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The effects of leaf litter on the filamentous alga *Cladophora* sp., with an emphasis on photosynthetic physioresponses

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ABSTRACT

Filamentous algae accumulate along the shorelines of lakes, rivers, and coasts on a vast scale, causing severe ecological risk and economic damage. It is important to identify a cost-effective and environmentally acceptable method to control filamentous algal growth. Previous studies have shown that deciduous leaf extracts inhibit the growth of filamentous algae. Therefore, the efficacy of three types of leaf litter extracts (ginkgo [*Ginkgo biloba* L.], metasequoia [*Metasequoia glyptostroboides* Hu & W.C. Cheng], and willow [*Salix babylonica* L.] leaf) were evaluated in this study for controlling the growth of filamentous algae (green algae, *Cladophora* Kutz sp.), with an emphasis on photosynthetic physioresponses. These experiments were conducted in a laboratory setting, and the responses of filamentous algae were measured in terms of photosynthesis parameters and growth (fresh weight). The fresh weight of *Cladophora* sp. was significantly inhibited by ginkgo and willow leaf extracts, whereas optimum quantum yield (F_v/F_m), maximal relative electron transfer rate ($rETR_{max}$), and initial slope (α) of *Cladophora* sp. were significantly ($P < 0.05$) lower after ginkgo and willow leaf extract treatments than those in the control. In contrast, metasequoia leaf extract exhibited no inhibition effect but slightly stimulated the growth of *Cladophora* sp., whereas there were no significant ($P > 0.05$) differences in the F_v/F_m, $rETR_{max}$, and α of *Cladophora* sp. between the metasequoia leaf extract treatment and the control. In addition, ginkgo and willow leaf extracts were found to be nontoxic to nontarget organisms within 96 h, such as eelweed [*Vallisneria natans* (Lour) H. Hara] and zebrafish (*Brachydanio rerio* Hamilton). These results suggest that ginkgo and willow leaf extracts may be useful in controlling the growth of *Cladophora* sp. and that photosynthesis inhibition may be the underlying mechanism.

Key words: *Cladophora* sp., growth, inhibitory effect, leaf litter extracts, photosynthetic physioresponses.

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INTRODUCTION

Filamentous algae (such as green algae [*Cladophora* Kutz spp.], water silk [*Spirogyra* Link spp.], and green algae [*Oedogonium* Him spp.]) grow along the shorelines of lakes, rivers, and coasts. Because of their ubiquity and luxuriant growth, filamentous algae have been widely regarded as nuisance plants in recent years (Higgins et al. 2012, Cattaneo et al. 2013). The overabundance of filamentous algae leads to negative consequences in terms of the economy, ecology, and human health (Tsuda et al. 2005, Higgins et al. 2008, Higgins et al. 2012) because these algae may interfere with freshwater uses, including drinking, swimming, boating, fishing, aesthetic appeal, and agricultural irrigation, etc. (Barrett et al. 1996, Ferrier et al. 2005). However, the decomposition of filamentous algae results in widespread hypoxic conditions with a high release of toxic hydrogen to bottom habitats (Lavery and McComb 1991, Berglund et al. 2003, Berezina and Golubkov 2008), which also negatively affects other aquatic fauna, seagrass beds, and feeding among wading birds (Everett 1994, Hansen and Kristensen 1997, Raffaelli et al. 1998, Caffrey and Monahan 1999).

Currently, there are three categories of remedial efforts to eliminate or control filamentous algae blooms in water bodies: chemical, physical, and biological approaches. Chemical approaches can effectively and rapidly remove filamentous algae blooms, but they may also elicit adverse effects for nontarget organisms (Caffrey et al. 1996, Caffrey and Monahan 1999). Physical treatments (including cutting, raking, and harvesting, etc.) for filamentous algae removal are typically time consuming, costly, and ineffective compared with chemical approaches (Caffrey 1990, Ghobrial et al. 2007). Biological methods tend to be more effective at killing neighboring competitors because bioactive substances consist of natural compounds and crude plant extracts (Caffrey and Monahan 1999, Ridge et al. 1999, Islami and Filizadeh 2011). However, biological methods are time consuming. Conversely, Ferrier et al. (2005) reported that filamentous algae (*Spirogyra* sp.) exhibited significant increased growth in the presence of agriculture byproducts, such as barley (*Hordeum vulgare* L.) straw. Furthermore, deciduous leaf litter from a range of woody species can suppress the growth of *Chlorella*, *Microcystis*, and *Cladophora* spp. effectively in both the laboratory and field trials (Ridge et al. 1999). Moreover, ginkgo (*Ginkgo biloba* L.), metasequoia (*Metasequoia glyptostroboides* Hu & W.C. Cheng), and willow (*Salix babylonica* L.) are three common trees often found near

ponds or lakes. The phytotoxic substances (e.g., acid, ester, and phenol compounds) isolated from ginkgo (Katonoguchi and Takeshita 2013), metasequoia (Ridge et al. 1999), and willow leaf (Choe and Jung 2002, Tsuda et al. 2005) have been shown to inhibit the growth of ryegrass (*Lolium* L. spp.) weed species or cyanobacteria. However, to our knowledge, the effects of these three common leaf litter extracts on filamentous algae have not yet been elucidated.

Because agricultural byproducts (such as barley straw) and deciduous leaf litter have inhibitory effects on filamentous algae, the primary inhibitory substances are polyphenols and ester compounds (Ridge and Pillinger 1996, Ridge et al. 1999). However, few of their inhibitory mechanisms have been clarified. Some studies suggest that the interruption of the electron transfer chain of photosystem II (PS II) may be the inhibitory mechanisms of polyphenols on *Microcystis* species (Leu et al. 2002, Dziga et al. 2007). Therefore, the aim of this study was to verify the inhibitory effect of three leaf litter extracts on *Cladophora* sp. growth, elucidate the inhibitory mechanism through photosynthesis, and evaluate the environmental safety of using leaf litter extracts. Growth (fresh weight), optimum quantum yield (F_v/F_m), the initial slope (α), and the relative electron transport rate (rETR, in micromoles of electrons per square meter per second] of *Cladophora* sp. were measured during a 96-h experiment, and an ecological safety experiment was also conducted.

MATERIALS AND METHODS

Algae collection and culture

Filamentous algae *Cladophora* sp. were collected from a pond near Shanghai Ocean University in October 2016, then isolated under a stereomicroscope,[1] and cultured in a laboratory for 1 wk before the experiments. These algae were precultured in 1/4 BG11 medium (Allen and Stanier 1968) at 25 °C under 60 μmol photons m^{-2} s^{-1} with cool-white light (12 : 12 h light : dark cycle).

Preparation of leaf litter extracts

Tested leaves (ginkgo, metasequoia, and willow) were all collected in Shanghai, China, from November to December 2015, washed to remove surface deposits and organic materials, and powdered (approximately 100 mesh) after drying for 48 h at 80 °C. For preparing the extract, 10 g of each leaf litter powder was dissolved in 500 ml distilled water in a 1,000-ml beaker and then soaked in water for 5 h at 70 °C. Then, the supernatant was filtered through 0.22 μm membrane filters[2] and diluted with distilled water to 2,000 ml. The dose of each extract was 5.00 g dry weight equivalent extract L^{-1} (g DW eq. extract L^{-1}) and stored at 4 °C.

Experimental design

Three species of leaf litter extracts were diluted with the water from the eutrophic pond to obtain a final concentration of 3.00 g dry weight equivalent extract per liter (g DW eq. extract L^{-1}). When the solutions were completely stabilized at 25 °C, a biomass of 1.00 g fresh weight *Cladophora* sp. was added to the beakers as the inoculum. A total of 12 groups were established to reproduce four treatments with three replicates per treatment: (1) ginkgo leaf, (2) willow leaf, (3) metasequoia leaf, and (4) the control (free of leaf litter extracts). All cultures were incubated for 96 h at 25 C in an artificial illumination incubator[3] under the same condition as the preculture. Measurements (fresh weight, color, and photosynthetic characteristics of *Cladophora* sp.) were performed at the beginning (t_0) and end (t_{96}) of the experiment.

Determination of growth and photosynthetic parameters

The growth of *Cladophora* sp. during the experiment was determined by measuring the differences between the fresh weight at 0 h and that at 96 h.

The cultures of *Cladophora* sp. under three leaf extracts and the control that had grown at 25 °C for 96 h were sampled separately to measure F_v/F_m and rETR with a double-modulation fluorescence monitoring system.[4] The minimum fluorescence (F_0) was determined by illuminating the sample with low-intensity light (600 Hz, 665 nm, 0.3 mmol photons m^{-2} s^{-1}) after the samples were placed in the dark for 8 min. Subsequently, the maximal fluorescence (F_m) was determined at a saturating pulse of 5,000 μmol photons m^{-2} s^{-1} for 0.8 s; the variable florescence (F_v) was defined as $F_v = F_m - F_0$, and the quantum yield of the photochemical energy conversion in PSII (optimal quantum yield) was calculated as F_v/F_m. The rETR versus light curves were determined under 15 photosynthetically active radiation (PAR) levels (every measurement lasted for 20 s). The parameters of the rETR versus light curves were analyzed according to a method published previously (Eilers and Peeters 1988):

$$\mathrm{rETR} = \frac{I}{aI^2 + bI + c}, \quad [1]$$

where I is the irradiance (in μmol m^{-2} s^{-1}), and a, b, and c are the adjustment parameters. The initial slope (α), and the $\mathrm{rETR}_{\max}$ are expressed as functions of the parameters a, b, and c as follows:

$$\alpha = \frac{1}{c}, \quad [2]$$

and

$$\mathrm{rETR}_{\max} = \frac{1}{b + 2(ac)^{1/2}}. \quad [3]$$

Ecological safety experiment

Selected as the nontarget test organisms, eelweed [*Vallisneria natans* (Lour) H. Hara] and zebrafish (*Brachydanio rerio* Hamilton) were exposed to the leaf extracts with significant algal inhibition effect. Six *V. natans* (the average fresh weight of the plant was 4.90 ± 0.50 g) and 16 *B. rerio* (the average weight of the fish was 0.14 ± 0.02 g) individuals

were placed into each aquarium[5] (capacity = 25 L) with a final concentration of 3 g L^{-1} of extract, and all experiments were conducted with three replicates. Fish survival was observed at 24, 48, 72, and 96 h, and *V. natans* photosynthetic fluorescence efficiency (F_v/F_m) was measured at 96 h. Before measurement, the *V. natans* leaves were adapted to darkness for 8 min, and the values were recorded by the double-modulation fluorescence monitoring system;[4] F_v/F_m was calculated as described, where

$$\frac{F_v}{F_m} = \frac{F_m - F_0}{F_m}.$$

Statistical analysis

Data (mean ± SD) proved to be normally distributed according to the Shapiro-Wilk test, and equal variance was evaluated by the Levene's test. One-way analysis of variance and post hoc (Duncan) tests were used to determine the differences between three extracts and the control, and an independent-samples t test was used to determine the differences between pretreatment and posttreatment results among each extract. A $P < 0.05$ was considered statistically significant. All analyses were conducted with PASW Statistic statistical software.[6]

RESULTS AND DISCUSSION

Effects of litter extracts on growth of *Cladophora* sp.

The growth inhibition or stimulation of *Cladophora* sp. by three extracts (ginkgo, willow, and metasequoia leaf) and the control after 96 h are presented in Figure 1. The growth of *Cladophora* sp. was significantly suppressed by ginkgo and willow leaf extracts and was stimulated by metasequoia leaf extract, compared with the control ($P < 0.05$). In addition, the color of the *Cladophora* sp. in the control and metasequoia leaf extract groups remained green; the fresh weight of the *Cladophora* sp. was 1.32 g in the control and 1.90 g in the metasequoia leaf extract group at the end of experiment. However, the *Cladophora* sp. in the ginkgo and willow leaf extract groups changed from green to brown and became fragmented, with a fresh weight that decreased significantly ($P < 0.05$). Furthermore, the fresh weights of *Cladophora* sp., 0.56 g in ginkgo leaf extract and 0.59 g in willow leaf extract at 96 h, were also significantly less ($P < 0.05$) than that at the pretreatment (1.00 g).

Algal growth can be controlled by terrestrial leaf litter, which can substantially inhibit the growth of filamentous algae (*Cladophora* Kutz *glomerata*) in a pond, in which mixed deciduous leaf litter (mostly oak [*Quercus* L. spp.], beech [*Fagus* L. spp.], and sycamore [*Platanus* L. spp.]) had been added (Ridge et al. 1999). However, conventional treatment requires long-term decomposition of these terrestrial leaf litters to inhibit the growth of filamentous algae. In the present study, the leaves were first pulverized into powder and then soaked for 5 h in water at 70 °C; after which, the extract was collected. Thus, the ginkgo and willow extracts produced significant growth inhibition of *Cladophora* sp. in the 96-h experiment (Figure 1). This method of deciduous leaf-growth inhibition is faster and more efficient compared with those in previous studies. In the future, this method may be applied in field trials to verify its actual effect.

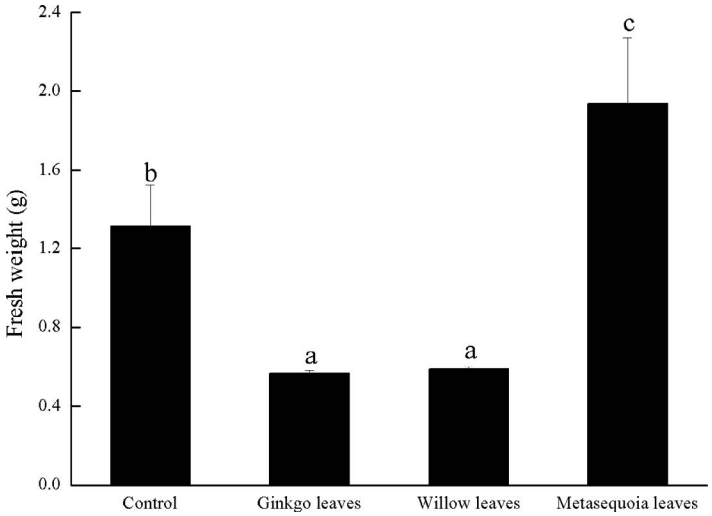

Figure 1. Change in the fresh weight of extract-treated *Cladophora* sp. after 96 h. The means ± SE are based on triplicates, and the different letters on the bars indicate the difference was significant at the $P = 0.05$ level.

Many studies suggest that allelochemicals, such as phenolic compounds, esters, and indole-like compounds, may be causing the inhibitory effects of plant extracts or exudates on algae. Phenolic compounds (such as tannins), which originate predominantly from lignin (barley straw or deciduous leaves) exhibit significant inhibition on the growth of filamentous algae, and oxidation may facilitate lignin solubilization and/or enhance toxicity of the solubilized material (Pillinger et al. 1994, Ridge et al. 1999, Ridge and Pillinger 1996). Choe and Jung (2002) showed that hexanedioic acid, dioctyl ester, 1,2-benzenedicaboxylic acid, and bis(2-ethylhexyl) ester were major antialgal chemicals. Laue et al. (2014) reported that polyphenols tannic acid, gallic acid, and indole alkaloid gramine were also antialgal chemicals. In addition, acetic acid and abscisic acid were screened for toxicity to clustered bellflower when concentrations were above 100 mg L^{-1} (Gibson et al. 1990). In the present study, the addition of ginkgo and willow leaf extracts produced significant inhibition of *Cladophora* sp. It is also possible that some phytotoxic substances might be produced from a high-temperature soaking treatment with deciduous leaves. Recently, Kato-noguchi and Takeshita (2013) reported that a phytotoxic substance (one of the phenolic compounds, 2-hydroxy-6-(10-hydroxypentadec-11-enyl)benzoic acid [HHPEBA]) was isolated in ginkgo litter, and HHPEBA may contribute to the inhibitory effect on the growth of neighboring plants, such as ryegrass weed species (*Lolium multiflorum* L.). In addition, 59 compounds were identified in willow leaf. The primary constituents were tritetracontane (15.2%), octadecenoic acid-1,2,3-propanetriyl ester (11.1%), hexadecanoic acid-methyl ester (10.5%), and 1,3-dioxane-4-(hexadecyloxy)-2-pentadecyl (10.3%) (Salem et al. 2011). Moreover, the presence of ester in the leaf may have a key role in the inhibitory effect on algal growth (Choe and Jung 2002).

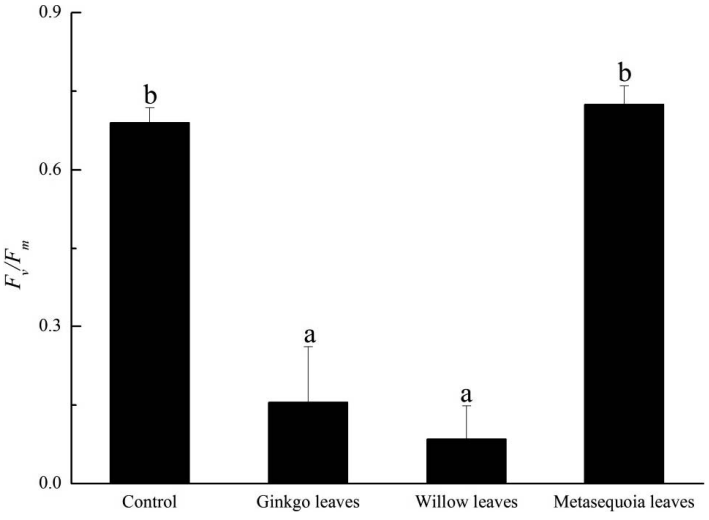

Figure 2. Change in the maximal photochemical efficiency (F_v/F_m) of extract-treated *Cladophora* sp. after 96 h. The means ± SE are based on triplicates, and the different letters indicate that the difference was significant at the $P = 0.05$ level.

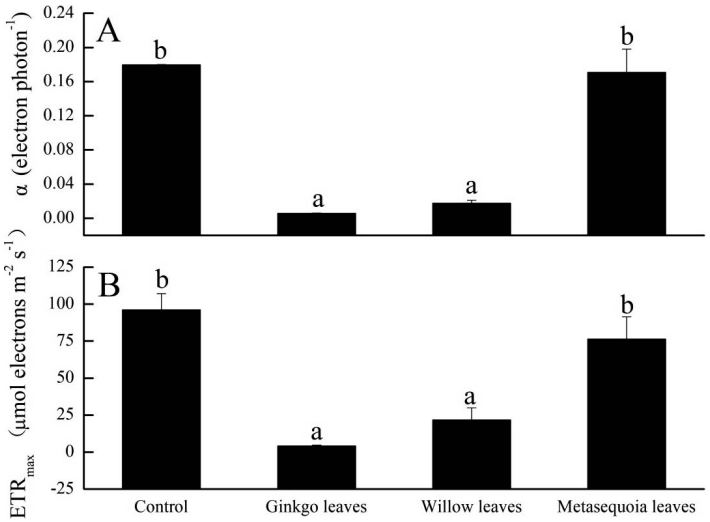

Figure 3. Changes in the initial slope (α) and maximal electron transport rate ($rETR_{max}$) of extract-treated *Cladophora* sp. after 96 h. The means ± SE are based on triplicates, and the different letters on the bars indicate the difference was significant at the $P = 0.05$ level.

Effect of litter extracts on photosynthetic parameters of *Cladophora* sp.

The F_v/F_m of *Cladophora* sp. in the ginkgo and willow leaf extract groups (0.155 and 0.085) were found to be significantly less than that in the control group and the metasequoia leaf extract group (0.690 and 0.725; $P < 0.05$; Figure 2). The α of *Cladophora* sp. in the control, ginkgo, willow, and metasequoia leaf extract groups were 0.180, 0.006, 0.018, and 0.171 electrons photon^{-1}, respectively, after 96 h (Figure 3A). The $rETR_{max}$ values of the corresponding groups were 95.95, 4.1, 21.55, and 76.35 μmol electrons m^{-2} s^{-1}, respectively (Figure 3B). Both the α and $rETR_{max}$ of *Cladophora* sp. in the ginkgo and willow leaf extract groups were significantly less than those in the control and metasequoia leaf extract groups. Compared with the control, the α of *Cladophora* sp. in the ginkgo, willow, and metasequoia leaf extract treatments decreased by 96.94, 90.25, and 5.00%, respectively. Similarly, the $rETR_{max}$ of *Cladophora* sp. in the corresponding groups decreased by 95.73, 74.40, and 20.43%, respectively.

Based on previous studies, alteration of algal photosynthesis is an important toxic mechanism of allelochemicals. In the present study, F_v/F_m, α, and $rETR_{max}$ results showed evident inhibition by ginkgo and willow leaf extracts. The decrease in these photosynthetic parameters indicated the inhibition of photosynthetic capacity because these parameters represent the capacity of a photosystem to convert light energy into chemical energy (Wang et al. 2016). An important allelochemical—polyphenols—which originate from straw, terrestrial leaf litter, or aquatic macrophytes, are suggested to inhibit photosynthesis primarily by blocking electron flow in a photosystem. For example, tellimagrandin II ($C_{41}H_{30}O_{26}$, a polyphenolic allelochemical produced by Eurasian watermilfoil [*Myriophyllum spicatum* L.]) and trachyloban-19-oic acid ($C_{20}H_{30}O_2$, isolated from escorcionera [*Iostephane heterophylla* (Cav.) Benth.]) were found to inhibit photosynthetic electron transport and one of the target sites in PS II between Q_A (the quinone secondary electron acceptor of PSII) and Q_B (a plastoquinone bound to PSII) (Leu et al. 2002, Hernández-Terrones et al. 2003). Similarly, sorgoleone, a *p*-benzoquinone ($C_6H_4O_2$) from sorghum [*Sorghum bicolor* (L.) *Moench* spp. *bicolor*], was also revealed to inhibit the electron transport between Q_A and Q_B (Gonzalez et al. 1997). Zhu et al. (2010) demonstrated that PSII, with a range from oxygen evolving complex to Q_B, is an important target site for the allelopathic inhibition of polyphenols (pyrogallic acid and gallic acid) on *Microcystis aeruginosa* (Kützing) Kützing.

In the present study, it is also possible that there were allelopathic substances, such as phenol compounds and/or ester compounds, in the ginkgo and willow leaf extracts. Therefore, the toxic mechanisms of these substances (especially for photosynthesis) to filamentous algae were speculated to inhibit the photosynthetic electron transport and also one of the target sites in PS II between Q_A and Q_B. In addition, the development of internal oxidative stress may lead to reduced photosynthetic activity to avoid the excess production of reactive oxygen and nitrogen species (Mittler 2002). Indeed, a reduction in photosynthetic oxygen release mediated by polyphenolic material (e.g., tannic acid and pyrogallol) has been observed in the cyanobacteria *M. aeruginosa* (Laue et al. 2014, Shao et al. 2009). Conversely, the growth of *Cladophora* sp. was significantly stimulated by metasequoia leaf extract, whereas there were interesting phenomena regarding changes in the photosynthetic parameters (F_v/F_m, $rETR_{max}$, and α) that exhibited identical results compared with the control (Figures 1–3). Although metasequoia extract contains a variety of known compounds (including 2-butaneone [C_4H_8O], cyclopentane [C_5H_{10}], β-myrcene [$C_{10}H_{16}$], cyclobutane [C_4H_8], furan [C_4H_4O], valeramide [$C_5H_{11}NO$], borneol [$C_{10}H_{18}O$], β-farnesene [$C_{15}H_{24}$], thymol [$C_{10}H_{14}O$], and α-pinene [$C_{10}H_{16}$]) in varying amounts (Lee et al. 2016), the metasequoia leaf

extract proved to be antibacterial/antifungal, and prokaryote were more sensitive to algicidal organic compounds than eukaryotes in most cases (Jančula et al. 2010, Bährs et al. 2013), which may explain why no inhibition effects were observed on filamentous algae. Additionally, the metasequoia leaf extract exhibited biological activity similar to that of ascorbic acid (Lee et al. 2016), which may be attributed to some promoting effects on filamentous algal growth. Therefore, the specific allelochemicals in deciduous leaf extracts that contribute to inhibitory mechanisms should be further isolated and identified in future research.

Ecological safety of litter extracts

The inhibition effect results for the eelweed and zebrafish nontarget test organisms exposed to the two leaf extracts (ginkgo and willow) and the control are presented in the present study. First, the appearances of eelweed did not change significantly in the two leaf extracts and the control. Second, the F_v/F_m results for the eelweed in the control, ginkgo, and willow leaf extracts were 0.729, 0.746, and 0.777, respectively, after 96 h (Figure 4). There were no significant differences in photosynthetic characteristics of the eelweed ($P > 0.05$; Figure 4). Additionally, the survival rate of the zebrafish was 100% in the two leaf extracts and the control.

Future studies are required to prove the effectiveness of common deciduous leaves (such as ginkgo and willow) against filamentous algae and their toxic effects to other aquatic organisms in an open aqua-ecosystem. In this regard, some people have found that some plant extracts can act as natural agent(s) to manage harmful cyanobacteria (*Microcystis* spp.) blooms in pond. Huang et al. (2014) observed that *Microcystis* spp. biomass decreased by more than 70% after 5 d and by more than 80% after 25 d after Canada goldenrod (*Solidago canadensis* L.) extract (0.01 and 0.05 g DW eq. extract L^{-1}) addition; each enclosure was approximately 1.00 m^2 in area and 1.20 m in depth, located in Shanghai, China. Zhang et al. (2016) also reported that a calamus (*Acorus calamus* L.) root extract–treated enclosure (0.02 to 0.10 g DW eq. extract L^{-1}, 1.44 m^2 in area, and 1.50 m in depth), decreased *Microcystis* biomass by 64.5 to 94.6% after 3 d, and the total algal biomass and chlorophyll *a* concentration decreased more than 90% for 7 d in a pond located in Jinzhou, Hubei Province, China. In addition, on a larger-scale field experiment, we also had a successful case. The Chinese herbal medicine Chinese goldthread (*Coptis chinensis* Franch.) extract has a remarkable removal effect on another floating plant giant duckweed [*Spirodela polyrhiza* (L.) Schleid.] that affects the landscape. In 2015, we conducted an on-site experiment on an artificial landscape water body (approximately 100 m^2 area with an average water depth of 0.5 m) in Gubei Community, Minhang District, Shanghai, China from July 3 to July 13. The results showed that the giant duckweed extract of 0.02 g DW eq. extract L^{-1} began to wither within 3 d after implementation and gradually died after 7-10 days (Shao et al., 2018). These antialgal-activity or herbicidal characteristics of these various extracts within ponds or other small water bodies are, therefore, encouraging from the applied perspective of using plant extracts as natural agent(s) to manage nuisance aquatic plant, such as harmful cyanobacteria blooms, duckweed mats, or filamentous algae.

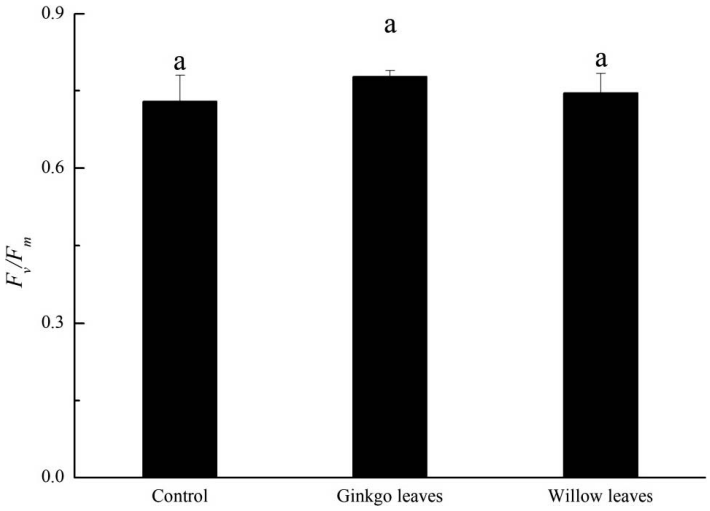

Figure 4. Changes in the maximal photochemical efficiency (F_v/F_m) of extract-treated eelweed after 96 h. The means ± SE are based on triplicates, and the different letters on the bars indicate the difference was significant at the $P = 0.05$ level.

CONCLUSION

Our study demonstrated that *Cladophora* sp. was effectively inhibited by ginkgo and willow leaf extracts at 3.0 g L^{-1}, and these two leaf extracts were safe for aquatic organisms, indicating that the two leaf types are a potential source of natural products to control filamentous algal blooms. The primary photosynthetic parameters were significantly less in the ginkgo and willow leaf extracts groups than were those in the control group. The results of the present study and previous studies concerning the inhibitory mechanism of allelochemicals (ester and phenol compounds) prove that the photosynthetic system (especially in PS II) is one of the targets of toxicity. In addition, multiple target sites (inhibition of PS II and enzymes) are a common characteristic of many allelochemicals that originate from terrestrial or aquatic plants (Leu et al. 2002, Shao et al. 2010), and some enzymatic activities, such as esterase activity, are found to be more sensitive and respond more rapidly than photosynthetic variables and cell growth (Wang et al. 2016). Therefore, the responses of enzymatic activities of algae should be investigated to further clarify the inhibitory mechanism. Finally, future studies are needed to prove the effectiveness of common deciduous leaves (such as ginkgo and willow) against filamentous algae in an open aqua-ecosystem.

SOURCES OF MATERIALS

[1]SMZ-168 Motic stereomicroscope, Motic Industrial Group Co., Ltd., Motic building, torch high tech. Industrial Development Zone, Xiamen, Fujian Province 361006, China.

[2]Membrane filters, Millipore, Sigma, 400 Summit Drive, Billerica, MA 01803.

[3]LRH-150-G ZHUJIANG artificial illumination incubator, Guangdong THK Scientific Instrument Co., Ltd., Shaoguan City Industrial Park Avenue Mu Xi, Guangdong province 512029, China.

[4]DUAL-PAM-100 double-modulation fluorescence monitoring system, Walz Heinz GmbH, Eichenring 6, Effeltrich 91090, Germany.

[5]SUNSUN aquarium, Sensen Group Co., Ltd., No. 61-79, Baima street, ma'ao Town, Dinghai District, Zhoushan City, Zhejiang Province 316015, China.

[6]PASW statistics software, version 22.0, IBM SPSS Statistics, 1 New Orchard Road, Armonk, NY 10504-1722.

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