metal and metalloid ions from their indigenous reservoirs, resulting in the contamination of terrestrial soils, aquatic rivers, marine oceans, and the atmospheric milieu and cause adverse impact on plant

Vol. 19 (Supplementary Issue 3A), September 2025, ISSN 0973-8916 (Print)., 2230-7303 (Online)
10.5530/ctbp.2025.3s.4

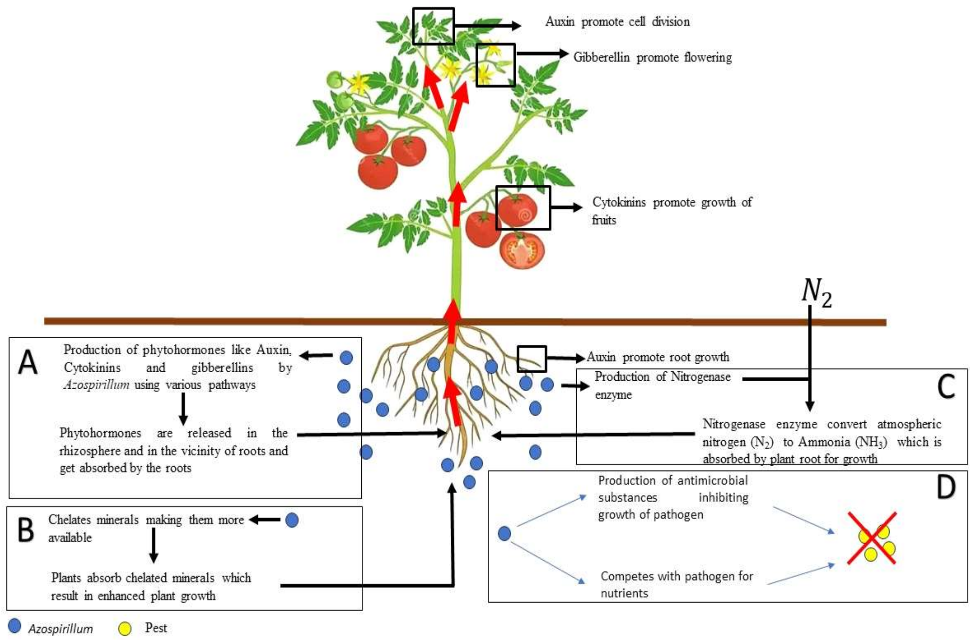

Fig. 3: Mechanism of plant growth promotion by *Azospirillum.*

health(82). An alternative conceivable mechanism for enhancing plant vitality involves mitigating metal toxicity within polluted soils and mine tailings, where, under typical circumstances, plant growth is substantially impeded (78). *Azospirillum* accumulate and absorb these toxic metals reducing their bioavailability to plants, which mitigates the stress these metals cause to plant (75).

The mechanism by which *Azospirillum* helps in promoting plant growth are summarized in Figure 3. *Azospirillum* colonizes in rhizosphere in the soil around the roots of the plant and produces variousphytohormones like auxin, cytokinins and gibberellins using various biochemical pathways in the root vicinity. Plant roots absorb these phytohormones and stimulate plant growth like auxin promote root growth and cell division, gibberellins promote flowering and cytokinins promote development of root.*Azspirillum* releases organic acids and various enzymes that chelates minerals making the minerals more available. Plants absorb that chelated minerals which result in enhanced plant growth.Also,*Azospirillum* adhere to root surface which lead to the formation of biofilm around the root surface, it then produces nitrogenase enzyme that convert atmospheric nitrogen to ammonia. Ammonia is absorbed by plant roots for growth.*Azospirillum* also acts as biological control agent by releasing certain antimicrobial compounds in soil that inhibit the growth of pathogens. *Azospirillum* even competes with pathogen for nutrients, which result in the reduction of pathogenic impact that leads to healthier plants.*Azospirillum* as biological control agent.

Interaction of *Azospirillum spp.* with staple crops

Staple crops forms the backbone of diets for a significant portion of population across the globe. They have high content of

Vol. 19 (Supplementary Issue 3A), September 2025, ISSN 0973-8916 (Print)., 2230-7303 (Online)
10.5530/ctbp.2025.3s.4

carbohydrate, that fulfils the substantial portion of daily caloric intake. The most common staple crops include cereals like rice, wheat, sugarcane and maize, which together account for over 50% of the world's caloric consumption (83). Along with serving as a dietary staple, these crops provide livelihood to millions of farmers. *Azospirillum,* offers a promising approach to enhance growth, improve nutrient use efficiency, and ensure sustainable agricultural practices for these crops (84).

Rice (Oryza sativa)

Rice serves as a pivotal dietary staple for approximately 50% of the world's population, making it one of the most extensively cultivated cereal crop(85). On an annual basis, over 3 billion individuals incorporate more than 100 kilograms of rice into their diets (81). Rice cultivation faces notable constraints, mainly due to the limited availability of water resources, additionally, urban and industrial encroachment in regions like Asia, already grappling with scarce arable land, poses challenges (86,87). The substantial financial investments required for the development of new rice-friendly lands further restrict the feasibility of acreage dedicated to rice-based agricultural systems in the foreseeable future (88).

Different species of *Azospirillum* exert diverse beneficial effects on rice plants. Their specific impact can vary according to various parameters such as strain used, application method, and various environmental factors (89). When used on rice, the bacterium *Azospirillum brasilense* increases the crop's overall productivity and lowers the requirement for nitrogen (90). Inoculating *A. brasilense* increases the uptake of mineral ions (91). After inoculating rice plants with *A. lipoferum*, NH_4^+ and PO_4^- absorption was also improved (92). The utilization of *Azospirillum* strain B510 within the rice agricultural framework provide resistance to pathogens and improve crop yield (93).

In a research study the productivity of rice was significantly increased after inoculation with *A. brasilense* strains Ab-V5 and Ab-V6, boasting a cellular concentration of 2×10^8 cells mL^{-1}, which was administered across four discrete dosage levels (0, 100, 200 and 300 mL ha^{-1}) (94). Furthermore, the researchers explored four distinct application methodologies, encompassing seed inoculation, in-furrow delivery during sowing, soil-based spraying immediately after sowing, and foliar application at the initial stages of tillering. Notably, a consistent pattern of effectiveness was observed across the various inoculation protocols. The optimal response was, when plants were subjected to an inoculum volume of 200 mL ha^{-1}. This specific treatment resulted in a striking 10% augmentation in crop yield relative to the control group, which did not receive the *A. brasilense* inoculation (94).

Azospirillum isolates isolated from north Bengal paddy fields, namely *Azospirillum brasilense, Azospirillum lipoferum, Azospirillum brasilense* and *Azospirillum halo praeferens*, significantly enhance plant growth when used to inoculate "*BRRI dhan-28*" seeds. Rice seeds subjected to inoculation were germinated within a petri dish. The germinated rice seeds from both the inoculated and control groups were then transplanted into earthen pots filled with soil. Various plant growth parameters were meticulously assessed and juxtaposed with those of the control group. The outcomes revealed that all isolate inoculations led to a notable increase in rice seed germination percentage when contrasted with the control. Moreover, the application of *Azospirillum* as an inoculant demonstrated a statistically significant enhancement in plant height, leaf count per plant, dimensions of leaves (both length and breadth), as well as the fresh and dry weight per plant in the rice cultivation (95). Inoculating the root of rice with *Azospirillum* resulted in the significant increment in elongation of roots, surface area of roots, root dry matter and development of lateral roots (96,97).

Sugarcane (Saccharum officinarum)

Sugarcane stands as a pivotal global commercial crop, cultivated all around the

Vol. 19 (Supplementary Issue 3A), September 2025, ISSN 0973-8916 (Print)., 2230-7303 (Online)
10.5530/ctbp.2025.3s.4

world. Functioning as the primary feedstock for white sugar, jaggery and khandsari, it further serves in mastication and the extraction of juice for beverage applications (98). The optimization of sugarcane crop yields not only bolsters agricultural productivity but also serves as a critical determinant in uplifting the economic well-being of participating farmers. One of the most important limiting factor for sugarcane growth is Nitrogen and chemical fertilizers are generally used to meet its demand (99). There are various drawbacks of using chemical fertilizers like they are expensive, detrimental to the environment and even contribute to global warming by greenhouse gasses emission(100). Nitrogen fertilizers add on a significant amount to total cost of the manufactured product requiring sugarcane as a raw product (101).

Azospirillum replace the need of adding N fertilizers by fixing nitrogen available in atmosphere (102). *Azospirillum brasilense* strain Az-V5 when tested on sugarcane variety 'RB86-7515,' protects the sugarcane plant from biotic and abiotic stress factors ultimately influencing the cell viability, root colonization and various other growth parameters including plant height, stalk diameter, tiller count, leaf characteristics and dry matter content in a positive manner (103). Inoculating Sugarcane plant with *Azospirillum brasilense* mitigate the drought stress and result in higher dry weight of shoot and root along with improved efficiency of water usage (104). *Azospirillum* spp. mitigates water stress tolerance under drought conditions, promoting improved root growth and nutrient uptake by improving root development (102).

Maize (Zea mays)

Maize has a pivotal role as a fundamental source of sustenance in numerous nations. In developed economies, it predominantly serves as a vital component of animal feed, while simultaneously fulfilling diverse roles within industrial and energy sectors (105). Maize plays a versatile and ever-evolving role within the broader framework of worldwide agricultural and food systems, exerting a significant impact on aspects related to food security and nutritional aspects (106.107).

A. brasiliense inoculation significantly improved maize growth in terms of plant height and biomass accumulation. Maize yield was notably higher in inoculated plants when compared to non-inoculated controls (108). *Azospirillum brasilense* when inoculated with zinc enhance fungal root colonization with increment in crop yields, nutrient uptake, root development and grain yield in maize under savannah conditions suggesting a synergistic effect between the bacterium and the micronutrient (109). Inoculating maize with *Azospirillum brasilense* Ab-V5 cells enriched with exopolysaccharides and polyhydroxybutyrate significantly improved the plant growth and grain yield even under low nitrogen input. The enriched bioinoculant enhanced stress tolerance and plant-microbe interactions, reducing dependency on chemical fertilizers (110). *Azospirillum brasilense* when inoculated in maize with different soil bioactivator, improved nutrient availability, microbial activity, increased maize yield and plant vigor. These findings suggest that integrating *A. brasilense* inoculation and bioactivators is a promising strategy for sustainable maize production, offering enhanced productivity and soil health benefits (111).

In a greenhouse-based experiment, cultivation of maize plants in pots filled with a mixture of vermiculite and perlite was done. These plants were subjected to various combinations of *Azospirillum spp*. with uniconazole treatments and were harvested after a 30-day period. The use of uniconazole resulted in a reduction in maize plant growth due to its inhibitory effect on gibberellin production. Multiple parameters were assessed, including plant height, fresh weight, and dry weight, as well as the fresh weight of both roots and shoots(112). Additionally, a gibberellin content analysis in the roots using gas chromatography-mass spectrometry was also conducted. The plants treated with

Vol. 19 (Supplementary Issue 3A), September 2025, ISSN 0973-8916 (Print)., 2230-7303 (Online)
10.5530/ctbp.2025.3s.4

Azospirillum spp. exhibited significantly greater height, fresh weight, and dry weight compared to the control plants. For instance, the height of *Azospirillum spp*.treated plants reached 23.5 cm, while the control plants only reached 18.5 cm. The fresh weight of *Azospirillum spp*.treated plants was 5.2 g, in contrast to the 3.8 g recorded for the control plants. Likewise, the dry weight of *Azospirillum spp*.-treated plants was 0.8 g, while the control plants registered 0.6 g. The level of gibberellin in the roots of *Azospirillum spp*.treated plants measured 0.70 ng/g fresh weight, while it was undetectable (n.d.) in the roots of the control plants (112).

Wheat (Triticum)

Wheat holds a significant position among cereal grains worldwide, serving as a crucial element in agriculture, consumption patterns, and international trade (113). Wheat remains a primary source of sustenance for a considerable portion of the global population(114). Multiple factors have jeopardized the long-term viability of traditional wheat cultivation systems, such as the deterioration of soil quality, limited water resources, labour and energy shortages, nutrient imbalances, reduced soil organic carbon levels, diverse persistent weed, pest populations, the proliferation of herbicide-resistant weed species, and emissions of greenhouse gases (115).

The relationship between *Azospirillum* and wheat is characterized by mutual benefits. Within this symbiotic partnership, wheat offers *Azospirillum* a carbon source and a living environment, while *Azospirillum* reciprocates by supplying the wheat plant with nitrogen and various advantageous substances. Numerous research studies have demonstrated that introducing *Azospirillum* into the wheat-growing environment leads to enhanced wheat growth and increased yield (114,115,116). Inoculating wheat with *A. brasilense* improve grain yield across multiple cultivars by increasing the accumulation of essential nutrients including nitrogen, phosphorus, and potassium (113). The co-application of *A. brasilense* with *R. pisi* improve biomass, root development and grain yield under water deficit and partial root drying stress in wheat plant. The combined inoculation mitigates the harmful effect of water stress maintaining leaf water content and photosynthetic efficiency (117). Wheat inoculated with *A. brasilense* showed a 10.3% higher grain yield compared to non-inoculated plants, with greater root and shoot biomass and nitrogen accumulation. Combining inoculation with a reduced Nitrogen application (50 kg N ha^{-1}) increased operating profit by 10.5%, demonstrating cost-effectiveness (118).

Conclusion

The bacterium *Azospirillum,* known for its ability to fix nitrogen and thrive independently, holds a significant position among rhizobacteria species due to its substantial contributions to plant growth. Its multifaceted growth-promoting mechanisms are intricately regulated. With a long history of use in agriculture, *Azospirillum* has been consistently applied to enhance crop productivity and overall plant development. The widespread adoption of *Azospirillum* inoculants in crop production has been well-documented and firmly established. Notably, these inoculants have demonstrated effectiveness in boosting grain yields across various staple crops. This microorganism demonstrates potential in enhancing the sequestration of various phytotoxins within plant roots, bearing implications not only for sustainable agriculture but also in ecological toxicology.

Despite considerable strides in research, important gaps persist, particularly in comprehensively understanding its genetic blueprint and molecular mechanisms. Addressing these gaps is crucial to broaden the scope of its potential applications. While existing studies highlight the potential of *Azospirillum* spp. to enhance plant growth and stress tolerance, there is a limited elucidation of the specific signalling pathways and genetic factors that modulate these responses across

Vol. 19 (Supplementary Issue 3A), September 2025, ISSN 0973-8916 (Print)., 2230-7303 (Online)
10.5530/ctbp.2025.3s.4

diverse crop species. Additionally, the influence of environmental factors, such as soil characteristics and climatic conditions, on the effectiveness of *Azospirillum* -plant associations remains inadequately explored. Addressing these gaps necessitates in-depth molecular and genetic studies that decipher the intricate signalling cascades and regulatory networks involved in *Azospirillum* -mediated effects on different crop varieties. Moreover, comprehensive field trials incorporating varying environmental conditions are warranted to validate and optimize the efficacy of *Azospirillum* spp. in diverse agricultural settings, paving the way for more targeted and sustainable applications in crop production.

Acknowledgement

Authors of this article acknowledge their gratitude to Amity Institute of Biotechnology, Amity University Uttar Pradesh, Noida, Uttar Pradesh for their support and encouragement.

Conflicts of Interest

The authors declare that they have no conflicts of interest.

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