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Inhibitory effects of total flavonoids from *Solidago canadensis* on growth, oxidative stress, and microcystin production in *Microcystis aeruginosa*

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Abstract

Cyanobacterium blooms caused by *Microcystis aeruginosa* eutrophication present a major threat to water resources protection. Plant-derived allelochemicals have attracted increasing attention as environmentally friendly alternatives for controlling harmful algal blooms. Here, we evaluated the inhibitory effects of total flavonoids extracted from the invasive plant *Solidago canadensis* on the growth and physiological and biochemical responses of *M. aeruginosa*. Algal cell density, photosynthesis-related pigments, oxidative stress indicators, antioxidant enzyme activities, and extracellular microcystin content were analyzed under different flavonoid concentrations (0–100 mg/L). Flavonoid treatment (20–100 mg/L) significantly suppressed algal growth in a concentration- and time-dependent manner, with algal density in the 100 mg/L group decreasing by nearly 50% compared with the control at day 12. Photosynthetic pigment contents, including chlorophyll a, carotenoids, and phycocyanin, were markedly reduced under flavonoid exposure, indicating impairment of the photosynthetic system. Meanwhile, hydrogen peroxide content increased significantly (more than 2 times), accompanied by enhanced antioxidant enzyme activities, suggesting the induction of oxidative stress. Malondialdehyde accumulation further confirmed membrane lipid peroxidation and cellular damage. In addition, extracellular microcystin content decreased with increasing flavonoid concentration. These results indicate that *S. canadensis* total flavonoids inhibit *M. aeruginosa* primarily by disrupting photosynthesis and inducing oxidative stress, supporting their potential as environmentally friendly algicidal agents for the management of cyanobacterial blooms.

Keywords: *Solidago canadensis*; *Microcystis aeruginosa*; Total flavonoids; Oxidative stress; Microcystin; Photosynthetic pigment

1. Introduction

Cyanobacterial blooms caused by eutrophication have become a major environmental problem worldwide and pose serious threats to aquatic ecosystems and water resource safety.[1] Excessive algae proliferation on the water surface reduces light penetration and dissolved oxygen, degrades aquatic vegetation, and causes organism mortality, thereby worsening water quality.[2,3] Among different types of algal blooms, cyanobacterial blooms dominated by blue-green algae are the most common in freshwater lakes and reservoirs.[4] In recent decades, the intensity and frequency of cyanobacterial blooms have increased significantly under the combined effects of anthropogenic activities and global climate change.[1,5] In China, large freshwater lakes such as Taihu Lake, Chaohu Lake, and Dianchi Lake have experienced frequent cyanobacterial outbreaks.[6,7]

Microcystis aeruginosa is one of the dominant species responsible for cyanobacterial blooms in freshwater ecosystems. Its massive proliferation not only disrupts aquatic ecological balance but also releases microcystins, a class of hepatotoxic cyanotoxins that threaten drinking water safety and human health by affecting organs such as the liver, skin, intestine, and the nervous system.[8-13] Therefore, effective control of cyanobacterial blooms has become an important issue in environmental science and water management.

Currently, cyanobacterial bloom control methods mainly include physical, chemical, and biological approaches.[14] Physical methods, such as ultrasonic algae control and shading, are environmentally friendly but often costly and inefficient for long-term management. Chemical algicides can rapidly suppress algal growth; however, their residues may cause secondary pollution and ecological risks. Biological controls also have limitations, including slow response and potential ecological disturbances. Consequently, environmentally friendly and sustainable algal control strategies remain highly desirable.

Recently, plant-derived allelopathic compounds have received increased attention as potential natural algicides due to their biodegradability and ecological compatibility. *Solidago canadensis*, a perennial herb in the Asteraceae family, is native to North America and has become a typical invasive alien species in China.[15,16] Owing to its strong interspecific competitive ability, this species often forms monodominant populations, leading to reduced biodiversity and ecological imbalance in invaded habitats.[17,18] Meanwhile, studies have demonstrated that *S. canadensis* possesses antibacterial, antioxidant, anti-inflammatory, and insecticidal activities, suggesting its potential as a natural bioresource.[19,20]

Flavonoids are important phenolic secondary metabolites widely distributed in plants and are known for their antioxidant and antibacterial properties.[21,22] Previous studies have shown that Asteraceae plants contain relatively high levels of flavonoid compounds,[23,24] and *S. canadensis* is also rich in total flavonoids with stable extraction efficiency and good biological activity.[25,26] Although flavonoids have been extensively studied for their pharmacological and antioxidant effects,[27–30] reports on the inhibitory effects of total flavonoids from *S. canadensis* on *M. aeruginosa*, especially regarding physiological and biochemical response mechanisms, remain limited.

Flavonoids have been widely reported to exhibit inhibitory effects on cyanobacteria; however, most previous studies have focused on individual flavonoid compounds, and integrated analyses of total flavonoids from invasive plant species remain limited. In particular, the combined effects of total flavonoids on growth, photosynthetic pigments, oxidative stress responses, and toxin production in *M. aeruginosa* have not been systematically elucidated. Therefore, this study aimed to investigate the inhibitory effects and underlying physiological mechanisms of total flavonoids extracted from *S. canadensis* on *M. aeruginosa*. We hypothesize that total flavonoids exert their algicidal effects by coordinating disruption of the photosynthetic system and the induction of oxidative stress, ultimately leading to reduced growth and toxin production. By integrating multiple physiological and biochemical indicators, this study aims to provide a more comprehensive understanding of flavonoid-mediated algal inhibition and to explore the potential application of invasive plant resources in environmentally friendly bloom control strategies.

2. Materials and methods

2.1. Extraction of total flavonoids from *Solidago canadensis*

Inflorescences of *S. canadensis* in full bloom were collected from Huanshan Road, Huainan Normal University, China. The samples were washed, air-dried, and further dried at 95 °C to constant weight. The dried materials were ground into powder and sieved for extraction. Total flavonoids were extracted using 70% ethanol at a material-to-liquid ratio of 1:20 (w/v) under ultrasonic conditions (40 °C, 30 mins). The extract was concentrated using a rotary evaporator (RV-211MO, Shanghai Yiheng Scientific Instrument Co., Ltd., China), followed by ethanol precipitation at 4 °C overnight. Chlorophyll was removed by petroleum ether extraction, and the final extract was concentrated and adjusted to a defined volume with deionized water for subsequent experiments. The flavonoid extract used in

the bioassays was prepared for independent biological replicates, and all algal exposure experiments were performed in triplicate.

2.2. Determination of total flavonoid content

A total of 30.1 mg of rutin standard, previously dried to constant weight at 105 °C, was weighed, dissolved in 60% ethanol, and diluted to 100 mL to obtain a standard solution with a mass concentration of 0.301 mg/mL. The absorbance values of rutin solutions at different concentrations were measured at 510 nm using a ultraviolet–visible spectrophotometer (UV2300II, Shanghai Tianmei Scientific Instrument Co., Ltd.) based on the $NaNO_2$–$Al(NO_3)_3$–NaOH colorimetric method.[31] The absorbance was measured after diluting 30 mL of the total flavonoid solution from *S. canadensis* 40-fold. Total flavonoid extraction was performed in three independent batches. The flavonoid contents of the three independent extracts were 17.24, 17.68, and 18.03 mg/mL, respectively, with a mean value of 17.65 ± 0.32 mg/mL.

2.3. Cultivation and treatment of *Microcystis aeruginosa*

Microcystis aeruginosa was purchased from the Freshwater Algae Species Bank of the Chinese Academy of Sciences (FACHB 1328). The culture temperature was maintained at 25 ± 1 °C, with a light intensity of 2800 lx and a 12/12 h light/dark cycle. For the experimental treatment, six total flavonoid treatments were established: control (CK) group (0 mg/L), 20, 40, 60, 80, and 100 mg/L; each treatment was replicated three times.

2.4. Density quantification and morphological alterations of algal cells

The linear relationship between algal density and absorbance was established using spectrophotometry.[32] An ultraviolet–visible spectrophotometer (UV2300II, Shanghai Tianmei Scientific Instrument Co., Ltd., China) was used to measure the absorbance of algal liquid at OD_{680} in the treatment and control groups. After 12 days of treatment, the samples were washed with phosphate buffer. Subsequently, the samples were dehydrated through a graded ethanol series (30–100%) and allowed to dry naturally.[33,34] Finally, scanning electron microscopy (Gemini SEM 300, Zeiss, Germany) was used to observe and characterize the cell morphology of *M. aeruginosa.*

2.5. Quantification of photosynthetic pigments

Spectrophotometry was used to quantify chlorophyll a, carotenoids, phycocyanin (PC), and allophycocyanin (APC). For chlorophyll a and carotenoid determination, the absorbance of the supernatant was measured at 470, 649, and 665 nm.[32,35] For PC determination, the absorbance of the supernatant was measured at 620 and 650 nm.[36] For APC determination, the absorbance values were measured at 620 and 650 nm.[36]

2.6. Detection of oxidative damage and antioxidant enzyme activity

The determination of hydrogen peroxide (H_2O_2) and malondialdehyde (MDA) was performed using previously reported methods with slight modifications.[36–38] Briefly, *M. aeruginosa* culture was centrifuged, and the algal cells were washed. Subsequently, precooled phosphate-buffered saline was added, and the mixture was lysed using an ultrasonic cell crusher, then centrifuged to obtain the supernatant. The contents of H_2O_2 and MDA, as well as the activities of superoxide dismutase (SOD) and peroxidase (POD), were determined using commercial assay kits (Nanjing Jiancheng Bioengineering Institute, China). The absorbance of the supernatant was measured at 405, 532, 550, and 420 nm using a ultraviolet–visible spectrophotometer, and the contents of H_2O_2 and MDA and the activities of SOD and POD were calculated accordingly.

2.7. Detection of extracellular microcystin content

Extracellular microcystin content was determined according to the method described by Li et al.[36] Briefly, 4 mL of *Microcystis* culture was centrifuged at 8,000 rpm for 10 mins, and the supernatant was directly used for quantification of extracellular microcystins. The extracellular microcystin content was measured using an enzyme-linked immunosorbent assay (ELISA) with a Lightary Microcystin ELISA Kit (Shanghai Guangyu Biotechnology Co., Ltd., China). Prior to the ELISA assay, the supernatant was appropriately diluted according to the density of *Microcystis* cells.

2.8. Statistical analysis

All experiments were performed with three biological replicates, and the data are presented as mean ± standard deviation. Statistical analyses were conducted using the Statistical Package for Social Sciences 25.0 software. For variables measured at a single sampling point, differences among treatments were evaluated using one-way analysis of variance (ANOVA) followed by Duncan's multiple-comparison test. For photosynthetic pigments measured across different flavonoid concentrations and exposure times, two-way ANOVA was performed to evaluate the main effects of concentration and time, as well as their interaction (time × concentration). Differences were considered statistically significant at $p < 0.05$.

3. Results

3.1. Effect of total flavonoids of *Solidago canadensis* DC on the growth and morphology of *Microcystis aeruginosa*

The growth of *M. aeruginosa* showed significant differences under different concentrations of total flavonoids from *S. canadensis* (Figure 1A). In the CK group, algal density increased continuously throughout the experimental period, reaching a maximum on day 12. In contrast, algal density in all flavonoid-treated groups (20–100 mg/L) increased during the early stage of exposure, reached a peak around day 5, and subsequently declined with prolonged treatment time. This trend suggests that the inhibitory effect of total flavonoids becomes more pronounced over time, particularly during the later stages of algal growth. The inhibitory effect became more pronounced in a concentration-dependent manner. On day 12, algal densities in the 60, 80, and 100 mg/L treatment groups were significantly lower than those in the CK group, indicating a clear concentration-dependent inhibitory effect on algal growth. These results indicate that total flavonoids effectively suppress algal proliferation, possibly by disrupting cellular metabolic processes and cell division under flavonoid stress.

Morphological observations further confirmed the inhibitory effect of total flavonoids on *M. aeruginosa* (Figure 1B). Cells in the control group maintained normal morphology with smooth and intact surfaces, whereas cells exposed to total flavonoids exhibited varying degrees of deformation, surface depression, and structural damage. The proportion of damaged and ruptured cells increased with increasing flavonoid concentration, suggesting that total flavonoids negatively affected cell integrity and normal growth of *M. aeruginosa*.

These structural alterations indicate that total flavonoids may impair membrane integrity and cellular stability, thereby contributing to the observed growth inhibition, suggesting that membrane disruption is an important mechanism underlying flavonoid-induced toxicity.

3.2. Effect of total flavonoids of *Solidago canadensis* on the photosynthetic pigments of *Microcystis aeruginosa*

Total flavonoids from *S. canadensis* significantly affected the photosynthetic pigment contents of *M. aeruginosa* (Figure 2). Two-way ANOVA revealed significant effects of concentration, time, and their interaction on all four pigments (Tables S1–S4; $p < 0.0001$). In the CK group, the contents of chlorophyll a and carotenoids augmented progressively with culture time. In contrast, under flavonoid treatments (20–100 mg/L), chlorophyll a and carotenoid contents showed a general trend of initial increase followed by a gradual decline with prolonged exposure, with the magnitude of decline varying significantly among concentrations (time × concentration interaction). Compared with the control group, both pigments were consistently lower in the treatment groups during the later cultivation stages, and the reductions became more pronounced with increasing flavonoid concentration and exposure duration. Significant differences among treatments were observed from day 4 onwards ($p < 0.05$), with the greatest decrease occurring in the 100 mg/L treatment group by day 12. These results indicate that total flavonoids inhibit the accumulation of major photosynthetic pigments, suggesting impairment of the photosynthetic apparatus. This reduction in chlorophyll a and carotenoids may be attributed to the disruption of chlorophyll synthesis or enhanced degradation under stress conditions, ultimately limiting light absorption and energy conversion efficiency.

Phycocyanin content exhibited a similar but more pronounced decreasing trend under flavonoid treatments. While PC content elevated steadily in the control group, it declined progressively in the treated groups after the early stage of exposure, particularly at higher concentrations (80–100 mg/L). The concentration-dependent inhibitory effect was statistically significant, with a moderate but significant time × concentration interaction. The more pronounced decline in PC suggests that phycobiliproteins, which are located on the surface of thylakoid membranes, may be more sensitive to flavonoid-induced stress. Damage to these light-harvesting complexes could further reduce photosynthetic efficiency and accelerate growth inhibition. In contrast, APC content increased continuously over the experimental period in all treatment groups and was generally higher than in the control group. Strikingly, chlorophyll a showed the strongest concentration effect among all pigments and the most pronounced time × concentration interaction. The increase in APC content may represent a compensatory response of the photosynthetic system under stress conditions, aimed at maintaining energy transfer efficiency. However, this compensatory mechanism appears to become saturated under prolonged high-dose exposure. In addition, APC has been reported to possess antioxidant properties, which may help mitigate oxidative damage induced by flavonoid exposure. Collectively, total flavonoids exerted differential, time-dependent effects on photosynthetic pigment components: while major pigments (chlorophyll a, carotenoids, and PC) showed concentration-dependent inhibition, APC exhibited a concentration-modulated compensatory increase with distinct temporal dynamics.

The consistent significance of time × concentration interactions across all four parameters highlights the critical necessity of multifactorial statistical analysis for understanding flavonoid-photosynthesis relationships. These findings suggest that total flavonoids disrupt photosynthetic function by differentially affecting pigment components, thereby inhibiting algal growth.

3.3. Effect of total flavonoids from *Solidago canadensis* on hydrogen peroxide content in *Microcystis aeruginosa*

The H_2O_2 content of *M. aeruginosa* was significantly affected by total flavonoids from *S. canadensis* (Figure 3). Throughout the experimental period, the H_2O_2 level in the CK group remained at baseline, whereas all flavonoid-treated groups (20–100 mg/L) exhibited significantly higher H_2O_2 levels than the control ($p < 0.05$). With increasing flavonoid concentration, H_2O_2 content generally increased, peaking in the 80 mg/L treatment group. Although the H_2O_2 content in the 100 mg/L treatment group decreased slightly compared with that at 80 mg/L, it remained significantly higher than that in the CK group. Overall, total flavonoid exposure resulted in a concentration-dependent increase in H_2O_2 accumulation in *M. aeruginosa*. These results indicate that total flavonoids induce the accumulation of reactive oxygen species (ROS), thereby triggering oxidative stress in *M. aeruginosa*. The elevated H_2O_2 levels suggest an imbalance between ROS production and scavenging capacity under flavonoid stress. The slight decrease in H_2O_2 content at the highest concentration (100 mg/L) may be associated with severe cellular damage or reduced metabolic activity, thereby limiting further ROS production. This pattern suggests that excessive flavonoid stress may lead to a decline in cellular activity rather than a continued increase in oxidative response.

3.4. Effect of total flavonoids from *Solidago canadensis* on antioxidant enzyme activities of *Microcystis aeruginosa*

Total flavonoids from *S. canadensis* significantly affected the antioxidant enzyme activities of *M. aeruginosa* (Figure 4). Compared with the CK group, SOD activity increased in all treatment groups (20–100 mg/L) and showed a concentration-dependent upward trend. The highest SOD activity was observed at 100 mg/L, which was significantly higher than that of the CK group ($p < 0.05$). The continuous increase in SOD activity indicates that *M. aeruginosa* activated its antioxidant defense system in response to flavonoid-induced oxidative stress. As a primary ROS-scavenging enzyme, SOD plays a key role in converting superoxide radicals into H_2O_2, thereby enhancing detoxification responses under stress conditions.

Peroxidase activity exhibited a similar response pattern but showed a peak at an intermediate concentration. POD activity increased with flavonoid concentration, reaching a maximum value at 60 mg/L, followed by a slight decline at 80 and 100 mg/L; however, it remained significantly higher than that in the control group ($p < 0.05$). This pattern suggests that POD activity is stimulated under moderate stress conditions but becomes inhibited or insufficient at higher flavonoid concentrations. The decline in POD activity at high concentrations may reflect enzyme inactivation or damage from excessive ROS accumulation, suggesting that the antioxidant defense system is overwhelmed under severe stress. The differential responses of SOD and POD further indicate an imbalance in the antioxidant system, where ROS generation exceeds the capacity of enzymatic scavenging. This also demonstrates the difference in sensitivity or tolerance to ROS between SOD and POD enzymes. These results suggest that while total flavonoids stimulated the antioxidant enzyme system to scavenge excessive ROS, the capacity of certain enzymes (like POD) might be partially compromised under high-concentration stress.

3.5. Effect of total flavonoids from *Solidago canadensis* on malondialdehyde and microcystin contents in *Microcystis aeruginosa*

Total flavonoids from *S. canadensis* significantly influenced the MDA and microcystin contents of *M. aeruginosa* (Figure 5). Compared with the CK group, MDA content in all treatment groups (20–100 mg/L) increased markedly at both 6 and 12 days, indicating enhanced lipid peroxidation under flavonoid exposure. At day 6, MDA content increased with increasing flavonoid concentration, reaching a maximum at 60 mg/L, followed by a decline at higher concentrations. A similar trend was observed at day 12, with the highest MDA level recorded at 60 mg/L, while the 100 mg/L treatment showed a lower value than the intermediate concentrations but remained higher than the control. The decrease in MDA content at the highest flavonoid concentration may reflect reduced cellular activity or extensive structural damage under severe stress; however, this interpretation remains tentative because cell viability was not directly measured in the present study. Overall, MDA accumulation in treated groups was significantly greater than in the control group ($p < 0.05$). These results indicate that total flavonoids induce severe oxidative damage to cellular membranes, as reflected by increased lipid peroxidation. The accumulation of MDA is consistent with enhanced ROS levels observed in previous sections, suggesting that oxidative stress plays a central role in flavonoid-induced toxicity.

In contrast, microcystin content decreased with

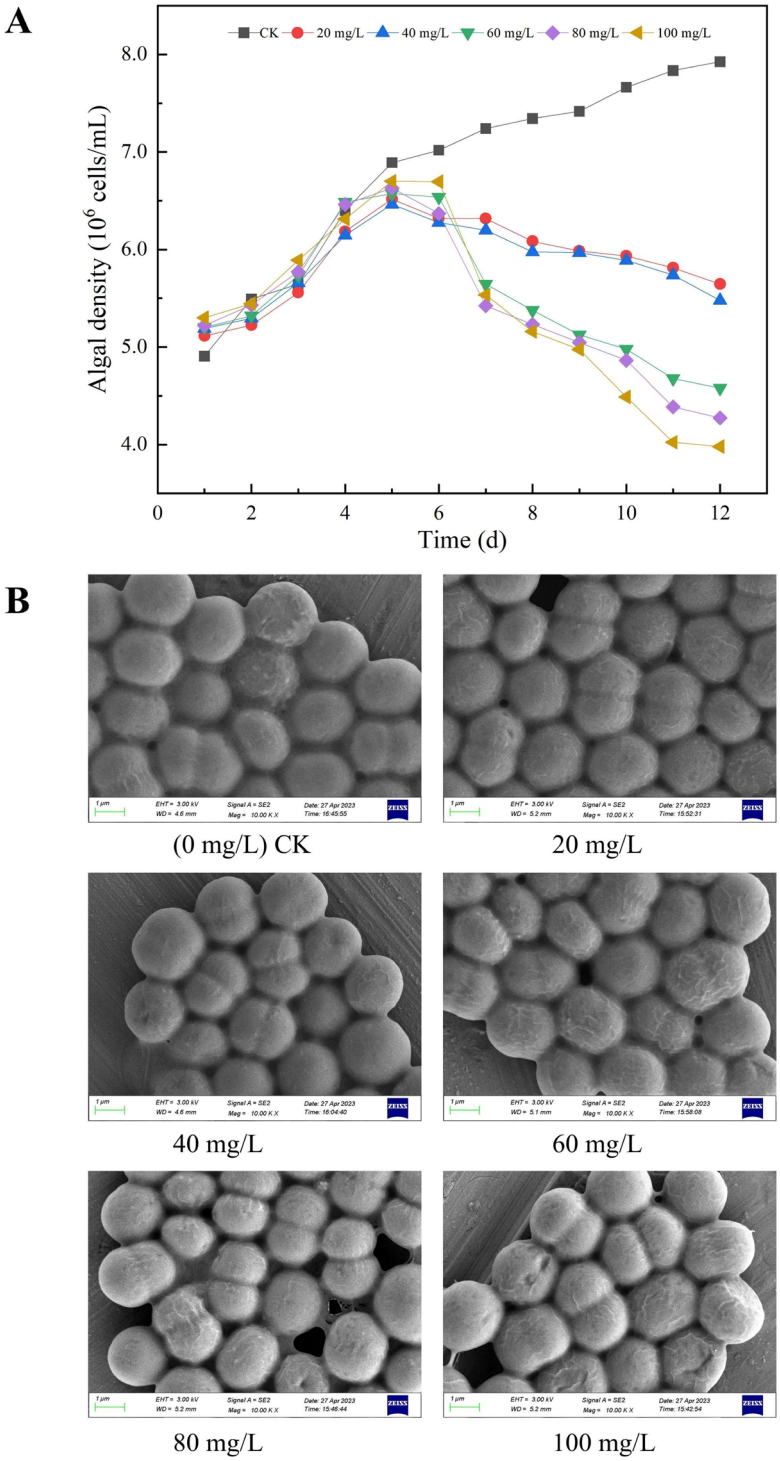

Figure 1. Effects of total flavonoids from *Solidago canadensis* on the growth and morphology of *Microcystis aeruginosa*. (A) Changes in algal cell density under different concentrations of total flavonoids (0, 20, 40, 60, 80, and 100 mg/L) during a 12-day exposure period. Data are presented as mean ± standard deviation (n = 3). (B) Scanning electron microscopy (SEM) images showing morphological changes of *M. aeruginosa* cells after 12 days of treatment. Scale bar: 1 μm; magnification: 10,000×. CK refers to the control group.

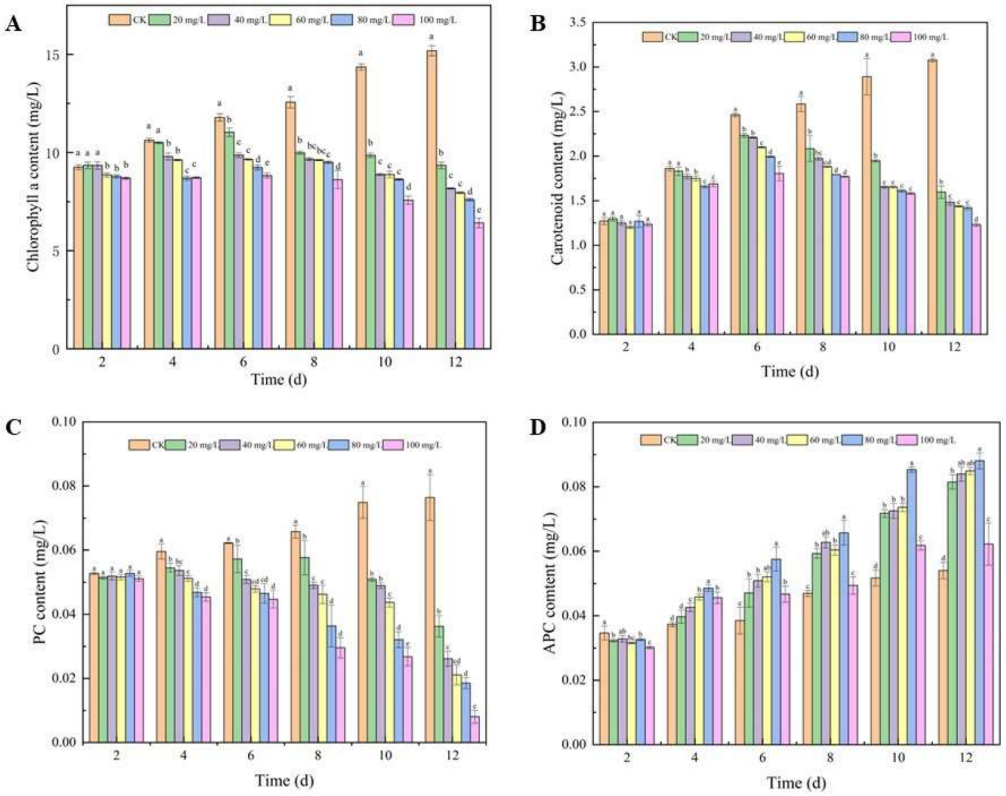

Figure 2. Effects of total flavonoids from *Solidago canadensis* on photosynthetic pigments of *Microcystis aeruginosa*. Changes in photosynthetic pigment contents of *M. aeruginosa* under different concentrations of total flavonoids from *S. canadensis* (0, 20, 40, 60, 80, and 100 mg/L) during the experimental period: (A) chlorophyll a, (B) carotenoids, (C) phycocyanin (PC), and (D) allophycocyanin (APC). Because the four pigments differed substantially in magnitude, they are presented as separate panels with independent Y-axis scales to allow clearer visualization of their respective changes. Data are presented as mean ± standard deviation (n = 3). Different lowercase letters indicate significant differences among treatments ($p < 0.05$). CK refers to the control group.

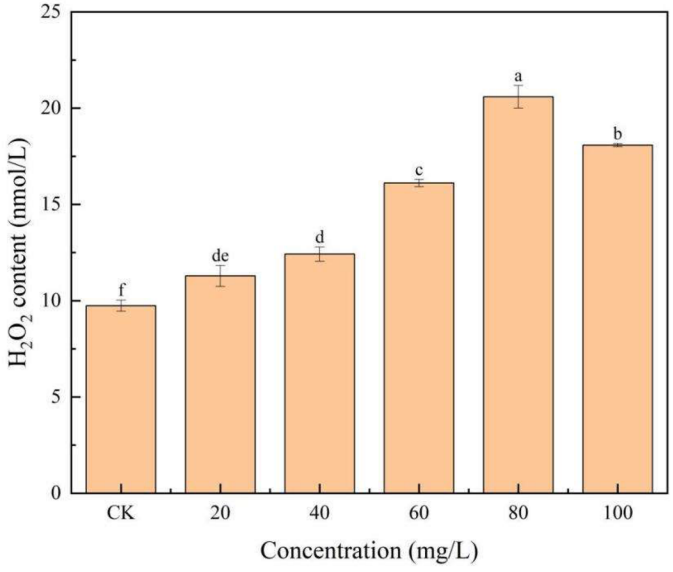

Figure 3. Effects of total flavonoids from *Solidago canadensis* on hydrogen peroxide (H_2O_2) content in *Microcystis aeruginosa*. Changes in H_2O_2 content of *M. aeruginosa* under different concentrations of total flavonoids from *S. canadensis* (0, 20, 40, 60, 80, and 100 mg/L). Data are presented as mean ± standard deviation (n = 3). Different lowercase letters indicate significant differences among treatments ($p < 0.05$). CK refers to the control group.

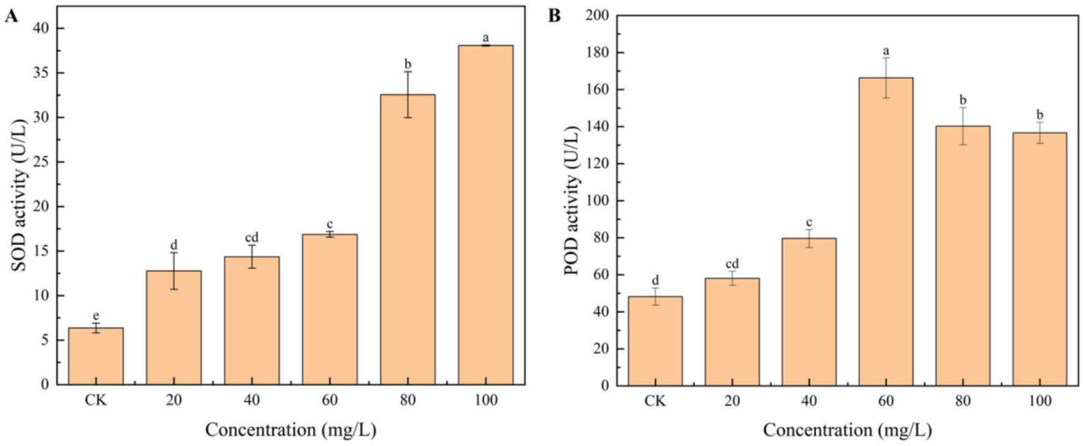

Figure 4. Effects of total flavonoids from *Solidago canadensis* on antioxidant enzyme activities of *Microcystis aeruginosa.* Changes in antioxidant enzyme activities of *M. aeruginosa* under different concentrations of total flavonoids from *S. canadensis* (0, 20, 40, 60, 80, and 100 mg/L): (A) superoxide dismutase (SOD) activity and (B) peroxidase (POD) activity. Data are presented as mean ± standard deviation (n = 3). Different lowercase letters indicate significant differences among treatments ($p < 0.05$). CK refers to the control group.

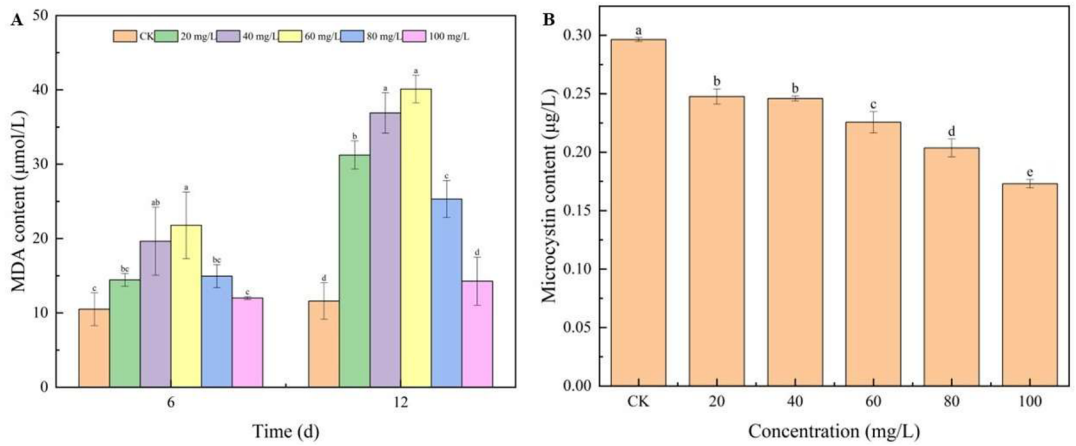

Figure 5. Effects of total flavonoids from *Solidago canadensis* on malondialdehyde (MDA) and microcystin contents of *Microcystis aeruginosa*. Changes in (A) MDA content at 6 and 12 days and (B) microcystin content of *M. aeruginosa* under different concentrations of total flavonoids from *S. canadensis* (0, 20, 40, 60, 80, and 100 mg/L). Data are presented as mean ± standard deviation (n = 3). Different lowercase letters indicate significant differences among treatments ($p < 0.05$). CK refers to the control group.

increasing flavonoid concentration. Compared with the control group, microcystin levels in all treatment groups were reduced to varying degrees, with the lowest content observed at 100 mg/L. Significant differences among treatments were detected ($p < 0.05$). The reduction in microcystin content may be attributed to the inhibition of algal growth and metabolic activity under flavonoid stress. In addition, severe cellular damage and disruption of physiological processes may limit toxin synthesis and accumulation. These results demonstrate that, while total flavonoids induced severe oxidative damage to the cellular membranes of *M. aeruginosa*, they effectively inhibited microcystin accumulation, suggesting a potential reduction in the environmental toxicity of cyanobacteria.

Overall, these findings suggest that total flavonoids not only inhibit algal growth by inducing oxidative damage but also reduce toxin production, highlighting their potential application as environmentally friendly agents for controlling harmful cyanobacterial blooms.

4. Discussion

Cyanobacterial blooms are characterized by rapid algal proliferation that leads to ecological imbalance and deterioration of water quality.[1-3] Flavonoid compounds have

been reported to exhibit inhibitory effects on *M. aeruginosa* growth.[39–41] In the present study, total flavonoids extracted from *S. canadensis* significantly inhibited the growth of *M. aeruginosa* in a concentration- and time-dependent manner, which is consistent with previous findings on the allelopathic effects of flavonoids.[36,42] However, compared with studies focusing on individual flavonoid compounds, our results provide a more integrated perspective by linking growth inhibition with coordinated changes in photosynthesis, oxidative stress, and toxin production. These findings suggest that the inhibitory effects of total flavonoids extend beyond growth suppression to include structural damage at the cellular level. Such morphological changes are likely associated with membrane disruption and loss of cellular integrity, which may represent an early step in flavonoid-induced toxicity.

Photosynthesis is essential for algal growth and biomass accumulation, and impairment of the photosynthetic system is a major pathway through which allelochemicals inhibit cyanobacteria.[43,44] Chlorophyll a, carotenoids, and phycobiliproteins are key components of the photosynthetic apparatus. The significant reductions in chlorophyll a, carotenoids, and PC observed in this study indicate that total flavonoids disrupted light-harvesting and energy-transfer processes. Previous studies have demonstrated that flavonoids can inhibit chlorophyll synthesis and damage photosystem function in *M. aeruginosa*.[39,45] The more pronounced decline in PC suggests that phycobiliproteins located on the outer surface of thylakoid membranes may be more sensitive to flavonoid-induced stress.[36,46,47] In contrast, the increase in APC content may represent a compensatory response aimed at maintaining photosynthetic efficiency under stress conditions.[48–50] Meanwhile, previous studies have suggested that changes in APC content may be associated with stress adaptation and the regulation of photosynthetic activity under adverse conditions.[37,49,50] Therefore, the increase in APC observed in the present study may represent a stress-related adjustment of the photosynthetic apparatus.

Oxidative stress is another important mechanism underlying algal inhibition by allelopathic substances. Environmental stress can lead to excessive accumulation of ROS, including H_2O_2, which disrupts cellular metabolism and damages biomolecules.[51,52] The elevated H_2O_2 levels observed in this study indicate that total flavonoids induced oxidative stress in *M. aeruginosa*. Antioxidant enzymes such as SOD and POD function as primary defense systems against ROS damage.[41,50,53-56] The continuous increase in SOD activity and the initial increase followed by a decline in POD activity suggest that antioxidant defenses were activated at moderate stress levels but became insufficient under higher flavonoid concentrations. Similar responses have been reported in cyanobacteria exposed to excessive oxidative stress, in which ROS production exceeds the capacity of enzymatic scavenging, leading to cellular damage.[57-60] It is worth noting that the disparity in alterations in SOD and POD enzyme activities under identical stress conditions implies differential sensitivity or tolerance of these two enzymes.

Malondialdehyde, an indicator of membrane lipid peroxidation, reflects the extent of oxidative injury in algal cells.[61] The significant increase in MDA content observed in flavonoid-treated groups indicates severe membrane damage caused by oxidative stress. Previous studies have reported similar increases in MDA levels in microalgae exposed to luteolin.[36] The decrease in MDA at higher concentrations may be related to reduced algal biomass due to extensive cell death rather than alleviation of stress,[53,62,63] which can be attributed to the reduction of algal cell density. Meanwhile, microcystin content decreased progressively with increasing flavonoid concentration, consistent with previous findings that other allelochemicals can suppress toxin synthesis or reduce toxin accumulation by inhibiting growth.[36,64,65] Although microcystins may function as protective molecules and strengthen toxin synthesis under stress conditions,[66–69] severe cellular damage likely limited toxin production in this study. Collectively, the reduction in extracellular microcystin content observed in this study may be associated with altered toxin synthesis, release, or degradation under flavonoid stress; however, the underlying mechanism could not be resolved in the absence of gene expression analysis of microcystin synthesis genes.

Overall, the present results suggest that total flavonoids from *S. canadensis* inhibit *M. aeruginosa* through a combined mechanism involving disruption of photosynthesis, induction of oxidative stress, imbalance of antioxidant defense systems, and membrane lipid peroxidation, ultimately leading to reduced algal growth and toxin production. The limitation of the present study is that the chemical composition of the total flavonoid extract was not characterized at the monomer level, and no positive control (e.g., copper(II) sulfate or a pure flavonoid such as quercetin) treatment was included. Future studies should identify major flavonoid constituents by high-performance liquid chromatography or liquid chromatography-mass spectrometry and assess the contributions of individual compounds and their potential synergistic effects, including positive controls to facilitate direct comparison of inhibitory efficiency and improve comparability of results.

5. Conclusion

Total flavonoids extracted from *S. canadensis* significantly inhibited the growth of *M. aeruginosa* and altered its physiological responses, particularly photosynthetic pigments, oxidative status, and microcystin content. These findings suggest that invasive plant-derived flavonoids may be effective, environmentally friendly agents for controlling cyanobacterial blooms. However, the active flavonoid constituents and the molecular basis of toxin regulation remain unresolved. Future studies should therefore combine compositional analysis with examination of the expression of microcystin biosynthesis genes to further clarify the underlying mechanisms.

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Conflict of interest

The authors declare that they have no competing interests.

Author contributions

Conceptualization: Ling Liu, Haitao Liu
Formal analysis: Haitao Liu
Investigation: Yule Zheng, Ling Liu, Haitao Liu
Methodology: Ling Liu, Haitao Liu, Yule Zheng
Writing–original draft: Haitao Liu
Writing–review & editing: Haitao Liu, Ling Liu, Lijuan Zhao, Conghui Li, Yu Kang

Availability of data

Data are available from the corresponding author upon reasonable request.

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