



Aquatic plant allelochemicals inhibit the growth of microalgae and cyanobacteria in aquatic environments

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Abstract

Excess nitrogen and phosphorus nutrients in the aquatic environment result in the growth of algal cells and water eutrophication, which adversely affect the aquatic environment and human health. Therefore, discovering a safe and efficient algae suppression method is necessary to ensure the ecological safety of water. Recently, the allelopathic effects of aquatic plants on algae have attracted extensive attention from researchers. This review demonstrates the current research hotspot of allelopathic algal inhibition in aquatic plants and lists the common aquatic plant species and allelochemicals. In addition, the inhibition mechanism of allelochemicals from aquatic plants on algae is systematically discussed. Moreover, the key factors affecting the inhibition of allelopathy in algae, such as pH, temperature, algal cell density, and concentration of allelochemicals, are summarized. The present utilization modes of allelochemicals on algae are also presented. Finally, the problems existing in the study of allelopathic algal inhibition of aquatic plants are highlighted, and suggestions for further research are proposed.

Keywords Aquatic plants · Allelopathy · Allelochemicals · Algae inhibition · Eutrophication · Inhibition mechanism

Introduction

Due to the large amount of wastewater containing nutrients such as nitrogen and phosphorus being discharged into the water body, eutrophication occurs frequently all over the world (Suresh et al. 2023). Eutrophication, also known as algal bloom, refers to the phenomenon of water pollution caused by the rapid growth of algal cells on the water surface (Zhao et al. 2015). When certain algae, including *Microcystis aeruginosa* and *Prymnesium parvum*, reach high concentrations in a specific range of water, they cause detrimental effects on the aquatic ecosystem of the surrounding area. When the algal bloom phenomenon occurs, a large number of algal cells float on the water's surface, which reduces the transparency of the water (Abadie et al. 2018), making it difficult for sunlight to penetrate the water and affecting the growth of aquatic plants. At the same time, algal blooms

consume a large amount of oxygen in the water, resulting in the death of aquatic organisms due to anoxia. Dead aquatic organisms and other organic matter are decomposed by microorganisms under anaerobic conditions, producing an unpleasant odor (Cheng et al. 2022). Some harmful algal can even produce toxins, which can accumulate in the food chain through their toxic effects on aquatic organisms, ultimately threatening human health (Liu et al. 2022). As a consequence, the inhibition of excess algal growth has become an urgent issue in environmental protection.

The main methods currently studied that can be used for algae removal are physical, chemical, and biological methods (Xie et al. 2023). Physical methods mainly include ultrasonic treatment (Kong et al. 2019), biochar adsorption (Cheng et al. 2022), mechanical fishing, etc. The physical approach poses a minimal risk of secondary water pollution. However, it is time-consuming and expensive, so this treatment method is unsuitable for large-scale use. Chemical methods are generally used to achieve algal growth inhibition and removal by dispensing chemical agents such as oxidants (Zhang et al. 2020), fungicides (Chavan et al. 2017), flocculants (Zhang et al. 2023), and photocatalysts (Fan et al. 2023; Yang et al. 2023). The chemical method is distinguished by its abbreviated processing time, expeditious

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effectiveness, and superior treatment efficiency. However, secondary pollution is a risk (Sun et al. 2015), and the chemicals may also be toxic to other organisms (Zhao et al. 2018). Biological methods, however, aim to create unfavorable conditions for algal growth (Kibuye et al. 2021). Standard methods such as the use of algae-killing bacteria, zooplankton, and allelopathy in plants are considered to be more economical and friendly methods for controlling cyanobacterial blooms (Jia et al. 2010) and degrading cyanobacterial toxins (Mohamed and Alamri 2012). Usually, allelopathic algal inhibition of aquatic plants provides a new viewpoint for biological algae inhibition, which has become the preferred method to improve eutrophic water in recent years.

“Allelopathy” was first proposed by Molisch (1937). Rice (1974) expanded the definition of allelopathy in the mid-1970s. Plants (including microorganisms) produce chemical compounds that are released into the environment. These compounds showed direct or indirect harmful effects on other plants. With a mature understanding of allelopathy, Rice (1984) extended the definition of allelopathy: plants that directly or indirectly cause positive or negative effects on other plants or microorganisms by releasing certain chemical substances into the surrounding environment. Currently, allelopathy refers to any process in which organisms produce bioactive metabolites that affect other neighboring plants or fungi (Legrand et al. 2003; Fa et al. 2010; Bajwa 2014). Plants produced secondary metabolites called allelochemicals (Long et al. 2021), which are considered environmentally friendly algacides due to their natural origin, low toxicity, high selectivity, and biodegradability (Wang et al. 2018b).

The purpose of this review is to understand the research hotspots of allelopathy by using a co-occurrence diagram. In addition, we examine the inhibition mechanisms and influencing factors of allelochemicals from aquatic plants. Moreover, this work aims to expose practical applications of allelochemicals to provide a basis for water ecological health management.

Current research hotspots

This paper used “allelopathy” and “algae” as search keywords in the Web of Science database to search for relevant documents published before December 15, 2022. A co-occurrence diagram of allelopathy was prepared in VOSviewer to analyze current international research hotspots (Fig. 1). The figure is divided into six clusters and different research topics.

In cluster 1, allelopathy involves competition. This theme covers keywords such as competition, macroalgae, and chemical defenses. Aquatic plants restrain algae growth by releasing allelochemicals, which is one of the essential method of obtaining effective competition (Qi et al. 2019b). Organisms

might inhibit the growth of other organisms by secreting allelochemicals, thus contributing to their advantage to growth in the environment. Cluster 2 shows the extraction of allelochemicals. This topic covers keywords such as inhibition, gallic acid, and usnic acid. Through allelopathy, the plant can secrete a variety of bioactive compounds, i.e., allelochemicals. Researchers can determine the types and contents of allelochemicals with algae-inhibiting effects by different extraction and identification methods, which can provide a reference for future research. Cluster 3 corresponds to the control of water eutrophication. This theme covers keywords such as submerged macrophytes, blue-green algae, growth inhibition, and aquatic macrophyte. Aquatic plants have attracted increasing attention owing to their rapid growth, abundant secondary metabolites, and direct contact with water, which have great potential in algae control applications. Most current studies focus on the use of allelopathy of aquatic plants to inhibit the growth of algae, thus providing ideas for the solution to eutrophication in water bodies. Cluster 4 corresponds to mechanisms of allelochemicals to inhibit algal growth. This topic covers keywords such as oxidative stress, chlorophyll fluorescence, and protease inhibitors. Plant allelochemicals reduce algal growth by different mechanisms and by now have been extensively studied. Cluster 5 corresponds to algal cells that are inhibited by allelopathy. This topic covers keywords such as phytoplankton, harmful algae, and *P. parvum*. Since allelopathy has different effects on different study subjects, the subjects can be restructured according to the type of algae present in the water that urgently needs to be addressed. Common types of algae cells inhibited by allelopathy mainly include *P. parvum*, *Heterosigma akashiwo*, *M. aeruginosa*, etc. *P. parvum* (Chromophyta: Haptophyceae) has been detected in both coastal and brackish waters and inland freshwaters (Feist and Lance 2021). Its euryhaline and eurythermal properties support aquatic ecosystems with different gradients (Taylor et al. 2021). The golden-brown marine alga *H. akashiwo* (Chromophyta: Raphidophyceae) is frequently observed in coastal waters globally and has been increasing in incidence and distribution (Ling and Trick 2010; Zhang et al. 2018). *M. aeruginosa* is a prominent species of freshwater cyanobacterium with worldwide distribution and a propensity for forming blooms (Dick et al. 2021). These types of algae are deemed to be a substantial threat to the well-being of aquatic ecosystems and are commonly singled out as objectives for allelochemical suppression. Cluster 6 shows the influencing factors of allelopathic algal inhibition. This topic covers keywords such as growth, toxicity, different nutrient conditions, and cell density. The strength of allelopathic inhibition of algae has different influencing factors, such as different nutrient conditions, distinct algal cell densities, and varying temperatures. The best algae-inhibiting conditions can be found by changing different factors.

study of allelopathy has shown that a large number of aquatic plants are capable of secreting allelochemicals that exert inhibitory effects on algae (Mohamed 2017). For instance, allelochemicals with inhibitory effects on algae have been collected from aquatic plants such as *Vallisneria* (Wang et al. 2022), *Pistia stratiotes* L. (Wu et al. 2013a), and *Phragmites australis* (Men et al. 2006). Allelochemicals produced by aquatic plants are listed in Table 2.

Aquatic plant species

Previous research on allelopathy was focused on terrestrial plants, but with the deterioration of aquatic ecosystems, algal blooms have become a global problem (Zhu et al. 2021). To solve this problem, researchers began to explore the allelochemicals from aquatic plants to inhibit algae in the late 20th century (Nakai et al. 1999). Aquatic plants have

Table 2 Aquatic plants and allelochemicals for inhibiting algae cells

Plant type	Botanical name	Effective suppression of algae	Major allelochemicals	Reference
Submerged plant	<i>Vallisneria</i>	<i>Microcystis aeruginosa</i>	Benzylic acid, sorbic acid, glycerol	Wang et al. (2022)
	<i>Ulva lactuca</i>	<i>Karodinium micrum</i> , <i>Prorocentrum donghaiense</i>	Unsaturated fatty acids	Tang and Gobler (2011)
		<i>Dunaliella salina</i> , <i>Chlorella salina</i>	Linoleic acid ethyl ester, propionic acid, 3-(methylthio)	El-Darier et al. (2021)
	<i>Hydrilla verticillata</i>	<i>Microcystis aeruginosa</i>	Vanillic acid, protocatechuic acid, ferulic acid, caffeic acid	Gao et al. (2011)
	<i>Potamogeton crispus</i>	Blue-green algae, diatom	Fatty acids, ketones, esters	Haroon and Abdel-Aal (2016)
	<i>Potamogeton pectinatus</i>	<i>Oscillatoria tenuis</i> , <i>Microcystis aeruginosa</i>	-	Ghobrial et al. (2015)
	<i>Myriophyllum spicatum</i>	Blue-green algae, diatom	Ketones, esters, alkaloids	Haroon and Abdel-Aal (2016)
		<i>Microcystis aeruginosa</i> , <i>Sele-nastrum capricornutum</i>	Polyphenol	Zhu et al. (2010)
		Blue-green algae, brown algae, Cryptophyceae	Gallic acids, nonanoic acids	Techer et al. (2016)
	<i>Sargassum fusiforme</i>	<i>Heterosigma akashiwo</i>	Fucosterol, α -linolenic acid, 24-hydroperoxy-24-vinyl-cholesterol	Sun et al. (2021b)
Floating plant	<i>Eichhornia crassipes</i>	<i>Microcystis aeruginosa</i>	Propionamide	Wu et al. (2018)
	<i>Nymphaea tetragona</i>	<i>Microcystis aeruginosa</i>	Total phenols, tannins	Chen et al. (2012)
		<i>Microcystis aeruginosa</i>	Gallic acid, kaempferol, coumaric acid, vanillic acid	Huang et al. (2015)
	<i>Pistia stratiotes</i> L.	<i>Microcystis aeruginosa</i>	Polyphenol, linoleic acids, linolenic acids, fatty acids	Wu et al. (2013a)
Emergent aquatic plant	<i>Arundo donax</i> L.	<i>Microcystis aeruginosa</i>	Esters, ketones, alkaloids, phenolic acids	Hong et al. (2011)
		<i>Microcystis aeruginosa</i>	Total phenols, tannins	Chen et al. (2012)
	<i>Alternanthera philoxeroides</i>	<i>Microcystis aeruginosa</i>	-	Zuo et al. (2012b)
		<i>Chlorella pyrenoidosa</i> , <i>Microcystis aeruginosa</i>	-	Zuo et al. (2012a)
	<i>Pontederia cordata</i>	<i>Microcystis aeruginosa</i> , <i>Scenedesmus obliquus</i>	-	Qian et al. (2019)
	<i>Phragmites australis</i>	<i>Scenedesmus obliquus</i>	Eathyl-2-methyl acetoacetate	Men et al. (2006)
		<i>Microcystis aeruginosa</i>	Total phenols, Tannins	Chen et al. (2012)
	<i>Typha orientalis</i>	<i>Chlorella pyrenoidosa</i> , <i>Microcystis aeruginosa</i>	Phenolic acids, Fatty acids, Ketones	Kang et al. (2020)
		<i>Microcystis aeruginosa</i>	Total phenols, Tannins	Chen et al. (2012)
	<i>Thalia dealbata</i>	<i>Microcystis aeruginosa</i> , <i>Anabaena flosaquae</i>	-	Zhang et al. (2011)

allelopathic effects on inhibiting algal cells in the aquatic environment, including submerged plants, floating plants, and emergent plants. Aquatic plants showing an inhibitory effect on algae are listed in Table 2, and the mechanisms involved in algal growth inhibition are shown in Fig. 2.

Submerged plants

Submerged plants inhibit algae mainly through three main processes: competition, shading, and allelopathy. Submerged plants can compete with algae in water for nutrient conditions, resulting in the inhibition of algal growth (Preiner et al. 2020). Additionally, submerged plants can impede incoming light and release allelochemicals, which can ultimately inhibit algal growth (Mohamed 2017). The ultrasonic cellulase extraction of *Vallisneria* produces benzylic acid, sorbic acid, and glycerol, which substantially inhibit the growth of *M. aeruginosa* (Wang et al. 2022). Similarly, Haroon and Abdel-Aal (2016) characterized allelochemicals secreted by *Potamogeton crispus* using gas chromatography–mass spectrometry (GC-MS) analyzer and demonstrated that fatty acids, esters, and ketones secreted by *P. crispus* also had inhibitory effects on cyanobacteria and diatoms.

Floating plants

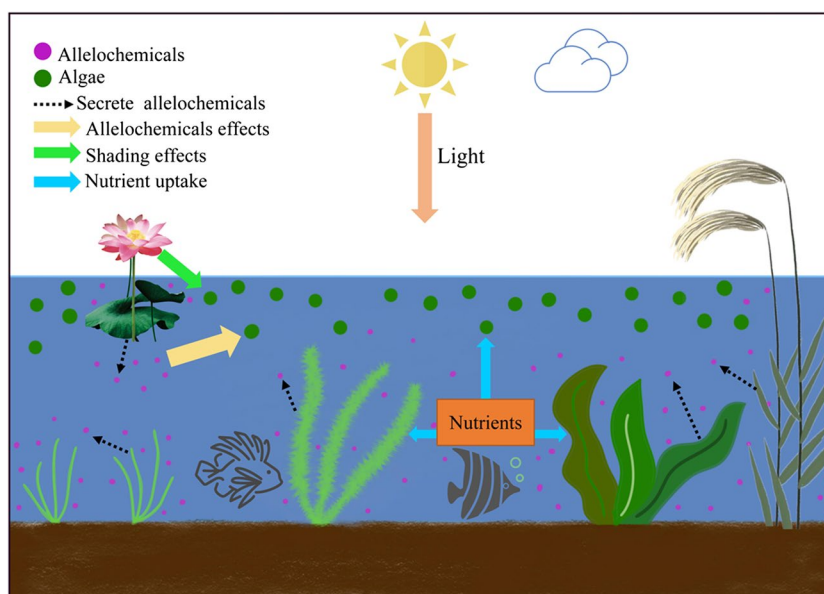
Floating plants typically have larger leaf structures that attenuate light and temperature in the water, ultimately hindering the growth of algae to some degree (Guo et al. 2014). It was also found that floating plants can further influence the growth of algae through the release of allelochemicals. The floating plants *Nymphaea tetragona* and *Nelumbo nucifera*

were found to have algae inhibition activity up to 75–82% on *M. aeruginosa* after 19 days of algae inhibition tests (Chen et al. 2012). When the concentration range of allelochemicals extracted from *P. stratiotes* L. was 60–100 mg/L, the allelochemicals had the most potent inhibitory effect on the growth of algae, with a relative inhibition ratio reached 50–90%. Furthermore, the chlorophyll-a (Chl-a) content in algae cell cultures was reduced by 50–75% within 3–7 days (Wu et al. 2013a). Wu et al. (2018) investigated the potential of propionamide, derived from the aquatic plant *Eichhornia crassipes*, for controlling cyanobacterial blooms. The results demonstrated that the inhibition rate of algae cells exceeded 90% when 2 mg/L propionamide was co-cultured with the cells for 7 days by semi-continuous addition. Additionally, they showed the gradual disintegration of algal cells.

Emergent plants

The stems and leaves of emergent aquatic plants extend out of the water, and the roots grow in the silt of the water bottom, inhibiting the growth of algae mainly through the release of allelochemicals from the roots (Qian et al. 2021). The aqueous extract of the roots of the aquatic plant *Thalia dealbata* could dramatically inhibit the growth of the cyanobacteria *Anabaena flosaquae* and *M. aeruginosa*. It mainly leads to a decrease in chlorophyll content and to inhibition of total dehydrogenase activity (Zhang et al. 2011). A similar situation was observed with the aqueous extract of *Arundo donax* L. after 7 days of cultivation. The percentage of inhibitions (PIs) was above 60% for all treatment groups, and the maximum almost reached 100%. In addition, the potential allelochemicals of *A. donax* L. mainly include esters, ketones, alkaloids, and phenolic acids (Hong et al. 2011).

Fig. 2 Anti-algae methods of aquatic plants



Inhibition mechanism of allelochemicals on algae growth

Allelopathy of aquatic plants has been shown to inhibit the growth of algae cells. Current studies have found that the mechanism of allelopathy against algae mainly includes the destruction of cellular structures, causing oxidative stress in cells as well as programmed cell death (PCD) and influencing the photosynthetic system and protein synthesis. The algae-inhibiting mechanism of allelochemicals is shown in Fig. 3.

Destruction of cellular structures

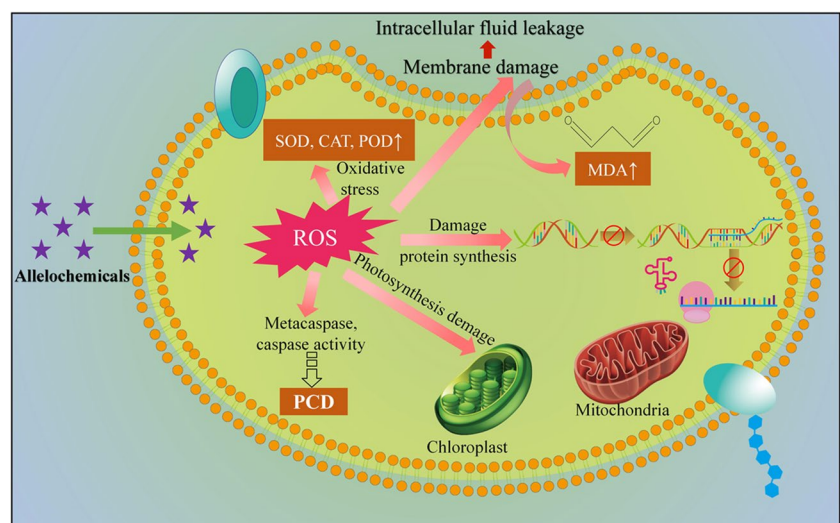
As a natural barrier between cells and organelles, allelochemicals initially influence the cytomembrane (Fink 2007). Allelochemicals destroy the permeability and integrity of the cytomembrane, and disturbances in cytomembrane integrity may lead to disruptions in organelle structure and function. The allelochemical ethyl-2-methyl acetoacetate (EMA) damaged the cytomembrane of *M. aeruginosa*, resulting in the leakage of substances from the algal cells and the destruction of the nucleus and mitochondrial structure (Li et al. 2007). After adding an extract of the aquatic plant *Vallisneria*, the cell morphology of *M. aeruginosa* changed dramatically. Wang et al. (2022) used concentrations of 0.5 g/L and 1 g/L test groups and observed extracellular attachments and slight cell damage. Similarly, in the 10 g/L and 20 g/L experimental groups, the membrane of algae cells was destroyed, resulting in leakage of intracellular fluid and the formation of columnar structures through cell connections. When *M. aeruginosa* cells were exposed to 14 mg/L pyrogallol acid (PA) for 72 h, the algal cells showed nuclear membrane rupture and extravasation of intracellular material, which eventually led to vacuolation (Lu et al. 2017).

Similarly, Tan et al. (2019) proposed that the shape of algal cells would change under the action of a particular concentration of allelochemicals, which manifested as protoplast contraction and cell wall separation, as well as reduced nuclear and chloroplast structures.

Causes of oxidative stress in algal cells

Oxidative stress is produced by an increase in the level of reactive oxygen species (ROS) and can induce damage to biological macromolecules (Staszek et al. 2021; Wang et al. 2022). Algae cells produce oxygen free radicals, including hydroxyl radical ($\text{HO}\bullet$), hydrogen peroxide (H_2O_2), and superoxide anion radical ($\text{O}_2\bullet^-$) and accumulate reactive oxygen species (ROS), under the stimulation of allelochemicals. Enzymes of the antioxidant system, superoxide dismutase (SOD), catalase (CAT) and peroxidase (POD), can reduce ROS so that the cells will continue their normal physiological activities. However, if there is an accumulation of ROS within a short time that exceeds the normal metabolic level of antioxidant enzymes, it will result in cellular demise, thus inhibiting algae growth. Kirpenko and Usenko (2013) proposed that under the influence of EMA, the concentration of ROS and lipid peroxide products in algae cells increased. At the same time, the activity of some antioxidant enzymes was inhibited. Malondialdehyde (MDA), the product of lipid peroxidation in algal cell membranes under stress, is commonly used to assess the degree of damage to cell membranes and to measure the degree of stress in algal cells (Zhu et al. 2021). In the semi-continuous co-culture system, after 108 h of exposure to allelochemicals produced by the aquatic plant *Cyperus alternifolius*, the MDA content of *M. aeruginosa* was 3.6 times higher than that of the control group and then decreased sharply (Zhu et al. 2014).

Fig. 3 Inhibition mechanism of allelochemicals



Causes of programmed cell death (PCD)

PCD is a genetically controlled biological process of cellular self-destruction that involves the transcription of specific genes and protein synthesis (Lockshin and Zakeri 2004; Bidle 2016). ROS are the bridge between allelopathy and PCD. When low-concentration allelochemicals stimulate algae cells, they act as signal molecules to regulate growth and development processes and activate defense mechanisms. In contrast, ROS trigger PCD when exposed to high concentrations of allelochemicals. Multiple caspase orthologs, such as paracaspases, metacaspases and caspases, have been shown to be involved in the PCD process in algal cells (Bidle 2016). Plants rely on caspases for oxidative stress to induce PCD (Klemenčič and Funk 2018; Qi et al. 2019a). Simultaneously, PCD-treated algae constantly show changes such as shrinkage, phosphatidylserine externalization, nuclear fragmentation, and condensation. Xu et al. (2022) conducted a study on the process of PCD induced by 5,4,-dihydroxyflavone (5,4,-DHF) in two cyanobacteria, *M. aeruginosa* and *Phytocystis globularis*. The findings revealed that 5,4,-DHF exhibited a considerable inhibitory effect on both algal species, and typical indicators of PCD, phosphatidylserine externalization and chromatin condensation, were detected in both species.

Impact on the photosynthetic system

Photosynthesis is one of the necessary conditions for the normal physiological metabolism of algae cells. The addition of allelochemicals markedly reduces pigment content by destroying the synthesis of photosynthetic pigments or stimulating the decomposition of photosynthetic pigments (Zhu et al. 2021). Furthermore, chlorophyll is one of the main pigments for photosynthesis in aquatic plants. The ethanol extract obtained by Sun et al. (2021b) from the brown microalga *Sargassum fusiforme* displayed the ability to substantially reduce the chlorophyll content of *H. akashiwo*, which negatively impacted the average growth of algae cells. When algal cells were treated with different concentrations of tannins, Chl-a inhibition in algal cells was 95% when treated with 140 mg/L tannins for 13 days, and the color of the exposure solution gradually turned yellow, suggesting that the photosynthesis of the algae was inhibited (Xie et al. 2023).

Many allelochemicals produced by aquatic plants are able to inhibit photosystem II (PSII). PSII is a highly conserved multiprotein pigmented membrane complex that catalyzes light-driven water splitting, oxygen evolution, and plastoquinone reduction, which is crucial for photosynthesis (Li et al. 2023b). While the physiological state of PSII can be measured by chlorophyll fluorescence (Henriques 2009), it primarily includes maximum photochemical efficiency (Fv/Fm), effective photochemical quantum yield (Y_{PSII}),

ETR, IK, α , and other photosynthetic parameters. Fv/Fm can measure the photosynthetic efficiency of PSII. With the increase in α -linolenic acid concentration (4, 6, 8 mg/L), the Fv/Fm ratios of *H. akashiwo* decreased dramatically (6.8–29.4%), which suggested that PSII was the potential mechanism for the inhibition effect (Sun et al. 2021b). The pyrogallol acid (PA) and gallic acid (GA) in the aquatic plant *Myriophyllum spicatum* inhibited the PSII activities of *M. aeruginosa* by 71.43% and 70.95%, respectively (Zhu et al. 2010). Analogously, Nakai et al. (2014) also found that allelochemicals produced by *M. spicatum* markedly inhibited PSII activity. Chlorophyll fluorescence parameters were restricted by the capacity of the electron transport chain and Calvin activity in photosynthesis (Xu et al. 2020). Toxicological studies have revealed that linoleic acid significantly impairs photosynthetic pigment content in *M. aeruginosa*, ultimately leading to the blockage of electron transport in the photosynthetic electron transfer chain, as reported by Ni et al. (2018). Leu et al. (2002) found that β -1,2,3-tri-O-galloyl-4,6-(S)-hexahydroxydiphenyl-D-glucose, known as tellimagrandin II, dramatically disrupted the electron transport chain in the cyanobacteria *Anabaena* sp. and *Synechococcus* sp. by enhancing the redox midpoint potential of nonheme iron.

PSII is often the primary target when algae cells are under pressure from the surrounding environment, and oxygen production is impacted by allelochemicals (Zhu et al. 2021). For instance, the respiration rate of algal cells began to decrease when the allelochemicals isolated from the terrestrial plant *Aloe vera* came into contact with the algal cells (Hongying and Hong 2008). Shao et al. (2010) also observed a 34% reduction in the rate of oxygen evolution in *M. aeruginosa* upon exposure to a concentration of 4 mg/L nonanoic acid. Furthermore, allelochemicals extracted from the aquatic plant *M. spicatum* adversely affected the respiration of the microalga *Selenastrum capricornutum* and the cyanobacterium *M. aeruginosa* (Zhu et al. 2010).

Influence on protein synthesis

Protein is a significant supporter of life functions and an essential component of cells. Allelochemicals are able to negatively affect algae growth by affecting protein synthesis. Chao (2013) discovered that allelochemicals reduced the protein content in approximately 80% of *M. aeruginosa* cells. Expression of the *psbA* gene encoding the D1 protein was markedly inhibited by pyrogallol acid, resulting in the failure of protein synthesis (Wu et al. 2013b). Similarly, Shao et al. (2010) investigated the effect of pyrogallol acid on gene expression in *M. aeruginosa* and found that protein was an important target site for pyrogallol acid inhibition, which affected the growth of *M. aeruginosa* by disrupting protein synthesis.

Factors affecting the inhibition of allelopathy in algae

As an effective competition strategy, the allelopathic effects of aquatic plants are certainly affected by the surrounding biotic and abiotic factors. It is of great value to discuss the allelopathy of aquatic plants under different influencing factors to reveal the regulation of allelopathy in aquatic ecological systems (Li et al. 2021b).

Abiotic factors represent all physicochemical factors in an ecosystem that have an impact on a particular biotic population and are behaviors from non-living to living. In contrast, biological factors are related to the activities of organisms and have an impact on the distribution of plant and animal species in a given biological community (Chaïb et al. 2021).

Abiotic factors

Light intensity

Light may cause changes in allelochemicals due to oxidation, polymerization, or degradation (Gross et al. 2007). It has been shown that light intensity substantially affects the production of allelochemicals. Through field manipulation experiments, Cronin and Lodge (2003) observed that leaf phenolics of the aquatic plant *Potamogeton amplifolius* were markedly increased by 72% by high light (35% of surface irradiance). The concentration of total phenolic compounds in *Potamogeton perfoliatus* and *M. spicatum* branches under sunlight was also higher than that in the shade (Choi et al. 2002). In addition, Bauer et al. (2012) proved that light and microbial treatment reduced the growth rate of cyanobacteria more than dark treatment, but the differences in algal growth were minor. In contrast, under low light intensity, the total phenolic content in the top tissue of *M. spicatum* was only 3.09% higher than that under high light intensity, but the content of phenolics in the stem was 112.77% higher than that under high light intensity (Ge et al. 2012). The biomass of *M. spicatum* was dramatically reduced with the decrease in light intensity. This may be due to the decomposition of some allelochemicals under light conditions, resulting in differences in algal inhibition (Nakai et al. 2014).

pH

The existing state of allelochemicals can be altered by a variety of pH levels (Li et al. 2021b). Hence, pH is a crucial influencing factor. The inhibitory effect of *Chrysochromulina polylepis* on *Heterocapsa triquetra* was stronger in alkaline growth medium than in neutral or acidic medium (Schmidt and Hansen 2001). Additionally, Noaman et al. (2004) noted that the pH level of the culture medium

strongly influenced the growth of *Synechococcus leopoliensis* as well as the production of secondary metabolites. The allelopathic effect of *Corallina pilulifera* was most significant when the pH value was 10 (Wang and Tang 2016). In the same way, Yamasaki et al. (2007) also proposed the influence of pH level on allelochemical activity.

Nutritional conditions

Allelopathy is regarded as a novel competitive mechanism among species, and aquatic plants tend to discharge a higher concentration of allelochemicals during times of nutrient scarcity, thus improving their competitiveness against algae (Rice 1984). Mjelde and Faafeng (1997) observed that when essential nutrients are lacking in aquatic systems, phytoplankton may be inhibited by aquatic plants. Similarly, Cagle et al. (2021) determined different parts of *P. parvum* culture under balanced N:P conditions, unbalanced N:P conditions, and P deficiency conditions. The results showed that the yield of allelochemicals was meager under balanced N:P conditions. However, the allelochemical concentration increases under the conditions of imbalance and P reduction. Similar to this test result, Graneli and Salomon (2010) found that allelopathy may be reduced or completely stopped if the cells of *P. parvum* grow under balanced N:P conditions. Within 24 h of supplying deficient nutrients to N-deficient or P-deficient cells, allelochemical production of P-deficient cells was reduced to less than half, the same phenomenon as adding inorganic N to N-deficient cells. An increase in the concentration of allelochemicals from the submerged plant *M. spicatum* could be observed under low phosphorus conditions (Gross 2003).

These studies suggest that nutrient availability in the environment can influence the production of allelochemicals by aquatic organisms and ultimately affect their allelopathic potential.

Temperature

The impact of temperature on the allelopathy of aquatic plants cannot be overstated. It is generally accepted that temperature plays a key role in the production and release of plant allelochemicals, primarily by influencing the enzymatic activity within the plants themselves as well as the rate of diffusion of these chemicals through the water (Li et al. 2021b). The effect of coumarin on *M. aeruginosa* at varying temperatures was studied by Hong et al. (2018). Compared with the control group (day/night, 25 °C/20 °C), the inhibition rate of algae cells decreased by 63.27% when the temperature increased by 2 °C during the day and decreased by 12.24% when the temperature increased by 2 °C at night. The results of the study demonstrated that the photosynthesis of *M. aeruginosa* and its resistance to allelochemicals were dramatically enhanced with an increase in temperature. Correspondingly, Nakai et al.

(2014) studied the effect of temperature on the inhibitory effect of eight allelochemicals (comprising five polyphenols and three fatty acids) produced by *M. spicatum* on *M. aeruginosa*. They revealed that the degree of growth inhibition in *M. aeruginosa* varied within a temperature range of 20–30 °C, with more significant growth inhibition observed at lower temperatures: at 20 °C, the number of algae cells decreased by 1.9 times as much as that at 30 °C.

Metal ions

Metal ions have specific effects on the allelopathic and algae-inhibiting activities of aquatic plants. Zuo et al. (2012a) observed that heavy metals (Ni, Pb, Cr, and Cu) in aquatic ecosystems reduced the algae-inhibiting potential of the aquatic plant *Alternanthera philoxeroides*. However, some elements other than heavy metals, i.e., inorganic anions F⁻, S²⁻, Cl⁻, SO₄²⁻, and metal cations K⁺, Na⁺, Ca²⁺, Mg²⁺, Zn²⁺, total Fe, and total Mn, could improve the algae inhibition potential of *A. philoxeroides*. The results showed a significant relationship between the allelopathic algae inhibition effect of *A. philoxeroides* and the concentrations of metal cations, but not inorganic anions, in the aquatic environment.

Freshness

Freshness will affect the activity of allelochemicals secreted by aquatic plants. When freshly harvested aqueous extract of the aquatic plant *A. donax* L. was co-cultured with *M. aeruginosa* for 7 days, the maximum percentage inhibitions (PIs) approached 100%. However, the allelopathic activity of the extracts decreased markedly after 2 months of storage, resulting in inhibition rates below 60% in all test groups (Hong et al. 2011). Kang et al. (2020) investigated the effect of extracts from reed (*P. australis*) and cattail (*Typha angustifolia*) on the growth of *M. aeruginosa* in different decomposition stages (fresh and dead). The researchers quantified the effective concentration 50 (EC₅₀) of the extract based on the concentration of dissolved organic carbon (C). The EC₅₀ value of fresh cattail extracts for 100 days was 19.3 mg C/L. According to the results derived from the EC₅₀ and the comparison of growth percentage at the maximum concentration of extracts, it can be concluded that the inhibitory effect of live plants on algae was comparatively more pronounced than that of dead plants.

Biotic factors

Species of aquatic plants and algae

Allelopathy is a phenomenon that is specific to certain species. In other words, the same species of plant or allelochemicals may produce diverse effects on various algal

species (Hilt and Gross 2008). Generally, donor organisms may have an impact on multiple target organisms, although not necessarily all of them. Additionally, target organisms possess sensitivity to a range of allelochemicals released by donor species, although not to all of them. Many studies have found that the allelopathy intensity depends on the taxonomic characteristics of donor and recipient species (Poulson-Ellestad et al. 2014; Konarzewska et al. 2020). Sylvers and Gobler (2021) studied the inhibitory effect of three culturable macroalgae, Irish moss (*Chondrus crispus*), sugar kelp (*Saccharina latissima*), and *Ulva* spp., on *Alexandrium catenella*. Co-culture experiments showed that with the exception of low levels of *C. crispus*, all species instigated cell lysis and resulted in a decrease in the number of *A. catenella* compared to the control group, with densities reduced by 17–74% in 2–3 days and 42–96% in similar to 1 week. Among the three seaweed species, *S. latissima* exhibited the strongest inhibitory effect on *A. catenella*, followed by *Ulva* spp. and *C. crispus*, respectively. The study highlights that different aquatic plant species display varying inhibition abilities against algae. Li and Hu (2005) isolated allelochemicals from the aquatic plant *Phragmites communis* Trin. that displayed potent inhibition of *Chlorella pyrenoidosa* and *M. aeruginosa* but no inhibition of *Chlorella vulgaris*. The allelopathic effects of freshwater stonewort, *Chara australis*, and *P. crispus* on microalgae were examined by Pakdel et al. (2013). The study analyzed the growth of *Anabaena variabilis* and *Scenedesmus quadricauda* in the presence and absence of macrophyte extracts, exudates, and live material. The results showed that all treatments had no significant impact on the growth of *S. quadricauda* but had a significant adverse effect on *A. variabilis*, with the most substantial effect on *C. australis*. This phenomenon confirms earlier findings that allelochemicals from macrophytes have specific receptor species. In another study, when the concentration of allelochemicals was 100 mg/L, the algae-inhibiting activity of *Ceratophyllum demersum* on *M. aeruginosa* was more potent than that of *Vallisneria spiralis* (Xian et al. 2006).

Concentration of allelochemicals

Allelopathy of plants can inhibit or promote the growth of algae, which mainly depends on the concentration of secreted allelochemicals. In the study by Xie et al. (2023), the inhibitory effects of polyphenols with different concentration gradients (1 mg/L, 20 mg/L, 50 mg/L, 80 mg/L, 110 mg/L, 140 mg/L) on *M. aeruginosa* were investigated. The results showed that the algal cell density in the experimental group dramatically decreased with increasing initial polyphenol concentration. The allelopathic

effects of aquatic plants on algae were observed to exhibit a relationship where low concentrations promoted growth and high concentrations inhibited growth. Wang et al. (2022) designed two concentration gradients, low-concentration (0.5 g/L and 1 g/L) and high-concentration (5 g/L, 10 g/L, and 20 g/L) extracts, to inhibit *M. aeruginosa* using the aquatic plant *V. spiralis* as the source of allelochemicals. Algal cell growth showed completely different trends between the low- and high-concentration treatments, indicating that allelochemicals from *V. spiralis* had low-concentration promotion and high-concentration inhibition on *M. aeruginosa*.

Growth phase

The sensitivity of algae to the allelopathy of aquatic plants is subject to variation based on the growth phase. It was observed that the allelochemicals of the aquatic plant *P. communis* inhibited *M. aeruginosa* more strongly at the initial growth stage (lag phase) than at the rapid growth stage (logarithmic phase) (Li and Hu 2005). Similarly, the growth stage of aquatic plants affects their allelopathy. A study indicates that aquatic plants show higher allelopathic activity during seedling stage (Sun et al. 2021a).

Different organs and tissues of aquatic plants

The variations in the distribution of allelochemicals among aquatic plants lead to disparate types and quantities of allelochemicals present within distinct plant tissues and organs. This, in turn, gives rise to differences in the effectiveness of algae inhibition. Chen et al. (2012) found that all tissues from eight tested macrophytes could markedly inhibit the growth of *M. aeruginosa*, in which the leaves of the aquatic plant *N. tetragona* and *N. nucifera*, two of the tested plants, exhibited higher activity than petioles.

Different extraction solvents

Extracting the same parts of aquatic plants with different solvents can also result in differences in the type and amount of allelochemicals. Ghobrial et al. (2015) employed aqueous extracts containing solvents of 50% and 100% acetone and ethanol to investigate the impact on *M. aeruginosa* and *Oscillatoria tenuis* of *Potamogeton pectinatus* and *C. demersum*. The results revealed that the aqueous extracts of 50% and 100% acetone and ethanol produced different effects on the growth of algal cells. The ethanol extract showed a more substantial inhibitory effect than the 50% acetone extract. The strongest inhibitory effect of the 50%

acetone extract of *Ceratophyllum* against *O. tenuis* was 1.05 mg/L, with the highest percentage rate (R) of 169.4. The highest inhibitory rate of the 50% ethanolic extract of *Ceratophyllum* against *O. tenuis* was 0.0083 mg/L, with an R of 74.32. In a study by Haroon and Abdel-Aal (2016), the chemical composition and anti-algal activity of crude extracts obtained from aquatic plants, namely, *P. crispus* and *M. spicatum*, were investigated. In this regard, various organic solvents with different polarities, such as petroleum ether, methylene chloride, chloroform, acetone, and methanol, were employed for the extraction process. The findings of the study indicated that the phytochemical composition and mass fraction varied significantly based on the extraction solvents and plant species. Among the different extracts evaluated, it was observed that the mixed extracts and chloroform extracts of the two plants demonstrated the most promising anti-algal activity.

Utilizing modes of allelochemicals for algae control

Growing aquatic plants

The rapid increase in nitrogen and phosphorus in water will cause eutrophication of the water, which poses a great threat to aquatic ecosystems and human health. Planting aquatic plants can effectively inhibit algal reproduction. Planting aquatic plants in water is often used for the construction of ecological floating beds (EFBs).

EFBs refer to an ecological technology for purifying water bodies floating on the surface of the water, mainly consisting of aquatic plants and taking macromolecule materials or inorganic nonmetallic materials as carriers and bases (Samal et al. 2019). Aquatic plants in the EFBs provide attachment sites for microorganisms through developed roots (Bi et al. 2019), secrete allelochemicals and purify eutrophic water bodies through absorption, competition, and shading. A 3-month experiment was conducted in a 326 m² lake located in the northwest corner of Xi'an (34°27' N, 108°93' E) Fengqing Park. The EFBs system uses *calamus*, *iris*, *lythum*, and *Hydrocotyle vulgaris* as vegetation and zeolite and sponge iron as fillers. The results showed a noteworthy decrease in the mean concentration of Chl-a and the density of algae (Wang et al. 2018a). Simultaneously, Svanys et al. (2014) observed that *M. spicatum* had consistent negative effects on *M. aeruginosa* biomass through mesocosm experiments in the Curonian Lagoon. Although planting aquatic plants in EFBs may effectively control the growth of algae, aquatic plants are vulnerable to low-temperature weather, their growth state is difficult to control, and dead plants are liable to cause secondary pollution to the water.

Addition of allelochemicals sustained-release microspheres (AC-SMs)

To solve the shortcomings of direct planting of aquatic plants, a method of extracting allelochemicals from aquatic plants and adding them artificially was proposed. In natural waters, aquatic plants continuously release allelochemicals into the water (Bauer et al. 2009). The use of AC-SMs aims to simulate the natural release process of allelochemicals to provide the possibility for the practical application of allelochemicals.

AC-SMs are prepared from allelochemicals and natural materials. The most commonly used preparation method is to mix allelochemicals and sodium alginate in distilled water as the basic material, then use an aqueous acetic acid solution containing chitosan and calcium chloride as the coagulation fluid, and finally add the basic material dropwise into the coagulation fluid to obtain beads. Chitosan and sodium alginate are two nontoxic and biodegradable natural polysaccharides (Rescignano et al. 2015). Li et al. (2023a) discovered that AC-SMs not only effectively reduced the toxicity of allelochemicals but also enhanced the ingestion, incorporation, and digestion abilities of *Daphnia magna* Straus. Moreover, the combination of chitosan and sodium alginate guarantees high encapsulation efficiency and good release performance of AC-SMs. The SMs of DHF prepared by Huang et al. (2016) showed a high drug-loading rate (47.18%) and encapsulation efficiency (67.65%). The theoretical release time was approximately 120 days, which has a long-term inhibitory effect on *M. aeruginosa* (>30 days). Linoleic acid SMs not only has high encapsulation efficiency (up to 62%) but also has good thermal stability (decomposition temperature of 236 °C) (Ni et al. 2015). In the process of algae inhibition by AC-SMs, Ni et al. (2013) observed that artemisinin SMs reduced the content of Chl-a and soluble protein in 30 days and increased the superoxide dismutase activity of *M. aeruginosa*. Additionally, AC-SMs dramatically reduced the content of phycobiliprotein in *M. aeruginosa*, but the stressed algae cells still had complete cell membrane structure, which indicated that the algae cells may undergo PCD (Sang et al. 2022). Additionally, according to the comparative proteomic analysis conducted by Li et al. (2021a), the SMs of luteolin markedly upregulated photosynthesis and protein homeostasis while downregulating the stress response, transcription, translation, transport, cell shaping, and cell division. This disruption negatively impacts the physiological and metabolic processes of the organism and impedes its growth. The primary inhibitory mechanism of artemisinin algaecides involves irreversible damage to the cell membrane. Jiang et al. (2022) noted that lipid peroxidation occurred in algal cell membranes after treatment with artemisinin SMs, and the permeability of the membrane increased. Similarly, Ni et al. (2018) noted that disruption of algal cell membranes was the main mechanism of linoleic acid

SMs. The algae-inhibiting effect of AC-SMs may be related to particle size. The inhibitory effect was found to be more significant when the particle size of artemisinin sustained-release microspheres (ASMs) was reduced to 2/10000 in comparison to artemisinin sustained-release granules (ASGs). It is possible that the particulate dimensions of ASMs are comparatively inferior to those of ASGs, which dramatically increases the effective contact area with *M. aeruginosa* and reduces the swelling rate of the sustained-release algal inhibitor (Jiang et al. 2022). Researchers have found that using AC-SMs before recruiting cyanobacteria would be more effective (Huang et al. 2016; Ni et al. 2020).

Summary and outlook

Allelopathy of aquatic plants has certain advantages in limiting water eutrophication caused by algal blooms, which provides a new idea for the remediation of eutrophication. Previous studies have mainly focused on the sources and types of allelochemicals, the separation of allelochemicals, the factors affecting allelochemicals, and the inhibition mechanism of allelochemicals from aquatic plants on algae, in addition to achieving some research results. However, there are currently numerous research endeavors that remain to be conducted with a view to achieving significant breakthroughs:

- (1) Currently, research on the effects of aquatic plants on algae remains mostly at the cellular level; while genetic level research mostly focuses on protein synthesis, other levels of research still need to be explored and discovered.
- (2) Most of the current studies are only at the laboratory level. However, in practical applications, the allelochemicals released by plants are located in complex and diverse environments. It is not possible to determine whether allelochemicals would still exert algal inhibition under multiple factors in the same or similar way as under laboratory conditions.
- (3) Allelochemicals with algae inhibitory activity have been widely recognized by research scholars, but their manufacture has not yet been scaled up, thus leading to high costs in application, which would be combined with other treatments, such as photocatalysis and UV irradiation, to make future growth and manufacture more scaled up to reduce application costs.

In conclusion, it is an eco-friendly water treatment method to use allelopathy in aquatic plants to inhibit algae. Currently, the research has made some achievements, but it still needs to be systematically studied in multiple aspects and at a deep level to be applied in the current environment.

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