Review Article

Action Mechanisms of Plant Growth Promoting Cyanobacteria in Crops In Situ: A Systematic Review of Literature

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1. Introduction

Nowadays, agriculture represents one of the most significant causes of environmental contamination [1, 2]. The accelerated growth of the world’s population demands greater food production. The World Health Organization (WHO) estimates that, by 2029, the world’s food production will have to be increased by 50% [3]. The agricultural soil in the world is severely damaged by use of chemical fertilizers and excessive irrigation, which have led to erosion, nutrient depletion, and salinity. In Canada and the United States alone, around 3 billion tons of topsoil is lost due to the use of inorganic compounds on crops [4].
Protection Agency (EPA) [8–10]. Some environmental problems caused by these compounds are soil fertility loss, inefficient nutrient-use, and low crop yields. Heavy metals and radioelements also accumulate, leading to the introduction of such compounds to the trophic chain and posing health hazards to living organisms [11–13].

All things considered, there is a need for other strategies that include compounds or aggregates other than conventional fertilizers in order to increase the crop yields without compromising the environment [14]. Biofertilizers, which consist of microbial inoculants such as bacteria and mycorrhizal fungi, have become the most promising option to increase nutrient availability in soils and plants, reduce dependence on expensive chemical fertilizers, and mitigate diseases related with crop handling, such as viroids, viruses, fungi, and pathogen bacteria [15–17]). Even when microbial inoculation has been adopted in several crop systems, their beneficial effects are difficult to reproduce, given their vulnerability to diverse types of environmental stress when exposed to conditions of drought, salinity, and extreme temperatures in the rhizosphere [18]. However, Swarna-lakshmi et al. [19] indicate that the use of biofertilizers that contain consortiums of autochthonous microorganisms with promoting growth plant rhizobacteria (PGPR) can improve their effect [20].

Cyanobacteria are prokaryotic photosynthetic microorganisms, and some are facultative heterotrophs, capable of using various sources of carbon and organic nitrogen, proliferating in all types of habitats, even if they are of extreme nature [21, 22]. Both their physiological plasticity and their ability to fix nitrogen, which allows the inorganic nitrogen of the air (N₂) to be transformed into organic nitrogen to be used by plants, making them ideal for their use as biofertilizers. These bacteria can also form symbiotic associations with plants and other microorganisms; since they are photosynthetic, they are able to use carbon dioxide (CO₂) and water to generate monosaccharides and oxygen, from which plants can also benefit [22–24]. There is even more to using cyanobacteria as biofertilizers, since their action as PGPR or their PGP traits have also been proven through the observation of various mechanisms such as nutrient solubilization, plant growth hormone production, and, indirectly, antagonism to pathogenic fungi through siderophore production [18, 20, 25]. Also, they contain a wide variety of vitamins and produce a diversity of secondary metabolites that are a source of bioactive molecules, which also have herbicidal, insecticidal, and immunosuppressive activities. [3].

According to Wang et al. [22], several researchers have analyzed the use of cyanobacteria as biofertilizers in rice crops throughout countries such as India, Japan, the Philippines, and Iran. The diverse studies revealed an increase of up to 19.5% in rice crop yields. Increased grain yields, plant weights, and leaf lengths were also reported: a 53% increase in the weight of rice plants, 66% in the length of roots, and 58% in the weight of leaves and stems [22]. In turn, the potential of cyanobacteria to increase nutrient bioavailability in other crops such as wheat, corn, beans, and cassava has been studied. However, field data on the plant promoting mechanisms of cyanobacteria are limited and disorganized. Additionally, there are no current review articles focused on describing such mechanisms, which means that the knowledge about the topic is still insufficient when considering subsequent implementation in experimental trials [20]. This is because the strong influence of external factors, especially in fluctuating environments, on the growth of cyanobacteria, also known as epigenetics, still constitutes a main problem [26, 27]. Therefore, through a systematic review of scientific literature published in the last 10 years, the main objective of this study was to describe the action mechanisms of various cyanobacterial genera on plant growth promotion in diverse crop systems in situ.

2. Materials and Methods

2.1. Search Strategy. The study was carried out in accordance with the Prisma statement, it proposes a methodology for systematic reviews [28]. A systematic literature search was performed in ScienceDirect and Scopus databases under three criteria: (a) sensitivity, with DeCS and AGROVOC descriptors, (b) specificity, with the combination of Boolean operators and terms defined according to the research problem, and (c) completeness, by means of non-DeCS descriptors, together with the gray literature found.

The search was performed using the general route [(cyanobacteria) AND (“growth promoting” OR biofertilizer OR PGPR)]. In ScienceDirect and Scopus databases, the time limits “2009 to present” and “limit to 2009–2018,” respectively, were used to cover the scientific literature published between these dates. Each specific route is presented below.

2.2. ScienceDirect. (“Cyanobacteria”) AND (“growth promoting” OR “biofertilizer” OR “PGPR”).

2.3. Scopus. (“Cyanobacteria”) AND (“growth promoting” OR “biofertilizer” OR “PGPR”).

In February 2018, the references found, together with the respective abstract, were registered in a Microsoft Office Excel database. Duplicates were eliminated.

2.4. Inclusion and Exclusion Criteria. The study included original research articles from the scientific literature of the last 10 years, written in English, which reported the action mechanisms of cyanobacteria on plant growth, types of crop used, and taxonomic classification of microorganisms involved in the mentioned process. The articles that described the use of ATCC strains and the performance of in vitro tests were excluded in order to analyze only the action of cyanobacteria as PGPR agents in natural and experimentally reproducible conditions. Data were extracted from each publication and tabulated for further analysis.

2.5. Reproducibility. The reproducibility of the study was assessed by using the search paths in the databases selected, together with the application of inclusion and exclusion criteria by two readers independently. Additionally, any
discrepancy related with article eligibility was resolved by a third reader.

2.6. Analysis of Results. The data extracted and analyzed were related with the taxonomic classification of cyanobacteria, the mechanisms that intervene in plant growth promotion, and the respective cyanobacterial genera involved. The information gathered also referred to the type of crops where biofertilizers with cyanobacteria were employed.

3. Results

After using the search protocol indicated, a total of 127 articles were obtained (ScienceDirect 20 and Scopus 107). Once 17 duplicates were deleted at the Microsoft Excel database, 110 publications were evaluated based on their title and abstract content; 69 of them were discarded since they did not meet the inclusion criteria. A total of 41 articles were analyzed; 20 of them met the exclusion criteria. The search protocol resulted thus in a total of 21 articles selected for systematic review (Figure 1).

Two articles classified as a thesis or a dissertation were added by exhaustivity for a total of 23 papers obtained, in accordance with the same inclusion and exclusion criteria. This gray literature was found in Google Scholar (Table 1, Figure 1).

3.1. Distribution of Studies according to the Country of Origin and Publication Year. The systematic search of the scientific literature published between 2009 and 2018 resulted in a total of 23 articles, carried out in 5 different countries (Figure 2), among which India and Egypt stand out with 14 and 4 publications, respectively, followed by Iran and Pakistan with 2 publications each, and finally, Russia with 1 publication. The high number of publications in these countries is probably due to rice and wheat being cultivated in about 13.5 million hectares of the Indo-Gangetic Plain (IGP) in and around South Asia, in countries such as India, Pakistan, Bangladesh, and Nepal. These crops contribute to 80% of the total production of these cereals and are an important part of the economy and food sustainability across much of Asia [4].

Besides, the considerable number of paddy fields in these countries creates the necessary conditions for the proliferation and establishment of cyanobacteria [17]. On the other hand, regarding publication year, the works obtained in the systematic review did not show a significant variation and, in fact, maintained an average of approximately two articles per year between 2009 and 2018.

3.2. Research Objectives. Although all literature analyzed was determined by the inclusion and exclusion criteria established and is based on the same research premise, their diverse research objectives can be classified in four subgroups according to certain general features (Table 2). Simultaneously, the objectives can be divided into two groups. The first one contains those of an observational kind, which focus on understanding the effect of cyanobacteria used as PGPR and their mechanisms or their PGP traits. The second group, also the most predominant in the studies analyzed in this systematic review, contains the distinctly experimental objectives, which attempt to explain, through different methodologies, the phenomena involved in the mechanisms used by cyanobacteria.

4. Discussion

4.1. Cyanobacterial Genera Used as PGP. Cyanobacteria are photosynthetic prokaryotic organisms highly able to colonize many habitats under diverse environmental conditions and, therefore, are widely found around the world [33]. Cyanobacteria are used in agriculture as biofertilizers and soil stabilizers since they can promote cell division and plant elongation [41]. They can directly or indirectly increase plant growth rate: directly, through the production of biologically active growth promoting substances such as phytohormones (auxins, gibberellins, and cytokinins) and indirectly when cyanobacteria prevent the plant deterioration caused by one or more pathogenic microorganisms [33]. In addition, they can use other mechanisms such as N2 fixation and polysaccharide production [36]. Filamentous cyanobacteria Nostoc sp. and Anabaena sp. are some of the most commonly reported cyanobacteria genera with PGP characteristics. Other genera such as Cylindrospermum, Calothrix, Plectonema, Phormidium, and Gloeotrichia have also been mentioned [4, 25].

Nowadays, the genera most commonly used as PGPR in most crops are Nostoc sp. and Anabaena sp. [4, 17, 18, 34, 43]. However, genera such as Cylindrospermum sp., Synechococcus sp., Aulosira sp., Syctogenema sp., Tolypothrix sp., Westiellopsis sp., Calothrix sp., Phormidium sp., and Oscillatoria sp. are also included in the reports (Figure 3) [4, 29, 31, 38]. A study conducted by [20] reports the capacity of two cyanobacteria isolates, identified as Anabaena sp. and Calothrix sp., to produce ammoniacal and indole compounds and to inhibit the effects of a pathogenic fungus. It was established that the combination of these cyanobacterial isolates and Provi dencia sp. bacteria led to an enhanced yield in a wheat crop [25, 31]. In another study by [17], several Anabaena sp. species, including A. spi rodies, A. variabilis, A. torulosa, and A. oscillarioides, were isolated and identified in paddy fields in Iran; a large proportion of these species was found in such soil during spring, therefore the season with the highest concentration of cyanobacteria population.

Discrepancies among the cyanobacterial species mentioned in studies may be attributed to their morphological or physiological differences, which include cell size and the presence of cell inclusions, such as gas vesicles and polyphosphate granules, and also, to the genotypic characteristics of existent taxa and their adaptive or resilience capacity [46].

4.2. Action Mechanisms of Cyanobacteria with PGPR or PGP Characteristics. Cyanobacteria play a significant role in the maintenance and improvement of soil fertility, by
improving yields, nutrient uptake, and growth in different types of crops. For that reason, they are considered natural biofertilizers [17, 20]. In order to cause such effects, cyanobacteria use diverse PGPR mechanisms (Table 3) such as the most often reported N₂ fixation [36]. Nevertheless, cyanobacteria are also able to implement other strategies, including increase in soil pores by using filamentous structures and adhesive substances, excretion of...
growth promoting substances such as hormones (auxins and gibberellins), vitamins and amino acids, increased capacity of soils to retain water, increased nutrient availability after their death, decreased salinity, prevention of weeds growth, and increased amount of soluble phosphate in soils through the excretion of organic acids and extracellular polysaccharides, among others [4, 17, 36]. Some cyanobacteria can secrete hydrogen cyanide, which functions as an antibacterial and antifungal substance, allowing the biocontrol of phytopathogens [41]. It should be noted that the quantity and quality of the excreted compounds vary according to the cyanobacterial species, their growth phase, and the environmental conditions to which they are exposed [4].

Cyanobacteria are major elements of biogeochemical cycles, specifically, carbon and nitrogen cycles [18]. Moreover, there is evidence of the capacity of free-living cyanobacteria such as *Synechococcus* sp., *Anabaena* sp., *Chlorogloeopsis* sp., and *Nostoc* sp. to establish symbiotic associations with a wide range of eukaryotic organisms (Panax, Medicago, Nicotiana or wheat, corn, bean, sugar beet, and rice crops), which constitutes an effective mechanism to promote plant growth [18]. There is also proof of the ability of cyanobacteria to excrete indole-3-acetic acid (IAA), amino acids, and other compounds to the environment, which can enter the root cortex, stimulating the growth of soil microbial populations [25].

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**Table 2: Research objectives**

| Research objective                                                                 | Reference                      |
|-----------------------------------------------------------------------------------|-------------------------------|
| To understand and evaluate the PGPR effect of various cyanobacterial strains on wheat and pea crops | [19, 20, 25, 29–31].          |
| To isolate and identify native plant-growth-promoting cyanobacterial strains in wheat and rice crops | [4, 32–36].                   |
| To determine the effectiveness of cyanobacteria colonization, their physical, metabolic and enzymatic effects, as well as their impact as biofertilizers in stressed soils, corn, and rice crops | [17, 37–40].                  |
| To identify the most promising combinations of plant growth promoting cyanobacteria for effective nutrient management in rice plants | [32, 35, 41–43].              |
| To improve rice plants efficiency in saline soil and decrease the electrical conductivity of the soil using N-fixing cyanobacteria as biofertilizers | [32, 44].                    |
| To determine the potential of a consortium of endogenous cyanobacteria and CBBs (cyanobacterial biofilmed fertilizers) for the bioremediation of soil and wheat crops growth under greenhouse conditions | [18, 31, 45]                  |

Source: own elaboration
A study conducted by Swarnalakshmi et al. in 2013 analyzes the effect of nitrogen-fixing cyanobacteria and phosphate solubilizers in wheat seeds under controlled conditions. When microbiological parameters, soil chlorophyll and nitrogenase activity, were estimated at 4 to 14 days after sowing, an increase in soil chlorophyll was found, due to the establishment of cyanobacterial biofilms. The treatments with the highest chlorophyll content and the highest acetylene reducing activity involved the genus *Anabaena* sp.; *Anabaena* sp. inoculants in soil recorded a 57.42% increase in available nitrogen, compared with the controls used in the study.

Adak et al. [32], Prasanna et al. [38], Salama [35], and Verma et al. [31] also reported nitrogen fixation by cyanobacteria as a PGPR characteristic in different crops. On the other hand, in the study conducted by Nisha et al. in 2018, the biofertilizers used were composed of two isolated strains of *Nostoc* sp. and led to the increase of key nutrients such as total Kjeldahl nitrogen (TKN) (7–16%), total organic carbon (TOC) (12%) and available phosphorus (17%) in saline soil. Regarding the mechanism of phosphate solubilization, it was reported that when this element is assimilated by cells during growth and then released, it decomposes as soluble organic phosphate compounds and is subsequently mineralized to orthophosphate, causing soil available phosphate to increase. Such is the reason for the significant role cyanobacteria application plays in inorganic phosphate mobilization by producing extracellular phosphatases and excreting organic acids. The study also showed that the treatment with cyanobacteria significantly increased carbon mineralization in soil. Finally, soil treated with cyanobacteria also showed an effect on nitrogen mineralization, where there was an increase of 22 to 60% in NH$_4^+$ + N. The heterocystic cyanobacteria used were able to fix N$_2$ by increasing TKN [45].

Singh et al. [40] evaluated the effect of the colonization of several strains of cyanobacteria in rice crop, at physical, metabolic, and enzymatic levels. This study presents the mechanisms of phytohormone production and bioactive compound excretion. The plants inoculated with *Plectonema boryanum* after 15 days showed a maximum plant and root length of 17.6 cm and 7.3 cm, respectively, a plant weight of 2.18 g, and after 30 days, 24.1 cm, 8.6 cm, and 3.1 g, respectively, compared with that of the control without cyanobacteria. Rice leaves showed a maximum accumulation of total phenol after the inoculation with *Anabaena oryzae* 30 days after sowing. The production of phenolic acids and flavonoids, involved in plant/microorganism interactions and in the promotion of the root being colonized by microorganisms, was also reported. Finally, there was evidence of various metabolites in the rhizosphere enhancing the growth of other cyanobacteria and higher plants. All things considered, the cumulative effect of metabolites such as phenolic compounds, flavonoids, and phytohormones like IAA and abscisic acid is thus proven; these, together with amino acids such as aspartic acid, glutamic acid, proline, valine, glycine, and alanine, produced and released by cyanobacterial inoculants in the plant rhizosphere, are directly responsible for the PGPR effect or PGP characteristics [25, 29, 31, 32].

4.3. Effects of Cyanobacteria Used as PGPR Microorganisms or Those Having PGP Characteristics. Soil-plant-microorganism interactions are complex and have the primary role in both plant health and productivity [42]. Many studies have suggested that plants protect themselves from damage originated in oxidative stress as well as from pathogens and adverse environmental conditions. The colonization of PGPR microorganisms, such as cyanobacteria in the root, is thus one of the main defense mechanisms that allow them to fight such types of problems [40]. Some of the most frequently reported effects of cyanobacteria as PGPRs are the improvement in plant growth and crop yields, reflected in the length of roots, leaves, and plant structures. Besides, it has been found that using cyanobacteria as biofertilizers reduces the use of nitrogen fertilizers by up to 50% [29]. The cyanobacteria is considered important in carbon, nitrogen, and oxygen cycles, since they are responsible for the production of 30% of the oxygen on the planet every year [45]. These microorganisms can also produce biocontrol agents, useful for the treatment of phytopathogenic microorganisms [37].

Nowadays, many of these effects continue to be reported by a number of authors. In a study carried out in Egypt, after applying a treatment with *Nostoc* sp., *Anabaena* sp., and...
Calothrix sp. cyanobacteria, Salama [35] reported increased height of rice plants with maximum values of 86.92 cm and 83.75 cm, compared with that of the controls, where values of 70.21 cm were obtained. Additionally, findings indicated that with the individual or combined inoculation of these cyanobacteria, both the crop yield and 1000 grain weight of rice plants significantly increased in comparison to treatments without inoculation. The influence of treatments with cyanobacteria was notorious in another study, carried out by Saadatnia and Riahi in 2009. Cyanobacteria were used in a rice crop in Iran, where germination was observed 2 days after sowing, and a 3 cm root length was also obtained, whereas the seeds in the control group germinated 5 days after sowing, with a 0.5 cm root length. The same study makes reference to previous research reporting a 69% increase in root length, 137.5% in plant fresh weight, 20% in plant dry weight, 28% in soil moisture, and 9.8% in soil porosity. The authors like Manjunath et al. [25], Osman et al. [29], and Shariatmadari et al. [19] report the production of phytohormones like IAA, stimulating the growth of crops in which the treatments with cyanobacteria were applied.

### 4.4. Types of Crops Where Cyanobacteria Biofertilizers Have Been Tested

Cropping systems of rice and wheat, cereals of high demand in Asia and much of the world, occupy about 24 million hectares of cultivated land in the Asian continent. It is precisely in this type of crops where the effect of microorganisms such as cyanobacteria has been studied in order to mitigate the decrease in yields and improve their sustainability [4, 17]. The potential of this type of microorganisms to increase nutrient availability in staple food crops of corn, bean, and cassava, as well as cotton crops, has also been studied [20, 29, 30, 38].

At present, the use of cyanobacteria as biofertilizers continues to be widely studied mainly in rice and wheat crops [17, 20, 25, 36]. However, the authors like Osman et al. [29], Prasanna et al. [37, 39], Shariatmadari et al. [19], and Swarnalakshmi et al. [19] also report in their studies the positive impact of cyanobacteria on pea, corn, bean, sugar beet, pumpkin, cucumber, potato, and tomato crops, pointing at the growing expansion of the use of biofertilizers based on cyanobacteria to improve yields of all kinds of crops.

### 5. Conclusions

Most studies on the use of cyanobacteria as biofertilizers and their mechanisms to promote plant growth in diverse types of crops come from the Asian continent and from part of Africa, which may be due to the largest cereal-producing countries in the world being located there, with extensive fields of corn and wheat, among other products. Although there were no studies conducted in the American continent, more specifically, in Latin America, the use of cyanobacteria as PGP microorganisms is shown as a promising practice to increase yields, soil quality, and crops typical in the region. This practice would benefit from the tropical weather of South American countries since it would substantially promote the proliferation of several cyanobacterial genera with PGP characteristics.

This systematic review evidenced various beneficial effects that cyanobacteria have on plants, such as a significant increase in plant and root length and a reduction in the use of chemical fertilizers in crops, with an ensuing progressive reduction of environmental pollution and production costs in agriculture.

The use of cyanobacteria as biofertilizers may be a promising strategy because these microorganisms show a great adaptability to environmental conditions; additionally, they contribute an important volume of biomass to soil, even after their death. They may also help in the regulation of biological functions in other microorganisms that are beneficial to soil, as many of the articles that we analyzed have shown. Thus, cyanobacteria abundance and diversity may change the soil’s conditions, the same as soil conditions may change cyanobacteria populations. This is an important reason to promote these types of studies, which may help in finding trends or differences in further studies that can guide decision taking.

### Data Availability

The research articles used to support the findings of this study are available from the corresponding author upon request at the e-mail: leonardo.rios@udea.edu.co.

### Conflicts of Interest

The authors have no conflicts of interest to disclose.
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