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Review

Potential Use of Aquatic Vascular Plants to Control Cyanobacterial Blooms: A Review

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Abstract: Intense "blooming" of cyanobacteria (blue-green algae) caused by eutrophication and climate change poses a serious threat to freshwater ecosystems and drinking water safety. Preventing the proliferation of cyanobacteria and reducing water nutrient load is a priority for the restoration of eutrophic water bodies. Aquatic plants play an important role in the function and structure of aquatic ecosystems, affecting the physiochemistry of the water and bottom sediments, primary production, and biotic interactions that support a balanced ecosystem. This review examines the inhibitory effect of aquatic vascular plants on harmful blooms of cyanobacteria. Aquatic plants are able to successfully inhibit the growth of cyanobacteria through various mechanisms, including by reducing nutrient and light availability, creating favorable conditions for the development of herbivorous zooplankton, and releasing allelopathic active substances (allelochemicals) with algicidal effect. Allelopathy is species-specific and therefore acts as one of the key mechanisms by which the development of cyanobacterial populations in aquatic ecosystems is regulated. However, allelopathic activity of aquatic vascular plants depends on various factors (species characteristics of aquatic plants, area, and density of overgrowth of water bodies, physiochemical properties of allelopathically active substances, hydrological and hydrochemical regimes, temperature, light intensity, etc.), which may regulate the impact of allelochemicals on algal communities. The paper also discusses some problematic aspects of using fast-growing species of aquatic vascular plants to control cyanobacterial blooms.

Keywords: aquatic vascular plants; water bloom; cyanobacteria (blue-green microalgae); phytoplankton; allelopathic activity; cells change (cellular damage)

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1. Introduction

The increase in frequency and duration of blue-green algal (cyanobacterial) blooms poses serious threats to the environment, including degradation of local and global water resources [1–6]. This is due to the production of a wide range of toxic secondary metabolites, namely cyanotoxins, by some species of planktonic microalgae (*Microcystis aeruginosa* (Kützing) Kützing; *Dolichospermum flosaquae* (Bornet & Flahault) P.Wacklin, L.Hoffmann & Komárek (=*Anabaena flosaquae* Brébisson ex Bornet and Flauhault); *Aphanizomenon flosaquae* Ralfs ex Bornet and Flahault; *Planktothrix agardhii* (Gomont) Anagnostidis and Komárek; *Planktothrix rubescens* (De Candolle ex Gomont) Anagnostidis and Komárek; *Cylindrospermopsis raciborskii* (Woloszynska) Seenaya and Sabbaraju (=*Raphidiopsis raciborskii* (Woloszynska) Aguilera, Berrendero Gómez, Kastovsky, Echenique and Salerno), etc.) [1,7–9]. Eutrophication and climate change are the two main factors contributing to the intensification and spreading of harmful blue-green algae blooms [1,2]. Many approaches that involve the use of synthetic chemicals to mitigate cyanobacterial blooms have been proposed [10–12]; however, recent studies demonstrate that aquatic vascular plants offer a promising solution through natural biological control of cyanobacterial blooms [5,12–17].

Aquatic vascular plants play an important role in the functioning and structure formation of aquatic ecosystems and ensure their sustainability [18–20]. They do so by affecting the physical and chemical properties of the water and bottom sediments, carbon fixation and biomass production, nutrient transformations, and biotic interactions that support a balanced ecosystem [21,22].

The purpose of this review is to examine the mechanisms by which aquatic vascular plants can control harmful blooms of blue-green algae (cyanobacteria) with a focus on the main benefits and some problematic aspects of their use.

2. Mechanisms of Aquatic Vascular Plants' Influence on Cyanobacterial Blooms

Aquatic plants reduce phytoplankton blooms, including cyanobacterial blooms, by releasing allelopathic compounds into the environment, altering physical and chemical parameters of the aquatic environment (e.g., light regime, inorganic nutrient concentrations), or by facilitating the development of herbivorous zooplankton [18,21,23]. The mechanism and degree of inhibition of phytoplankton by aquatic macrophytes (benthic and floating aquatic plants) varies depending on the area that they occupy in a water body (Figure 1).

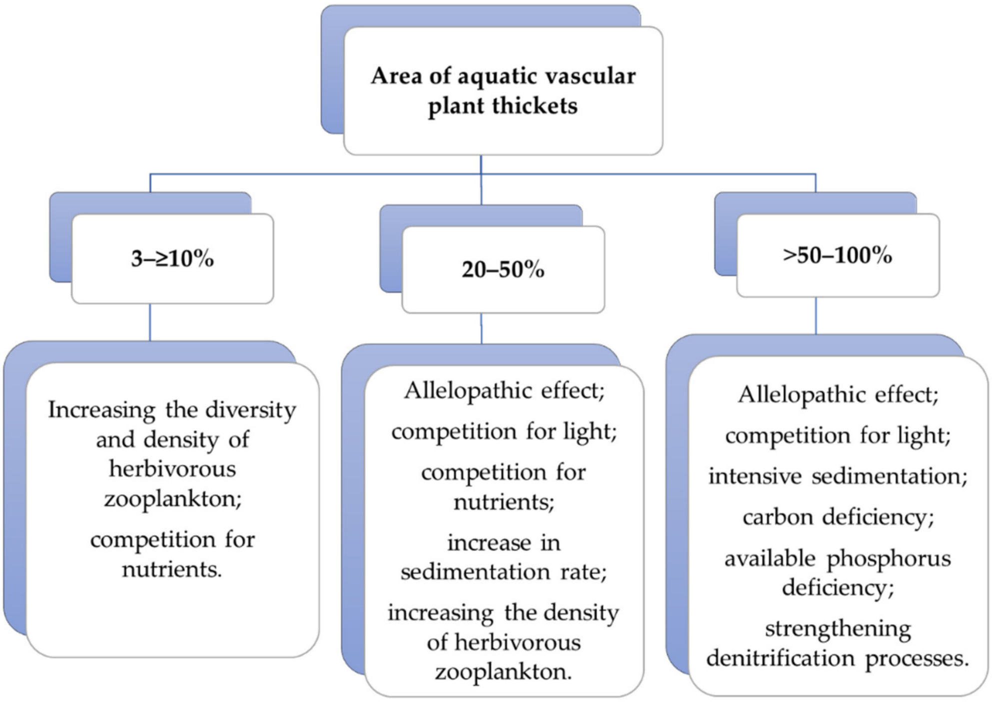


Figure 1. The mechanism of inhibition of cyanobacteria and other phytoplankton growth depends on the relative area of aquatic macrophyte thickets [21,24,25].

Aquatic vascular plants inhibit phytoplankton by reducing the solar radiation available for photosynthesis (shading effect) [26–28]. This is a particularly common mechanism for floating-leaved plants such as *Trapa natans* L., *Nuphar lutea* L. Smith, *Pontederia crassipes* Mart., *Pistia stratiotes* L. [23,28–30] (Figure 2). Large, dense thickets of *Trapa natans* may absorb more than 95% of incident sunlight and inhibit the growth of other plants and their associated microscopic flora and fauna to become the dominant species in aquatic environments [28,31–33]. A similar pattern of competitive exclusion was described for *Pontederia crassipes* or common water hyacinth (former name *Eichhornia crassipes* Mart.), water lettuce (*Pistia stratiotes*) and yellow waterlily (*Nuphar lutea*) [23,28,34].

Figure 2. Floating aquatic plants (*Trapa natans* L., *Nuphar lutea* (L.) Smith) in the Kyiv Reservoir (Dnipro River, Ukraine).

Reductions of cyanobacterial biomass, which is often observed in thickets of aquatic plants, may be associated with competition for nutrients [18,35,36]. The competition for nutrients applies especially to the effects of non-rooted, floating leaf plants, because submerged rooted plants absorb essential nutrients from the bottom sediments, which supports their active growth even under very low dissolved nutrient concentrations in the water column [18,36–38]. Essien et al. [22] demonstrated that the distribution of *Pistia stratiotes*, *Lemma* sp., *Nymphea lotus* L. and *Pontederia crassipes* is associated with large quantities of organic matter in the water. These authors also noted that these plants play a significant role in improving water quality by taking up organic and inorganic substances from the aquatic environment. Such reduction in nutrient concentrations can contribute to decreasing the intensity of cyanobacterial blooms.

Aquatic vascular plants can indirectly affect the amount of nutrients in the water. The presence of submerged macrophytes increases the surface area available for periphyton and, as a consequence, competition for nutrients between phytoplankton and periphyton [18,39]. In addition, under anoxic conditions formed in the areas overgrown with macrophytes, heterotrophic denitrification increases [18,21,40]. This promotion of denitrification leads to a decrease in nitrate concentration and changes the ratio of nitrogen species, which can limit the growth of cyanobacteria [21].

Some authors report that the density of planktonic algae may decrease due to intensified sedimentation. However, this trend is usually observed in larger microalgae species or those lacking flagella or gas vacuoles [41,42]. Many species of planktonic blue-green algae (cyanobacteria), including *Aphanizomenon flosaquae*, *Dolichospermum flosaquae*, *Microcystis aeruginosa*, *Planktothrix agardhii* and *Planktothrix rubescens*, have gas vacuoles that ensure their buoyancy [11,43–45]. This mechanism of reducing the intensity of blue-green algae development by aquatic vascular plants appears to play a secondary role.

Aquatic vascular plants are known to serve as a refuge for zooplankton [18,46]. Shallow lakes support higher zooplankton densities within or close to the areas overgrown with aquatic vascular plants during the day [47]. Given that most species of zooplankton are herbivorous, increased densities of zooplankton will decrease cyanobacteria abundance. Many authors note that the high species richness and development of high densities of zooplankton in dense beds of submerged aquatic plants [48–51], and their exometabolites (phenolcarboxylic acids) stimulate *Daphnia magna* Straus fertility [52]. However, it should be noted that helophytes and floating leaf plants create poorer physicochemical conditions for the development of large populations of aquatic animals compared to submerged plants [48,53]. In addition, cyanotoxins produced by blue-green algae are released in large quantities and can adversely affect zooplankton. Thus, this indirect mechanism does not always play an important role.

In view of the above, allelopathy appears to be the most effective mechanism to control cyanobacterial development in aquatic communities. Allelopathic interactions occur due to the synthesis and release of specific allelochemicals by plants [21,24,54–57]. Many macrophyte species, as active producers of these substances, inhibit the development of cyanobacteria [21,24].

3. The Main Groups of Allelopathically Active Substances of Aquatic Vascular Plants with Algicidal Action

The allelopathically active compounds (allelochemicals) with algicidal effects can be categorized [58,59] into four main groups based on their biosynthesis pathways: polyphenols, nitrogen-containing compounds, fatty acids, and terpenoids.

Structural formulae of polyphenols include an aromatic ring with one or more hydroxyl groups. Depending on peculiarities of chemical structure, they are divided into simple phenols, phenolcarbonic acids, coumarins, flavonoids, quinones, and tannins [60]. Algicidal activity of exometabolites of aquatic vascular plants is determined by their physical and chemical properties [15,58,61,62]. Polyphenols containing hydroxyl groups in "ortho" and/or "para" position cause a stronger inhibitory effect on blue-green algae compared to polyphenols with a "meta" position of hydroxyl groups [12,63,64]. Polyphenols (including shikimate pathway-producing polyphenols) are one of the main classes of allelochemicals in *Myriophyllum spicatum* L., *Phragmites communis* Trin. and *Trapa natans* [65–69]. The algicidal activity of phenolic compounds of *M. spicatum* was first described in 1987 by Planas et al. [70]. It was later discovered that species of *Myriophyllum* produce various phenolic allelochemicals that inhibit the growth of cyanobacteria, especially cyanobacteria that cause harmful algal blooms [5,71]. The total content of phenolic compounds in *M. spicatum* can reach up to 12% (dry weight), and the content of algaecide telimagrandin II—up to 2% [72]. The influence of phenolcarboxylic acids on epiphytic algae has also been demonstrated [73,74]. In this case, gallic, salicylic, and caffeic acids show the highest allelopathic activity, changing the dominant epiphytic algae when the ecological state of water bodies changes.

Nitrogen-containing compounds include alkaloids, amines, amino acids, and their derivatives. Among these allelopathically active compounds, alkaloids are highly toxic to algae and include a large group of secondary metabolites containing one or more nitrogen atoms, often in the heterocyclic ring, and have alkaline properties [75,76]. Some aquatic vascular plants, such as *Nuphar lutea*, produce acaloids (resorcin, etc.) and are highly active against not only phytoplankton species but also zooplankton, including crustaceans [57,77].

Fatty acids are carboxylic acids possessing long aliphatic carbon chains (saturated or unsaturated). The shorter the carbon chain and the more unsaturated the bonds in the fatty acid, the higher is the toxic effect on algae [12,61]. Plants such as *Potamogeton natans* L., *Nuphar lutea*, *Nymphaea alba* and *Myriophyllum spicatum* are considered to be the most active producers of allelochemical fatty acids. The proportion of fatty acids among volatile organic compounds in these plants may exceed 60–70% [5]. Although fatty acids are common compounds in plant metabolism, release of large quantities by vascular plants can inhibit microalgal growth.

Terpenoids is the common name for a class of hydrocarbons and their oxygen-containing derivatives (alcohols, aldehydes, carboxylic acids, and esters, etc.) [59,78]. Only a limited number of substances in this class have algicidal effects compared to polyphenols, alkaloids, and fatty acids [58]. In addition, their ability to inhibit algal growth is considerably weaker compared to other allelopathic compounds. A typical example of a substance belonging to this class with toxic effects on blue-green algae is terpenoid β-ionone [58,79].

The most promising species for biological control of cyanobacteria due to their production of allelopathic compounds are *Nuphar lutea*, *Myriophyllum spicatum*, *Ceratophyllum demersum* L., *Phragmites communis* and *Elodea canadensis* Michx., as well as plants of genera *Eichhornia*, *Pistia*, *Potamogeton*, *Typha* and *Trapa* [5,16,80,81]. Table 1 represents the main allelochemicals of aquatic vascular plants that possess algicidal properties.

Table 1. The main allelopathically active compounds of some aquatic vascular plant species, which have inhibitory effects on phytoplankton.

Macrophyte Species	**Allelopathically Active Compounds**	**Phytoplankton Species, Subjected to Inhibitory Effects**	**Literature Source**
Hydrophytes			
Spiked water-milfoil (*Myriophyllum spicatum* L.)	Tannins (telimagrandin II); Phenolic acids (gallic, ellagic, pyrogallic); Flavonoids ((+)-catechin); Fatty acids (nonanoic, oleic, petroselinic)	*Limnothrix redekei* (Goor) Meffert, *Microcystis aeruginosa* (Kützing) Kützing, *Planktothrix agardhii* (Gomont) Anagnostidis and Komárek,	[66,82,83]
Whorled water-milfoil (*Myriophyllum verticillatum* L.)	Phenylpropanoids (α-asarone)	*Limnothrix redekei*, *Microcystis aeruginosa*	[84,85]
Water caltrop (*Trapa natans* L.)	Phenolic acids (benzoic, p-hydroxybenzoic, salicylic, cinnamic, α-resorcylic, protocatechuic, coumaric, vanillic, gallic, caffeic, ferulic, syringic, ß-resorcylic and sinapinic)	*Microcystis aeruginosa*, phytoplankton in general	[5,69]
Yellow waterlily (*Nuphar lutea* (L.) Sm.)	Fatty acids (hexadecanoic acid, tetradecanoic acid); Esters of phthalic acid (dibutyl phthalate, diisobutyl phthalate)	*Microcystis aeruginosa*	[5]
Canadian waterweed (*Elodea canadensis* Michx.)	Flavonoids (luteolin 7-O-diglucuronide, apigenin 7-O-diglucuronide, chrysoeriol 7-O-diglucuronide)	*Microcystis aeruginosa*	[81,86]
Common water hyacinth (*Pontederia crassipes* Mart. = *Eichhornia crassipes* Mart.)	Amines (N-phenyl-1-naphthylamine, N-phenyl-2-naphthylamine); Fatty acids (linoleic acid)	*Microcystis aeruginosa*, *Microcystis* sp., green microalgae	[87,88]
Coontail (*Ceratophyllum demersum* L.)	Esters of carboxylic acids (3-hydroxy-2,2,4-trimethylpentyl ester of 2-methylpropanoic acid); Ethers of phthalic acid (dibutyl phthalate)	*Aphanizomenon flosaquae* Ralfs ex Bornet and Flahault, *Microcystis aeruginosa*, *Pseudanabaena limnetica* (Lemmermann) Komarek, *Oscillatoria tenuis* C. Agardh ex Gomont, green microalgae	[5,82,89]
Water lettuce (*Pistia stratiotes* L.)	Phenylpropanoids (α-asarone); Fatty acids (linoleic acid, γ-linolenic acid)	*Microcystis aeruginosa*, *Synechococcus leopoliensis* (Raciborski) Komárek, phytoplankton in general	[90,91]

Table 1. *Cont.*

Macrophyte Species	Allelopathically Active Compounds	Phytoplankton Species, Subjected to Inhibitory Effects	Literature Source
Sago pondweed (*Potamogeton pectinatus* L.)	Terpenoids (lactone diterpenes)	*Microcystis aeruginosa*, *Oscillatoria tenuis*, green microalgae	[5,79,92]
Floating pondweed (*Potamogeton natans* L.)	Terpenoids (lactone diterpenes, furan diterpenes)	*Microcystis aeruginosa*, green microalgae	[93]
Floating fern (*Salvinia natans* L.)	Ethers of phthalic acid (dibutyl phthalate)	*Microcystis aeruginosa*	[94]
Helophytes (partly submerged plants)			
Common reed (*Phragmites communis* Trin. (=*Phragmites australis* (Cav.) Trin. ex Steud))	Phenolic acids (p-coumaric acid, ferulic acid, vanillic acid, syringic acid, caffeic acid, gallic acid); Fatty acids (tetradecanoic acid, palmitic acid, nonanoic acid and stearic acid)	*Microcystis aeruginosa*, *Chlorella pyrenoidosa* H.Chick	[65,95]
Narrowleaf cattail (*Typha angustifolia* L.)	Phenolic acids and their derivatives (syringic acid, isoferulic acid)	*Dolichospermum flosaquae*, *Microcystis aeruginosa*,	[96,97]
Broadleaf cattail (*Typha latifolia* L.)	Fatty acids (linoleic acid, α-linolenic acid)	*Dolichospermum flosaquae*, *Microcystis aeruginosa*, *Chlorella vulgaris* Beijerinck, *Chlorella pyrenoidosa*	[79,98,99]

4. Physiological and Biochemical Mechanisms of Allelopathic Effect of Aquatic Vascular Plants on Cyanobacteria

Allelopathically active compounds, as well as other stressors, affect a number of physiological and biochemical processes in phytoplankton species (Table 2), including water bloom agents, and thereby limit their growth and development (Figure 3) [58,100–102].

Table 2. The mechanism of inhibitory action of some allelopathically active substances of aquatic vascular plants on cyanobacteria.

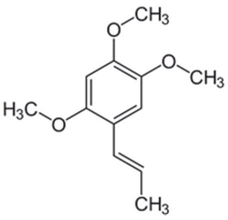
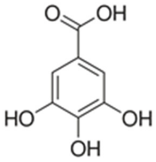
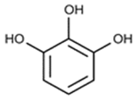
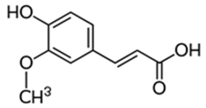
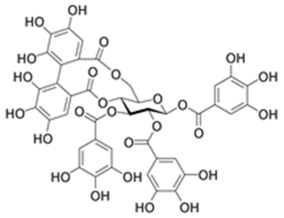
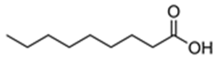
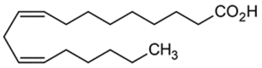
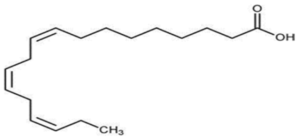
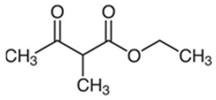
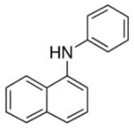
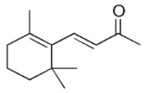
Allelopathically Active Compounds	Structural	Mode of Action
Polyphenols		
α-Asarone		Inhibition of respiration, inhibition of growth [79]
Gallic acid		Inhibition of photosystem II (PSII), reduction of chlorophyll content, oxidative stress [12,58,103]
Pyrogallic acid		

Table 2. *Cont.*

Allelopathically Active Compounds	Structural	Mode of Action
Ferulic acid		Reduction of membrane potential, reduction of chlorophyll content [58]
Telimagrandin II		Inhibition of photosystem II (PSII); inhibition of alkaline phosphatase activity [79,103]
Fatty acids/esters		
Nonanoic acid		Inhibition of oxygen evolution, inhibition of growth [103,104]
Linoleic acid		Oxidative stress, reduction of chlorophyll content, blocking the transport of electrons [58,105]
α-Linolenic acid		Inhibition of growth [58]
Ethyl 2-methylacetoacetate		Oxidative stress, changes in the structure of cell membranes, inhibition of growth [12,16,106]
Nitrogen-containing compounds		
N-phenyl-1-naphthylamine		Oxidative stress, inhibition of growth [107]
Terpenoids		
β-Ionone	 β	Distortion of thylakoids [108]

4.1. Disturbance of Cell Structure

Acting as natural barriers for cells and organelles, biomembranes are the first structures to be affected by allelochemicals [56]. Disturbance of the membrane integrity leads to disruption of the organelles' structure and function. In some algal species, the degree of unsaturation of fatty acids increases under the influence of macrophytic allelochemicals and, as a consequence, there is an increase in fluidity and a decrease in selective permeability of cell membranes [12,16,109]. According to Li et al. [101], ethyl 2-methylacetoacetate causes changes in cell membranes of *Microcystis aeruginosa*. Moreover, the shape of microalgal cells changes at some concentrations of allelochemical substances that is manifested in the protoplast shrinking and its separation from the cell wall, shrinking of the nucleus volume, and impairment of the chloroplast structure [12].

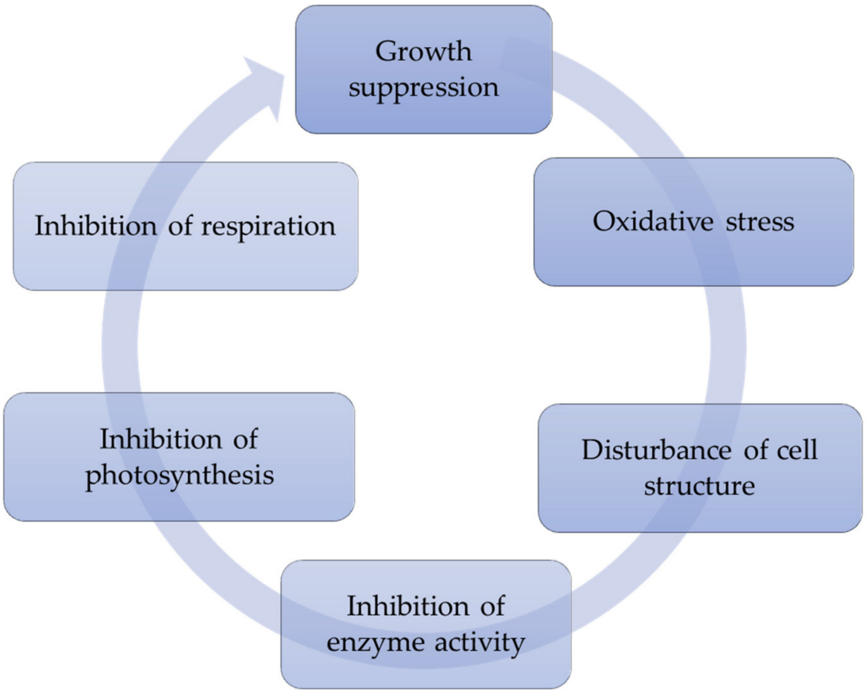


Figure 3. Physiological and biochemical mechanisms of influence of allelopathically active compounds of aquatic vascular plants on target phytoplankton species.

4.2. Oxidative Stress

Oxidative stress is considered one of the most important physiological and biochemical effects of allelopathically active substances of aquatic vascular plants on phytoplankton [16,110,111]. Under the influence of ethyl 2-methylacetoacetate, the concentration of reactive oxygen species (ROS) and products of lipid peroxidation in algal cells increases, and the activity of some antioxidant enzymes is inhibited [16]. Allelochemicals may increase the activity of some enzymes and inhibit others due to various functional differences in enzymes [79]. Lourenção et al. [102] recorded a sharp decrease in superoxide dismutase (SOD) activity in *Microcystis aeruginosa* with addition of *Pistia stratiotes* extracts, while the activity of other enzymes that offer antioxidant protection was not inhibited. Lourenção et al. [102] demonstrated that superoxide dismutase (SOD) in *Microcystis aeruginosa* is a main target for bioactive substances, which are present in aqueous and ethanolic extracts of *P. stratiotes*.

Phenolic compounds dissolved in the waters of continental reservoirs, under certain conditions, affect the photosynthetic activity of planktonic algae, especially those that cause water blooms. The main sources of the formation of the pool of extracellular phenols are intravital and postmortem secretions of aquatic vascular plants. During biogenic leaching, easily oxidized phenols are transformed into the corresponding quinones, which, penetrating into algae cells, change the normal course of their photosynthesis. In this case, the processes of non-cyclic and cyclic phosphorylation are inhibited. Depending on the amount of quinone entering the cells of algae, their photosynthetic activity slows down or may stop completely [13,112].

4.3. Inhibition of Extracellular Enzyme Activity

Many phytoplankton species produce extracellular enzymes that enable them to use complex substrates to sustain life or colonize habitats [113]. A decrease in the activity of extracellular alkaline phosphatase is one of the main inhibitory effects of polyphenols on phytoplankton [79,80]. This enzyme is synthesized by many microalgal species experiencing inorganic phosphorus deficiency. Inactivation of alkaline phosphatase in conditions of phosphorus deficiency leads to the death of algal cells. This enzyme is especially important for homeostasis of blue-green algae [113].

4.4. Inhibition of Photosynthesis and Respiration

Allelopathically active substances of aquatic vascular plants inhibit the growth of cyanobacteria by reducing the rates of photosynthesis and respiration [12,79,114]. A decrease in microalgal respiratory rate occurred after exposure to α-asarone and allelochemicals isolated from *Phragmites communis* [79]. The effect of allelopathy on algal photosynthesis can be manifested in disruption of electron flow in the photosynthetic electron transport chain, a reduction in pigment content, and a change in chlorophyll-a fluorescence [17,81,83]. Many allelopathic compounds produced by aquatic vascular plants (telimagrandin II, gallic acid, pyrogallic acid etc.) inhibit photosystem II (PS II) [81,100,103]. Damage to PS II can be mitigated by de novo synthesis of the D1 protein, which is a key subunit of PS II [81,115]. Nevertheless, allelochemicals such as pyrogalic acid inhibit expression of the psbA gene that encodes the D1 protein in *Microcystis* Lemmermann and *Cylindrospermopsis* G.Seenayya and N.Subba Raju, and thus prevents protein synthesis, which promotes adaptation to stress [111]. Zhu et al. [83] showed that polyphenols strongly inhibit the photosynthetic transport of electrons in cyanobacteria but do not have a significant effect on photosynthesis of green algae, in particular because of differences in localization and structure of the photosynthetic apparatus. In addition, it has been shown that under the influence of certain allelochemical substances, in particular linoleic acid, ferulic acid, and pyrogallol of *Microcystis aeruginosa,* the concentration of the photosynthetic pigment chlorophyll-a is significantly reduced [58,105]. Inhibition of photosynthesis, the main physiological process in competing autotrophs, is an effective strategy for survival and colonization of aquatic habitats and is typical for many macrophyte species [100,113]. Given that aquatic vascular plants have a selective ability to inhibit the development of certain phytoplankton species, they can serve as an effective means of biocontrol against cyanobacterial agents of harmful blooms in water bodies.

5. Factors Affecting the Allelopathic Activity of Aquatic Vascular Plants

Allelopathic activity of aquatic vascular plants depends on various biotic and abiotic factors [12,16,79,81,113,116]. The complex of biotic factors that determine the impact of aquatic vascular plants on phytoplankton includes the density and benthic or surface areal cover of aquatic vegetation, species-specific features, and the growth stage of aquatic plants. Among the abiotic factors, the hydrological regime (flow rate, water exchange intensity, etc.) and physicochemical conditions (temperature, irradiance, nutrient concentration, pH, dissolved oxygen content, etc.) in water bodies are crucial.

5.1. Biotic Factors

5.1.1. Area and Density of Overgrown Areas of Aquatic Vascular Plants

A number of studies demonstrated an inhibitory effect of aquatic vascular plants on phytoplankton growth in a wide range of macrophyte areal cover (3–100%) [21,25,74,117]. The potential impact of allelopathy is particularly notable in water bodies with a high level of macrophyte coverage, 20% or more [21,24,118]. In this case, the density of macrophyte thickets plays an important role. Studies show a negative allelopathic effect of higher aquatic plants on phytoplankton at a biomass density of 1 to 10 g/dm^3 (wet weight) [82,119].

5.1.2. Species-Specific Features and Growth Stage of Plants

Allelopathy is a species-specific phenomenon, that is, the same plant species or allelochemical may cause different effects on different species of algae [21,59,82,120]. For example, *Ceratophyllum demersum* significantly suppresses the growth of *Anabaena* species but does not inhibit the growth of *Chlorella* and *Scenedesmus* species [121]. The allelochemical ethyl 2-methylacetoacetate, isolated from *Phragmites communis*, shows high inhibitory activity against *Microcystis aeruginosa*, but has almost no influence on *Chlorella vulgaris* Beijer. [65]. Allelopathically active compounds of some species, for example, *Myriophyllum spicatum*, *Nuphar lutea*, *Pistia stratiotes*, *Typha latifolia* L., inhibit both prokaryotic and eukaryotic microalgae [79,82].

Aquatic vascular plants produce various allelochemical compounds, which have unequal inhibitory effect on phytoplankton species [16,57]. However, a number of studies have shown that prokaryotic algae are more sensitive to exometabolites of aquatic vascular plants compared to eukaryotic algae [21,58]. Allelopathically active compounds produced by plants belonging to the same phylum, or even genus may have diverse effects on phytoplankton [79,82,120]. Among Cyanobacteria, species of *Dolichospermum* (Ralfs ex Bornet and Flahault) P.Wacklin, L.Hoffmann and J.Komárek (=*Anabaena* Bory ex Bornet and Flahault), *Microcystis* Lemmermann and *Oscillatoria* Vaucher ex Gomont are highly sensitive to a wide range of allelochemicals [82,120]. In addition, allelopathic influence of aquatic vascular plants on toxic *Microcystis* strains is more pronounced than on non-toxic strains [120,122,123]. *Ceratophyllum demersum* causes a higher inhibitory effect on the microcystin-producing strain of *Microcystis aeruginosa* compared to *Microcystis panniformis* Komárek, Komárková-Legnerová, Sant'Anna, M.T.P.Azevedo, and P.A.C.Senna, which does not produce toxins [123]. This effect can be explained by the fact that under conditions of stress caused by microcystins, aquatic vascular plants produce and release allelochemicals more intensively [122,123].

The sensitivity of algae to allelopathy from aquatic vascular plants also varies depending on the growth phase and initial cell density of microalgae. *Microcystis aeruginosa* is inhibited by allelochemical compounds of *Phragmites communis* to a greater extent at the initial growth phase (lag phase) than at the rapid growth phase (logarithmic phase) [65]. The growth stage of aquatic vascular plants can also affect their allelopathic activity. Some authors report that younger and actively vegetating aquatic vascular plants demonstrate higher allelopathic activity [124,125].

5.1.3. Concentration of Allelopathically Active Compounds and Exposure Duration

Allelochemicals of aquatic vascular plants demonstrate both inhibitory and stimulating effects on cyanobacteria depending on the concentration of these compounds in water [59,81]. Wu et al. [90] studied the effect of allelochemicals isolated from *Pistia stratiotes* on the growth of *Microcystis aeruginosa*, as well as its release of microcystin-LR. Low concentrations (20–60 mg/dm^3) stimulated growth of algal cultures, while high concentrations (100–200 mg/dm^3) caused an inhibitory effect on growth and decreased release of microcystin-LR. Along with the concentration of allelochemical compounds, the duration of their effect is also important. The inhibitory effect of N-phenyl-1-naphthylamine on *Microcystis aeruginosa* was more substantial at lower doses and longer exposures [107].

5.2. Abiotic Factors

5.2.1. Hydrological Regime

Hydrological conditions, particularly the flow rate, water exchange rate, and water level regime, are important abiotic factors influencing the distribution, species composition, and metabolic activity of aquatic vegetation [126–129]. Freshwater aquatic vascular plants and planktonic microalgae develop intensively in both lentic and lotic ecosystems [113]. However, high density and species diversity of plants are usually observed at low and moderate flow rates, while the fast flow is limiting to their growth [79,113,129]. Water flow rate causes an indirect effect on plant photosynthesis, in particular by regulating the availability of dissolved nutrients [126,130]. Photosynthesis and rate of nutrient uptake by freshwater vascular plants positively correlate with lower flow rates such as 0–0.1 m/s [127,129,130]. Under these conditions, greater production and release of allelochemicals by aquatic vascular plants are observed, as well as greater accumulation of these compounds in the water [79]. Alternatively, there is intensive leaching and dilution of allelochemicals in faster water flows [79,131]. In this regard, the allelopathic influence of aquatic vascular plants on algae is considered to be more pronounced in lake systems than in river systems [79].

It should also be noted that the most promising potential for controlling blue-green algae, which cause water blooms, pertains to shallow areas of water bodies, where the content of phenolic compounds reaches 2 mg/dm^3. In addition, 0.2–0.4 mg/dm^3 was found to be sufficient to control water bloom, depending on the pool of these compounds [63,132] present in thickets of aquatic vascular plants.

5.2.2. Physicochemical Conditions

Among physicochemical factors that influence the growth, distribution and allelopathic activity of aquatic vascular plants, the nutrient concentration, temperature regime and light intensity should be primarily mentioned [80,113].

Low availability of nutrients increases biotic competition and enhances the allelopathic activity of aquatic vascular plants [54,133–135]. Phosphorus limitation causes *Myriophyllum spicatum* to intensify the release of telimagrandin II [81,113].

Fitzgerald [136] noted that aquatic vascular plants inhibit the growth of microalgae in aquatic environments with limited nitrogen [79]. A similar trend was observed by Mjelde and Faafeng [137], who found that aquatic vascular plants inhibit the development of phytoplankton in lakes with low content of this nutrient. Therefore, the release of allelochemicals by aquatic vascular plants is an effective protection and survival strategy in various stressful conditions.

Aquatic plants demonstrate optimal rates of photosynthesis at relatively high temperatures (between 20 and 35 °C [23,138,139]), and an increase in their growth and local distribution follows seasonal increases in water temperature [23,140]. An increase in water temperature contributes to the accumulation of aquatic vascular plant biomass and increased release of allelopathically active substances [59,85]. For example, the intensive development of *Myriophyllum verticillatum* is observed in August, and during this period it causes the strongest allelopathic inhibition of phytoplankton species [85]. The temperature largely determines the rate of synthesis and release of allelopathically active compounds by aquatic vascular plants, affecting the activity of enzymes involved in the biosynthesis of allelochemicals and the diffusion rate of these compounds in water.

Increased temperature may contribute to the development and spread of species such as *Pontederia crassipes*, *Pistia stratiotes* and *Nuphar lutea* [23,30]. *Pontederia crassipes* (common water hyacinth) inhibits the growth and activity of enzymes in *Microcytis aeruginosa* at temperatures less than 25 °C [141,142]. The optimal temperature range for the growth of water hyacinth is 25–30 °C, maximal–33–35°C [139]. Plant species *Pontederia crassipes* and *Pistia stratiotes* are known to be among the most common species in regions with warm climates [34,143].

The stability of allelochemical compounds in water depends on temperature and other factors such as light intensity, pH level and dissolved oxygen content [59,103,144,145]. Nakai et al. [103] showed that increasing temperature (from 20 to 30 °C) and light intensity (from 25 to 75 μmol m^{-2} s^{-1}) reduce inhibition of *Microcystis aeruginosa* growth, and that this process is mediated by the impact of polyphenols ((+) catechin, eugeniin, ellagic acid, gallic acid and pyrogallic acid) and fatty acids (nonanoic acid, cis-6-octadecenoic acid and cis-9-octadecenoic acid), which are also produced by *Myriophyllum spicatum* [6]. Other researchers report the effect of light intensity on the stability of allelopathically active phenolic compounds in water [144,146]. Light can cause chemical changes in allelopathically active substances due to stimulation of their oxidation, polymerization or degradation [144].

Different conditions of pH and dissolved oxygen content also affect the degradation of allelochemicals, thus modifying allelopathic effects [59,62,147]. Under high values of pH ($\geq$10) polyphenols transfer from molecular to ionic state and easily undergo oxidized polymerization, which reduces their bioavailability and toxicity [62]. Alkaloids, in contrast, exist in the molecular state at low pH [59]. For these reasons, when using aquatic vascular plants as producers of allelopathically active substances to control blue-green algal blooms, the low stability of these compounds under the influence of various abiotic factors should be considered. High pH and dissolved oxygen concentrations are the consequence of intensive growth processes and high metabolic activity of aquatic vascular plants. The low level of these indicators is associated with the intensification of accumulated phytomass decomposition. Therefore, selective extraction of biomass of fast-growing species of aquatic vascular plants should be conducted to prevent these stressful conditions.

6. The Advantages and Considerations of Using Aquatic Vascular Plants to Control Harmful Cyanobacterial Blooms

Analysis of the literature demonstrates that many species of aquatic vascular plants are characterized by significant potential for restoring water quality, and their introduction into areas of harmful "blooms" is an effective biological method to control these processes. Aquatic vascular plants are able to inhibit the growth of cyanobacteria both directly, releasing allelopathically active substances with algicidal effect, and indirectly, reducing the concentration of nutrients in water, access to light, etc.

In practical terms, allelopathy is a promising approach to fight against cyanobacterial blooms. Allelopathically active compounds produced by aquatic vascular plants are characterized by high selectivity and show a pronounced inhibitory effect against cyanobacteria, which cause harmful blooms. Their impact on other algae and aquatic organisms may be minimal or non-existent, implying that these natural mechanisms of action on cyanobacteria are environmentally safe.

Direct application of synthetic algicidal compounds into water bodies to control the growth of water-blooming pathogens may disrupt the aquatic ecosystem due to their high concentration in local areas. In addition, it may lead to fast inactivation of toxic agents and eliminate the effect of inhibitory concentrations [12,148,149]. In this regard, the use of slow-release algicides is a more effective and environmentally safer way to tackle harmful algal blooms. The combination of this approach with the allelopathic inhibiting effect of aquatic vascular plants is of particular interest.

Aquatic vascular plants affect the nutrient cycle in aquatic ecosystems. Along with associated periphyton algae, they act as "traps" for nutrients, helping to restore water-quality status and preventing biomass increase of planktonic cyanobacteria species. Different mechanisms of the growth inhibition of harmful algal taxa may act simultaneously and synergistically (for example, reduction in access to bioavailable nutrients and development of the allelopathic effects).

Despite apparent advantages, some problematic aspects should be considered in the use of aquatic vascular plants to fight against harmful algal blooms. Increasing anthropogenic eutrophication leads to excessive reproduction of aquatic vascular plants, and more competitive species may completely displace less competitive ones. For example, the increased invasive potential is typical for *Pontederia crassipes*, *Pistia stratiotes*, *Trapa natans* та *Nuphar lutea* [23,28,34,150–152]. Rapidly growing aquatic vascular plants change physicochemical conditions and affect the structure and function of all hydrobionts, including fish. Abundance of fish populations as well as their diversity decrease in aquatic environments where the native structural complexity is reduced by invasive, non-indigenous species (NIS). One of the main reasons for this phenomenon might be a change in the "predator–prey" interaction pattern [153,154] and blockage of waterways and fish movement [22]. Excessive growth of aquatic vascular plants can cause anoxic conditions that lead to increased mortality of fishes and other aquatic fauna by reducing light penetration in the water column to support photosynthesis [29,34]. Therefore, mass reproduction of aquatic vascular plants can negatively impact productivity of fish populations. Selection of certain macrophyte species to prevent harmful cyanobacterial blooms should take into consideration their effects on aquatic animals such as fishes. It should be noted as well that the decomposition of their biomass may be accompanied by the release of organic and inorganic substances into the water and cause secondary pollution of water bodies.

Therefore, the use of fast-growing species of aquatic vascular plants to prevent harmful cyanobacterial blooms is an environmentally safe and effective method if accompanied by further selective or complete removal of their phytomass, as well as control of allochthonous nutrients, which contribute to their intensive reproduction.

7. Conclusions

The use of aquatic vascular plants to limit harmful algal blooms caused by cyanobacteria has a number of valuable advantages. First, they are able to limit cyanobacterial blooms by reducing dissolved nutrient concentrations in aquatic ecosystems. However, their main advantage is synthesis and release of compounds into the aquatic environment that are allelopathically specific against physiological processes of some groups of algae such as cyanobacteria. The use of these natural mechanisms to control the blue-green algae abundance is much safer for aquatic ecosystems compared to synthetic chemical compounds that can lead to secondary pollution of water bodies. However, literature analysis shows that allelopathic activity of aquatic plants depends on many biotic and abiotic factors such as the species characteristics of aquatic vascular plants, pool of biologically active compounds of exometabolites of aquatic vascular plants, area and density of their thickets in water bodies, physicochemical properties of allelopathically active substances, hydrochemical and hydrological regime, and temperature and irradiance levels. In addition, some rapidly growing macrophyte species (e.g., *Pontederia crassipes*, *Pistia stratiotes*, *Trapa natans*, *Nuphar lutea*) are able to inhibit the growth of other plants, as well as related microscopic flora and fauna, and monopolize aquatic habitats. Large dense thickets of such aquatic plants can change the "predator–prey" system, clog waterways and obstruct fish migrations, and reduce oxygenation of water bodies, which is one of the most common causes of fish productivity decline. Therefore, these species-specific effects and other characteristics should be considered in the selection of the species of aquatic vascular plants for harmful algal bloom control.

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