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Review

Edible Terrestrial Cyanobacteria for Food Security in the Context of Climate Change: A Comprehensive Review

Midori Kurahashi and Angelica Naka *

Biosystems and Biofunctions Research Center, Tamagawa University, Tokyo 194-8610, Japan; t_kurahashi@lab.tamagawa.ac.jp

* Correspondence: angelica.naka@lab.tamagawa.ac.jp

Abstract: This review examines the history of consumption, life cycle, and culture conditions of seven edible mucilaginous terrestrial cyanobacterial strains—*Nostoc flagelliforme*, *Nostoc commune*, *Nostoc sphaeroides*, *Nostoc sphaericum*, *Nostoc verrucosum*, *Aphanothece sacrum*, and *Nostochopsis lobatus*—as resilient and sustainable food sources in the face of climate change. Traditionally consumed across various cultures and known for their resilience in extreme environments, these cyanobacteria offer high nutritional value, including proteins, vitamins, and essential fatty acids, making them promising candidates for addressing food security. Their ability to fix nitrogen reduces reliance on synthetic fertilizers, enhancing agricultural applications by improving soil fertility and minimizing dependence on fossil fuel-derived chemicals. Unlike conventional crops, these cyanobacteria require minimal resources and do not compete for arable land, positioning them as ideal candidates for low-impact food production. Despite these advantages, the review highlights the need for scalable and cost-effective cultivation methods to fully realize their potential in supporting a resilient global food supply. Additionally, it underscores the importance of ensuring their safety for consumption, particularly regarding toxin content.

Keywords: cyanobacteria; *Nostoc*; *Aphanothece*; *Nostochopsis*; food security; climate adaptation; sustainable agriculture

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1. Introduction

To date, society has relied heavily on fossil resources as raw materials for industrial and economic development. However, the escalating severity of climate change highlights the urgent need to identify sustainable and carbon-neutral alternatives to replace fossil-based resources [1,2]. Essential requirements for new raw materials include carbon neutrality, sustainability, scalability, and the capacity to support large-scale production. In this context, microalgae have emerged as a highly promising candidate, attracting global attention for their potential to meet these criteria [3–5].

Efforts to cultivate microalgae on a large scale have been undertaken in several countries, including the United States, China, Spain, and Australia. However, a significant barrier persists: the high costs associated with microalgae production [6]. The cost of producing microalgal biomass depends on various factors, including the production system and scale. In general, the most expensive stage is harvesting and dewatering, followed by cultivation costs such as nutrient supply and energy consumption [7–9]. This cost challenge has limited their widespread adoption as raw materials for societal applications through artificial cultivation [10].

Microalgae represent a diverse and polyphyletic group, encompassing a wide range of taxa classified through molecular phylogenetics. Among eukaryotes, these include Chlorophyta (green algae), Bacillariophyta (diatoms), Chrysophyta (golden algae), Dinophyta (dinoflagellates), Euglenophyta (euglenoids), and Phaeophyta (brown algae) [11]. Within prokaryotes, Cyanobacteria, also known as blue-green algae, stand out as a group with significant ecological and industrial potential [12].

To address the challenge of reducing production costs, attention has shifted to terrestrial cyanobacteria, a subgroup of microalgae with a long history of use as a food source [13,14]. These cyanobacteria exhibit several advantageous characteristics that make them promising candidates for cost-effective cultivation. Notable features include their ability to fix both atmospheric carbon and nitrogen, form protective external sheaths, grow with minimal water requirements, thrive across a wide range of temperatures, and produce high levels of exopolysaccharides. Together, these attributes enhance their potential as a sustainable and scalable raw material [15].

To the best of our knowledge, while individual studies on terrestrial cyanobacteria exist—covering aspects such as taxonomy, physiology, adaptation to extreme environments, biofertilizer potential, secondary metabolite production, biotechnological applications, and their use as a food source—a comprehensive synthesis in the form of a review is currently lacking. This review compiles existing research and provides insights into the distribution, life cycle, culture conditions, applications, and associated risks and challenges of cyanobacteria. Such a synthesis is crucial for evaluating their potential applications and identifying knowledge gaps and future research priorities, including optimizing cost-effective large-scale cultivation techniques, ensuring their safety for consumption, and assessing their agricultural applications, among others [16]. In this review, we focus on seven edible mucilaginous terrestrial or semi-aquatic cyanobacterial strains: *Nostoc flagelliforme* (Bornet and Flahault) Wolle 1887: 285, *Nostoc commune* Vaucher ex Bornet and Flahault 1888: 203, *Nostoc sphaeroides* Kützing ex Bornet and Flahault 1886: 212, *Nostoc sphaericum* Vaucher ex Bornet and Flahault 1886: 208, *Nostoc verrucosum* Vaucher ex Bornet and Flahault 1886: 216, *Aphanothece sacrum* (Suringar) Okada 1953: 17, and *Nostochopsis lobatus* Wood em. Geitler. Providing an overview of the journal papers published to date on this high-potential group of microalgae is expected to be valuable for assessing their potential applications in agriculture, food, pharmaceuticals, and other fields—particularly in the context of climate change—and for identifying directions for future research [17].

2. Terrestrial Edible Cyanobacteria: *Nostoc* spp., *Aphanothece sacrum*, and *Nostochopsis lobatus*

Terrestrial edible cyanobacteria, including *Nostoc* spp., *Aphanothece sacrum*, and *Nostochopsis lobatus*, play important roles in sustainability and biotechnology, with applications spanning agriculture, food, pharmaceuticals, and eco-friendly materials. Their adaptability to diverse environments, including terrestrial and semi-aquatic habitats, and their capacity to produce bioactive compounds underscore their potential. However, challenges such as toxin production and ecological risks necessitate careful management. This section examines their distribution, biology, culture conditions, applications, and associated risks, while assessing their potential to support sustainable development and drive innovation across various industries.

2.1. Distribution

The cyanobacteria we selected are distributed worldwide, often thriving in extreme environments within terrestrial or semi-aquatic habitats, and forming both microscopic and macroscopic colonies (Table 1). *Nostoc flagelliforme*, for instance, is found predominantly in

arid and semi-arid regions, such as the Loess Plateau in China, where it forms macroscopic colonies on soil surfaces under extreme conditions like droughts and high evaporation rates, demonstrating resilience in deserts and saline environments [1,18–21]. Its habitats are characterized by extreme conditions such as low precipitation (50–300 mm annually) and high evaporation rates, with temperatures ranging from −17 °C to 35 °C, and surface temperatures reaching up to 66 °C in summer [18].

Table 1. Habitat and key features of *Nostoc* and related cyanobacteria.

Cyanobacterium	Habitat	Key Features	References
Nostoc flagelliforme	Arid and semi-arid regions, Loess Plateau (China), deserts, saline environments	Forms macroscopic colonies, tolerates droughts, high evaporation rates	[1,18,21]
Nostoc commune	Global: polar to tropical regions, nutrient-poor soils, rocks, freshwater surfaces	Withstands extreme temperatures, desiccation cycles, soil stabilization	[22–24]
Nostoc sphaeroides	Mountain paddy fields, Zouma Town (China), nutrient-rich soils	Forms spherical macrocolonies, thrives in winter, vulnerable to herbicides	[25–27]
Nostoc sphaericum	High-altitude regions, Andes (South America), lakes, rivers, wetlands	Forms spherical colonies (10–25 mm), thrives at high altitudes	[28,29]
Nostoc verrucosum	Cool, clear, shallow streams, Japan, riverbeds	Requires low temperatures, high water clarity, vulnerable to habitat loss	[30–33]
Aphanothece sacrum	Clean streams, rivers, Kyushu (Japan), stony substrata	Endemic to Japan, endangered, inhabits oligotrophic, mineral-rich waters	[14,34–39]
Nostochopsis lobatus	Tropical, temperate climates, riverbeds, Nan and Mekong Rivers (Thailand)	Forms gelatinous colonies, thrives in clean/moderately clean water	[40–45]

Nostoc commune is a globally distributed cyanobacterium found in diverse habitats, ranging from polar regions to tropical areas [22]. It commonly inhabits nutrient-poor soils, rocks, freshwater surfaces, and occasionally marine environments. Its ability to withstand extreme temperatures and desiccation cycles makes it prevalent in deserts, dry grasslands, mountains, and other challenging habitats, where it contributes to soil stabilization and land restoration [22–24].

Nostoc sphaeroides is predominantly found in mountain paddy fields, particularly in regions such as Zouma Town, Hubei Province, China, where it thrives in nutrient-rich soils with neutral to slightly alkaline water [25]. It forms spherical macrocolonies in irrigated fields during the winter months and typically disappears during summer rice cultivation [27]. However, historical habitat destruction due to agricultural changes, including herbicide use, has significantly reduced its natural presence [25,26].

Nostoc sphaericum is a cyanobacterium predominantly found in high-altitude regions such as the Andes, thriving at elevations above 3000 m. It inhabits lakes, rivers, and wetlands across Peru, Bolivia, Ecuador, and northern Chile, forming spherical colonies (10–25 mm) in Andean wetlands and lagoons [28,29].

Nostoc verrucosum is found in cool, clear, shallow streams, typically attached to well-lit riverbeds [30,31]. It is particularly prevalent in Japan, where it is known as "Ashitsuki", with regions such as Toyama Prefecture serving as key habitats [30,32]. The species requires stable conditions, including low temperatures and high water clarity, which restrict its distribution and make it vulnerable to habitat loss caused by river development and pollution [30,33].

The unicellular cyanobacterium *Aphanothece sacrum*, originally identified as *Phylloderma sacrum* and commonly referred to as "Suizenji-nori", is a freshwater species endemic to Japan. It is predominantly found in clean streams and rivers, where it often attaches to stony substrata [34–37]. Its natural distribution is limited to the Kyushu region of Japan, particularly in Kumamoto and Fukuoka Prefectures [14,34]. This species inhabits pristine environments and is highly sensitive to environmental changes such as water pollution and eutrophication, which threaten its sustainability and have led to its inclusion on the Ministry of the Environment Japan Red List 2017 as an endangered species [14,34]. *Aphanothece sacrum* thrives in cool, oligotrophic, and mineral-rich waters with stable flow conditions [14,38,39].

Nostochopsis lobatus is a freshwater cyanobacterium found in tropical, temperate, arid, and cold climates, although it is absent in polar regions [40]. It thrives on riverbed rocks and cobbles in shallow streams, forming spherical to irregularly lobed gelatinous colonies up to 5.5 cm in diameter [41–44]. The species is particularly abundant in tropical and subtropical regions, with notable occurrences in India and northern Thailand [45]. In Thailand, it is prevalent along the Nan and Mekong Rivers, especially during the dry season, when water conditions favor its growth [43]. In temperate zones, its colonies are smaller and more sparsely distributed [40]. Its natural habitat includes clean to moderately clean water with optimal light and nutrient levels [45].

2.2. Life Cycle and Reproduction

Nostoc and related cyanobacteria typically undergo a complex life cycle comprising both vegetative and reproductive phases [12], as shown in Figure 1 based on available research on Nostoc. During vegetative growth, they form macroscopic, gelatinous colonies composed of filaments [46]. These species reproduce asexually through fragmentation, wherein parts of the colony break off and develop into new colonies [16]. They also produce resting spores called akinetes, which enable survival under unfavorable conditions until more suitable environments are restored [17]. Additionally, *Nostoc* and some related species differentiate specialized cells known as heterocysts, which are essential for nitrogen fixation and allow them to thrive in nitrogen-deficient environments [3,22]. Moreover, *Nostoc* and certain related cyanobacteria can produce hormogonia—short, motile filaments—that facilitate dispersal and colonization of new habitats under specific environmental conditions, such as desiccation or nutrient deprivation [12]. These adaptive strategies, including vegetative growth, spore formation, fragmentation, and motile filament production, make cyanobacteria highly resilient and versatile across diverse environmental conditions.

Nostoc flagelliforme exhibits a unique adaptation to extreme dryness, cycling between dehydration and rehydration. This species can survive prolonged dry periods, reactivating its metabolic processes within hours of water availability [21]. It grows very slowly in natural environments, with an annual growth rate of less than 6% [13]. Its reproduction involves the formation of colonial filaments, with desiccation playing a critical role in maintaining structural integrity [20].

Nostoc commune forms macroscopic colonies composed of trichomes embedded in an extracellular polysaccharide matrix. It reproduces vegetatively through trichome fragmentation and does not differentiate into akinetes [24]. The organism alternates between desiccated and hydrated states, maintaining viability for over 100 years in its dry state. Upon hydration, photosynthesis and nitrogen fixation resume, enabling survival and colonization in transiently wet environments [22,24].

The life cycle of *Nostoc sphaeroides* includes developmental stages from hormogonia to mature colonies. Hormogonia are motile fragments that develop into non-organized filaments, which then form spherical macrocolonies. These colonies exhibit structural differentiation, with the outer filaments demonstrating higher photosynthetic activity compared to the inner layers [26,47]. The presence of polysaccharides enhances colony resilience to environmental stresses [47,48].

Nostoc sphaericum undergoes a complex life cycle characterized by morphological adaptations to environmental changes. It alternates between desiccated and hydrated forms, relying on the production of akinetes and hormogonia for survival and dispersal. These structures enable it to withstand prolonged dry periods and flooding, conditions typical of its habitat [49].

The colonies of *Nostoc verrucosum* consist of trichomes embedded within an extracellular matrix. This cyanobacterium is capable of nitrogen fixation, enabling it to thrive in nutrient-poor environments [33]. It produces trehalose and extracellular polysaccharides, which enhance stress tolerance, although it remains sensitive to desiccation [50]. Reproduction occurs through filament fragmentation and spore formation typical of cyanobacteria.

Aphanothece sacrum produces a thick extracellular matrix composed of exopolysaccharides, which plays a crucial role in its life cycle by providing structural support and protection against environmental stress [14]. This species is characterized by an irregular or dispersed arrangement of rod-shaped cells that form multicellular colonies, enveloped in a gelatinous mucilage. These colonies can float and range in size from microscopic to macroscopic, growing up to 20 cm in length [14,34–36]. Reproduction in *A. sacrum* primarily occurs through binary fission, a mechanism common among unicellular cyanobacteria. During this process, cells divide in one plane, perpendicular to their long axis, contributing to colony growth and maintenance [36]. Additionally, genetic analysis has revealed that *A. sacrum* occupies a unique phylogenetic position among cyanobacteria, attributed to specific ferredoxin genes involved in its metabolic processes [34].

Nostochopsis lobatus forms mucilaginous colonies that are spherical when young and transition into amorphous shapes as they mature, with colors ranging from green to rusty [42]. Like other members of the order Nostocales, *Nostochopsis lobatus* reproduces through a combination of vegetative cell division, filament fragmentation, the formation of akinetes under stress conditions, and the release of motile hormogonia that germinate into new colonies under favorable conditions [41]. Unlike other Nostocales, its microscopic structure includes trichomes with lateral branching and heterocysts located in intercalary, terminal, or lateral positions [42]. These heterocysts play distinct roles in nitrogen assimilation and reproduction, highlighting the species' nitrogen fixation capabilities. Additionally, akinetes serve as survival structures during adverse conditions, demonstrating the organism's adaptability and resilience in fluctuating environments [41,51].

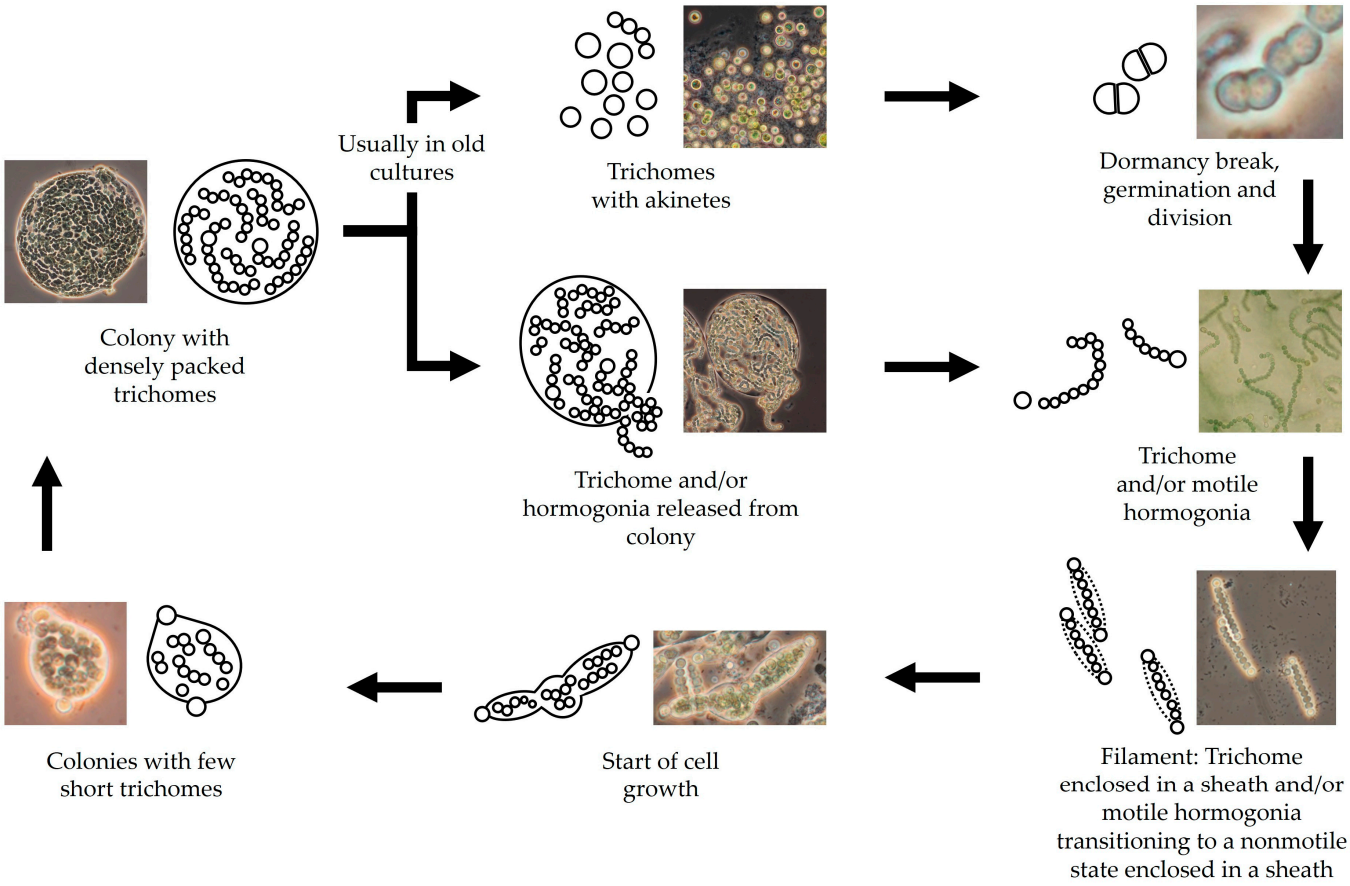


Figure 1. The life cycle of *Nostoc* is summarized and schematized based on information from the literature [17,20,26,40,41,46,49,52–54]. Several strains of *Nostoc* can differentiate into various cell types, including vegetative cells with photosynthetic ability, heterocysts for nitrogen fixation, motile hormogonia, and akinetes, with the latter two considered dispersion mechanisms. In *Nostoc flagelliforme*, globular colonies are not formed. In *Nostochopsis lobatus*, branching occurs from the main trichome, and heterocysts can be both intercalary and lateral.

2.3. Culture Conditions and Large-Scale Culture

Culturing cyanobacteria requires careful control of environmental factors, presenting both challenges and opportunities for various applications. This section discusses the optimal culture conditions for the cyanobacterial species presented in this review, as summarized in Table 2. *Nostoc flagelliforme* thrives in alkaline environments, with a pH range of 8.0–9.5 being ideal for growth, as it inhibits contamination by other algal species [55]. Temperature is critical, with an optimal range of 25–30 °C facilitating colonial filament development and extreme temperatures above 35 °C or below 15 °C impeding growth [20]. Light intensity is another key factor; 60 µmol photons m^{-2} s^{-1} provides optimal conditions for colony formation, whereas higher intensities, such as 180 µmol photons m^{-2} s^{-1}, accelerate cellular growth but limit colony development [20]. In laboratory experiments, *Nostoc flagelliforme* is typically cultivated in the BG-11 medium [56]. Fed-batch cultivation methods have been successfully employed, achieving in increased biomass concentrations of up to 1.16 g·L^{-1} and exopolysaccharide production of 124 mg·L^{-1}, demonstrating its potential for scalable production [55].

Nostoc commune thrives at temperatures between 20 °C and 33 °C, and can endure extremes ranging from −269 °C to 70 °C in its desiccated state [22,57]. It grows optimally at a pH range of 3 to 10, and tolerates salinity up to 20 g NaCl per kg [22]. High light intensity enhances photosynthesis and nitrogen fixation, particularly after rehydration [24]. While the BG-11 medium is commonly used for cultivation, fertilizer-based media have proven effective for reducing costs without compromising growth [58]. Large-scale cultivation has been successfully implemented in bioreactors and outdoor systems by optimizing conditions such as aeration and mixing [52,58]. Laboratory studies show that colonies form macrocolonies within 28 days and continue to grow thereafter [52].

The cultivation of *Nostoc sphaeroides* requires a neutral-to-slightly alkaline pH (7.0–7.5) and nitrogen-free BG-11 medium to support its nitrogen-fixing capability [47,59]. Optimal growth occurs at 25 °C under continuous illumination, with white light at 90 μmol m^{-2} s^{-1} promoting biomass production, blue light enhancing phycobiliprotein accumulation, and red light increasing biomass yield [27]. Regular medium renewal every 10 days ensures sustained growth, allowing macrocolonies of 2–20 mm to form within 4 weeks and achieve high oxygen evolution rates (approximately 150 μmol O_2 mg^{-1} h^{-1}) [59]. Although large-scale cultivation faces challenges such as colony morphogenesis and quality consistency, advances in photobioreactor technology have improved production capabilities, making *Nostoc sphaeroides* a valuable resource for food and bioactive compounds [26,27,59].

Nostoc sphaericum can be cultivated under controlled conditions using nitrogen-free BG-11 medium. Optimal conditions include temperatures of 22–30 °C, light intensities of 28–30 μmol m^{-2} s^{-1}, and a neutral to slightly alkaline pH (6.5–7.0) [49,60,61]. Large-scale cultivation often utilizes spray-drying techniques to produce hydrocolloids, which are stable across a range of pH and temperature conditions. These hydrocolloids have applications in food, pharmaceuticals, and water treatment [61,62].

Nostoc verrucosum grows optimally at 13–18 °C, with 18 °C commonly used in laboratory settings [30,50]. It thrives in modified nitrogen-free BG11 medium, supplemented with biotin (1 mg L^{-1}), thiamine (2 mg L^{-1}), and cyanocobalamin (1 mg L^{-1}), buffered at pH 7.5 [31,50]. Fluorescent light at 2–4 μmol m^{-2} s^{-1} supports its growth [31]. Large-scale cultivation has been demonstrated in cylindrical tanks with controlled conditions, producing biomass for applications in cosmetics and functional foods [32]. However, its specific growth requirements and sensitivity to environmental changes pose challenges for scaling up [30,50].

According to records, *Aphanothece sacrum* is the only microalga that has been cultivated as a food source for more than 300 years, with its cultivation dating back to 1763 in an oligotrophic freshwater aquafarm in Asakura City, Fukuoka Prefecture, Japan [14,39]. It requires specific conditions for optimal growth and enhanced exopolysaccharide production. The organism grows best at a temperature of approximately 20 °C [14,34]. Light intensity also affects its growth, with optimal conditions ranging between 40–80 μmol m^{-2} s^{-1} under continuous light or a 12:12 light/dark cycle [14,34]. Unlike many cyanobacteria, *Aphanothece sacrum* does not thrive in conventional culture media such as BG-11 but grows effectively in synthetic media specifically designed to meet its unique nutritional requirements, such as AST and AST-5xNP [14,34]. These media formulations are based on the mineral composition of its natural oligotrophic freshwater habitat, which is mineral-rich [34,38]. Although specific pH requirements are not detailed, the cyanobacterium generally thrives in conditions that replicate its natural environment, likely neutral to slightly alkaline.

Table 2. Culture conditions of *Nostoc* and related cyanobacteria.

Cyanobacterium	Optimal Conditions	References
Nostoc flagelliforme	pH: 8.0–9.5 Temperature: 25–30 °C Light: 60 µmol photons m^{-2} s^{-1} Medium: BG-11 Fed-batch cultivation	[20,55,56]
Nostoc commune	pH: 3–10 Temperature: 20–33 °C Light: High intensity post-rehydration Medium: BG-11 or fertilizer-based	[22,24,58]
Nostoc sphaeroides	pH: 7.0–7.5 Temperature: 25 °C Light: 90 µmol photons m^{-2} s^{-1} (white light) Medium: Nitrogen-free BG-11	[27,47,59]
Nostoc sphaericum	pH: 6.5–7.0 Temperature: 22–30 °C Light: 28–30 µmol photons m^{-2} s^{-1} Medium: Nitrogen-free BG-11	[49,60,61]
Nostoc verrucosum	pH: 7.5 Temperature: 13–18 °C Light: 2–4 µmol photons m^{-2} s^{-1} Medium: Modified nitrogen-free BG-11 supplemented with biotin, thiamine, and cyanocobalamin	[30,31,50]
Aphanothece sacrum	Temperature: approximately 20 °C Light: 40–80 µmol photons m^{-2} s^{-1} Medium: AST or AST-5xNP (synthetic)	[14,34,39]
Nostochopsis lobatus	pH: 7.5–7.8 Temperature: 20–30 °C Light: 80–300 µmol photons m^{-2} s^{-1} Medium: Nitrogen-free BG-11 with supplements	[41,45,63]

Nostochopsis lobatus is a diazotrophic cyanobacterium capable of growing in nitrogen-free media by fixing atmospheric nitrogen. However, the addition of ammonium nitrogen enhances its growth, reducing the doubling time from 82.4 to 32.9 h [41]. Optimal growth conditions include a temperature range of 20–30 °C, depending on the study, with some experiments reporting a specific range of 25 ± 1 °C [45,63]. The pH is typically maintained near neutral to slightly alkaline, with common values between 7.5 and 7.8 [41,45]. Light conditions involve intensities of 80–300 µmol m^{-2} s^{-1} with continuous illumination, although one study utilized a light-dark cycle of 15:9 [43,45,63]. The culture medium commonly used is nitrogen-free BG-11, which supports atmospheric nitrogen fixation. However, supplementing the medium with phosphorus (10 mg/L as K_2HPO_4) and iron (3 mg/L as $FeNH_4$ citrate or Fe-EDTA), either separately or together, enhances biomass yield, pigment production, and antioxidant properties, including the synthesis of phycobiliproteins like phycocyanin and phycoerythrin [45]. In one study, immobilized cultures exhibited superior growth compared to free cultures, likely due to better nutrient accessibility and stability [45]. *Nostochopsis lobatus* has also been successfully cultured in BG-11 broth, BG-11 semi-solid agar, cylindrical acrylic tanks with aeration, and transparent plastic bags [43,45,63].

2.4. Food Consumption History and Potential Uses

The cyanobacteria discussed in this review have a long history of consumption, have diverse applications across various cultures and industries, and are used for soil restoration because of their nitrogen fixation ability (Table 3). *Nostoc flagelliforme* has been consumed in China for more than 2000 years, valued as a delicacy known as "Facai" (hair-like vegetable) [18]. Its bioactive compounds, including nostoflan, exhibit antiviral properties against viruses such as HSV-1 and influenza [13]. Additionally, it is recognized for its antioxidant properties, making it a promising ingredient for functional foods and nutraceuticals [56].

Table 3. The traditional names and applications of *Nostoc* and related cyanobacteria.

Cyanobacterium	Region: Traditional Name	Applications	References
Nostoc flagelliforme	China: "Facai" or hair-like vegetable	Consumed in China for over 2000 years. Functional foods, nutraceuticals, antiviral and antioxidant properties.	[13,18,56]
Nostoc commune	Peru: "Llullucha"	Consumed for centuries in Asia, particularly in China, and in Peru. Functional food, therapeutic applications, soil restoration, sustainable cultivation.	[23,52,58,64–66]
Nostoc sphaeroides	China: "Ge-Xian-Mi"	Used historically as food and medicine. Pharmaceuticals, cosmetics, Controlled Ecological Life Support Systems (CELSS).	[25,48,59]
Nostoc sphaericum	Peru: "Cushuro"	Combating anemia and malnutrition, phycogastronomy, food preservation.	[28,60,67]
Nostoc verrucosum	Japan: "Ashitsuki"	Its cultural importance dates back to the eighth century. Natural antimicrobial agent, antimelanogenic applications, cosmetics.	[30,32]
Aphanothece sacrum	Japan: "Suizenji-nori"	Culinary uses, anti-inflammatory, bioengineering, therapeutic applications.	[14,34,35,38,39,68–70]
Nostochopsis lobatus	Thailand: "Lon"	Pharmaceuticals, cosmetics, anti-inflammatory and anti-gastric ulcer properties.	[42–44,63,71]

Nostoc commune has been consumed for centuries in Asia, particularly in China, where it is recognized for its nutritional and medicinal properties in texts such as the Compendium of Materia Medica [64]. It is rich in proteins, polysaccharides, vitamins, and minerals and exhibits antioxidative, anti-inflammatory, and anti-carcinogenic activities, making it valuable as a functional food [23,65]. In Peru, it is known as "Llullucha" and used in traditional dishes, particularly in high-altitude regions where its nutritional content is highly beneficial [66]. Beyond its use as food, its bioactive compounds hold potential for therapeutic applications, while its environmental benefits include nitrogen fixation and soil restoration [58]. Sustainable cultivation is essential to meet growing demand and to conserve wild populations [52].

Nostoc sphaeroides has been consumed for centuries, particularly in China, where it is known as "Ge-Xian-Mi". Historically, it has been used as both food and medicine to treat ailments such as inflammation, burns, hypertension, and chronic fatigue [25,48]. It is traditionally prepared in soups, salads, and fried dishes, and its high nutritional value—including proteins, vitamins, and antioxidants—has drawn modern scientific interest [48,59]. Additionally, its polysaccharides exhibit antioxidant and moisture-retaining properties, making it valuable for pharmaceutical and cosmetic applications [48]. *Nostoc sphaeroides* also shows potential for use in Controlled Ecological Life Support Systems (CELSS) because

of its rapid growth, oxygen production, and high nutrient density, which are particularly beneficial for space missions and extreme environments [59].

Nostoc sphaericum, known as "Cushuro" in Peru, has a long history of consumption. It is rich in protein (28%), carbohydrates (62%), and minerals such as calcium (377 mg/100 g) and iron (4.76 mg/100 g), making it a valuable food for combating anemia and malnutrition [28]. It is used in traditional dishes, modern phycogastronomy, and avant-garde cuisine, including as an ingredient in edible films for food preservation [67]. Additionally, its bioactive compounds, such as mycosporine-like amino acids, show potential for UV protection and antioxidant applications [60].

Nostoc verrucosum, or "ashitsuki", has been consumed in Japan since at least the eighth century, with mentions in the "Man'yoshu" and regional names such as kotobuki-nori and shiga-nori underscoring its cultural importance [30,32]. It contains n-1 fatty acids with antibacterial activity against gram-positive bacteria, suggesting its potential as a natural antimicrobial agent [30]. Additionally, its aqueous and methanol extracts exhibit antioxidant activity, with IC_{50} values of 294.6 µg/mL and 172.8 µg/mL, respectively [32]. *Nostoc verrucosum* also shows promise in cosmetics because it inhibits melanin synthesis and tyrosinase activity, making it a potential antimelanogenic agent [32].

Aphanothece sacrum has a long history of consumption in Japan, confirming its safety for human use. It is commonly incorporated into soups and marinades or served as a garnish for sashimi (thinly sliced raw fish) and is valued for its gelatinous texture and bioactive components [14,34,38]. Beyond its culinary uses, this cyanobacterium produces unique polysaccharides such as sacran, which have been studied for their anti-inflammatory properties and functional material applications, including liquid crystalline gels and bionanocomposites [68–70]. The structural and functional versatility of sacran highlights its potential in the food, pharmaceutical, and bioengineering industries [35]. Additionally, the inhibitory effect of freeze-dried *A. sacrum* on the development of diabetic cataracts underscores its promise as a therapeutic agent [39]. Furthermore, sacrolide A, an oxylipin macrolide derived from *A. sacrum*, exhibits antimicrobial and cytotoxic activity, further expanding its potential as a source of bioactive compounds [38].

Nostochopsis lobatus has a long history of use as food, particularly in Thailand, where it is known as "Lon" and traditionally prepared in dishes such as the salad "Yum Lon" [43]. It is rich in nutrients, including proteins, carbohydrates, vitamins, and essential minerals such as selenium and iron [43]. Beyond its nutritional value, *Nostochopsis lobatus* exhibits significant bioactivity, including anti-pyretic, antioxidant, anti-inflammatory, and anti-gastric ulcer properties [42,63,71]. Its polysaccharides are being explored for applications in pharmaceuticals and cosmetics, including as hyaluronidase inhibitors and anti-allergy agents [63]. Furthermore, its ability to synthesize bioactive compounds such as nostochopcerol highlights its potential as a source of novel therapeutic agents [44].

2.5. Risks, Challenges, and Considerations for Sustainable Utilization

Despite their numerous benefits, the cyanobacterium discussed in this review also present risks, including toxin production, ecological impacts, and challenges associated with cultivation. For example, the over-exploitation of natural populations of *Nostoc flagelliforme* has led to its endangered status in China, prompting government protection measures to regulate harvesting and trade [55]. The species' slow natural growth rate, combined with its sensitivity to prolonged hydration, limits productivity and complicates large-scale cultivation efforts [21]. Open culture systems, while cost-effective, require careful management to maintain productivity and prevent losses [55]. Despite these challenges, safety evaluations have confirmed *Nostoc flagelliforme* as a safe food source, with

no adverse effects observed in toxicity studies, bolstering its potential as a functional food and nutraceutical ingredient [72].

Nostoc commune poses risks such as the potential production of β-N-methylamino-L-alanine (BMAA), a neurotoxin associated with neurodegenerative diseases [66]. Overharvesting and environmental degradation threaten wild populations, while habitat destruction impacts biomass quality [52,64]. Sustainable large-scale cultivation faces challenges, including maintaining consistent yields and quality under variable conditions, as well as reducing production costs through optimized methods, such as fertilizer-based media [58].

The sustainable use of *Nostoc sphaeroides* is challenged by habitat destruction caused by to agricultural practices, including excessive use of herbicides and fertilizers, which have significantly reduced natural populations and driven up market prices [25,26]. Large-scale cultivation faces issues such as inconsistent yields, high production costs, and difficulties in maintaining optimal growth conditions, including controlled light, temperature, and pH [47,59]. Advances in cultivation technology and sustainable harvesting practices are essential to address these challenges while balancing economic demand and ecological conservation [25,27,48].

The sustainable use of *Nostoc sphaericum* faces challenges such as habitat loss in high-altitude wetlands, highlighting the need for conservation efforts [28,61]. Potential antinutritional factors also require further investigation to ensure safety [73]. Scaling production presents economic and technical challenges, including the development of eco-friendly and cost-effective methods for its applications in food, pharmaceuticals, and water treatment [61,62].

The sustainability of *Nostoc verrucosum* is threatened by habitat loss due to river development, pollution, and climate change, as it depends on cool, clear streams with stable conditions [30,33]. Declining populations in Japan have led to local protections, such as those implemented in Toyama Prefecture [30]. Its sensitivity to environmental changes and specific growth requirements pose significant challenges for large-scale cultivation, necessitating precise control of temperature, light, and nutrients [31,50]. Conservation efforts and sustainable cultivation practices are crucial to preserving its ecological and cultural value [30,33].

Aphanothece sacrum holds significant potential for sustainable applications, particularly in nutraceuticals and pharmaceuticals; however, its utilization faces several challenges. Its natural habitats are highly specific, requiring oligotrophic, mineral-rich waters that are increasingly threatened by urbanization and water pollution [14,38]. As a result, effective and advanced aquaculture techniques must be developed to support its cultivation [34]. The extraction of its polysaccharide sacran involves resource-intensive processes that require optimization for scalability and sustainability [35,69]. Furthermore, bioactive compounds such as sacrolide A, which exhibit antimicrobial and cytotoxic properties, raise concerns about potential food toxicity. To address this issue, precooking treatments have been suggested to deactivate sacrolide A in the raw alga, thereby preventing food intoxication [38,68]. Research into innovative cultivation and extraction methods is essential to overcome ecological, economic, and technological barriers while ensuring the sustainable use of *A. sacrum* for various applications.

Nostochopsis lobatus has gained attention for its bioactive compounds with therapeutic potential. It produces nostochopcerol, a novel antibacterial monoacylglycerol [44], while its polysaccharides exhibit strong hyaluronidase inhibitory activity, suggesting applications in anti-aging and anti-inflammatory treatments [63]. Additionally, *Nostochopsis lobatus* is a rich source of pigments and antioxidants [45] and contains corrinoid compounds such as pseudo-vitamin B12 [71]. Its traditional medicinal uses further underscore its therapeutic value [42]. However, the sustainable exploitation of *Nostochopsis lobatus* for nutritional

and therapeutic applications faces several challenges. These include a need for a deeper understanding of its chemical and biological properties, optimization of bioactivity and bioavailability, improved extraction efficiency, and scalability for large-scale production while maintaining high yields and consistent quality. Addressing these challenges is crucial to ensuring its sustainable utilization without ecological or health risks.

3. The Potential of Cyanobacteria in Climate Change Adaptation and Food Security

Terrestrial edible cyanobacteria, including *Nostoc flagelliforme*, *Nostoc commune*, *Nostoc sphaeroides*, *Nostoc sphaericum*, and *Nostoc verrucosum*, along with *A. sacrum* and *Nostochopsis lobatus*, offer significant potential for addressing climate change, food security, and sustainable agriculture. These cyanobacteria are recognized for their ability to fix atmospheric carbon dioxide [12,74]. By capturing and converting carbon dioxide into organic compounds through photosynthesis, they contribute to carbon neutrality [3]. The adaptation of cyanobacteria to various environments, including arid and nutrient-poor conditions, underscores their resilience and potential for ecological restoration [12,46]. In the context of climate change, these traits make them valuable for rehabilitating degraded lands and preventing desertification.

From a nutritional perspective, cyanobacteria have been used as food in many cultures due to their high protein content [16]. For example, *Nostoc commune*, *Nostoc flagelliforme*, and *Aphanothece sacrum* are traditionally consumed in Asia, providing essential nutrients such as amino acids to populations in vulnerable areas [15,16]. The rich protein composition of these cyanobacteria makes them well-suited to address malnutrition and food insecurity, particularly in regions with limited agricultural resources. As climate change intensifies food shortages due to extreme weather events, declining soil fertility, and freshwater scarcity, cyanobacteria offer a sustainable and climate-resilient protein source. Their ability to thrive in non-arable lands with minimal freshwater requirements aligns with global efforts to develop climate-smart food systems. Additionally, the production of edible polysaccharides and bioactive compounds further enhances their value for both nutritional and pharmaceutical applications [15].

In agriculture, these cyanobacteria play a pivotal role due to their nitrogen-fixing ability. The presence of heterocysts in species like *Nostoc commune* allows them to convert atmospheric nitrogen into bioavailable forms, enriching soil fertility and reducing the need for synthetic fertilizers [3,12]. This capability is especially valuable in sustainable farming practices, such as rice cultivation, where cyanobacteria can improve yields while minimizing environmental impact [10]. As climate change intensifies unpredictable weather patterns, including prolonged droughts and soil degradation, nitrogen-fixing cyanobacteria could help maintain soil health, reduce dependency on chemical fertilizers, and support regenerative agricultural practices.

To fully harness the potential of these cyanobacteria, the development of large-scale, cost-effective culturing methods is essential. Innovations in cultivation techniques, such as solid media systems and open pond systems, may offer promising solutions for large-scale production [10,75]. Additionally, mimicking natural conditions, such as alternating wet and dry cycles, has been shown to enhance the productivity and stability of these systems [46,74]. For example, *Nostoc flagelliforme*, known for its slow growth rate in desert-like conditions, could be cultured under controlled conditions that replicate its natural habitat to ensure steady biomass yield. Adapting these cultivation methods to integrate climate-resilient strategies, such as utilizing brackish or wastewater for growth, could further enhance sustainability while reducing the strain on freshwater resources. Moreover, incorporating carbon capture technologies into large-scale production systems could maximize their

role in climate mitigation by directly absorbing CO_2 emissions from industrial sources. Integrating these strategies with renewable energy sources and sustainable water-use practices could enhance the economic viability of cyanobacteria cultivation while supporting global efforts to adapt to climate change. Further research into optimizing cultivation techniques and expanding their applications could unlock their full potential as a raw material or bio-resource for a sustainable future. Conducting mathematical or statistical analyses, including numerical Strengths, Weaknesses, Opportunities, and Threats (SWOT) assessments, with a focus on cultivation methods, large-scale production techniques, and cyanotoxin assessment, would help ensure safety for consumption and potential use as fertilizer while identifying the most suitable species for future food security. By incorporating climate risk assessments into these analyses, it may also be possible to anticipate how shifting environmental conditions could influence cyanobacterial growth, productivity, and resilience, ensuring their long-term viability as a sustainable solution in the face of climate change.

4. Conclusions

Cyanobacteria, such as *Nostoc flagelliforme*, *Nostoc commune*, *Nostoc sphaeroides*, *Nostoc sphaericum*, *Nostoc verrucosum*, *Aphanothece sacrum*, and *Nostochopsis lobatus*, offer several benefits in addressing climate change challenges. These terrestrial edible cyanobacteria can enhance soil fertility, water retention, and contribute to sustainable food and biofertilizer solutions, making them valuable for climate-resilient agriculture. Their nutritional value and ability to adapt ecologically highlight their potential as food sources, particularly in regions vulnerable to food insecurity. These cyanobacteria can thrive in both laboratory and open-culture conditions, supporting large-scale cultivation. Future research should focus on optimizing cultivation methods, developing cost-effective techniques that replicate natural growth conditions, and enhancing their resistance to environmental stresses. Integrating these organisms into agroecosystems can improve agricultural productivity and support climate adaptation strategies. Continued research and technological investment will be crucial to scaling their use and ensuring their contributions to climate change adaptation and resilient food systems.

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