MINI-REVIEW



Biotechnological approaches for suppressing *Microcystis* blooms: insights and challenges

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Abstract

Cyanobacterial harmful algal blooms, particularly those dominated by *Microcystis*, pose significant ecological and health risks worldwide. This review provides an overview of the latest advances in biotechnological approaches for mitigating *Microcystis* blooms, focusing on cyanobactericidal bacteria, fungi, eukaryotic microalgae, zooplankton, aquatic plants, and cyanophages. Recently, promising results have been obtained using cyanobactericidal bacteria: not through the inoculation of cultured bacteria, but rather by nurturing those already present in the periphyton or biofilms of aquatic plants. Fungi and eukaryotic microalgae also exhibit algicidal properties; however, their practical applications still face challenges. Zooplankton grazing on *Microcystis* can improve water quality, but hurdles exist because of the colonial form and toxin production of *Microcystis* control blooms through allelopathy and nutrient absorption. Although cyanophages hold promise for *Microcystis* control, their strain-specificity hinders widespread use. Despite successful laboratory validation, field applications of biological methods are limited. Future research should leverage advanced molecular and bioinformatic techniques to understand microbial interactions during blooms and offer insights into innovative control strategies. Despite progress, the efficacy of biological methods under field conditions requires further verification, emphasizing the importance of integrating advanced multi-meta-omics techniques with practical applications to address the challenges posed by *Microcystis* blooms.

Key points

- A diverse range of biotechnological methods is presented for suppressing Microcystis blooms.
- Efficacy in laboratory experiments needs to be proved further in field applications.
- Multi-meta-omics techniques offer novel insights into Microcystis dynamics and interactions.

Keywords Microcystis · Cyanobacterial bloom · Biotechnological control · Field application · Multi-meta-omics

Introduction

Cyanobacterial harmful algal blooms (cyanoHABs) refer to the rapid proliferation of cyanobacteria in water systems that cause disturbances in ecosystems. Some cyanobacteria produce diverse toxins that pose threats to aquatic animals, livestock, and even humans (Shahmohamadloo et al. 2023, 2020; Zeng et al. 2021a). Among the globally prevalent cyanoHABs, Microcystis is the most dominant in Asia, North America, South America, and Europe (Arif et al. 2023; Den Uyl et al. 2021; Huo et al. 2021; Mânica and Lima 2023; Park et al. 2021; Schweitzer-Natan et al. 2023). For instance, Lake Taihu, China, has been famous worldwide for Microcystis blooms since the shutdown of the water-supply system in Wuxi in 2007, prompting intensive research (Chen et al. 2024; Huang et al. 2024). Microcystis blooms are also prevalent in freshwater systems in Korea, such as the Nakdong River and Daechung Reservoir (Chun et al. 2019, 2020; Le et al. 2023a), particularly after the completion of the Four Major Rivers Restoration Project (Park 2012). In Lake Erie, a significant cyanoHAB in 2014 led to the suspension of the water supply for more than 500,000 residents in Toledo, Ohio (Steffen et al. 2017).

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The intensification of cyanoHABs has been attributed to the combined effects of eutrophication and climate change (Burford et al. 2020; Geletu 2023; Thomalla et al. 2023). In particular, cyanobacteria are adapting better to elevated temperatures caused by global warming (Guo et al. 2023; Wang et al. 2023; Yang et al. 2023). In addition, cyanoHABs promote the production of methane, a greenhouse gas (Li et al. 2021; Wang et al. 2022b). Increased methane oxidation by *Methylomonas* during the post-bloom period can facilitate the recovery of water quality in eutrophicated reservoirs (Yu et al. 2023), but cyanoHABs still stimulate methylotrophic methanogenesis and accelerate global warming (Zhu et al. 2022). Therefore, increased methanogenesis by cyanobacteria coupled with rising temperatures synergistically exacerbate cyanoHABs.

Various approaches, including physical, chemical, and biological methods, have been proposed to suppress *Microcystis* blooms and improve water quality (Lusty and Gobler 2020; Zang et al. 2020; Zhang et al. 2023c). However, physical methods for *Microcystis* removal are generally costly, and chemical methods can leave persistent substances that pose toxicity risks to water quality, aquaculture facilities, and drinking-water sources (Buley et al. 2021; Santos et al. 2021). In contrast, biological methods are regarded as more

favorable owing to their nontoxic nature and highly specific effects on the target cyanobacteria. Furthermore, the recent integration of high-throughput sequencing and bioinformatic/ecoinformatic techniques has created an opportunity to obtain novel insights and enhance the reliability and effectiveness of biological methods. This review focuses on analyzing biotechnological approaches for suppressing *Microcystis* blooms, assessing their field applicability, and prospecting innovative techniques based on genomics and multi-meta-omics.

Biotechnological approaches for *Microcystis* suppression using diverse biotic agents

Biotechnological methods for suppressing *Microcystis* can be categorized into microorganism- and macroorganismbased methods. Microorganisms comprise bacteria, fungi, eukaryotic microalgae, zooplankton, and viruses, whereas macroorganisms include aquatic plants. Each organism either directly attacks *Microcystis* or indirectly influences it by releasing allelopathic compounds. This review focuses on biotic agents that have been isolated and used to suppress *Microcystis* (Fig. 1).

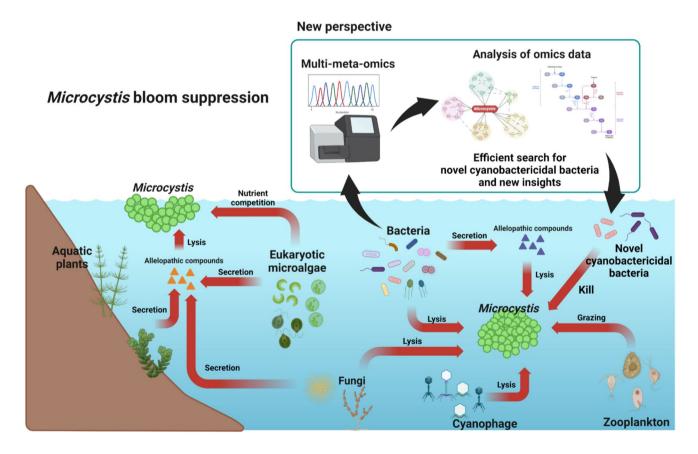


Fig. 1 Overview of diverse biotechnological approaches for suppressing Microcystis

Cyanophages

Cyanobactericidal bacteria are considered to be crucial biological facilitators for *Microcystis* suppression. These bacteria exploit both direct and indirect modes of action against *Microcystis*. Direct activity involves physical contact between cyanobactericidal bacteria and *Microcystis*, whereas indirect activity involves the secretion of secondary metabolites (Table 1). *Streptomyces globisporus* G9 and *Stenotrophomonas* sp. KT48 kill *Microcystis aeruginosa* by direct cell-to-cell attack (Lyu et al. 2022; Zeng et al. 2021b). However, direct cyanobactericidal bacteria have been scarcely reported when compared with indirect ones. The multifaceted effects of indirect activity, mediated by allelopathic compounds, often surpass those of direct activity. Indirect mechanisms involve the degradation of cell

 Table 1
 Summary of control mechanisms for Microcystis bloom using cyanobactericidal bacteria

Mechanism	Mode of action	Species	Effective concen- tration	Initial cell den- sity of <i>Micro-</i> cystis	Growth inhibi- tion	Duration	Reference
Direct	Cell-to-cell con- tact and lysis	Aeromonas bestiarum HYD0802- MK36	1×10^7 cells/mL	5×10^4 cells/mL	91.0%	2 days	Park et al. (2022)
	Cell-to-cell con- tact and lysis	Streptomyces glo- bisporus G9	5% (v/v)	1×10^6 cells/mL	96.7%	6 days	Zeng et al. (2021b)
	Lysis	<i>Stenotropho- monas</i> sp. KT48	10% (v/v)	5.2×10 ⁶ cells/ mL	95.2%	10 days	Lyu et al. (2022)
Indirect	Secretion of algicidal compounds in filtrate	Bacillus sp. YZ1 and Brevibacil- lus sp. CBS	10% (v/v)	1×10^7 cells/mL	95.0%	5 days	Liu et al. (2022)
		Bacillus altitudi- nis G3	5% (v/v)	4.0×10 ⁶ cells/ mL	99.8%	72 h	Hou et al. (2023)
		Brevibacillus sp.	3‰ (v/v)	7×10^7 cells/mL	100.0%	96 h	Liu et al. (2023)
	Secretion of seven algicidal compounds in cell-free supernatant (cyclo (leu-pro), cyclo (phe-pro), norharman, trans-3-indolea- crylic acid, hypoxanthine, kanosamine, and betaine) Secretion of	Bacillus sp. AK3	5% (v/v)	2.59×10 ⁶ cells/ mL 1.07×10 ⁷ cells/	82.6% 98.5%	3 days	Boonbangkeng et al. (2022)
	algicidal compounds in filtrate	Morganella morganii	10% (v/v) 5.65×10 ⁷ cells/ mL	mL	98.3%	6 days	Mankiewicz-Boc- zek et al. (2022)
	Secretion of pyoluteorin	Pseudomonas sp. Go58	3.1×10 ⁸ cells/ mL	1.83×10 ⁵ cells/ mL	>95.0%	2 days	Chen et al. (2023)
	Flocculation and lysis by algicidal com- pounds	Paenibacillus sp. A9	6% (v/v)	-	80.9%	96 h	Jia et al. (2023)
	Secretion of algicidal compounds in filtrate	<i>Streptomyces</i> sp. HY	5% (v/v)	5×10^6 cells/mL	93.0%	2 days	Zhang et al. (2023a)
Direct/indirect	Secretion of paucibactin A and direct lysis	Paucibacter aquatile DH15	2.1×10 ⁴ CFU/ mL	2×10^6 cells/mL	94.9%	36 h	(Le et al. 2022a, 2023b)

wall components, modulation of gene expression, and disruption of antioxidants or photosynthetic systems (Zhang et al. 2022b). For example, Bacillus altitudinis G3 secretes both thermolabile and thermostable algicidal substances that affect photosynthetic activity and reactive oxygen species production, selectively killing *M. aeruginosa* (Hou et al. 2023). The filtrate of Bacillus sp. YZ1 and Brevibacillus sp. CBS, when applied at a density of 1×10^7 cells/mL, caused more than 95% lysis of *M. aeruginosa* cells within 5 days (Liu et al. 2022). Similarly, the filtrate of a novel Brevibacillus sp. caused complete cell lysis within 4 days at a concentration of 2.1×10^5 cells/mL (Liu et al. 2023). Paenibacillus sp. A9 uses a "flocculation-lysis-degradation" mechanism, where it initially secretes polysaccharides containing carboxyl groups to flocculate Microcystis, followed by lysing it with algicidal active compounds (Jia et al. 2023). In contrast, Bacillus sp. AK3 secretes seven antimicrobial compounds into the cell-free supernatant (Boonbangkeng et al. 2022). This supernatant, when inoculated into Microcystis bloom water, strongly inhibited the growth of Microcystis and Pseudanabaena and promoted the growth of Chlorella, indicating a specific inhibitory effect. Recently, Paucibacter has emerged as a dual-acting bacterium against Microcystis, exerting both direct and indirect effects with a high cyanobactericidal effect of 94.9% within 36 h (Le et al. 2022a). Through indirect action, *Paucibacter* secretes paucibactin A, which exhibits an algicidal effect of 81.6% within 24 h. Moreover, paucibactin A undergoes 87.4% photolysis within 24 h, rendering it an environment-friendly substance without a persistent impact on aquatic ecosystems (Le et al. 2023b). Additionally, various bacteria such as Paucibacter aquatile DH15, Paenibacillus sp. A9, and Stenotrophomonas geniculata can degrade microcystin, a toxin produced by Microcys*tis* (Jia et al. 2023; Le et al. 2022a; Xie et al. 2023).

Cyanobactericidal bacteria are more abundant during bloom-declining periods, but they are often successfully isolated during bloom periods (Le et al. 2022a; Mankiewicz-Boczek et al. 2022; Zhang et al. 2019). Therefore, periphyton, which consists of diverse attached eukaryotic microalgae and bacteria, has been suggested as a promising strategy to reduce cyanobacterial blooms owing to its ability to stimulate the growth of cyanobactericidal bacteria (Le et al. 2023c). Biofilms on aquatic plants may serve as reservoirs of algicidal bacteria in the natural environment (Miyashita et al. 2019). These approaches can enhance the control of Microcystis blooms by fostering the growth of only periphyton or aquatic plants, without the inoculation of cultured bacteria or allelopathic compounds and. Because such methods promote already existing cyanobactericidal bacteria and organic matter-degrading bacteria in the water column, they can achieve eco-friendly bloom control at a lower cost.

Fungi

The process of eliminating cyanobacterial cells and their degradation by fungal strains remain largely unknown. Currently, only a few species with the ability to inhibit and lyse cyanobacterial cells have been identified. Direct and indirect attacks are the modes of fungal action used to lyse Microcystis species. For example, Trichaptum abietinum and Lopharia spadicea degrade M. aeruginosa and M. flos-aquae, and the lysis mechanism involves mucus secretion by fungal mycelia upon direct contact with cyanobacterial cells (Jia et al. 2010; Wang et al. 2010). Irpex lacteus, Trametes versicolor, and Bjerkandera adusta also successfully eliminate Microcystis cells by direct attack (Han et al. 2011). In addition, algicidal fungi can indirectly attack cyanobacteria by releasing algicidal compounds that inhibit growth or by secreting lytic enzymes that damage the cell wall and plasma membrane. T. versicolor also inhibits M. aeruginosa by producing decomposing enzymes such as cellulase, β -glucanase, and protease (Dai et al. 2018). Trichoderma citrinoviride culture filtrate inhibits the growth of *M. aeruginosa*, indicating algicidal activity through fungal secretions rather than a direct attack (Mohamed et al. 2014). Aureobasidium pullulans produces β -N-acetylglucosaminidase, an enzyme capable of breaking down bacterial peptidoglycan, a major component of the cyanobacterial cell wall (Mohamed et al. 2020). Recent studies have shown that certain fungal species can degrade microcystins. Phanerochaete chrysosporium, a white-rot fungus, not only destroys algal cells but also reduces the expression of microcystin genes (Zeng et al. 2020). Penicil*lium chrysogenum* inhibits the growth and antioxidant system of *M. aeruginosa* by secreting extracellular substances, specifically penicillin V and G (Han et al. 2021b). This interaction leads to the altered expression of genes involved in microcystin synthesis and photosynthesis in M. aeruginosa. Moreover, Penicillium sp. GF3 effectively degrades microcystin-LR (Kuzikova et al. 2023). Algicidal fungi are expected to be an environment-friendly control method because they can decompose toxins and cells simultaneously (Mohamed et al. 2014; Kuzikova et al. 2023). However, there are numerous challenges in directly using them for onsite treatment, so the use of fungal extracts is now regarded as a more practical method.

Eukaryotic microalgae

Microcystis and eukaryotic microalgae compete under different environmental conditions, such as temperature, nutrients, and light (Hu et al. 2021). The colonial *Microcystis* exhibits more resistance to light stress and chemical materials than eukaryotic algae (Fang et al. 2018; Zhang and Benoit 2019), and Microcystis and its exudates have allelopathic effects on Scenedesmus quadricauda and Chlorella pyrenoidosa (Wang et al. 2017). However, recent studies indicate a decline in the competitive ability of colonial M. aeruginosa against Scenedesmus obliquus with respect to the macro-nutrient phosphorus (P) (Wang et al. 2022d). Furthermore, S. obliguus exhibits greater resistance and outcompetes M. aeruginosa in freshwater salinization caused by climate change, agriculture, and use of deicing salts (Gao et al. 2023). At different temperatures and P concentrations, M. aeruginosa and C. pyrenoidosa showed different patterns of competition (Ren et al. 2021). Although C. pyrenoidosa predominated at low temperatures and high P concentrations, M. aeruginosa suppressed C. pyrenoidosa at higher temperatures through more efficient P-uptake systems and allelopathic effects.

Microcystis can be inhibited by the allelopathic effects of eukaryotic microalgae. Oocystis borgei competes with M. aeruginosa for nutrients and hinders its growth through allelopathic effects, thereby disrupting the membrane system and esterase activity (Wang et al. 2022c). Scenedesmus sp. FACHB-1229 produces allelochemicals 1,2-benzenedicarboxylic acid and bis(2-methoxyethyl) ester that suppress M. aeruginosa FACHB-3550 and FACHB-905, respectively (Song et al. 2022). However, *Microcystis* also has allelopathic effects on eukaryotic algae such as S. quadricauda, C. pyrenoidosa, and Cyclotella meneghiniana (Wang et al. 2017). Furthermore, the allelopathic effects vary depending on the growth phase of *M. aeruginosa* and species of microalgae, which complicates the practical applications of eukaryotic microalgae in inhibiting Microcystis in the field (Wang et al. 2022c).

Zooplankton

Zooplankton and Microcystis have miscellaneous interactions, involving not only the grazing of Microcystis but also defense against zooplankton (Davis and Gobler 2010; Ger et al. 2014). Daphnia pulex, Hyalella azteca (Davis and Gobler 2010), Notodiaptomus iheringi (Leitao et al. 2018), cyclopoid copepods (Urrutia-Cordero et al. 2015), Eudiaptomus gracilis, and Daphnia magna (Ger et al. 2018a) are known to graze on Microcystis. According to Mohamed et al. (2018), *M. aeruginosa* is completely consumed by Cyclops vicinus. The highest grazing rate of C. vicinus was observed when the cell density of *M. aeruginosa* peaked. In a hypereutrophic pond, Daphnia pulicaria reduced the biomass of Microcystis by up to 19.7 times when compared with that of the control (Chislock et al. 2013). However, many zooplankton species cannot graze on Microcystis because of three main reasons: (1) As Microcystis does not provide key nutrients (particularly essential fatty acids) to zooplankton, Cladocera and Copepoda prefer nutrient-rich eukaryotic microalgae over Microcystis (Ger et al. 2018a). (2) Zooplankton have difficulty ingesting Microcystis cells because of its colonial forms (Geng et al. 2013; Xiao et al. 2018). Pseudodiaptomus hessei, Moina micrura, Ceriodaphnia cornuta, Brachionus angularis, Brachionus falcatus, and Keratella sp. can digest filamentous cyanobacteria but not the colonial forms (Kâ et al. 2012). (3) Microcystis produces various secondary metabolites as a defense mechanism against zooplankton (Harke et al. 2016). For example, trypsin and chymotrypsin derived from M. aeruginosa PCC 7806 suppress the activity of digestive proteases in Daphnia magna (Agrawal et al. 2005). Xu et al. (2023) observed that Microcystis exudates damaged the mitochondrial membrane potential of Daphnia, causing impaired mitochondrial function. Microcystin, a notorious cyanobacterial toxin, is also lethal to *Daphnia* (Bownik 2016).

Zooplankton contribute to improved water quality by directly grazing on *Microcystis*, but *Microcystis* colonization presents a significant challenge to this grazing activity (Chislock et al. 2013; Xiao et al. 2018). Under continuous disturbances, *Microcystis* cells form small colonies that are easy to ingest, whereas intermittent disturbances cause them to form larger colonies that are difficult for zooplankton to consume (Yang et al. 2020). Thus, successful control necessitates the simultaneous optimization of numerous environmental conditions (Ger et al. 2018b).

Aquatic plants

Aquatic plants are fundamental primary producers that play a key role in maintaining water clearance in aquatic ecosystems. Macrophytes are regarded as prospective tools for controlling cyanobacterial blooms because they produce chemical compounds that can suppress bloom-forming cyanobacteria (Maredova et al. 2021; Nezbrytska et al. 2022; Wang and Liu 2023). However, the detailed mechanisms underlying the cyanobactericidal effects have not yet been fully identified. Submerged macrophytes possess distinct allelopathic properties, along with effective nutrient absorption (Maredova et al. 2021; Nezbrytska et al. 2022; Wang and Liu 2023). The various aquatic plants recognized for their ability to inhibit the growth of *M. aeruginosa* are listed in Table 2.

Among emergent macrophytes, *Typha angustifolia* exhibits more pronounced inhibitory effects on *M. aeruginosa* than *Acorus calamus* and *Phragmites australis* (Kang et al. 2020; Maredova et al. 2021). *Pistia stratiotes*, a free-floating macrophyte, demonstrates substantial growth inhibition with both aqueous and ethanolic extracts (Lourenção et al. 2021). However, the study conducted by Maredova

Table 2 Summary of Microcystis bloom control using aquatic plants

Habitat	Species	Types used in experi- ments	Effective concentra- tion	Initial cell density of Microcystis	Growth inhibition ^a	Duration	Reference
Emergent	Acorus calamus	Ethanolic extracts	1% (200 µL)	1.2×10 ⁶ cells/mL	Μ	72 h	Maredova et al. (2021)
	Phragmites australis	Extracts at different decomposition stages (fresh and dead)	Various levels of EC ₅₀ (mg C/L)		Н	0.2, 10, 30, 50, 100 days	Kang et al. (2020)
	Typha angustifolia	Extracts at different decomposition stages (fresh and dead)	Various levels of EC ₅₀ (mg C/L)		Н	0.2, 10, 30, 50, 100 days	Kang et al. (2020)
Free-floating	Pistia stratiotes	Ethanolic extracts	25 mg/L	2.3×10^5 cells/mL	Н	6 days	Lourenção et al. (2021)
		Aqueous extracts	3% (200 µL)	1.2×10^6 cells/mL	М	72 h	Maredova et al. (2021)
Rooted floating	Nymphoides peltata	Aqueous extracts	10% (200 µL)	1.2×10^6 cells/mL	М	72 h	Maredova et al. (2021)
Submerged and floating-leaves	Potamogeton natans	Aqueous extracts	1% (200 µL)	1.2×10^6 cells/mL	М	72 h	Maredova et al. (2021)
	Stratiotes aloides	Ethanolic extracts	3% (200 µL)	1.2×10^6 cells/mL	М	72 h	
Submerged	Ceratophyllum	Ultrasonic cellulose extraction	5 g/L	Around 50 μg Chl-a/L	Н	120 h	Li et al. (2023)
	Ceratophyllum demersum	Aqueous extracts (anaerobic soak- ing)	3 g/L	$1-2 \times 10^6$ cells/mL	Н	15 days	Han et al. (2021a)
	Ceratophyllum submersum	Ethanolic extracts	1% (200 µL)	1.2×10^6 cells/mL	М	72 h	Maredova et al. (2021)
	Chara globularis	Aqueous extracts	0.1% (200 µL)	1.2×10^6 cells/mL	Н	72 h	Maredova et al. (2021)
	Chara tomentosa	Aqueous extracts	10% (200 µL)	1.2×10^6 cells/mL	М	72 h	Maredova et al. (2021)
	Egeria densa	Organic extracts	0.5, 1, 3, 6 g/L	10 ⁵ cells/mL	H, M, P, P	10 days	Wijesinghe et al. (2023)
	Elodea canadensis	Aqueous extracts	10% (200 µL)	1.2×10^6 cells/mL	М	72 h	Maredova et al. (2021)
	Elodea nuttallii	Aqueous extracts	10% (200 µL)	1.2×10^6 cells/mL	М	72 h	Maredova et al. (2021)
	Hydrilla verticillata	Ethanolic extracts	10% (200 µL)	1.2×10^6 cells/mL	М	72 h	Maredova et al. (2021)
	Hydrocleys nym- phoides	Aqueous extracts	10% (200 µL)	1.2×10^6 cells/mL	М	72 h	Maredova et al. (2021)
	Myriophyllum alterniflorum	Aqueous extracts	1% (200 µL)	1.2×10^6 cells/mL	М	72 h	Maredova et al. (2021)
	Myriophyllum hetero- phyllum	Aqueous extracts	10% (200 µL)	1.2×10^6 cells/mL	М	72 h	Maredova et al. (2021)
	Myriophyllum spicatum	Extracts	100 mg/L	10 ⁶ cells/mL	Н	9 days	Kitamura et al. (2023)
		Ultrasonic cellulose extraction	5 g/L	Around 50 µg Chl-a/L	Н	120 h	Li et al. (2023)
		Ethanolic extracts	100% (200 µL)	1.2×10^6 cells/mL	Н	72 h	Maredova et al. (2021)
		Plant	5 cm apical shoot (0.42 g dw/L)	471 μg Chl-a/L	Н	7 days	Jeong et al. (2021)
		Plant	5 g fw/L	1×10^{6} cells/mL	Н	3 days	Zhu et al. (2010)
		Plant	1 g fw/L	1×10^{6} cells/mL	Н	7 days	He et al. (2016)
		Plant	12 cm apical shoot (2 g fw/L)	4.5×10^6 cells/mL	Н	12 days	Gao et al. (2022)
	Potamogeton crispus	Aqueous extracts	10% (200 µL)	1.2×10^6 cells/mL	М	72 h	Maredova et al. (2021)
	Potamogeton prae- longus	Aqueous extracts	10% (200 µL)	1.2×10^6 cells/mL	М	72 h	Maredova et al. (2021)
	Potamogeton pusillus	Aqueous extracts	10% (200 µL)	1.2×10^6 cells/mL	М	72 h	Maredova et al. (2021)
	<i>Vallisneria</i> sp.	Ultrasonic cellulose extraction	5 g/L	Around 50 μg Chl-a/L	Н	120 h	Li et al. (2023)
		Ultrasonic cellulase extraction	5 g/L	Around 50 µg Chl-a/L	Н	5 days	Wang et al. (2022a)
	Vallisneria ameri- cana	Aqueous extracts	0.3% (200 µL)	1.2×10^6 cells/mL	М	72 h	Maredova et al. (2021)
	Vallisneria natans	Aqueous extracts (anaerobic soak- ing)	3 g/L	100–200 × 10 ⁴ cells/ mL	Н	15 days	Han et al. (2021a)

^a*H*, inhibition rate of > 50%; *M*, inhibition rate < 50%; *P*, promoting

et al. (2021) indicated that P. stratiotes, Nymphoides peltata, and Stratiotes aloides have only stimulatory effects on cyanobacteria. Ceratophyllum and Chara, which are submerged macrophytes, exhibit high allelopathic abilities, except Chara tomentosa, which has a stimulatory effect (Han et al. 2021a; Li et al. 2023; Maredova et al. 2021). Egeria, Elodea, and Hydrocleys do not hinder the growth of M. aeruginosa, whereas Elodea nuttallii and Hydrilla verticillata have algicidal abilities against Aphanizomenon gracile (Maredova et al. 2021; Wijesinghe et al. 2023). Within the genus Myriophyllum, M. spicatum has strong algicidal effects, whereas M. alterniflorum has a stimulatory effect on Microcystis (Gao et al. 2022; He et al. 2016; Jeong et al. 2021; Kitamura et al. 2023; Li et al. 2023; Maredova et al. 2021; Zhu et al. 2010). Of the studies on *M. spicatum*, Gao et al. (2022), He et al. (2016), Jeong et al. (2021), and Zhu et al. (2010) directly treated the plant itself. Moreover, M. spicatum selectively inhibits the growth of M. aeruginosa, exerting a robust effect especially on unicellular cyanobacterial strains, including various M. aeruginosa strains and Synechocystis sp. (Jeong et al. 2021). Potamogeton *praelongus* is the only species with inhibitory effects in its genus, whereas three other species, including P. natans with floating leaves, exhibit stimulatory effects (Maredova et al. 2021). Vallisneria demonstrates high growth inhibition of M. aeruginosa, except for V. americana, which has a stimulatory effect on Microcystis but an algicidal effect on Aphanizomenon (Han et al. 2021a; Li et al. 2023; Maredova et al. 2021; Wang et al. 2022a).

Most studies have verified the algicidal effects of allelopathic substances extracted from aquatic plants. Whole plants were also effective in controlling blooms in some experiments. To obtain more consistent results for comparison, it is necessary to establish standardized criteria in experimental settings, such as substance concentration, mesocosm volume, and treatment duration. Several recent studies have reported algicidal bacteria isolated from the symbiotic microbiota of aquatic plants (Chen et al. 2023; Imai et al. 2021; Jiang et al. 2019; Miyashita et al. 2019). Further research should consider both the allelopathic effects of the plant and the effects of algicidal bacteria originating from plant biofilms.

Cyanophages

Cyanophages are viruses with a specific affinity for cyanobacteria. Since the identification of SM-1 in 1969, more than 10 cyanophages that infect *Microcystis* have been identified to date (Aranda et al. 2023; Safferman et al. 1969). These cyanophages are categorized into three families: *Myoviridae*, *Siphoviridae*, and *Podoviridae* (Aranda et al. 2023; Zhu et al. 2023). Previously identified cyanophages such as Ma-LMM01, MaMV-DC, and MaCV-L exhibit highly strain-specific lysis of Microcystis (Li et al. 2013; Ou et al. 2013; Yoshida et al. 2006). However, new findings indicate that MaMV-DC infects not only Microcystis aeruginosa FACHB-524 but also M. flos-aquae TF09 and M. wesenbergii DW09 (Wang et al. 2019). Me-ZS1, MinS1, and Mae-Yong924-1 also infect various Microcystis species via lysis (Lin et al. 2020; Qian et al. 2022; Zhang et al. 2022a). Morimoto et al. (2023) reported that M. aeruginosa interacts with both broad and narrow host-range cyanophages. Broad hostrange cyanophages increase with Microcystis abundance, whereas narrow host-range cyanophages are less abundant and fluctuate less. Because Microcystis blooms typically consist of multiple Microcystis strains, strain-specific cyanophages could reveal this issue in field applications. However, the potential of cyanophages for bloom control is increasing, considering the recent isolation of novel broad host-range cyanophages and their observed increase even during the bloom period.

Field applications and limitations of biotechnological approaches

Several biotechnological approaches for inhibiting *Micro*cystis have been extensively validated in the laboratory. However, it is crucial to apply these results in the field under varying environmental conditions to determine their efficacy against natural Microcystis blooms. Nevertheless, biological methods have fewer field application reports and less impact on controlling natural Microcystis blooms than chemical methods. Among the few field applications, Paucibacter aquatile DH15, a cyanobactericidal bacterium, successfully removed 90.7% natural Microcystis blooms in a 1000-L-scale mesocosm within 2 days, with the microbial and eukaryotic communities monitored during this process (Le et al. 2022b). Notably, an increase in eukaryotic algae was observed following Microcystis decline, contributing to the long-term inhibition of *Microcystis* and maintaining a healthy ecosystem by preserving primary production. In addition, periphyton, a mixture of heterotrophic and photoautotrophic microorganisms, effectively reduced Microcystis blooms in a field experiment (Le et al. 2023c). This study demonstrated the effectiveness of periphyton not only against Microcystis but also against Dolichospermum blooms, offering a wide-range potential for various cyanobacterial blooms. Biological algicides derived from cyanobactericidal bacteria are also being used to control Microcystis in the field. For example, using biological algicides derived from Bacillus sp. T4 as an adsorbent, Park et al. (2024) confirmed the removal of Microcystis aeruginosa in

50-L and 10-ton reactors. Paucibactin A produced by *Paucibacter aquatile* DH15 was 91.6% efficient in removing natural *Microcystis* in a 12-L microcosm (Le et al. 2023b).

Field applications to control Microcystis blooms using other organisms are less common. Ger et al. (2018b) proved that Pseudodiaptomus forbesi ingests Microcystis by identifying the microcystin synthase E(mcyE) gene in the gut of P. forbesi from the upper San Francisco Estuary. Additionally, the Microcystis mcyE gene has been detected in the guts of various zooplankton species (Bosmina spp., Daphnia spp., Bythotrephes longimanus, and Eudiaptomus gracilis) in the eutrophic Lake Peipsi, Estonia (Agasild et al. 2019). These findings suggest the possibility of using zooplankton to control Microcystis in the field. Amorim and Moura (2020) conducted 100-L-scale mesocosms in the Tapacurá reservoir in Brazil, manipulating submerged macrophytes (Ceratophyllum demersum), large herbivorous zooplankton, and nutrients. They discovered that the presence of macrophytes, both alone and in combination with zooplankton, significantly reduced cyanobacterial biomass by up to 84.8%. In Chagan Lake, China, the combined restoration of filter-feeding bivalves and submerged macrophyte (Hvdrilla verticillate) effectively reduced nutrient concentrations and cyanobacterial biomass, thereby alleviating eutrophication (Du et al. 2023).

Through a meta-analysis of field experiments utilizing chemical, bacterial, physical, and/or plant-based treatments, Anantapantula and Wilson (2023) evaluated their effectiveness on the water quality, including parameters such as phytoplankton pigment, cell density, cyanobacterial toxins, and taste/odor compounds. They concluded that only four chemicals, namely, copper sulfate, hydrogen peroxide, peracetic acid, and simazine, were significantly effective in controlling natural blooms and improving water quality. None of the bacterial, physical, or plant treatments alone showed a statistically significant effect. However, the authors emphasized that field data are still limited for drawing firm conclusions. This indicates that sufficient data from large-scale field experiments have not yet been accumulated enough. Therefore, more field experiments are needed to understand the current limitations of each method and to search for better alternatives.

Future directions with genome sequencing and multi-meta-omics

Various biological methods have been introduced, yet their application and success rates in the field remain limited when compared with those of chemical and physical methods. Nevertheless, advances in biotechnological techniques are paving the way for novel approaches to suppress *Microcystis* from a unique perspective. For instance, Roseomonas and Rhodobacter, which exhibit a phylosymbiotic pattern with Microcystis genotypes, can enrich the metabolic potential of Microcystis (Perez-Carrascal et al. 2021). Controlling these symbiotic bacteria could indirectly contribute to reducing Microcystis blooms. Furthermore, genome sequencing of Microcystis allows for the identification of genetic diversity by examining variations in gene repertoires among different strains, thereby elucidating functional differentiation along the evolutionary route (Zhang et al. 2023b). Moreover, it facilitates the identification of algicidal substances and their mechanisms. For example, lysine is toxic to Microcystis, as it blocks peptidoglycan biosynthesis (Kim et al. 2023). Cai et al. (2024) analyzed the gene composition in metagenomeassembled genomes of bloom microbiome in comparison with complete Microcystis genomes. They reported that the microbiome and Microcystis had complementary biochemical pathways involved in C, N, S, and P cycling.

Research on the periodic succession in microbial communities during Microcystis blooms has increased in recent years (Chen et al. 2024; Le et al. 2023a; Smith et al. 2021). These findings offer new insights into the interactions within cyanobacteria-associated bacterial communities, including the specific bacterial communities associated with Microcystis genotypes and the diverse responses of successive freeliving and particle-attached bacterial communities during different stages of bloom development (Chun et al. 2020; Liu et al. 2019). Network and indicator analyses permit the straightforward identification of bacterial species that interact closely with Microcystis and have a high potential for bloom control. This approach is expected to provide innovative strategies for combating blooms effectively. For example, Vampirovibrionales, a non-photosynthetic obligate-parasitic cyanobacterium, was first proposed as a bloom terminator on the basis of a network analysis (Chun et al. 2020).

Multi-meta-omics techniques, along with microbial community analyses, allow us to understand the detailed mechanisms underlying cyanobacterial bloom formation and extinction (Wang et al. 2021; Yan et al. 2022). Proteomic and metabolomic studies have identified the metabolic processes of Microcystis under various environmental conditions (Huang et al. 2024). Transcriptomics has revealed that allelopathic chemicals derived from plants notably downregulate essential genes related to biosynthetic pathways for carbohydrate assembly during the carbon fixation cycle and peptidoglycan construction in M. aeruginosa (Gil and Eom 2023). In addition, the transcriptomic study by Wang et al. (2024) discovered that *Microcystis* exposed to β -cyclocitral exhibit reduced photosynthetic activity and upregulation of stress-related genes, leading to cell death pathways. These results provide insight into the potential role of biological

metabolites in inducing programmed cell death *Microcystis* to control blooms. Using a multi-meta-omics approach is expected to enhance our understanding of how *M. aeruginosa* responds to different environmental conditions, distinct microbial communities, and coexisting aquatic plants, thereby contributing to breakthroughs in cyanobacterial bloom control.

Concluding remarks

CyanoHABs pose a significant threat to freshwater ecosystems by adversely affecting drinking water quality and agricultural activities. Microcystis is responsible for most cyanoHABs globally. This review presents recent findings in biotechnological research on Microcystis control, weighs the advantages and disadvantages of each method, and suggests future directions. The biotic agents examined in this review include cyanobactericidal bacteria, fungi, eukaryotic microalgae, zooplankton, aquatic plants, and cyanophages. Among these agents, cyanobactericidal bacteria use both direct lysis of cells and secretion of algicidal compounds to indirectly kill bacteria. Furthermore, newly reported bacteria that use both methods enable the highly efficient control of Microcystis. Although numerous biological methods have demonstrated success, their control efficiencies in field applications are generally lower than those of chemical and physical methods. Therefore, a future approach to control Microcystis was proposed: a comprehensive understanding of microbial interactions during *Microcystis* blooms by using advanced molecular and bioinformatic/ecoinformatic tools, such as high-throughput sequencing and multi-metaomics. It is imperative to adopt the latest techniques and apply them more frequently in the field to achieve tangible advancements. Ultimately, we anticipate new insights into the unknown mechanisms surrounding Microcystis outbreaks.

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Data Availability Data sharing is not suitable for this mini-review paper because no new data was created.

Declarations

Ethics approval This article does not contain any studies with human participants or animals performed by any of the authors.

Conflict of interest The authors declare no competing interests.

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