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Cyanobacteria and microalgae as potential sources of biofertilizers: a review

Cianobacterias y microalgas como fuentes potenciales de biofertilizantes: una revisión

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Abstract

Cyanobacteria and microalgae represent promising sources for sustainable production of biofertilizers and biostimulants, which can improve crop yield and quality and contribute to food security. However, despite their potential, their exploration remains incomplete, hindered by technical and economic challenges that arise when attempting to scale up production. The primary focus of this review is to delve into the active chemical compounds responsible for the biofertilizing and biostimulating roles of cyanobacteria and microalgae. In addition, it explores the essential unit operations involved in transforming their biomass into potential bioproducts. Moreover, this review highlights studies that have employed cyanobacteria and microalgae as sources of biofertilizer in various crops, describing their mode of action and application. By integrating cyanobacteria and microalgae processing with other advanced biotechnological, the viability of these products for sustainable agriculture can be significantly enhanced.

Keywords: agriculture, biostimulant, growth-promoter, nitrogen fixation

Resumen

Las cianobacterias y las microalgas representan fuentes prometedoras para la producción sostenible de biofertilizantes y bioestimulantes, que pueden mejorar el rendimiento, la calidad de los cultivos y contribuir a la seguridad alimentaria. Sin embargo, a pesar de su potencial, su exploración sigue siendo incompleta, obstaculizada por los desafíos técnicos y económicos que surgen cuando se intenta escalar la producción. El objetivo principal de esta revisión es profundizar en los compuestos químicos activos responsables de las funciones de biofertilización y bioestimulación de las cianobacterias y las microalgas. También, explora las operaciones unitarias esenciales involucradas en la transformación de su biomasa en potenciales bioproductos. Además, esta revisión destaca estudios que han empleado cianobacterias y microalgas como fuentes de biofertilizante en diversos cultivos, describiendo su modo de acción y aplicación. Mediante la integración del procesamiento de cianobacterias y microalgas con otras herramientas biotecnológicas avanzadas, se puede mejorar significativamente la viabilidad de estos productos para la agricultura sostenible.

Palabras clave: agricultura, bioestimulante, fijación de nitrógeno, promotor de crecimiento

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INTRODUCTION

Sustainable agriculture is predicated on the ability to guarantee food security worldwide for the foreseeable future. Current agricultural practices depend largely on chemical fertilizers, as these are inexpensive and provide immediate availability of nutrients to crops that feed an ever-increasing human population (1.1% per year). Although such products have helped many countries to increase crop yield, it has also raised many issues (Baweja et al., 2019).

Combined with the application of pesticides and overirrigation, current agricultural practices often result in loss of soil fertility, environmental pollution, greenhouse gas emissions, overuse of water resources, damage to human and animal health, and food insecurity. These negative side-effects occur partly due to inefficient utilization of nitrogen-based fertilizers (e.g., urea, anhydrous ammonia, and ammonium nitrate) by plants, with only approximately half of the applied fertilizer being effectively absorbed (Govindasamy et al., 2023). The remaining half contributes to surface water pollution, leading to eutrophication and acidification (Kollmen and Strieth, 2022). To ameliorate environmental conditions and promote soil remediation without compromising food security, a radical change away from current agricultural practices is necessary. A proposed solution is the widespread adoption of biofertilizers and biopesticides (Boraste et al., 2009; Mutale-Joan et al., 2023).

Biofertilizers are defined as biologically based compounds that exhibit beneficial properties for plant growth and development (Gonçalves, 2021). These properties extend beyond nutrient provision and encompass enhanced nutrient absorption, atmospheric nitrogen fixation, improvement of soil conditions, and promotion of plant growth (Mącik et al., 2020). Biofertilizers are classified by the taxa used to create them as well as their mode of action (Boraste et al., 2009). Common taxa used as sources of biofertilizers include mycorrhizal fungi, rhizobacteria, nitrogen-fixing rhizobia, macroalgae, microalgae, bacteria, and cyanobacteria (Kalayu, 2019; Malusá et al., 2012). Modes of action are comprised of various mechanisms such as nitrogen fixation, potassium solubilization, and phosphorus mobilization, which contribute to the availability of macronutrients. Additionally, zinc-iron solubilizing bacteria and plant growth-promoting rhizobacteria play a crucial role in enhancing the availability of micronutrients (Joshi et al., 2020).

Of the aforementioned taxa, cyanobacteria (e.g., *Arthrospira* spp.) have gained significant attention due to the diversity of products that can be produced from its biomass, catering to industries including food, feed, pharmaceuticals, nutraceuticals, cosmeceuticals, and research (Badr et al., 2019). As biofertilizers, these microorganisms, are highly effective due to their nitrogen fixation capabilities and the abundance of bioactive compounds in their biomass, including but not limited to growth hormones, vitamins, and amino acids (Carvajal-Muñoz and Carmona-Garcia, 2012; Singh et al., 2016; Rakshit et al., 2021). While other taxa share this mode of action, cyanobacteria and microalgae have superior nutrient and active compound release abilities (Abinandan et al., 2019). Some of the active compounds produced by cyanobacteria include pigments, amino acids, polysaccharides, phytohormones, vitamins, and bioactive metabolites such as carotenoids, indole alkaloids, terpenoids, mycosporine-like amino acids, non-ribosomal peptides, and polyketides (Kollmen and Strieth, 2022; Poveda, 2021). These compounds can contribute to plant growth enhancement, increased resistance to biotic and abiotic stress, and improved soil conditions (Martínez-Francés and Escudero-Oñate, 2018; Renuka et al., 2018).

Microalgae are also highly valued as sources of biofertilizers and biostimulants. Their capacity for gradual nutrient and active compound release, coupled with their nutrient content consisting of nitrogen, phosphorus, potassium, magnesium, calcium, and other microelements, underscore the potential of this taxon for enhancing agricultural productivity (Coppens et al., 2016; Saeid and Chojnacka, 2018). As biostimulants, microalgae are a source of phytohormones, sulfated exopolysaccharides (EPS), amino acids, antibiotics, fungicides, bactericides, vitamins, carotenoids, micro and macroelements, promoting the development of plants in diverse growth phases and improving the crop yields and soil structure (Abinandan et al., 2019). Both microalgal- and cyanobacterial-based biofertilizers share additional beneficial properties, including detoxification of pollutants and excretion of plant growth promoting substances, alleviating biotic and abiotic stresses on crop plants (Mącik et al., 2020). Cyanobacteria as effective biofertilizers is not new to science; the first report evaluating their potential application was published in 1939 (Boussiba, 1988). Despite long-standing interest and research spanning nearly a century, global utilization of cyanobacterial or microalgal biofertilizers has not yet been achieved, and this will remain the case until significant challenges are addressed.

Common barriers to the adoption of biofertilizers include lack of knowledge of species present in agroecosystems (Simbaña, 2019), low nutrient contents relative to chemical fertilizers (Carvajal-Muñoz and Carmona-Garcia, 2012), and low technical and economic feasibility for large scale production. Examining unique cases, like the paddy rice fields in China, offers valuable insights. Nitrogen-fixing cyanobacteria were first applied to Chinese rice fields in 1939, and subsequent research has consistently highlighted the numerous benefits to rice cultivation that arise from soil inoculation with microorganisms (Bao et al., 2021; Kim et al., 2018; Qiu et al., 2002; Song et al., 2021).

The objective of this review is to consolidate existing knowledge on cyanobacterial and microalgal biofertilizer technology, with the aim to facilitate access to crucial information for biofertilizer production. This review provides a comprehensive examination of biofertilizer modes of action, and the various stages involved in their production, specifically from cyanobacterial or microalgal biomass. Furthermore, this review includes a comprehensive review of diverse primary research and review articles written in English or Spanish published from 1988 to 2023 that showcase the biofertilizing and biostimulating properties of these microorganisms on commonly cultivated crop plants. The retrieved articles underwent a rigorous screening process to identify those demonstrating promising outcomes of cyanobacteria or microalgae as a biofertilizer source across various crops or offering crucial insights on the topic. The articles that were considered included updated definitions and robust experimental methodologies with accompanying quantitative results.

RESULTS AND DISCUSSION

Modes of action

Cyanobacterial and microalgal extracts vary in their modes of action which define their utility as biofertilizers or biostimulants. Four key mechanisms, nitrogen fixation, phosphate solubilization, plant growth promotion, and soil conditioning are explored below.

Nitrogen fixation

Nitrogen is one of the macronutrients needed for plant development and it is crucial in all enzymatic reactions in plants cells. Nitrogen deficiency will limit plant growth and reproduction. Despite comprising 78% of the Earth's atmosphere, nitrogen in the form of dinitrogen gas (N_2) is inaccessible to plants due to the triple bond between atoms that render it chemically stable (Esch, 2014). The process to transform dinitrogen gas into a useable form for plants is called biological nitrogen fixation (Mącik et al., 2020).

There are two types of nitrogen-fixing microorganisms: free-living (non-symbiotic) bacteria, including *Azotobacter* sp., *Azospirillum* sp. and cyanobacteria such as *Anabaena* and *Nostoc*, and symbiotic bacteria such as *Rhizobium*, *Frankia*, and *Mesorhizobium*. Nitrogen fixation in cyanobacteria is a light-stimulated process and depends upon several biotic and abiotic factors such as moisture and temperature (Esch, 2014; Issa et al., 2014).

Crops benefit from nitrogen-fixing cyanobacteria, which not only provide nitrogen fertilizer but also contribute to the organic matter in biofertilizers. This organic matter comprises a diverse array of compounds, such as amino acids, vitamins, auxins, and the biomass of the cyanobacteria themselves (Bao et al., 2021). This is very useful for agriculture and has several positive effects on the soil and plants enhancing growth and crops yield. Algal-based biofertilizers are considered the best alternative source of nitrogenous chemical fertilizers since they are fuel-independent, cost-effective, and easily available without causing soil and water pollution (Dineshkumar et al., 2020).

Cyanobacteria possess the ability to convert atmospheric nitrogen into a usable form, despite the sensitivity of the enzyme responsible for this process, nitrogenase, to oxygen. To overcome this challenge, cyanobacteria have evolved strategies such as spatial separation, achieved through specialized cells called heterocysts (Figure 1), which create an environment with low oxygen levels conducive to nitrogen fixation. Additionally,

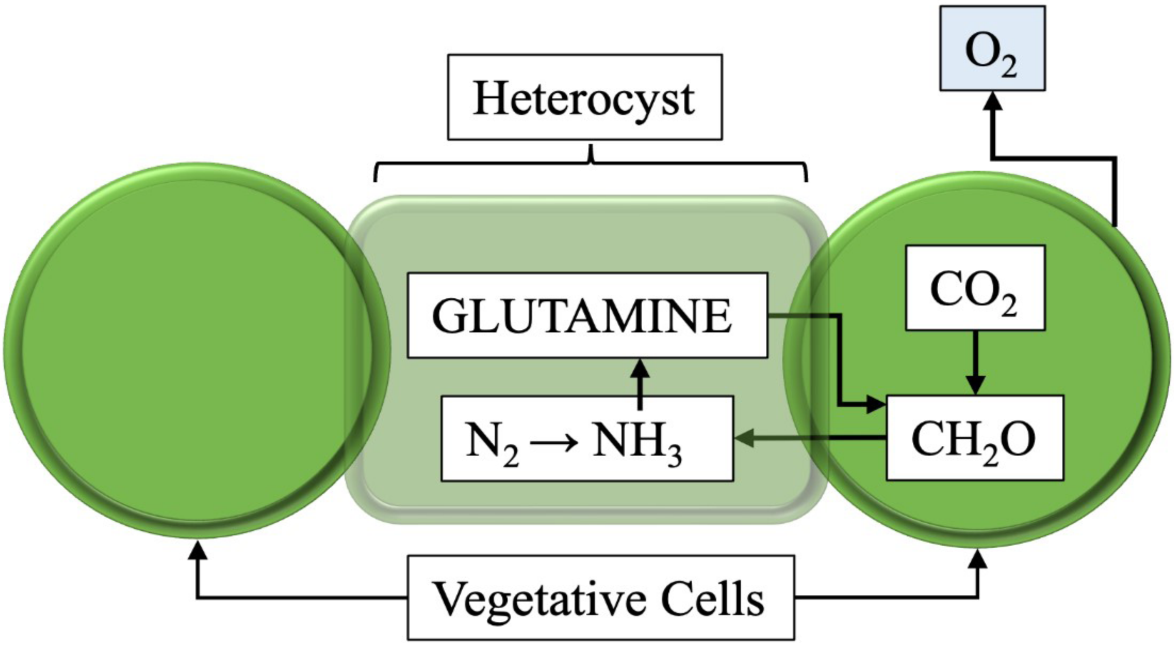

Figure 1. Diagram illustrating nitrogen-fixation by heterocysts, photosynthesis by vegetative cells, and chemical exchange between both. Adapted from Kollmen and Strieth (2022).

cyanobacteria employ temporal separation by carrying out nitrogen fixation during the night when photosynthesis and oxygen production are reduced. Some cyanobacteria even employ a combination of these strategies to maximize their nitrogen-fixing potential. These adaptations enable cyanobacteria to thrive by efficiently harnessing atmospheric nitrogen (Stal, 2015).

Phosphate solubilization

Phosphorus is a key element for several plant developmental processes (respiration, photosynthesis, energy regulation, and biosynthesis of macromolecules). Although phosphorus is naturally present in soil, most of it exists in an insoluble form, rendering it unavailable for plant uptake (Ray et al., 2013). Phosphorus-solubilizing microorganisms play a vital role in enhancing plant nutrition by effectively increasing the availability of phosphate for plant uptake and utilization. Commercially produced phosphate-solubilizing biofertilizers (PSB) are described based on strains, microbial density, and biological activity (Rakshit et al., 2021).

Harvested microalgal and cyanobacterial biomass involved in the biological remediation of phosphorus from wastewater can be used as slow-release phosphate biofertilizers, enhancing plant growth. This application has proven to be useful to avoid phosphorus toxicity due to high concentrations of commercial phosphate fertilizers (Ferreira et al., 2023; Osorio-Reyes et al., 2023; Ray et al., 2013). Cyanobacteria have demonstrated the ability to enhance the solubility of less soluble forms of phosphorus, including calcium phosphate ($Ca_3(PO4)_2$), ferric phosphate ($FePO_4$), aluminum phosphate ($AlPO_4$), and hydroxyapatite ($Ca_5(PO_4)_3OH$). This capacity has been observed in various environments, such as soil, sediments, and in laboratory settings (Afkairin et al., 2021).

Several genera of cyanobacteria, including *Anabaena*, *Calothrix*, *Nostoc*, and *Scytonema*, are capable of phosphate solubilization. Recent research by Bispo et al. (2023) found that the microalgae *Chlorella* sp. also exhibits this trait. In a study conducted by Toribio et al. (2020), the phosphate solubilization capacity of 28 cyanobacteria isolated from aquatic environments was investigated. Among the tested strains, only two strains belonging to *Nostoc* spp. showed significant bioactivity in terms of phosphate solubilization. This suggests that phosphate solubilization ability may vary among different cyanobacterial species. Furthermore, a recent study by Afkairin et al. (2021) compared the phosphorus solubilization capabilities of *Anabaena* sp. with a commercially available product based on a bacterial consortium consisting of *Citrobacter freundii*, *Enterobacter cloacae*, *Pseudomonas putida*, and *Comamonas testosterone*. The results indicated that *Anabaena* sp. exhibited higher phosphorus solubilization than the bacterial consortium product.

Additional research is needed to identify specific cyanobacterial and microalgal species that exhibit phosphorus-solubilizing capabilities, enabling the optimization of their fertilizing and growth-promoting properties in agricultural products. More information on the process of phosphate solubilization by soil microorganisms is provided by Khan et al. (2014)

Plant growth agents

Plant biostimulants are defined as products that have the ability to enhance a plants' nutritional processes and growth, irrespective of their nutrient content. Biostimulants often enhance the rate and efficiency of nutrient uptake as well as the tolerance to abiotic stress (Colla and Rouphael, 2020). Biostimulant activity of cyanobacterial extracts is related to the content of primary metabolites, key amino acids, vitamins, osmolytes, and polysaccharides.

Cyanobacteria and microalgae also produce essential phytohormones that promote plant growth. These include but are not limited to: (i) auxins, which increase growth level, biomass production, stress tolerance, and oil content, (ii) cytokinins, which promote cell division in plant roots and shoots, enhance growth rates, increase oil content, and stress tolerance, (iii) gibberellins, which promote biomass production and growth rate by stem elongation, seed germination, dormancy, and flowering, and (iv) abscisic acid, known to impart stress tolerance, and ethylene, which is involved in programmed cell death, improved growth rates, and biomass production (Baweja et al., 2019; Kumar et al., 2018; Rai et al., 2018). The table 1 highlights some species of microalgae and cyanobacteria known to produce specific phytohormones.

Soil conditioning

The foundation of sustainable agriculture lies primarily in the soil, as it forms the fundamental basis for crop production. Agricultural soils often lack nutrients such as nitrogen, phosphorus, potassium, and iron due to organic matter loss, increasing fertilizers consumption up to two hundred million metric tons (Abinandan et al., 2019). Cyanobacterial and microalgal extracts have been demonstrated to have bioremediation properties capable of enhancing soil fertility, soil aggregate stability, and performing heavy metal removal. In addition, depending on the soil, these extracts can form microbial crusts, thin, inconspicuous communities of microorganisms that develop on soil surfaces with high carbon and nitrogen content, improve soil enzyme activities, increase water drop penetration, and decrease evaporation during dry periods (Acea, 2003; Deviram et al., 2020; Garcia-Pichel, 2023; Lichner et al., 2013; Malam Issa et al., 2007; Renuka et al., 2015).

Starting with soil fertility, the application of microalgal and cyanobacterial extracts enhances soil microbial activity and promotes beneficial microbial interactions (e.g., nutrient cycling, biostimulation, and the production of bioactive compounds). This, in turn, increases the availability of soil organic carbon and other essential macro- and micronutrients (Renuka et al., 2018). Species such as *Chlorella* sp., and *Arthrospira platensis* increase soil total nitrogen and available phosphorus (Alobwede et al., 2019). This property becomes particularly advantageous during rainy and winter seasons for reclaiming alkaline soils, as the extracts can form a thick layer on the soil surface. This layer enriches organic plant production by increasing soil organic matter, specifically carbon, which subsequently enhances the growth of soil microbiota (Abinandan et al., 2019; Joshi et al., 2020). Additionally, many strains belonging to the order Nostocales have the capacity to retain water, release phosphate and nitrogen, produce substances with antiviral and antibacterial activities, and take up nutrients from water (Badr et al., 2019).

Soil aggregate stability is increased due to the properties of exopolysaccharides (EPS), which comprise approximately 25% of total cyanobacterial biomass. These EPS function as binding agents on soil particles within the upper crust, promoting soil aggregation, and resulting in the accumulation of organic content. This process enhances the water-holding capacity of the top layer of soil and

Table 1. Phytohormone-producing microalgae and cyanobacteria, adapted from Lu and Xu (2015)

Phytohormone	Cyanobacteria	Microalgae
Auxin	• *Synechocystis* sp. • *Chroococcidiopsis* sp. • *Anabaena* sp. • *Phormidium* sp. • *Oscillatoria* sp. • *Nostoc* sp.	• *Scenedesmus armatus* • *Chlorella pyrenoidosa* • *Chlorella minutissima*
Ethylene	• *Synechococcus* sp. • *Anabaena* sp. • *Calothrix* sp. • *Scytonema* sp. • *Cylindrospermum* sp.	• *Chlorella pyrenoidosa*
Abscisic acid	• *Synechococcus leopoliensis* • *Nostoc muscorum* • *Trichormus variabilis* • *Anabaena variabilis*	• *Chlamydomonas reinhardtii* • *Dunaliella* sp. • *Draparnaldia mutabilis* • *Chlorella minutissima*
Cytokinin	• *Synechocystis* sp. • *Chroococcidiopsis* sp. • *Anabaena* sp. • *Phormidium* sp. • *Oscillatoria* sp. • *Calothrix* sp. • *Chlorogloeopsis* sp. • *Rhodospirillum* sp. • *Trichormus* sp. • *Nostoc* sp.	• *Chlorella minutissima*
Gibberellic acid	• *Anabaenopsis* sp. • *Cylindrospermum* sp. • *Phormidium foveolarum*	• *Chlorella* sp. • *Chlamydomonas reinhardtii*
Salicylic acid	• *Calothrix* sp. • *Nostoc* sp.	• *Chlorella* sp. • *Nannochloropsis oceanica*

reduces soil erosivity. Consequently, the improved soil moisture and organic content create favorable conditions for the survival and growth of plant-growth promoting rhizobacteria (Kumar et al., 2018; Pathak et al., 2018).

Cultivation and downstream processing

Cultivation

Several methods are available for microalgae and cyanobacteria cultivation. Cultivation can be achieved through either open or closed systems, with environmental parameters customized to the desired metabolic pathway and final application, some of which may be specific to the strain being used. Successful cultivation relies on careful management of these parameters, including temperature ranges (16-27 °C), salinity (12-40 g/L), light intensities (15-135 mmol/m^{2}s), pH, mixing conditions, nutrient composition, and gas exchange. Besides these factors, the growth of microalgae is affected by mixing, culture depth, dilution rate, and harvest frequency (Bartosh and Banks, 2007; Mata et al., 2021).

According to the metabolic pathway, cyanobacteria can be cultured by four distinct modes of nutrition: photoautotrophic, heterotrophic, mixotrophic, and photoheterotrophic (Sharma et al., 2014).

Autotrophic cultivation is the most common growth system since the carbon source is CO_2 of the atmosphere and the energy is supplied by the sunlight. It has low cost, but the growth rate is low compared to the heterotrophic and mixotrophic systems. In the heterotrophic process, carbon and energy sources are supplied as organic carbon substrate. The main advantages of heterotrophic cultivation are high biomass productivity and high growth rate. On the downside, risk of contamination by other microorganisms is plausible, although it can be ameliorated or controlled under greenhouse conditions. In mixotrophic cultivation, microalgae can ingest both organic compounds and CO_2 as carbon source, and both light and organic carbon supply energy to the system. Mixotrophic conditions have advantages such as high growth rate, high biomass density, prolonged exponential growth phase, and reduction of photoinhibitory effect. The disadvantages are high cost and risk of contamination (Arias et al., 2021; Zuccaro et al., 2020).

The two most common systems of microalgae cultivation are open systems such as open ponds, tanks, and raceway ponds (i.e., shallow open ponds in which culture is circulated by a paddlewheel) and controlled closed systems using bioreactors (Sharma et al., 2014). Some of the advantages of open cultivation systems are low cost and lower energy requirement for culture mixing. However, open systems have elevated risk of contamination and are susceptible to weather changes and, it is difficult to control growth parameters such as evaporation rate, temperature, pH. Closed cultivation systems, also known as photobioreactors (PBRs), run under controlled conditions (Chew et al., 2018).

The design of PBRs is versatile because it can be used indoors or outdoors and is customizable according to the specific requirements and growth conditions. The major limitation with these systems is the capital cost involved in installation and maintenance. Closed bioreactors include various types such as flat panel (flat plate), vertical/inclined tubular, helical, airlift, horizontal/serpentine tubular airlift, bubble column, membrane, or hybrid type PBRs (Kim, 2015; Narala et al., 2016)

Although there are multiple cultivation methods, species selection is the most important step defining the sustainability and economic feasibility of a cultivation system (Rizwan et al., 2018). For some taxa, effective cultivation methods have already been recognized. For example, raceways ponds are often used to cultivate *Arthrospira* spp., *Dunaliella* spp., *Anabaena* spp., *Phaeodactylum* spp., *Pleurochrysis* spp., *Chlorella* spp. and *Nannochloropsis* spp., while photobioreactors are used for the cultivation of *Porphyridium* spp., *Phaeodactylum* spp., *Arthrospira* spp., *Nannochloropsis* spp., *Chlorella* spp., *Haematococcus* spp., and *Tetraselmis* spp. (Ronga et al., 2019). For visual representations of raceway ponds and other cultivation methods, please refer to Bitog et al. (2011) and Masojídek and Torzillo (2008). The composition of culture media can vary significantly based on the nutritional requirements and growth conditions of each species. BG-11 is a commonly used medium for cyanobacterial cultivation, but various specialized culture media are also available. For example, variants of the Z8 medium for seawater or hypersaline cyanobacteria, among others.

Harvesting and dewatering

Cyanobacterial harvesting is the removal of biomass from the culture medium. Harvesting requires efficient solid-liquid separation technologies that can be divided into two groups: methods based on gravity or buoyancy such as sedimentation, flocculation, centrifugation, and mechanical methods where a filter or screen is used (Tan et al., 2020).

Cyanobacteria cell size vary from less than 1 µm in diameter up to 100 µm (some tropical forms in the genus *Oscillatoria*), and microalgae cell sizes vary between 5 and 20 µm (Allaf and Peerhossaini, 2022; Richmond and Hu, 2013). Therefore, these methods are challenging because of the small size, and the selection depends on the nature of the cell, concentration of biomass, equipment costs. Solid-liquid separation technique must have large volume capacity, be highly reliable, have low capital and operating costs and be constructed with materials compatible with the culture media (Rizwan et al., 2018; Santos and Pires, 2020).

Drying is often the last harvesting step required to remove moisture content for downstream processing. Common drying methods include spray drying, sun-drying freeze drying – lyophilization, and fluidized bed drying. Spray drying is the most widely method for drying high-value products due to its speed, suitability for large-scale production, and ability to preserve nutrients better than other drying methods, such as microwave drying, despite its high energy demand and cost-intensive nature (Khoo et al., 2020; Rizwan et al., 2018). Sun-drying is also noteworthy for being a relatively cost-effective and highly environmentally friendly method, although it may exhibit some inefficiencies when applied to samples with elevated moisture contents (Kim, 2015).

Harvesting and dewatering processes for microalgae and cyanobacteria are tailored to the specific system, considering the species, growth conditions, and desired final product. Typically, a two-stage approach is necessary for biomass recovery since individual cells are too small for filtration alone. A common strategy involves a combination of flocculation followed by flotation or gravity sedimentation.

Improving the efficiency, cost-effectiveness, and energy consumption of harvesting technologies is essential. The development of enhanced techniques aims to achieve higher recovery efficiencies while minimizing costs and energy requirements. The ideal harvesting technique should enable a high biomass recovery while maintaining moderate operational costs, energy usage, and maintenance efforts (Khoo et al., 2020). Advancements in these areas will contribute to the overall viability and commercial feasibility of microalgae and cyanobacteria production.

Cell disruption

Biomass drying is typically followed by cell lysis to release the desired metabolites. Cell disruption methods can be categorized into mechanical and non-mechanical approaches. Mechanical methods rely on the application of shear forces: bead milling, high-speed homogenizer, high-pressure homogenizer, and energy transfer: microwave irradiation, ultrasonication, pulsed electric field, steam explosion, hydrothermal liquefaction and freeze dry. Non-mechanical methods involve acid, basic, or enzymatic hydrolysis, organic solvent extraction, and osmotic shock (Corrêa et al., 2021; Rahman et al., 2022).

During cell disruption, intracellular molecules can be extracted using organic solvents, ionic liquids, supercritical CO_2 (where carbon dioxide reaches a state with unique solvent properties, typically at temperatures above 31 °C and pressures above 72.8 atmospheres), or supercritical mixtures of CO_2 and solvents. High-pressure homogenization generally exhibits higher disruption efficacy compared to other mechanical methods. Ultrasonication is effective in disrupting cells and achieving high extraction yields but consumes significant energy and may be less effective for highly concentrated algae. Bead milling offers high-rate cell disruption and is practical for large-scale operations, although the degree of disruption depends on the characteristics of the beads used. Chemical methods are practical but may leave solvent residues in the biomass. Ultrasonication and chemical lysis can result in protein degradation, so careful selection of enzymes is crucial for maintaining protein functionality and integrity during enzymatic lysis (Grossmann et al., 2020; Nitsos et al., 2020; Rizwan et al., 2018; Wang et al., 2020).

In recent years, several novel concepts have emerged in downstream processing, particularly in relation to cell disruption methods. These methods include CO_2 explosion, electricity-based techniques, osmotic shock, ionic liquids, viral cell lysis, and contact-based disruption (Tan et al., 2020). One potential approach is the integration of harvesting and cell disruption, which reduces the number of downstream stages, leading to reduced capital investment and operating costs. Techniques such as coagulation-flocculation or electroflotation can be employed for this purpose (Nitsos et al., 2020; Oliveira et al., 2018).

Following cell disruption, the resulting disrupted cells can be solubilized and/or separated through centrifugation to obtain soluble and insoluble protein fractions. In agricultural applications, there is often no requirement for further purification of the disrupted cells. This streamlined approach to downstream processing offers potential benefits in terms of cost-effectiveness and simplicity, particularly for agricultural purposes.

Biorefinery approach

Biorefining is a sustainable process by which biomass is converted into value-added products and energy by integrating bioprocessing and chemical technologies, while minimizing environmental impacts. Cyanobacteria can produce a range of biochemicals used for food, cosmetics, medical research, wastewater treatment, among others. To harness the potential of cyanobacteria, a biorefinery approach is employed, which includes cultivation, biomass harvesting, extraction of desired compounds (Bhalamurugan et al., 2018; Rizwan et al., 2018).

Microalgae and cyanobacteria cultivated in domestic wastewater can serve as a source of biofertilizers, effectively integrating crucial nutrients such as nitrogen, phosphorus, potassium, magnesium, zinc, and iron from the wastewater.

Studies have demonstrated the potential of microalgal consortia, such as *Chlorella* sp. and *Scenedesmus* sp., in nutrient removal (78-98%) from domestic wastewater (Silambarasan et al., 2021). Similarly, *Spirulina* spp. have shown promise in wastewater bioremediation and as nutrient sources for biofertilizers (Mahapatra et al., 2018). A biorefinery approach for microalgae-based biofertilizers, as highlighted by Khan et al. (2019), can effectively manage wastewater pollution, generate biomass, and produce biofertilizers.

To optimize the utilization of wastewater sources and ensure an optimal supply of biofertilizers, understanding the dynamics of various wastewater sources and nutrient translocation is crucial. The biorefinery approach, with its zero-waste concept, plays a significant role in cost-effective, environmentally friendly agriculture, ultimately enhancing food quality and sustainability.

Policy framework

In recent years, the production and commercialization of biofertilizers have undergone separate regulations from traditional fertilizers. Government health agencies now issue certifications and permits for these products. Some regions and countries have already passed initial legislation on this matter; discussed below are the case studies of Europe, India, and Colombia.

The European market for biostimulants has been significant, with approximately 8.5 million hectares of treated area in 2016. As a result, there is a growing need for a unified European Regulation to govern the market placement of biostimulants. Distribution requirements varied across countries, ranging from simple composition analysis and conformity checks to more comprehensive assessments of composition, efficacy, and safety (Traon et al., 2014). The new European Fertilizer Regulation 2019/1009 now defines six Product Function Categories (PFCs): fertilizers, liming materials, soil improvers, growing media, inhibitors, and plant biostimulants as well as blends of those PFCs.

India has a robust legal framework concerning biofertilizers. In 2006, the Indian Ministry of Agriculture issued an order, later amended in 2009, to incorporate biofertilizers into the Essential Commodities Act of 1955 and the order for fertilizer control of 1985. Currently, 11 biofertilizers, including nitrogen fixers, are approved under the Fertilizer Control Order (FCO). However, despite these regulations, the biofertilizer and biopesticide industry in India still faces legal barriers and challenges in ensuring quality compliance (Arjjumend and Koutouki, 2020; Khurana and Kumar, 2022).

In Colombia, the registration requirements for bio-inputs used in agriculture are established by the Instituto Colombiano Agropecuario (ICA). These requirements include several aspects: demonstrating compatibility with other agricultural inputs through efficacy testing, ensuring compliance with safety parameters such as the absence of *Salmonella*, coliforms, and viable helminth eggs, and conducting a physicochemical characterization that includes determining the percentage of organic carbon, pH levels, and concentration of heavy metals.

The results of these evaluations are used to determine the appropriate uses, doses, and labeling information to be included in the registration documentation (ICA, 2020).

In the development of new legal provisions for biofertilizers, it is crucial for policy makers and industry stakeholders to consider the latest scientific knowledge on microbial species that are beneficial for plant growth (Malusá and Vassilev, 2014). This approach will facilitate the formulation of regulations that promote the effective and safe use of biofertilizers, harnessing the potential of microbial species to enhance agricultural productivity and sustainability.

Stability and storage

Biofertilizers are composed of biomass or living microorganisms, and therefore require careful handling and storage to maintain their viability. It is important to use biofertilizers before their expiration date. Biofertilizers are also sensitive to soil conditions, and specific pH and humidity levels must be achieved to ensure their effectiveness. Various delivery methods are employed to apply biofertilizers to plants and the rhizosphere, including soil drench or drip fertigation, foliar spray application, and seed treatment. Cyanobacteria and microalgae extracts are available in liquid/aqueous form or as liquid-soluble powder (biomass) for soil amendment. They are commonly used as foliar sprays on cereal crops, vegetables, and flowers (Bello et al., 2021). Careful attention to storage, expiration dates, soil conditions, and application methods ensures the optimal performance of biofertilizers in promoting plant growth and productivity.

Formulations of biofertilizers require a suitable carrier that possesses specific characteristics such as being inert, nontoxic, organic, cost-effective, and easy to handle. The carrier should also have a high capacity to adhere to seeds and/or root tips. Commonly used carriers include peat soil, vermiculite, charcoal, farmyard manure, and mud (Rakshit et al., 2021). It is important to note that not all biofertilizer formulations require sterilized carriers; some formulations may intentionally include non-sterile carriers to introduce a diverse microbial community, while others are sterilized to ensure inoculant viability and prevent dispersion of pathogens. For the transportation and distribution of cyanobacteria and microalgae, Castelló et al. (2018) found that acidification and vacuum packing in bioriented polyamide/polypropylene bags stored at 4 °C were effective alternatives. These methods ensure the preservation and viability of the microorganisms during transportation. In the case of algal liquid fertilizer, Deepika and MubarakAli (2020) developed and evaluated a formulation by mixing dried algal powder of *Chorococcum* sp. with distilled water. The mixture was then boiled in a water bath at 100 °C, followed by filtration to obtain a standardized solution. This solution can be further diluted to prepare different concentrations of the liquid fertilizer for application on various crops. These methods do not produce biologically active biofertilizers, thereby limiting the benefits of their application to their nutritional and phytochemical content.

By selecting appropriate carriers and employing suitable techniques for transportation and formulation, the effectiveness and practicality of biofertilizers can be optimized, facilitating their application, and enhancing their benefits in agricultural practices. Hence, biofertilizer formulations are diverse, and depend mainly on its mode of action, the microorganism selected, and the target crop.

Evaluating biofertilizing activity

Depending on the application's method of cyanobacterial extracts, different gains can be observed and quantified in crops. Above ground applications include soilless (hydroponic) systems, after-harvest application, and foliar application. Furrow/trench application, soil treatment and seed primer are some belowground approaches. Benefits from aboveground applications include increased plant growth rates and development, increased abiotic stress tolerance (e.g., ability to withstand drought and salinity, freezing conditions, or extreme temperature and pollution) and enhanced nutritional value, including higher micronutrient and chlorophyll contents. With belowground applications, soil fertility, root nodulation, and lateral root spread are increased (Bello et al., 2021).

For evaluating the biofertilizing activity, growth parameters such as plant height, number of leaves per plant, leaf weight per plant, fresh weight/dry weight; yield attributes like neck thickness, bulb diameter and bulb weight are quantified (Dineshkumar et al., 2020). Additionally, assessing metabolic activities, soil improvement, nitrogen fixation, nutrient availability, plant nutrition, and physicochemical characterization of plants are other important methods used for this purpose (Ramakrishnan et al., 2023; Toribio et al., 2021).

Biofertilizer quality can be evaluated based on several parameters. In China, for example, eight factors are considered to determine the fertilizing activity: (i) amount of living cells, (ii) carbon and water content, (iii) pH, (iv) size of carrier (for solid biofertilizers), (v) appearance, (vi) contamination, (vii) expiry period, and (viii) microbial density. According to the Chinese standard, microbial density is considered most important for determining fertilizing activity of nitrogen-fixing bacteria, phosphorus solubilizing bacteria, and a selection of other microorganisms including cyanobacteria, although the importance of density may vary by species (Mącik et al., 2020).

In Table 2, a selection of previous studies demonstrating biofertilizer potential of various cyanobacteria on twenty different crops are presented.

Current trends

Genetic engineering

Cyanobacteria exhibit rapid development compared to microalgae and plants, and their genetic manipulation is highly feasible. To harness their potential, it is crucial to identify novel strains capable of producing high-value products and genetically modify economically significant strains to enhance product yield. The discovery

Table 2. Example selection of studies demonstrating positive effects of various cyanobacteria and microalgae as biofertilizers

Crop	Microorganisms	Effects	References
Aloe (*Aloe barbadensis* Mill)	• *Oscillatoria annae*	Increased fresh weight of leaves from 22 g to 124.30 g.	(Moorthy and P, 2012)
Basil (*Ocimum basilicum* L.)	• *Nostoc* sp. • *Anabaena* sp. • *Tolypothrix* sp. • *Leptolyngbya* sp. • *Synechocystis* sp.	Increased plant growth (≤ 32%), and number (≤ 24%) and fresh weight (≤ 26%) of leaves.	(Hristozkova et al., 2018; Santini et al., 2022)
Basket willow (*Salix viminalis*)	• *Microcystis aeruginosa* • *Anabaena* sp. • *Chlorella* sp.	Stimulated metabolic processes. Increased stability of cytomembranes and intensified activity of net photosynthesis, transpiration, stomatal conductance, dehydrogenases, RNase, acid, and alkaline phosphatase.	(Grzesik and Romanowska-Duda, 2015)
Bean (*Phaseolus vlgaris*)	• *Chlorella vulgaris* • *Tetradesmus dimorphus* • *Arthrospira platensis*	Increased plant height, fresh weight, dry weight, and number of leaves at both vegetative growth and fruiting stage.	(Refaay et al., 2021)
Broadleaf plantain (*Plantago major* L.)	• *Cylindrospermum michailovskoense* • *Anabaena vaginicola*	Increased phenol and flavonoid content.	(Chookalaii et al., 2020)
Cucumber (*Cucumis sativus*)	• *Nostoc* (SAB-M612)	Increased root-to-shoot ratios. Increased stem length (50%), leaf production (30%), fresh weight (close to 50%) and leaf thickness.	(Toribio et al., 2020)
Chinese chives (*Allium tuberosum*)	• *Chlorella fusca*	Increased leaf width and fresh weight.	(Kim et al., 2018)

Crop	Microorganisms	Effects	References
Cotton (*Gossypium herbaceum*)	• *Anabaena* sp. • *Nostoc* sp.	Increased seed germination rate, yield, amount of available nitrogen, biomass, and plant height.	(Prasanna et al., 2016)
Lettuce (*Lactuca sativa*)	• *Chlorella vulgaris* • *Anabaena spp.*	Increased germination rates and number of pigments (chlorophyll a, chlorophyll b and carotenoids) in seedlings.	(Bhalamurugan et al., 2018; Me-namo and Wolde, 2013)
Maize (*Zea mays*)	• *Chlorella vulgaris* • *Arthrospira platensis.*	Increased growth performance at the early stages, seed germination rates and yield.	(Dineshkumar et al., 2019)
Okra (*Abelmoschus esculentus*)	• *Anabaena* sp.	Enhanced bioavailability of macro- and micronutrients in the rhizosphere.	(Manjunath et al., 2016)
Onion (*Allium cepa*)	• *Arthrospira platensis* • *Chlorella vulgaris*	Increased macro- and micronutrient availability and growth parameters of plant: height, leaf numbers, leaves weight, fresh weight, and dry weight.	(Dineshkumar et al., 2020)
Pea (*Pisum sativum*)	• *Nostoc entophytum* • *Oscillatoria angustissima*	Increased germination percentage, stimulated growth parameters, and photosynthetic pigment fractions.	(Osman et al., 2010)
Radish (*Raphanus sativus*)	• *Anabaena variabilis* • *Nostoc muscorum*	Enhanced growth rate and yield.	(Rodgers et al., 1979)
Rice (*Oryza sativa* L.)	• *Anabaena variabilis* • *Gloeocapsa* sp.	Enhanced yield and growth (≤15%) of rice plants, and disease control. Decreased chemical nitrogen fertilizer input.	(Araujo Vidal et al., 2018; Bao et al., 2021)
Roma tomato (*Solanum lycopersicum* 'Roma')	• *Acutodesmus dimorphus*	Increased plant growth and production of flowers.	(Bhalamurugan et al., 2018)
Spinach (*Spinacia oleracea*)	• *Chlorella fusca*	Increased leaf thickness, number of leaves, fresh weight, and yield. Increased yield, number of leaves, and root length.	(Kim et al., 2018; Salamah et al., 2019)
Tomato (*Solanum lycopersicum*)	• *Nannochloropsis oculata* • *Chlorella vulgaris* • *Scenedesmus* sp.	Improved fruit quality through increased in carotenoid and sugar levels.	(Coppens et al., 2016; Simbaña, 2019)
Wheat (*Triticum aestivum* L.)	• *Chroococcidiopsis* sp. • *Anabaena* sp.	Increased seed germination rate, shoot length, tillering, number of lateral roots, spike length, and grain weight.	(Hussain and Hasnain, 2011)

of novel genes contributing to biotechnologically important components can be facilitated through the creation of metagenomic libraries.

There are several approaches based on recombinant DNA technology that include plasmid DNA isolation, restriction enzyme analysis, homologous recombination, and plasmid construction (Figure 2). Genetically modified traits involved in maintaining soil fertility and health include genes such as *fdxH* (necessary for maximum nitrogenase activity and optimal growth under N_2-fixing conditions), *nif* genes (first example of nitrogenase activity detected in photosynthetic non-diazotroph), *chlL* (introduces N_2-fixing genes directly into a chloroplast genome) (Abinandan et al., 2019).

Also, the utilization of cyanobacterial nanoparticles to enhance food production and combat diseases is still in its early stages. Furthermore, the practical application of engineered nanoparticles in agriculture is limited or lacking substantial evidence (Govindasamy et al., 2022).

Cyanobacteria have emerged as promising microbial cell factories for sustainable synthesis of biochemicals and biofuels. However, to make these processes economically viable, improvements are needed. Hitchcock et al. (2020) suggest three key areas for improvement: (i) enhancing the efficiency of marker-less genome modification, including optimization of CRISPR-based technologies, (ii) developing replicative shuttle plasmids for heterologous gene and operon expression, and (iii) achieving tighter regulatory control of introduced pathways to increase strain stability over the long term. These advancements, in combination with 'omics' and genome-scale metabolic analyses, as well as protein and pathway engineering, have the potential to significantly optimize strain performance and product yield. Regarding CRISPR, progress in cyanobacteria is hindered by challenges such as chassis-organism-specific Cas9 toxicity, among other difficulties, impeding widespread implementation of CRISPR-based editing in these organisms (Patel et al., 2023). Therefore, a better understanding of the molecular aspects of cyanobacteria are crucial to reach their full potential in agriculture and other biotechnological applications.

One way to access intracellular material in microalgae is to genetically modify them to release the materials into the growing medium, instead of disrupting the cells. However, genetic engineering

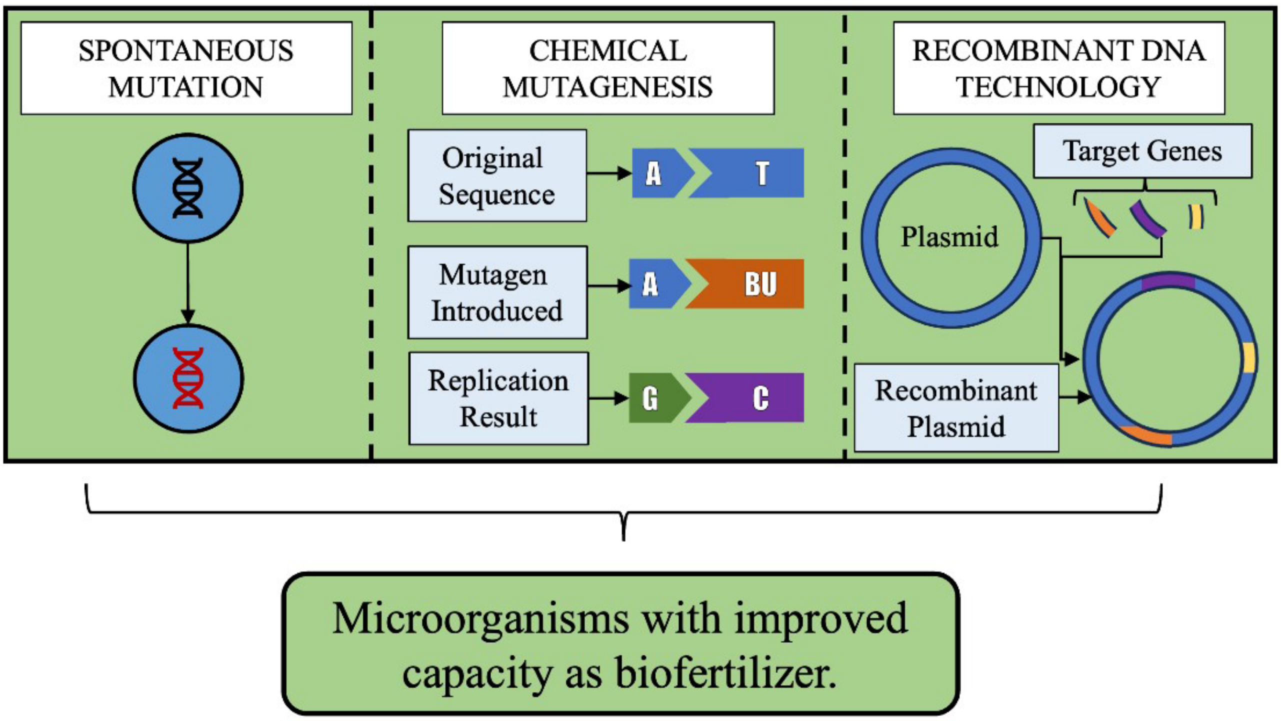

Figure 2. Diagram illustrating the three most common genetic engineering methods employed to enhance traits in microalgae and cyanobacteria, aiming to optimize their suitability for application as biofertilizers. Adapted from Figure 4 in Abinandan et al. (2019).

of microalgae is challenging due to their complex structure and genes being in multiple locations. This makes it difficult to enhance extracted products through genetic engineering, compared to other microorganisms like bacteria (Rahman et al., 2022). Although several genetic engineering techniques have been developed, this application requires significant investment in the future.

Commercial aspects

The global biofertilizer market, valued at 2.8 billion USD in 2022, is projected to reach 5.2 billion USD by 2028. By 2023, the market size is estimated to be 3.1 billion USD. Some examples of available algae-based biofertilizers are presented in Table 3. The utilization of biofertilizers has been proven to reduce agricultural input costs while enhancing long-term crop productivity (Markets and Markets, 2023). Leading commercial players in microalgal and cyanobacterial products include Cyanotech Corporation (U.S.), DIC Lifetec Co. Ltd. (Japan), Cellana Inc. (U.S.), Alltech, Inc. (U.S.), Algaetech International Sdn Bhd (Malaysia), BlueBioTech GmbH (Germany) and Parry Nutraceuticals Limited (India) (Mutale-Joan et al., 2023).

CONCLUSIONS

Fertilizers derived from microalgae or cyanobacterial extracts are characterized by their abundance of nutrients and metabolites, making them valuable for enhancing crop production. These fertilizers also contain plant-growth promoting regulators that further contribute to their effectiveness in improving agricultural yields. This technology is nonetheless limited by several biological, culture system and downstream processing factors that restrict large scale production. Given the imperative need to transition towards more sustainable agriculture, it is crucial to advance cultivation and extraction technologies. Possible solutions to the current challenges include (i) the isolation and selection of cyanobacteria based on the desired product, (ii) integrating molecular biology and omics in strain improvement, as well

Table 3. Selection of some commercial algae-based biofertilizers

Product (Country of origin)	Active compounds	Benefits
AgriAlgae ® Foliar (Spain)	L-amino acids, phytohormones, vitamins, minerals, pigments, peptides, polyunsaturated fatty acids, polysaccharides.	Increase in the crop yield, wettability, increase in number of bigger and heavier fruits, promotion of tissue regeneration, increase in resistance against abiotic stress.
KELPAK® (Colombia)	Organic-mineral fertilizer, made from seaweed (*Ecklonia maxima*), with auxin and brassinosteroid precursors.	Stimulate plant growth, generates higher biomass, and increases fruit set.
Optimar Algas Marinas ® (Spain)	Extracts from seaweed (*Ascophyllum nodosum*), and alginic, folic and gluconic acids.	An increase in cell size is produced by the induction of protein synthesis.
Algifert-K-Powder ® (Norway)	Extracts from seaweed (*Ascophyllum nodosum*), trace minerals and carbohydrates.	Correct nutrient deficiencies, improve fruit set, and help plants endure drought stress.
Nitrozyme ® (United Kingdom)	Highly concentrated and purified extract of marine kelp, rich in growth-promoting compounds.	Promote plant growth at all stages.
GOLPACK ® Algae (Chile)	Algae extract with a composition rich in macro and microelements, vitamins, carbohydrates and natural phytohormones.	Favor rooting, vegetation, fruiting, and fruit quality.

as selection of favorable culture conditions, and (iii) development of high efficiency and low-cost downstream process stages capable of reducing operational costs. Life cycle assessments should be performed to guarantee the feasibility of cyanobacteria-based fertilizers.

The primary constraint associated with the utilization of cyanobacteria as a fertilizer lies in the uncertain technical and economic viability at a large scale. The existing technologies for biomass concentration and processing entail significant energy requirements and necessitate optimization through the integration of multiple dehydration and drying processes. Furthermore, the adoption of a biorefinery approach is imperative as it enables the utilization of all process outputs within the framework of a circular bioeconomy.

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AUTHOR CONTRIBUTIONS

All authors contributed to the study conception. Camila Andrea Marín Marín and Juan Martín Delgado Naranjo led the search and Camila Andrea Marín Marín wrote the main manuscript text, José Alberto Estrada Peláez assisted with table elaboration, and Mariana Peñuela Vásquez and Paola Andrea Zapata Ocampo did a preliminary review of the manuscript and added valuable information. All authors read and approved the final manuscript.

CONFLICT OF INTEREST

The authors report no conflicts of interest.

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