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# Allelopathic effects of submerged macrophytes on phytoplankton

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## ABSTRACT

As a survival and resource-competition strategy, submerged macrophytes are supposed to release the secondary metabolites, named allelochemicals, to affect phytoplankton development. The species-specific inhibition and easy degradation of plant allelochemicals make them possible to control the algal bloom efficiently and environment-friendly. This paper aims to review the research advances in allelopathy of submerged macrophytes on phytoplankton, which covers the following aspects: species-specific inhibition of submerged macrophytes to phytoplankton, potential allelochemicals, their inhibitory modes, physiological mechanisms, impacts of environmental factors and possibility of application in water management. Research methodology on allelopathy needs to be improved from the viewpoint of ecology. It is proposed to do more comparable bioassays, more joint laboratory and field experiments to figure out release and degradation dynamics of allelochemicals and their interactions with biotic and abiotic factors, which will be helpful to reveal the allelopathic mechanisms from gene to ecology, and provide scientific guidance for its application in aquatic ecosystem management.


**Keywords**: Allelochemical, combined action, continual action, environmental impacts, membrane disturbance, oxidative stress, photosynthesis inhibition, programmed cell death, release contents, submerged macrophytes.

## 1. INTRODUCTION

With increasing anthropogenic nutrients loading and global warming in recent decades, more and more shallow aquatic ecosystems are suffering accelerated shifts from clear-water states dominated by submerged macrophytes to phytoplankton-prevalence turbid-water states along with frequent harmful cyanobacterial blooms (40,61,63,69). During the process of water quality improvement and ecological restoration practice worldwide, reestablishment of aquatic vegetation especially submerged macrophytes in eutrophic water bodies was proposed as a crucial step (32,64,68), due to their irreplaceable roles including improving the water transparency by reducing the sediment suspension, maintaining the biodiversity by providing refuges and habitats for various microorganisms. Besides, submerged macrophytes can effectively suppress the phytoplankton development by releasing the allelochemicals, which has been supposed to be one of the important strategies for submerged macrophytes to compete for nutrients and light availability with phytoplankton (22,30,77,80).

Hasler and Jones observed significantly lower phytoplankton density in ponds cultured with *Elodea canadensis* Michx. and *Potamogeton foliates* L., compared with the ponds without plants under the same nutrients and light conditions (27). Since then, there have been increasing field observations proving that allelopathy was involved in interaction of submerged macrophytes with phytoplankton (47,48,60). Although it is not clear, how much contribution of allelopathy is during the interactions between the submerged macrophytes and phytoplankton, many researchers have been attracted to this field to determine its mechanisms and explore the potential ways for application in harmful algal bloom control and water ecosystem management. Their research mainly includes the (i). Assessment of allelopathic-effects of various plants on target phytoplankton species (31,37,39,56), (ii). Isolation and identification of plant allelochemicals (12,26,54,92,93,99), (iii). Bioassays of

identified allelochemicals (38,55,56,57), (iv). Quantitative analysis of allelochemicals released into water environment (20,26,55,57), (v). Elucidation of physiological mechanisms and (vi). Modes of their action for allelopathic inhibition in phytoplankton etc. (29,39,44,74, 76,88,106).

The review aims to (i). Demonstrate the status quo on allelopathy of submerged macrophytes against phytoplankton (from phenomenon to mechanisms, mainly including results on specific allelopathic inhibition against phytoplankton species), (ii). Extraction and identification of potential allelochemicals, (iii). Modes of action from the viewpoint of ecology, (iv). Physiological mechanisms and (v). Impacts of environmental factors. We have analysed the key problems on each aspect. The possibility of application in the control of water eutrophication and harmful algal blooms has been discussed and future studies have also been proposed in the end.

## 2. SPECIES-SPECIFIC ALLELOPATHIC INHIBITION

The allelopathic antialgal effects of submerged plant species belonging to family of Haloragidaceae, Ceratophyllaceae, Potamogetonaceae, Hydrocharitaceae and Najadaceae (Table 1), were evaluated using various bioassay systems, such as plant-algae coexistence systems, dialysis bags, plant extracts and plant exudates with different target phytoplankton species (31,37,56), which are typical methods to assess the allelopathic effects of submerged plants. Although there are few literatures directly comparing the allelopathic effects of different plant species, species-specific effects are obvious both for submerged plants and phytoplankton.

Apparently the various plant species demonstrated different antialgal activities. When investigating sensitivity of *Raphidocelis subcapitata* Kor. and *Microcystis aeruginosa* Kütz. to exudates from two *Potamogeton* species, *P. maackianus* showed stronger inhibitory effects on *M. aeruginosa*, whereas *P. malaianus* had stronger effects on *R. subcapitata* (101). Compared with *Egeria densa* Planch. and *Cabomba caroliniana* A., *Myriophyllum spicatum* Linn. demonstrated the strongest inhibitory effects on both *M. aeruginosa* and *R. subcapitata* in plant-algae mixed-culture system as well as in the methanol extract assays (54). The inhibitory effects of 9-macrophyte species (*E. densa*, *C. caroliniana*, *M. spicatum*, *Ceratophyllum demersum* L., *Eleocharis acicularis* L., *Potamogeton oxyphyllus* Miq., *Potamogeton crispus* L., *Limnophila sessiliflora* Vahl., and *Vallisneria denseserrulata* Mak.) on the growth of cyanobacteria, (*M. aeruginosa*, *Anabaena flos-aquae* Breb., and *Phormidium tenue* Kütz.), were evaluated in a comparable coexistence assay, which indicated that only *M. spicatum* and *C. caroliniana* inhibited the growth of all cyanobacteria, with stronger effects of the former (56). According to these results, *M. spicatum* was deemed to be one of the strongest allelopathic species. However, it was not always the strongest inhibitor, which depended upon target phytoplankton species. A slightly stronger reduction on volume-based, chlorophyll-based and particle-based growth of *Scenedesmus obliquus* Kütz. by *E. canadensis* than *M. spicatum* was observed in co-culture systems and filtrate assays (45). When it came to cyanobacteria *Aphanizomenon flos-aquae* L., *C. demersum* exerted stronger growth and photosynthesis inhibition than *M. spicatum* (39).

Table 1. Reported submerged macrophytes with allelopathic activity against the phytoplankton species

| Family | Species | Sensitive algal species | References |
|---|---|---|---|
| Haloragidaceae | *Myriophyllum spicatum* L. | *Microcystis aeruginosa* Kütz. | 54,56 |
| | | *Pseudokirchneriella subcapitata* | |
| | | *Anabaena flos-aquae* Breb. | 39 |
| | | *Phormidium tenue* Kütz. | |
| | *Myriophyllum verticillatum* L.. | *Limnothrix redekei* Goor. | 32 |
| | | *Stephanodiscus minutulus* Kütz. | |
| | *Myriophyllum aquaticum* Vell. | *Microcystis aeruginosa* Kütz. | 95 |
| | *Myriophyllum brasiliense* Vell. | *Microcystis aeruginosa* Kütz. | 71 |
| | | *Anabaena flos-aquae* Breb. | |
| Ceratophyllaceae | *Ceratophyllum demersum* Linn. | *Oscillatoria limnetica* Lemm. | 37 |
| | | *Anabaena flos-aquae* Breb. | 39 |
| Potamogetonaceae | *Potamogeton malaianus* Miq. | *Microcystis aeruginosa* Kütz. | 82 |
| | | *Scenedesmus obliquus* Kütz. | 28 |
| | *Potamogeton maackianus* A. | *Microcystis aeruginosa* Kütz. | 82 |
| | *Potamogeton pusillus* L. | *Microcystis aeruginosa* Kütz. | 78 |
| | *Potamogeton illinoensis* Morong | Phytoplankton | 81 |
| | *Potamogeton foliosus* L. | Cyanobacteria | 27 |
| | | *Chlorella* spp. | |
| Hydrocharitaceae | *Stratiotes aloides* L. | *Scenedesmus obliquus* Kütz. | 50,51 |
| | | Natural phytoplankton | |
| | *Elodea nuttallii* Planch. | *Microcystis aeruginosa* Kütz. | 98 |
| | *Hydrilla verticillata* L. | *Microcystis aeruginosa* Kütz. | 98 |
| | *Vallisneria spiralis* L.. | *Microcystis aeruginosa* Kütz. | 98 |
| Najadaceae | *Najas minor* All. | *Scenedesmus obliquus* Kütz. | 28 |

Cyanobacteria was more susceptible to allelopathic inhibitors than eukaryotic algae in most cases. Live *C. demersum*, and its extracts induced a decline in the number of dominated cyanobacteria species *Oscillatoria limnetica* Lemm., cyanobacteria biomass and its percentage contribution to total algal biomass and an increase in the biomass and percentage contribution of green algae, especially *Chlorella* sp. and *Chlamydomonas* sp. (37). More cyanobacteria than other phytoplankton species were inhibited by the extracts of *Stratiotes aloides* L. (49). In a plant-algae mixed culture system, the cell density of *M. aeruginosa* was significantly affected by 5g FW/L of *M. spicatum*, whereas that of *R. subcapitata* was not affected by any treatment of *M. spicatum* (106). The field dialysis tube experiment performed in a lake dominated by *M. verticillatum* showed a decline in chlorophyll a content and PSII activity for cyanobacteria *Limnothrix redekei* Goor. and the diatom *Stephanodiscus minutulus* Kütz., but not for the green alga *Scenedesmus armatus* Chodat. (31).

Species-specific inhibition of submerged plants on phytoplankton was a useful characteristic for water environmental manager and engineer to develop the specific targeting technology to control certain algal species especially harmful cyanobacteria, without obvious impacts on non-target organisms. In future, it is necessary to do more research on effects of allelopathic plants towards different aquatic organisms including phytoplankton, zooplankton and fish, etc. in a more ecology-relevant and comparable bioassay systems.

## 3. POTENTIAL ALLELOCHEMICALS

Allelochemicals are often secondary metabolites biosynthesized and excreted by allelopathic plants, which are responsible for allelopathic process from plants to algae. So, it is a crucial step to find them for probing into the essence of allelopathy. With rapid technology development in analytic chemistry and phytochemistry, much progress has been made during recent decades.

### 3.1 Active fractions of plant extracts

To identify the allelopathically active compounds of each plant species, bioassay-directed extraction procedures were employed to uncover their chemical characteristics in advance. Gross *et al*. (25) found that fractions extracted by 50% methanol for *Najas marina* L.. and 50% acetone for *C. demersum* yielded the strongest inhibition against filamentous cyanobacteria i.e. *Anabaena* sp. and *Anabaena variabilis* as well as chroococcal *Synechococcus elongates* Nag., and at least two further purified fractions for both plants, one being hydrophilic and one moderately lipophilic, were active. Methanolic extracts of *Elodea nuttallii* Planch. and *E. canadensis* inhibited the growth of cyanobacteria (*S.elongates*, *Synechococcus* sp., *Synechococcus nidulans* Prin., *Pseudanabaena catenata* Lau. and *Anabaena variabilis* Kütz) and further fractionation of extracts indicated the hydrophilic and slightly lipophilic compounds were responsible for algal growth reduction (15). The active compounds of *S. aloides* were moderately lipophilic according to the extraction using solid phase extraction methods (49). The ethyl acetate fraction of aqueous extracts from *N. marina* and *Najas minor* All. inhibited the growth of *M. aeruginosa* (84).

Polyvinylpolypyrrolidone (PVPP) test was a classical method to remove the phenolic compounds from the extracts. Together with bioassays, it was a convenient way to test whether phenolic compounds are in plant extracts and demonstrate antialgal activities (42). Algal inhibition activities of PVPP treated extracts showed no significant differences from the extracts without treatments, which indicated that the active substances in *S. aloides* should not be phenolic compounds. For *E. nuttallii*, *E. canadensis*, *H. verticillata* and *V. spiralis*, the cyanobacterial inhibitory rates of plant exudates after PVPP treatment became significantly weaker, which provided evidence that the above four submerged plants released phenolic compounds into the surrounding water to inhibit cyanobacterial growth (15,98).

### 3.2 Chemical classes of potential allelochemicals

In search for allelochemicals, the actual agents of submerged macrophytes to exert the allelopathic inhibition on phytoplankton, polyphenols, fatty acids, terpenoids and alkaloids were among the main chemical classes.

**(i). Polyphenols**: Polyphenols, with at least one benzene hydroxyl as their basic structure, are widespread in submerged plant tissues, i.e. *M. spicatum*, *P. lucens*, *E. nuttallii*, *H. verticillata*, and *V. spiralis* (4,31,46,91,99). Total phenolic contents can reach up to 12% based on dry weight both for *M. spicatum* and *M. verticillatum*, as well as 3.7% for *Myriophyllum sibiricum* Kom. (23). The major algicidal tellimagrandin II in apical meristems of *M. spicatum* was assessed up to 2% (4,23 ). With hydrophilic character, polyphenols were supposed to be easily released into culture medium from donor plants

and they were the earliest detected in surrounding water of submerged macrophytes. Nakai *et al*. (55) revealed the release of four polyphenols by *M. spicatum* exhibiting the growth inhibition effects, i.e. ellagic, gallic and pyrogallic acid and (+)-catechin. The vanillic, protocatechuic, ferulic and caffeic acid were identified in the culture solutions of *H. verticillata* and *V. spiralis* (20).

**(ii). Fatty acids**: Fatty acids, carboxylic acids with saturated or unsaturated aliphatic chains, were supposed as one important class of antialgal allelochemicals for submerged macrophytes. *M. spicatum*, *E. nuttallii*, *P. malaianus*, *H. verticillata* and *V. spiralis* were reported to produce fatty acids (19,34,57). Pentadecanoic, linoleic, alpha-linolenic and stearic acids were among the most potent anti-algal allelochemicals from *E. nuttallii* (85), and lactic, succinic, hexanedioic, capric, lauric, tartaric, azelaic, palmitic and stearic acids were detected in the culture solutions of *E. nuttallii*, *H. verticillata* and *V. spiralis* (19,57). Nonanoic, linoleic and α-linolenic acid, with strong inhibitory effects on the growth of *M. aeruginosa*, existed in the culture solutions of *M. spicatum* (57). The (Z, Z)-9,12-octadecadienoic, tetradecanoic and hexadecanoic acids were identified as the potent allelochemicals for *Chara vulgaris* L. against the toxic *M. aeruginosa* (103). These results provided evidence that fatty acid allelochemicals were also released into water environment by submerged macrophytes.

**(iii). Terpenoids**: Terpenoids, derived from the five-carbon isoprene units assembled and modified in thousands of ways with various functional groups, are the largest group of natural products. There were nearly 30 terpenoids isolated and identified in the genus *Potamogeton*, including *P. pectinatus*, *P. lucens*, *P. perfoliatus*, *P. natans*, and *P. ferrugineus* (7,12,91,92,93). However, there was little evidence that they could be detected in culture solutions of *Potamogeton* species.

**(iv). Alkaloids**: Alkaloids, a group of naturally occurring chemical compounds that contain mostly basic nitrogen atoms, have already been found in plant tissues of *E. nuttallii*, i.e. 2-ethyl-1,4-diazine, 2-ethyl-5-methylpyrazine, indole, l-nicotine, 5-methylthiazole, and 7-methylquinoline, etc. (83). One of the antialgal compounds isolated from the leaves of *V. spiralis*, 2-ethyl-3-methyl-maleimide, was a simple alkaloid with the highest content and strong inhibitory effects on *M. aeruginosa* (99). The presence of alkaloids in nine *Potamogeton* species was detected by thin-layer chromatography (62). Yet there were no further reports, to find what they exactly are?

For most submerged macrophytes, multiple antialgal allelochemicals were isolated and identified. Alkanes, organic acids, terpenoids and ketones were mixed in the volatiles of *E. nuttallii* (85). Fatty acids, polyphenols and terpenoids were found in several *Potamogeton* species (34,102). These compounds precisely speaking, were only defined as potential allelochemicals, their specific contribution to allelopathy of their donor plants against target algae needs further illumination.

## 4. GAPS BETWEEN RELEASE CONTENTS AND EFFECTIVE DOSE

Concentration was crucial to determine the allelopathic activity of a single allelochemical. If there existed one main allelochemical for one plant species, it should be

released at a concentration, enough to effectively inhibit the target algae species. However, the match hasn't been found so far. Instead, a big gap between release amounts and effective dose for investigated allelochemicals is obvious.

**4.1 Contents of allelochemicals**

Compared with qualitative analysis of plant allelochemicals, there have been fewer reports about their quantitative analysis, though it is important to assess their contribution to allelopathic effects of donor plants on algae. The mean phenolic content in submerged plants including *E. nuttallii*, *C. demersum*, *M. spicatum* and seven *Potamogeton* species, was 29 mg/g DW, which was significantly lower than in floating and emergent species (75). However, the total phenolics content of *Myriophyllum* extracts with Folin-Ciocalteau assay was much higher, ranging from 57 to 108 mg/g DW (26,46). The content of tellimagrandin II in apical meristems of *M. spicatum* and *M. sibiricum* was 24.6 mg/g DW and 11.1 mg/g DW, respectively (46). Total phenolic content in plant tissues of *H. verticillata* was 16.65±0.21 mg/g DW, significantly higher than that of *E. nuttallii* and *V. spiralis*, averagely at 12.91±0.32 mg/g DW. The content of caffeic acid for *H. verticillata* was the highest (1.2 mg/g FW), among the vanillic, protocatechuic, ferulic and coumaric acids (94,98).

Allelopathy of submerged macrophytes on phytoplankton occurs in water bodies, then anti-algal secondary metabolites should be released into water by donor plants and reach up to effective dose. However, current research indicated that the allelochemical contents in surrounding water of donor plants were low, not exceeding 100 μg/L. The released amounts of total phenolic compounds only accounted for 1.0% of production of polyphenols by *M. spicatum* (23). The released content for ellagic, gallic and pyrogallic acid and (+)-catechin detected in culture solutions of *M. spicatum* at density of 100g FW/L was 76.6, 62.8, 5.2 and 16.6 μg/L, respectively (55). Total phenolic contents determined in the culture solutions of *E. nuttallii*, *H. verticillata* and *V. spiralis* were about 73.32, 33.02 and 74.15 μg/L, only 0.8%, 0.3% and 1.0% of those in corresponding plant tissues, respectively (98). The contents of vanillic, protocatechuic, ferulic and caffeic acid in the culture solutions of *H. verticillata* and *V. spiralis* at 10g FW/L were among 0.9-29.7 μg/L (20).

**4.2 Effective dose of allelochemicals**

Although many secondary metabolites were identified and isolated from the submerged plant tissues or culture solutions, not all of them exerted strong antialgal effects. According to the dose-response curves of each allelochemical in acute toxicity tests, the most effective inhibitors were those with the lowest 50% effective concentrations during a certain period, such as nonanoic acid at 0.5 mg/L and pyrogallic acid at 0.65 mg/L when targeting the cyanobacteria *M. aeruginosa* after 15-day exposure (55,57). Oleic acid inhibits the freshwater green alga *R. subcapitata* obviously with a 72 h $EC_{50}$ at 0.47 mg/L (38). However, most potential allelochemicals showed significant algal growth inhibition at a much higher concentration. The six compounds isolated and identified from *P. maackianus* inhibited the growth of *R. subcapitata* at 20 mg/L (102). $EC_{50}$ value of ρ-coumaric and vanillic acid on toxic *M. aeruginosa* was 0.26 mM and 0.34 mM, equal to 38.00 mg/L and 57.17 mg/L, respectively (104). Ferulic acid at a concentration above 0.31 mM equal to 60 mg/L, significantly suppressed the cyanobacterial cell density after 48 h exposure (89). Initial algal density influenced the $EC_{50}$ value, which increased for gramine from 0.5 to 2.1mg/L with initial algal

density for cyanobacterium *M. aeruginosa* rising from $5\times10^4$ to $5\times10^5$ cells/mL (33). In this way, it should be necessary to define which potential allelochemicals as potent ones, and whether there are other modes of action for identified allelochemicals should be investigated.

## 5. POSSIBLE MODES OF INHIBITION

Acute toxicity tests were often used to compare the antialgal activity of submerged macrophytes and their secreted allelochemiclas as mentioned in section 4.2. However, comparing with the effective dose i.e. $EC_{50}$ in acute bioassays, detected content of any allelochemical released into surrounding water by submerged macrophytes is much less, seemingly impossible to exert effective algal growth inhibition in an acute levels. To figure out, how the allelochemicals released from the submerged macrophytes effectively inhibit the target phytoplankton species at releasing levels, it is crucial to reveal the release and transport modes of allelochemicals before their attack on algal cells. Here two direct modes of action based on the releasing characteristics and indirect possibilities were proposed.

### 5.1 Continuous action

When testing allelopathic effects of submerged macrophytes on phytoplankton, both plant-algae coculture systems and plant filtrates or culture water assays were used frequently. However, significant differences in algicidal effects were always observed between the two bioassays. *M. spicatum* in coexistence culture system inhibited the growth of three cyanobacterial species (*M. aeruginosa*, *A. flos-aquae* and *P. tenue*), with $EC_{50}$ values of 1, 3.5 and 2 g FW/L, respectively. However, growth curve of *M. aeruginosa* in the initial addition culture solution of *M. spicatum* at 100 g FW/L were as same as that of control, whereas the $EC_{50}$ was about 65 g FW/L by the quasi-continuous addition of the culture solution of *M. spicatum* (56). Strong growth inhibition of *S. obliquus* occurred in the physical presence of *C. globularis*, *E. canadensis* and *M. spicatum*, but no or significantly weaker effects were observed when treating with filtrates from the three macrophytes (45). The allelopathic effects on *S. obliquus* were found in the presence of *P. malaianus*, but not in its filtrates (97). The main reason for their significant differences should be the supply patterns of allelochemicals between the presence of plants and its culture solution. That is, plants may continuously release the antialgal allelochemicals throughout the cultivation period, whereas there is no supplement of allelochemicals after initial addition.

To mimic the continuous release of plant allelochemicals, a repeated exposure treatment for three allelochemicals was designed. Compared to the high-dose (2.5 mg/L) single exposure group, stronger inhibition on cyanobacterial growth was observed in the low-dose (0.5 mg/L) repeated exposure group, and the inhibition ratio of nonanoic acid, N-phenyl-1-naphthylamine and caffeic acid was 1.8, 1.1 and 1.6 times higher. In this way, the growth of *M. aeruginosa* was significantly inhibited by N-phenyl-1-naphthylamine, when the single dose was as low as 0.1 mg/L, with an inhibition ratio up to 50.25% on the $7^{th}$ day (17). During a continuous daily exposure of pyrogallic acid at a single daily dose above 0.5 mg/L, pyrogallic acid exerted its inhibitory effect on growth and metabolism of the cyanobacterium *M. aeruginosa* (44). These results indicated that submerged macrophytes suppress the phytoplankton development successfully by continuously releasing the allelochemicals.

However, the repeated exposure pattern mentioned above did not associate with the release pattern of plant active substances. To assess the contribution of five polyphenols and three fatty acids to the allelopathic effects of *M. spicatum* on *M. aeruginosa*, Nakai *et al*. (58) determined daily release contents of the eight compounds in culture solutions of *M. spicatum* and calculated their release rates, which must be a first and only report on the release pattern of submerged plant allelochemicals so far as we know. Therefore, it is necessary to enhance the combined research on release and antialgal pattern of typical allelochemicals.

**5.2 Combined action**

Based on the facts that submerged macrophytes simultaneously release various allelochemicals into the water environment, it was easily to deduce that these chemicals might exert a stronger antialgal effects through additive and synergistic action than a single chemical, for which there is growing evidence from recent studies on joint effects of allelochemicals.

The four phenolic compounds of *M. spicatum*, mixed in the concentration found in culture solution, exerted synergistic growth and photosynthesis inhibition on *M. aeruginosa* (55,106), which was observed for the binary and ternary combination of benzoic acid, 4-hydroxybenzoic acid and gallic acid in a mixture with the ratio equivalent to 50% effective concentration of the individuals (86). The joint effects of multiple fatty acids of *P. malaianus* also showed synergistic inhibition (34). During our investigation on the combined effects of nonanoic acid, N-phenyl-1-napthtylamine and caffeic acid on the growth of *M. aeruginosa*, it was found that the combined toxicity of mixtures with equal concentration ratio showed synergism and the joint inhibitory effects became weaker with increase in caffeic acid proportion in the mixtures, which indicated mixing ratios and the individual activity of allelochemical were two major influencing factors. What's more, in 9-day joint bioassays, the inhibitory ratio of all mixtures increased over time till $7^{th}$ or $8^{th}$ day, which demonstrated a time-dependent joint toxicity, reminded us of an underestimate on the combined effects in a traditional 72-h exposure bioassay (18).

**5.3 Indirect action**

The two direct modes of action mentioned above are based on the release characteristics of allelochemicals. In addition, there might be other indirect patterns, since a complicated situation is faced for allelochemicals after releasing into the water environment, where interactions with biotic or abiotic environment are inevitable. On the one hand, their degradation or transformation is likely to enhance or weaken their antialgal activity. Oxidation products of polyphenols released by *M. spicatum* were also antialgal (55).

On the other hand, more attention should be paid to the mutual effects of allelochemicals and microorganisms. Microorganisms are proposed as mediators to involve in the allelopathy of plants on phytoplankton, by directly transforming the structures and characteristics of allelochemicals, or forming a new community detrimental for target phytoplankton under exposure to allelochemicals (9,10). Several bacterial isolates associated with *M. spicatum*, i.e. *Matsuebacter* sp., *Agrobacterium vitis* Ophel &Kerr and *Pseudomonas* sp. were capable of growing with tannic acid as the sole carbon and energy source, and their presence in the vicinity of *M. spicatum* might be the reason why tellimagrandin II and other hydrolysable polyphenols disappeared fast after excretion, which had implications for allelochemical interference with phytoplankton (52). Microbes in this situation mostly play a

negative role for allelopathic effects on phytoplankton. However, whether they are positive to this process is still an open question. Lower algal growth rate cultured in photolytically and microbially degraded tannic acid in lake water than cultured in respective dark treatments was observed for 3 weeks (5), which highlights the importance of microbial degradation and photolytic processes influencing the allelopathic effects. Will microbes be beneficial or detrimental for the successful inhibition of target algal species by the allelochemicals released from submerged macrophytes in natural waters? All the hypothesis needs more evidence to testify.

## 6. PHYSIOLOGICAL INHIBITION MECHANISMS

Researchers on ecotoxicology and molecular biology usually pay more attention, to how the identified allelochemicals affect the target algae at cellular levels. There are numerous papers trying to elucidate the physiological mechanisms of the inhibition process. Cell membrane disturbance, photosynthesis inhibition, damage of antioxidant system and programmed cell death were supposed to be four main physiological mechanisms according to the available related literature.

### 6.1 Cell membrane disturbance

Cell membrane is the first protective wall of any cells, and it is always the first attack target for any antialgal allelochemicals. Membrane potential reflected the differences in electric potential between the interior and the exterior of algal cells, that of *M. aeruginosa* was significantly inhibited by ferulic acid (89). Among pyrogallic acid, gallic acid, (+)-catechin, caffeic acid, protocatechuic acid, nonanoic acid and cis-9-octadecenoic acid, nonanoic acid damaged the cell membrane and severely altered the internal cell complexity of *M. aeruginosa* and *P. subcapitata* (87). Membrane integrity of *M. aeruginosa* cells was significantly ravaged when the concentration of ferulic acid was greater than 1.56 mM after 48 h exposure (89).

### 6.2 Photosynthesis inhibition

Various evidences showed that allelochemicals released by submerged macrophytes affected the structure and function of photosynthesis system. The content of photosynthetic pigments of *M. aeruginosa* obviously reduced the exposure to pyrogallic acid (41). After 2-day exposure for *M. aeruginosa*, the contents of both phycocyanin and allophycocyanin per cell were decreased by nonanoic acid at 4 mg/L concentration and oxygen evolution was inhibited even at 0.5 mg/L concentration (73). The relative content of chlorophyll a, phycocyanin and allophycocyanin of *M. aeruginosa* decreased to 52.7%, 15.3% and 7.6%, respectively, after treated by *M. aquaticum* culture water for 5 days (95). Chlorophyll a and carotenoic contents of *Phaeodactylum tricornutum* Bohlin. were significantly inhibited by the hydroquinone at concentrations above 0.4 μM (100).

Chlorophyll fluorescence measurements have been widely applied to analyse the effects on algae photosynthesis (31). The non-photochemical quenching (NPQ) and effective quantum efficiency (Yield) of *M. aeruginosa* were influenced significantly, when coexisted with submerged plant *M. spicatum* as well as its four allelopathic polyphenols, two of which are pyrogallic and gallic acids. They respectively at a concentration of 2.97 mg/L and 2.65 mg/L caused significant reduction in photosystem II (PSII) and whole electron transport chain

activities of *M. aeruginosa* (106). Inhibitions of $F_v/F_m$, $F_v'/F_m'$ occurred more quickly than cell growth under stress from ferulic acid. Meanwhile, the stimulation of non-photochemical quenching (NPQ) of *M. aeruginosa* cell was also observed, which was a feed-back mechanisms induced by photosystem II blockage (89).

*psb*A gene encodes D1 protein, a key subunit of PS II. Photosynthesis related gene i.e. *psb*Aand *fab*Z of *M. aeruginosa* were up-regulated under exposure to 1-4 mg/L pyrogallic acid, whereas *rec*A and *grp*E showed no significant changes under the pyrogallic acid stress (74). N-phenyl-2-naphthylamine reduced the transcript abundance of *psa*B and *psb*C of *Chlorella vulgaris* Beij. to 3% and 1% of the control, respectively, together with a decrease in chlorophyll content, which indicated that the compound inhibited photosynthesis of this aquatic organism (66). *rbc*L encodes the large subunit of ribulose-1,5-bisphosphate carboxylase oxygenase (Rubisco) in algae, *psb*D1 encoding the D2 protein that forms the reaction center of PS II, and *psa*B encoding one of the reaction center subunits of photosystem I. The transcription of *psa*B, *psb*D1 and *rbc*L was inhibited by N-phenyl-2-naphthylamine, implying that it was a blocker of the whole electron transport chain (67). Hydroquinone exerted great influences on the transcription of *psb*A and *psa*B at above 0.3 μM after 24 h (100).

**6.3 Oxidative stress**

Malondialdehyde (MDA), the oxidative product of unsaturated fatty acids, was also one of several low-molecular-weight end products formed via the decomposition of polyunsaturated fatty acids hydroperoxides. It was usually used as a biomarker for lipid peroxidation to reflect the cellular oxidative damage (3). Superoxide dismutase (SOD) was mainly responsible for $O_2$ removal as the first line of resistance against reactive oxygen species (ROS). The activity of antioxidant enzymes such as SOD, catalase (CAT) and peroxidase (POD) were always stimulated, and the contents of MDA were increased for target green alga and cyanobacteria exposed to allelopathic plants or their secreted compounds (97), which provided the early evidence for oxidative stress through allelopathy of submerged macrophytes. The lipid -peroxidation product MDA increased significantly in gramine-treated cells. The effects of gramine on enzymatic and non-enzymatic antioxidant were in different manners. The activity of SOD was decreased after gramine exposure. The CAT activity was increased after 4 h but decreased from 60 h. Both the contents and the regeneration rates of ascorbic acid (AsA) and reduced glutathione (GSH) were increased after 4 h exposure to gramine. Only GSH content was still increased after 40 h exposure (33). The activities of the antioxidant enzymes, SOD, POD, and CAT of *C. vulgaris* exposed to 2.5 mg/L N-phenyl-2-naphthylamine were 2.47, 3.24 and 4.27 times higher than control, which showed a decrease when the compound concentration was increased to 4 mg/L (66). Their activities in *M. aeruginosa* were also affected by N-phenyl-2-naphthylamine, 1 mg/L of which caused a 3.9-folds higher level of MDA than control (67). Hydroquinone induced the responses of SOD, CAT, glutathione peroxidase (GPX), glutathione S-transferase (GST) and GSH (100).

The unfavorable superoxide anion radicals ($O_2^{\cdot-}$) was derived from the electron leakage of electron transport pathways, which was also the precursor of several other ROS and the main factor to limit $O_2$ reactivity. Both ρ-coumaric and vanillic acid triggered the generation of $O_2^{\cdot-}$, which might induce a lipid peroxidation which may change cell membrane penetrability,

thereby leading to the eventual death of *M. aeruginosa* (104). The relative ROS levels in the cells of *M. aeruginosa* after 2, 24 and 48 h of exposure to 8 mg/L of gramine were 1.5 times, 2.6 times and 4.3 times higher than controls, respectively, which was a significant increase (33). Tryptamine induced an increase in hydrogen peroxide ($H_2O_2$) production in the cultures of both *Aphanizomenon gracile* Lemm. and *Ankistrodesmus falcatus* Corda. (8). Among the six polyphenols and two long-chain fatty acids, only (+)-catechin and pyrogallic acid could induce ROS formation in *M. aeruginosa* and *R. subcapitata* (88). Pyrogallic acid induced the dose-dependent generation of intracellular $O_2^{\cdot-}$ and consequently $H_2O_2$ and the hydroxyl radical ($OH^{\cdot}$) in *M. aeruginosa*, especially under light conditions (76). DNA strands and cell membrane of *M. aeruginosa* were two targets of ROS induced by pyrogallic acid, which indicated that oxidative damage was an important mechanism of pyrogallic acid against *M. aeruginosa* (43).

*prx* is a gene encoding for peroxiredoxin (Prx) that could catalyze the reduction of $H_2O_2$, alkyl hydroperoxides and peroxynitrite, using the thioredoxin and other thiol containing reducing agents as electron donors. In response to pyrogallic acid stress, expression of *prx* was up-regulated even at 1 mg/L, indicated that oxidant damage may be the mechanism for the allelopathy of pyrogallic acid to *Microcystis* cells (74).

### 6.4 Programmed cell death

Reactive oxygen species (ROS) acting as a chemical oxidizer causing macromolecular damage as mentioned above, also exists as a signalling molecule to trigger the programmed cell death (PCD) in phytoplankton along with nitric oxide (NO) (70,105). When co-cultured with 0.5-6g FW/L of *M. spicatum*, Caspase-3-like activity of cyanobacteria was significantly higher than control, accompanied by DNA fragmentation, disintegration of ultrastructure, increase of intracellular ROS and NO, and high mortality of *M. aeruginosa*, which indicated that PCD in *M. aeruginosa* was induced by *M. spicatum* (29). Polyphenols released by this submerged species were demonstrated to activate caspase-3-like activity, and could also induce DNA fragmentation and disintegration of cell ultrastructure of *M. aeruginosa*, which were the hallmarks of PCD (96). Although there have been several reports observed PCD of phytoplankton species under environment stress (90,107), but the PCD induced directly by allelopathic plants or their allelochemicals needed more research.

### 6.5 Other mechanisms

Besides the four pathways mentioned above, there must be other unrevealed mechanisms, as the growth of *M. aeruginosa* was significantly inhibited by *p*-benzoquinone, rather than its photosynthesis (1). There were several test endpoints showing the impacts of plant allelochemicals on the physiological process of phytoplankton cells. Intracellular esterase activity is very sensitive parameter, which in *M. aerugniosa* was significantly inhibited by the allelochemicals pyrogallic acid, gallic acid, protocatechuic acid, caffeic acid, cis-9-octadecenoic acid, nonanoic acid and ferulic acid (87,89). A significant inhibition in esterase activity was detected at every time point in green algae *Desmodesmus armatus* Chodat. and *Scenedesmus vacuolatus* Vall. and the diatom *S. minutulus* at 30 μmol/L tannic acid (14).

Allelochemicals from submerged macrophytes could affect the respiration process of phytoplankton cells by accelerating dark respiration rate, stimulating the transcription of respiration related genes, such as *nad*1 and *cob* (100,106).

There is also another possibility for antialgal allelochemicals, to suppress the growth and development of phytoplankton by altering their nutrients uptake systems, especially by reducing the related enzyme activities. Alkaline phosphatase (APA) could hydrolyse the organic phosphorus compounds once there was an inorganic phosphate limitation. The influence of *M. spicatum* exudates and one of main allelochemicals, tellimatrandin II, on APA activity was obvious with an exponential dose-response relationship (26). However, no obvious effects from *P. malaianus* to APA activity of *S. obliquus* were observed in a co-culture experiment (97).

Based on current research, there are multiple molecular target sites for allelochemicals of submerged macrophytes, which means that the allelopathic effects may be a complex process. Furthermore, it is necessary to consider the exposure patterns including concentrations, which should be in accordance with the release patterns in natural water environment during the further studies.

## 7. IMPACTS OF ENVIRONMENTAL FACTORS

Allelopathy phenomenon was first observed in field conditions and was finally also applied to water environment management. So, the impacts of environment conditions including biotic and abiotic factors might play important roles in the growth of allelopathic plants and target phytoplankton species, the biosynthesis and exudation pathway of single allelochemicals, the diffusion and transformation of the exuded allelochemicals, and the whole inhibition process. However, the related research till now is scarce. Following are the some research advances.

### 7.1 Nutrients levels

Based on the carbon-nutrient balance hypothesis (CNBH), a high carbon/nutrients ratio in the environmental conditions would result in an increased production of carbon-based secondary compounds (6). To test this influential theory, the controlled experiments and the investigation under in situ conditions were both conducted during the past decades. When setting the final concentrations of 0.6-4.8 mM N-$NO_3$, nitrogen availability did not influence the total phenolic compounds in plant tissues and culture water of *M.spicatum*, however, tissue concentrations of the major polyphenol tellimagrandin II increased at low nitrogen levels (24). The total phenolic contents in plant tissues of *M. spicatum* and its culture water were much higher under low nitrogen (0.06 mM) and high nitrogen (4 mM) levels than the control (0.5 mM). However, (+)-catechin and ellagic acid in plant culture solutions showed opposite trends (21).These results implied distinct differences among the different individual compounds. During a 4-year investigation of the seasonal and inter-annual variability of the total phenolic compounds and the individual phenolics in *M. verticillatum*, correlations between the total phenolic compounds and carbon/nutrients ratio were observed in some but not all years, especially in apical meristems. Plant tissue phosphorus content accounted also for the variability in TPC in some years (4). Nutrient (P or K) limitation decreased the sensitivity of *S. elongates* to allelochemicals from the *S. aloides* (49).

### 7.2 Light

Light first affected the photosynthesis process of submerged macrophytes and also influenced the production and release of allelochemicals. Higher light levels triggered an increase of tissue-bound and exuded phenolic compounds for *M. spicatum*, whereas, tissue concentrations of the major allelochemical tellimagrandin II increased in low light (24). The decrease in *M. aeruginosa* growth exposure to the allelochemicals produced by *M. spicatum* at 25 μmol $m^{-2}s^{-1}$ was 1.5 times of that at 75 μmol $m^{-2}s^{-1}$ (53). The inhibitory effects of the exudates from *S. aloides* on the growth of green alga *S. obliquus* was stronger at 35 μmol $m^{-2}s^{-1}$ than that at 105 μmol $m^{-2}s^{-1}$ (50). Although flavonoid biosynthesis depended less on the external conditions, high irradiance triggered luteolin diglucuronide biosynthesis, but not apigenin or chrysoeriol diglucuronides (16).

### 7.3 Temperature

When investigating the inhibition of growth and photosynthetic activity of the cyanobacterium *M. aeruginosa* mediated by eight allelochemicals of *M. spicatum*, the growth decrease rate at 20℃ was 1.9 times of that at 30℃ (53). Temperature affected most phenolic compounds negatively except for luteolin diglucuronide (16).

### 7.4 pH

The possible influence of pH on the allelopathic inhibition from submerged macrophytes to phytoplankton was probably due to its impact on the structure and characteristics of specific classes of allelochemicals, e.g. phenolic and fatty acids. With the increase of pH, polyphenols might transform from molecular states to ionic ones, more importantly, they are easily to form oxidized polymerization, which reduced bioavailability and toxicity. Hydroquinone completely inhibited the algal growth even after 4 days at pH 7.0, whereas toxicity vanished rapidly within 48 h and phototroph growth recovered at pH 11. When pH rose above 10, the toxicity of tannic acid, gallic acid and hydroquinone towards *D. armatus* and *M. aeruginosa* vanished (2).

## 8. APPLICATION IN WATER MANAGEMENT

Although there are still several open questions concerning the allelopathy from submerged macrophytes to phytoplankton, its application to control harmful algal blooms, or reestablish submersed vegetation community to stabilize a clear-water state, is supposed to be possible. So far the possible ways used to control the phytoplankton development we can think out include introduction of living plants into water bodies, preparation of dry plant tissues, extracts and natural allelochemicals or their synthetic analogues.

We are not quite sure about how much allelopathy contributes to the successful reestablishment of submerged macrophytes in eutrophic shallow lakes, which was once turbid with plenty of phytoplankton. However, some reports indicated that allelopathy of submerged macrophytes was one of important factors to assist in the restoring process. A forceful fact that the decrease in phytoplankton density and changes in phytoplankton community structure was significantly related to the biomass and coverage of submerged plants, rather than nutrients concentrations in field experiments or investigations (11,13,37,47,48,60). To test whether *E.*

*nuttallii* can control the phytoplankton biomass, two mesocosm experiments were conducted for 4-8 weeks, and the results showed a consistently lower phytoplankton biomass when exposed to *Elodea* than control, which suggested the obvious contribution of *Elodea* allelopathy to phytoplankton inhibition, since zooplankton grazing and competition for nutrients and light by plants were excluded (80). Under field-like conditions, consistent negative effects of *M. spicatum* on cyanobacteria biomass were observed in mesocosms (77). These studies provided the direct evidence that allelopathy strategy is obviously involved in the successful rehabilitation of submerged plants in aquatic ecosystems. However, more research is needed to reveal where and when the contribution of allelopathy is obvious. Hence, it is necessary to do more field studies to consider the impacts of biotic and abiotic factors.

The use of dry plant tissues currently seems to be reported not for submerged macrophytes, but for the agricultural byproducts, such as barley straw, rice straw and hull, etc (72). There has been a long history for barley straw used in UK, ranging from household ponds to reservoirs (65). As for submerged macrophytes, there are few trials to use dry plant tissues, instead, effective fractions isolated from the crude plant extracts must be more promising.

What motivated numerous researchers to search for active allelochemicals from the submersed plant tissues or plant exudates is their potential application by introducing pure compounds directly into turbid water to suppress the cyanobacteria development. Although several natural compounds are derived from the terrestrial plants, however, anthraquinone, stilbenes and isoquinoline alkaloids showed the algaecidal activity for prevention and management of cyanobacterial blooms (36). So far, there is not much successful practice to control the cyanobacteria growth with pure allelochemicals. Gallic and nonanoic acid were selected to inhibit the cyanobacterial growth in lentic hydrosystems during a 28-day mesocosm experiments, which indicated that gallic acid was more efficient than nonanoic acid in suppressing the cyanobacterial growth at concentrations as low as 1mg/L. What's worthy of mention is that a successive application of gallic acid and nonanoic acid was used to test whether it could completely eliminate the cyanobacterial growth (79). In future, we should do more mesocosm experiments in controlled conditions in combination with inhibitory modes of allelochemicals.

Besides, sustained-release microspheres of allelochemicals were proposed as a new ecological way for the practical treatments of water undergoing algal blooms in recent years. Over 90% inhibitory ratio on *M. aeruginosa* was observed when exposed to 0.3 g/L of linoleic acid micropheres, which also affected the algal antioxidant enzymes activity and decreased the production and release of microcystins (59). The continual-release beads of 5,4'-dihydroxy-flavone (DHF) had long-term inhibitory effects (> 30 d), whereas those of "direct-added" DHF to cells lasted a maximum of 10 d, which demonstrated that the successful application of allelochemicals offered great potential to control the harmful cyanobacterial blooms, especially at the initial stage of development (35). In future, there should be more attempts to use potent allelochemicals or their synthetic analogues directly to suppress the cyanobacterial development.

## 9. FUTURE PROSPECTIVES

It is indisputable that allelopathy of submerged macrophytes on phytoplankton is widespread in aquatic ecosystem, which is one of the influential factors to affect the natural and artificial succession and competition of plants and phytoplankton. So, to reveal the full mechanisms from molecules to ecology are quite meaningful, which require our more attention on the following aspects.

(i). **Assessment of allelopathic activity:** To identify whether one compound is plant allelochemical, or which one is more active and more contributory, it needs more comparable toxicity tests to assess their inhibitory activity against target phytoplankton species, including referenced target organisms, culture conditions, testing end-points and evaluation criterion, which is better to set up a standard or guideline, to avoid the difference among various laboratories towards same target for same allelochemical. It will be more efficient and comparable to screen responsible allelochemicals for plant allelopathy and it will be very helpful for the further research probing into their inhibitory mechanisms.

(ii). **Clarifying ecological mechanisms**: During the past decades, there have been more and more concerns on identification of allelochemicals and their physiological mechanisms. However, few are about the intermediate process of allelochemicals before arriving into target phytoplankton cells. What happens during this phase? How environment variables affect the allelochemicals' behaviour and activity? It is urgent to figure out their environmental behaviour, including production and release dynamics, degradation or transformation rhythm of allelochemicals in water environment and the interactions with biotic and abiotic factors, etc. It needs more field or mesocosm experiments to reveal its ecological mechanisms. A pivotal step is to study the modes of action of allelochemicals after release from donor plants. One possibility is to inhibit the growth and physiology of target phytoplankton cells directly by continual and joint action of the main responsible allelochemicals. Another strategy is to form a new compound during transformation and transportation course in surrounding water environment, or alter the microorganism community structure to indirectly suppress the survival and development of certain phytoplankton species. The above hypothesis needs more research to test.

(iii). **Systematic research:** Finally, systematic research should be done so that adequate evidences could be obtained from the multiple aspects including the allelopathic anti-algal phenomenon, chemical behaviour of responsible allelochemicals, their inhibition modes and mechanisms from gene to ecological views.

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