

Inhibition of Submerged Macrophytes on Phytoplankton

I. Field Evidence for Submerged Macrophyte Inhibition on Phytoplankton Biomass

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It is known that phytoplankton biomass or turbidity are lower in waters with submerged macrophytes than those without submerged plants at a given nutrient level. We hypothesize that presence of submerged macrophytes would lower phytoplankton biomass below levels expected by total phosphorus levels through various mechanisms and that phytoplankton biomass would decrease more as the biomass increase of the submerged macrophytes. To find submerged macrophytes effectively lowering phytoplankton growth, we conducted spatial field surveys at 21 water bodies and a temporal monitoring at Seung-un 1 Reservoir, Anmyeondo Island. We measured chlorophyll *a* concentrations and total phosphorus (*TP*) concentrations from waters in patches of submerged macrophytes with measurements of submerged plant biomass. Majority of our sites with submerged macrophytes showed much less chlorophyll *a* concentrations than the predicted ones from literature. Among submerged macrophytes studied, *Myriophyllum spicatum* and *Hydrilla verticillata* showed patterns of lowering chlorophyll *a*/*TP* ratios with increase of their biomass in both spatial and temporal surveys.

Key words : submerged macrophytes, phytoplankton, chlorophyll *a*, total phosphorus

INTRODUCTION

Recently, many Korean freshwater ecosystems have become eutrophic due to rapid industrialization and economic development causing serious ecological and economical problems. Considerable research interests are focusing on regulating phytoplankton water-blooms, especially cyanobacterial water-blooms using physical, chemical and biological approaches. A recent addition on regulating cyanobacterial water-blooms is using aquatic vascular plants, especially submerged plants (Van Donk and de Bunk, 2002). However, lake management studies using aquatic macrophytes are mainly concentrating on nutrient absorption of plants to compete with phy-

toplankton (Romero *et al.*, 1999; Coveney *et al.*, 2002; Dierberg *et al.*, 2002). A recent study reviewed on interactions among macrophytes, phytoplankton, and periphyton, and summarized mechanisms of macrophyte inhibition on phytoplankton as light, temperature, nutrient competition, and allelopathy (Van Donk and de Bunk, 2002). *Myriophyllum* (Planas *et al.*, 1981; Gross and Sütfield, 1994; Gross, 1999; Nakai *et al.*, 2000; Nakai *et al.*, 2005) and *Chara* (Crawford, 1979; Jasser, 1995) are the two most studied submerged macrophytes in regarding to allelopathic inhibition on phytoplankton. In particular, *M. spicatum* has been reported to produce several polyphenol compounds and fatty acids to reduce *Microcystis aeruginosa* growth (Nakai *et al.*, 2000; Nakai *et al.*, 2005). However, we are

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still missing strong evidence for allelopathy of submerged macrophytes (Van Donk and de Bunk, 2002; Gross *et al.*, 2007).

In recent years, many studies on submerged macrophytes have reported that phytoplankton biomass or turbidity are lower in waters with submerged macrophytes than those without submerged plants at a given nutrient level (Scheffer *et al.*, 1993; Rooney and Kalff, 2003; Takamura *et al.*, 2003). Especially, Rooney and Kalff (2003) reported chlorophyll *a*: total dissolved phosphorus (TDP) ratios decreased with increasing cover of submerged macrophytes. Also, it has been shown that chlorophyll *a* levels were lower with submerged macrophytes than without macrophytes at a given limiting nutrient level (Takamura *et al.*, 2003).

For the first step to search for allelopathic submerged macrophytes, we hypothesize that presence of submerged macrophytes would lower phytoplankton biomass below levels expected by total phosphorus levels through various mechanisms such as light, temperature, carbon limitation, and periphytic growth. Phytoplankton biomass would decrease more with the biomass increase of the submerged plants.

We attempted to screen submerged macrophyte candidates lowering phytoplankton biomass regardless of the suppression mechanisms. In this study, we surveyed 21 water bodies with submerged macrophytes in summer and a reservoir from spring to fall to detect any lowering effects on phytoplankton biomass by submerged macrophytes using chlorophyll *a*/TP ratios.

MATERIALS AND METHODS

1. Study sites and sample collection

Forty three water bodies in South Korea were selected from Gyeonggi-do, Chungcheongnam-do, and Chungcheongbuk-do and surveyed between August 8 and August 15 in 2006 (Table 1, Fig. 1). Among the surveyed sites, 21 water bodies had submerged macrophytes. In addition, Seung-un 1 Reservoir in Anmyeondo Island was monitored every other week between June and September, 2006. Seung-un 1 Reservoir have most of common submerged species including *M. spicatum*, *H. verticillata*, *Ceratophyllum demersum* and *Potamogeton macckianus* in it.

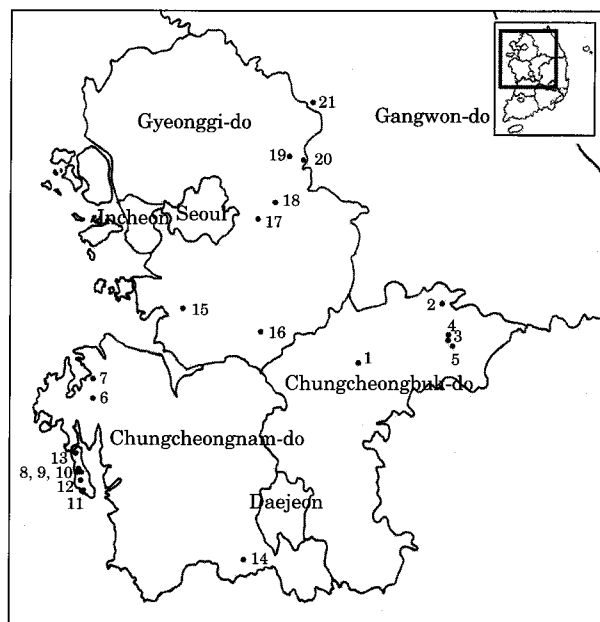


Fig. 1. Distribution of 21 water bodies with aquatic submerged macrophytes surveyed in August, 2006. Seungun 1 Reservoir (#8) was monitored monthly from June to September, 2006.

Physical and chemical parameters such as water temperature, dissolved oxygen (DO), electric conductivity (EC) were measured using multi-parameter equipment (YSI 600XL, YSI 650MDS) in 19 water bodies except for Yogolje and Gakgi Reservoir.

Water samples were collected from the patches of submerged macrophytes and from open waters, using a Van Dorn water sampler (Wildco, USA), transferred directly to 4 L polyethylene bottles, and kept at 4°C with ice during transport to the laboratory. During field surveys, we had sunny days except for 2 sites. Water samples for the measurement of total phosphorus concentration were transferred to 100 mL high density polyethylene bottle and stored at -20°C until analysis. Submerged plants, such as *H. verticillata*, *C. demersum*, *P. macckianus*, *M. spicatum*, and *Chara* species, were sampled using a quadrat (0.4 × 0.4 m) with replications (n=3). Collected plants were dried at room temperature in shade for one week. Dried plant samples in replications were mixed into one composite sample followed by weighing.

Total phosphorus was analyzed by persulfate digestion method (Strickland *et al.*, 1972) using

Table 1. List of study sites where submerged macrophytes occurred, province, species, their biomass, total phosphorus and chlorophyll *a* concentration in their patch.

No	Site	Province	Species	Biomass (g m ⁻²)	TP (µg L ⁻¹)	Chl. <i>a</i> (µg L ⁻¹)
1	Yogolje	Chungcheongbuk-do	<i>Chara</i> sp.	13.1	239.7	24.7
2	Uirim Reservoir	Chungcheongbuk-do	<i>Myriophyllum spicatum</i> <i>Potamogeton distinctus</i>	22.5 18.8	42.1	2.0
3	Gakgi Reservoir	Chungcheongbuk-do	<i>Potamogeton crispus</i>	24.0	37.7	5.7
4	Dogok Reservoir	Chungcheongbuk-do	<i>Potamogeton berchtoldii</i>	25.8	33.3	4.2
5	Eoui Pond	Chungcheongbuk-do	<i>Chara</i> sp. <i>Potamogeton malaianus</i> var. <i>latifolius</i>	11.3 44.0	46.6 33.3	6.4 1.4
6	Pungjun Reservoir	Chungcheongnam-do	<i>Ceratophyllum demersum</i>	15.0	77.7	14.0
7	Jigok Reservoir	Chungcheongnam-do	<i>Hydrilla verticillata</i> <i>Ceratophyllum demersum</i> <i>Potamogeton maackianus</i>	27.1 16.9 26.0	77.7 66.6 95.4	16.4 12.0 54.3
8	Seung-un 1 Reservoir	Chungcheongnam-do	<i>Potamogeton maackianus</i> <i>Hydrilla verticillata</i> <i>Ceratophyllum demersum</i> <i>Myriophyllum spicatum</i>	115.8 71.0 31.0 69.6	39.9 44.4 124.3 71.0	8.1 4.9 29.7 17.1
9	Seung-un 2 Reservoir	Chungcheongnam-do	<i>Hydrilla verticillata</i>	33.3	48.8	5.2
10	Seung-un 3 Reservoir	Chungcheongnam-do	<i>Potamogeton maackianus</i>	27.1	51.0	10.8
11	Jipo Reservoir	Chungcheongnam-do	<i>Hydrilla verticillata</i>	73.8	35.5	2.1
12	Chunsandong Reservoir	Chungcheongnam-do	<i>Myriophyllum spicatum</i>	47.7	48.8	8.9
13	Changgi Reservoir	Chungcheongnam-do	<i>Hydrilla verticillata</i> <i>Myriophyllum spicatum</i> _q	45.8 105.8	51.0 51.0	17.1 8.8
14	Nonsan Reservoir	Chungcheongnam-do	<i>Hydrilla verticillata</i>	159.2	55.5	4.2
15	Daesung Reservoir	Gyeonggi-do	<i>Myriophyllum spicatum</i>	11.7	66.6	31.7
16	Gosam Reservoir	Gyeonggi-do	<i>Chara</i> sp. <i>Ottelia alismoides</i>	23.8 25.6	46.6 48.8	2.5 1.1
17	A pond for rice fields, Neungnae-ri	Gyeonggi-do	<i>Myriophyllum spicatum</i>	22.3	71.0	15.7
18	Back marsh, Sujong-myeon	Gyeonggi-do	<i>Hydrilla verticillata</i>	36.5	37.7	3.7
19	Sangchun Reservoir	Gyeonggi-do	<i>Hydrilla verticillata</i>	42.5	42.1	2.1
20	Marshy land, Geumdae-ri	Gyeonggi-do	<i>Myriophyllum spicatum</i>	29.8	108.7	59.1
21	Sewol Reservoir	Gangwon-do	<i>Hydrilla verticillata</i> <i>Limnophila sessiliflora</i>	10.0 3.8	39.9 39.9	3.1 5.6

spectrophotometer equipment (Beckman, DU-65). For chlorophyll *a* concentration, we filtered 100 mL of sample water through 47 mm GF/C glass microfibre filters (Whatman International Ltd, England) to concentrate phytoplankton. After filtration, the filters were transferred and stored in film canisters pre-washed with 90% acetone at -20°C refrigerator until extraction. Chlorophyll *a* was measured using a fluorometer (Turner

Designs, Trilogy™) according to EPA Method 445.0, without acidification step. Calibration was performed with fluorometric chlorophyll standards (Turner designs, 2006).

2. Chlorophyll *a*/TP ratio

According to the study of Vollenweider and Kerekes (1982), chlorophyll *a* concentrations (µg

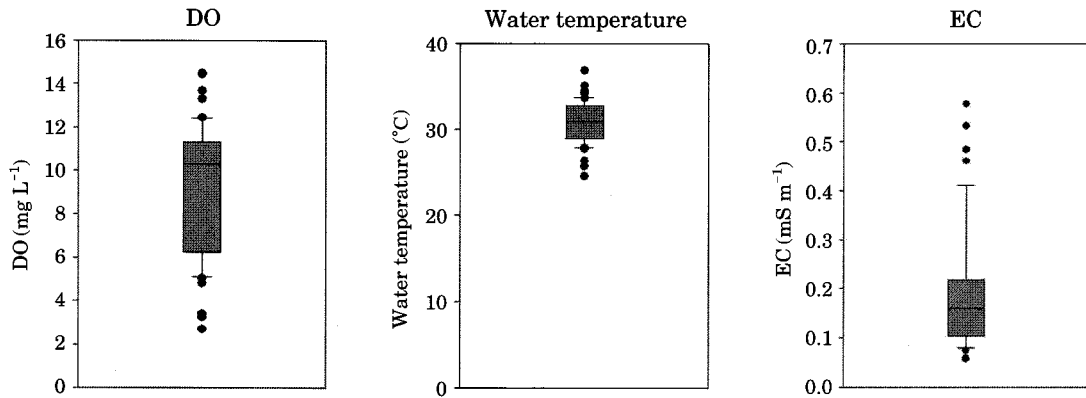


Fig. 2. Dissolved oxygen (DO), water temperature, and electric conductivity (EC) in 21 water bodies in August 2006.

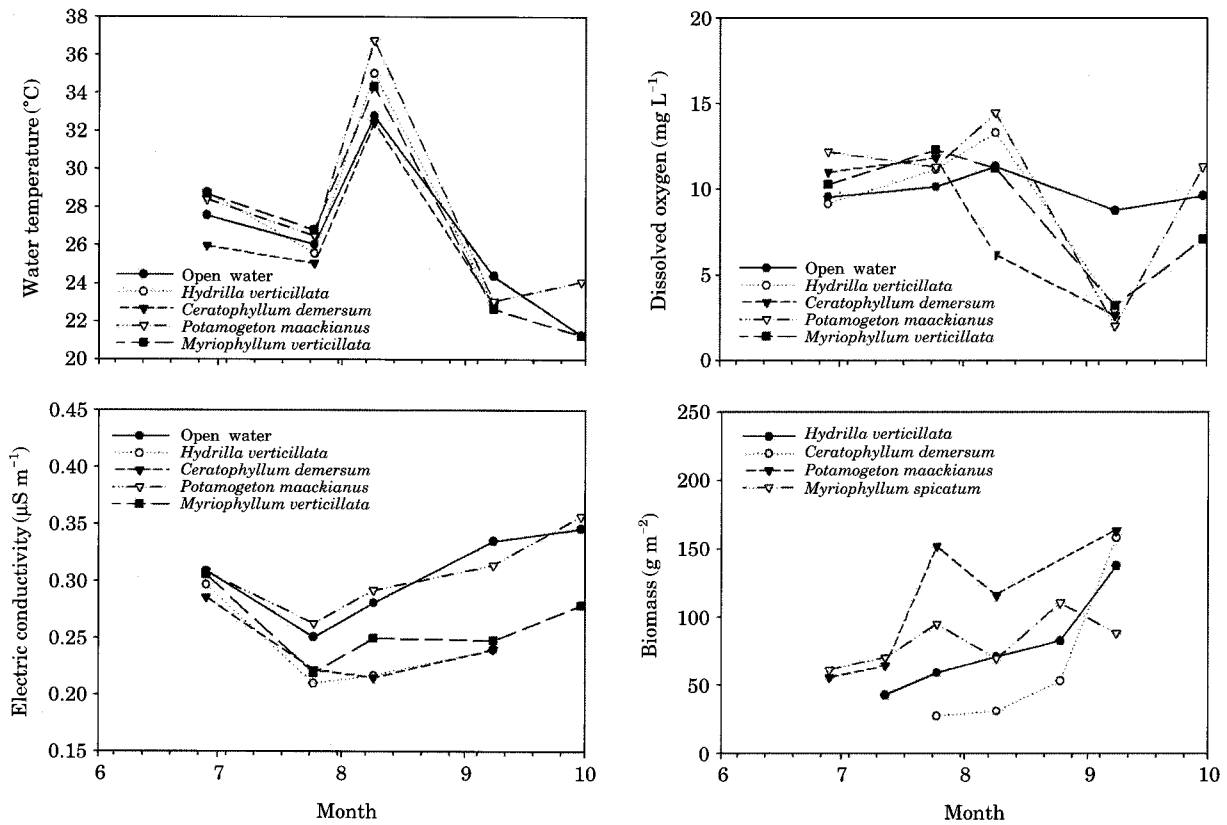


Fig. 3. Monthly change of water temperature, dissolved oxygen, electric conductivity, and biomass in Seung-un 1 Reservoir from June to September, 2006. Because we could not find two submerged plants, *Hydrilla verticillata* and *Ceratophyllum demersum* on June 28 and did not collect *Potamogeton maackianus* on August 25, these data are missing from the graph.

L^{-1}) are determined by total phosphorus concentration (TP),

$$\text{Chlorophyll } a = 0.28 TP^{0.96} \quad (1)$$

This equation can be represented as follows :

$$\text{Chlorophyll } a/TP^{0.96} = 0.28 \quad (2)$$

Chlorophyll a/TP ratio would exhibit approximately same value as $\text{Chlorophyll } a/TP^{0.96}$ and is easy to understand. We used chlorophyll a/TP

ratio to compare lowering capacity of submerged macrophytes on phytoplankton biomass. If a submerged plant lower phytoplankton growth, we expect that the chlorophyll *a*/TP ratio would decrease as the submerged plant biomass increases.

RESULTS

We summarized physical and chemical factors such as water temperature, dissolved oxygen (DO), and electric conductivity (EC) of 19 water bodies (Fig. 2). Dissolved oxygen averaged 10.2 mg L^{-1} while the mean water temperature was 30.7°C during the study. Electric conductivity ranged from $0.059 \text{ }\mu\text{S m}^{-1}$ in Sewol Reservoir to $0.577 \text{ }\mu\text{S m}^{-1}$ in Seung-un 2 Reservoir and averaged $0.192 \text{ }\mu\text{S m}^{-1}$.

Biomass of each submerged macrophyte, total phosphorus concentration and chlorophyll *a* concentration in water sampled from patches of submerged macrophytes were summarized in Table 1. Surveyed water bodies in this study showed generally low chlorophyll *a* concentration levels with a range of $1.1 \sim 59.1 \text{ }\mu\text{g L}^{-1}$ (average: $12.7 \text{ }\mu\text{g L}^{-1}$). Total phosphorus levels were in a range of $33.3 \sim 239.7 \text{ }\mu\text{g L}^{-1}$.

Seung-un 1 Reservoir showed seasonal changes in physical and chemical factors and in submerged macrophyte biomass from June to September, 2006 (Fig. 3). Usually water temperature was slightly higher in patches of submerged plants. Dissolved oxygen concentrations in patches of submerged plants were lower than that of open water on September 8, 2006 implying that decomposition of macrophytes occurred at the time. Open water and patches of *P. maackianus* showed higher EC than those of *Hydrilla* and *Myriophyllum* patches. *Potamogeton maackianus* and *M. spicatum* grew up earlier in the season while *C. demersum* and *H. verticillata* grew up later in the season.

Majority of our sites with submerged macrophytes in the present study showed much less chlorophyll *a* concentrations than the predicted lines from other studies (Kim and Hwang, 2004; Lee *et al.*, 2007) (Fig. 4). Five samples from 2 reservoirs (Wonchun Reservoir and Sindae Reservoir in Suwon, Korea) collected in August, 2006 showed much higher chlorophyll *a* concentration than the predicted lines. Wonchun Reservoir showed average TP concentration of $122 \text{ }\mu\text{g P L}^{-1}$

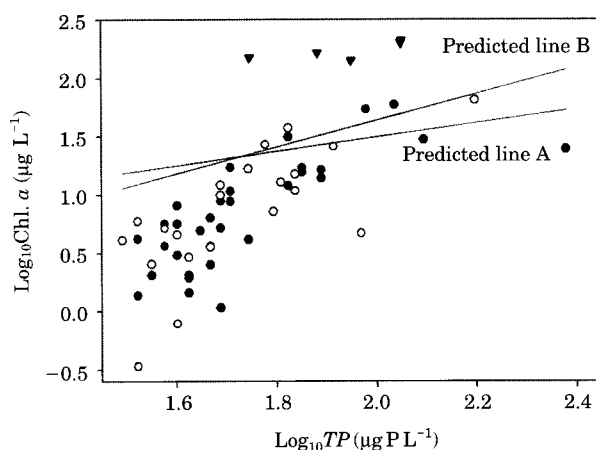


Fig. 4. Relationship between total phosphorus (TP) and chlorophyll *a* (Chl. *a*) of studied waters in the patches of submerged macrophytes (●), open areas without submerged macrophytes (○). For comparison, we showed relationship between TP and Chl. *a* from 5 samples of two eutrophic reservoirs without submerged macrophytes (Wonchun Reservoir and Sindae Reservoir) (▼) collected in August, 2006. Equation for predicted line A: $y=0.61 \times x + 0.27$, predicted line B: $y=1.14 \times x - 0.64$.

between March and August and average Secchie depth of 0.63 m between June and July in 2006. Sindae Reservoir showed average TP concentration of $290 \text{ }\mu\text{g P L}^{-1}$ between March and November and average Secchie depth of 0.59 m between June and November in 2006. Total phosphorus concentrations and chlorophyll *a* concentrations in waters from the patches of submerged macrophytes in the studied sites showed significant linear relationship on log-log scale ($y=1.87 \times x - 2.40$, $n=31$, $r^2=0.568$, $p < 0.0001$). Total phosphorus concentrations and chlorophyll *a* concentrations in open waters of the studied sites showed similar significant linear relationship on log-log scale ($y=2.21 \times x - 2.96$, $n=22$, $r^2=0.507$, $p=0.0002$).

In the spatial surveys, most submerged plants except for *C. demersum*, showed a tendency to decrease in chlorophyll *a*/TP ratios as plant biomass increase (Fig. 5).

There are six submerged macrophytes collected from only one site (Table 2). Water from the patches of 5 submerged plants in this category showed values of chlorophyll *a*/TP much lower than those predicted from literature (Vollenweider, and Kerekes, 1982; Kim and Hwang, 2004; Lee *et*

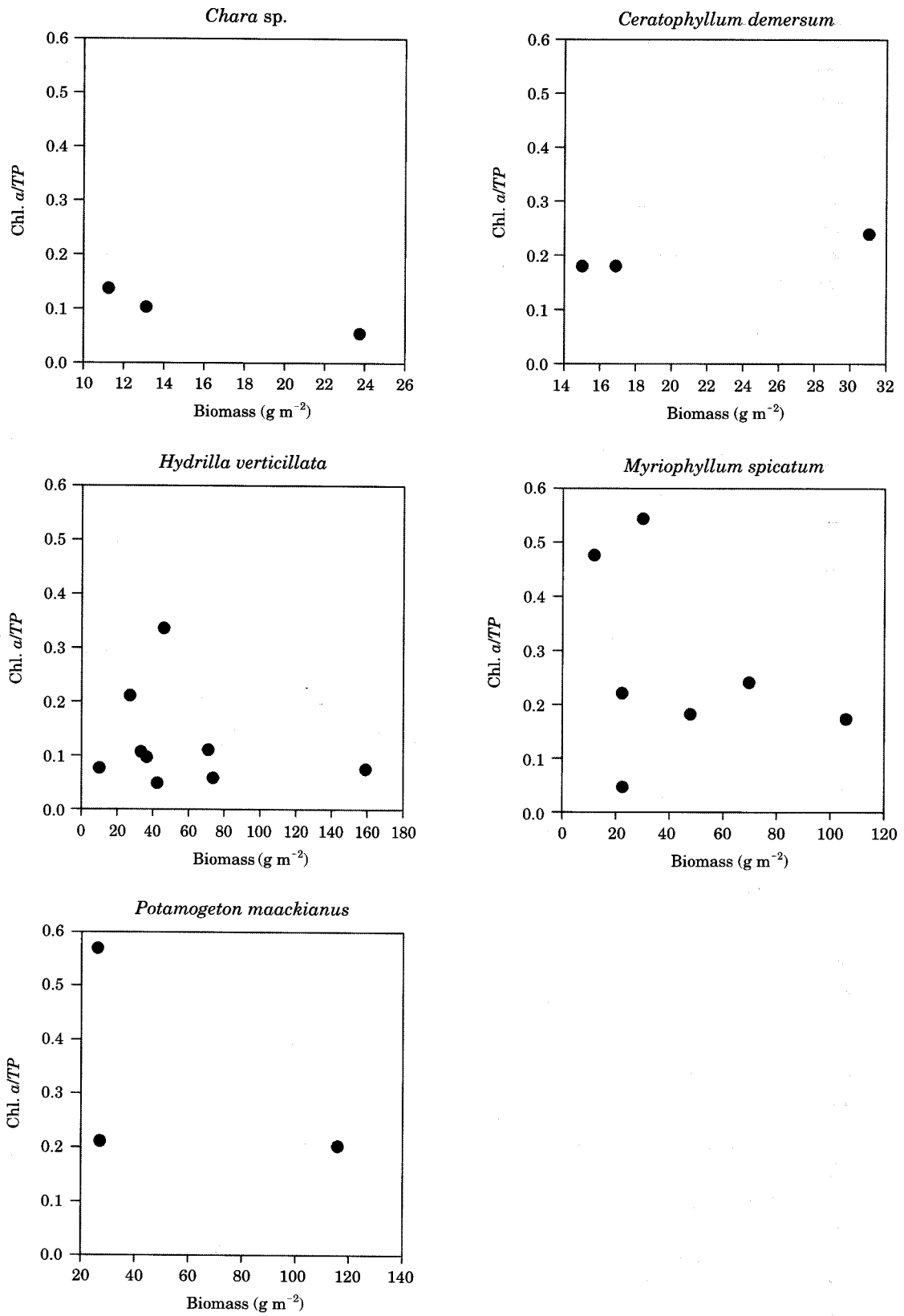


Fig. 5. Relationship between chlorophyll *a* (Chl. *a*) and total phosphorus (TP) based index (Chl. *a*/TP) ratio and biomass of 5 submerged plants in different water bodies in August.

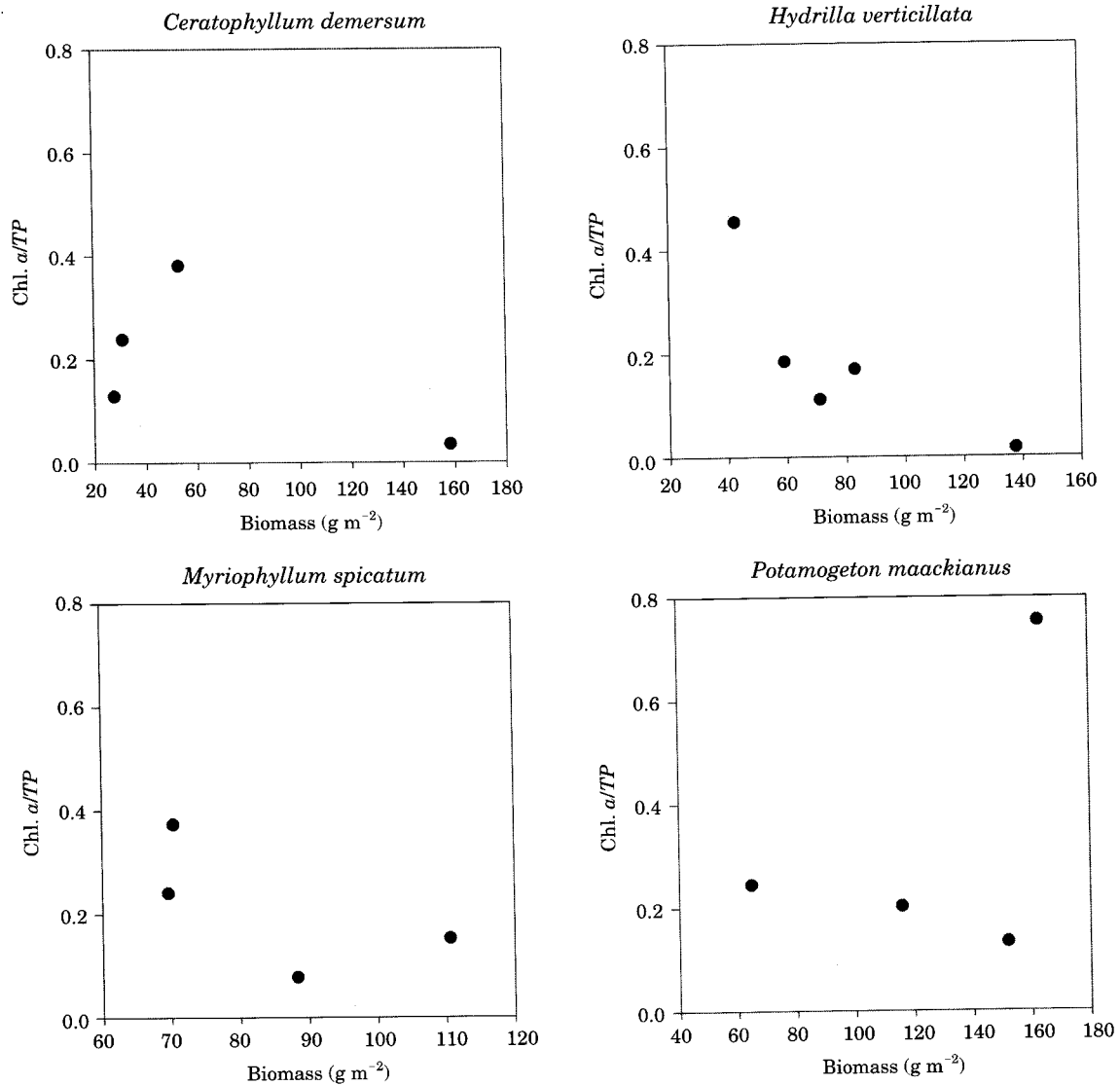


Fig. 6. Relationship between chlorophyll *a* (Chl. *a*) and total phosphorus (TP) based index (Chl. *a*/TP) ratio and biomass of 5 submerged plants in Seung-un 1 Reservoir from June to September, 2006.

al., 2007).

Similar lowering pattern was found in Seung-un 1 Reservoir (Fig. 6). In Seung-un 1 Reservoir, water from patches of submerged plants except for *P. maackianus* showed decreasing chlorophyll *a*/TP ratios as plant biomass increased.

DISCUSSION

Surveyed water bodies in this study appeared to have lower chlorophyll *a* concentration levels compared to the levels predicted from eutrophicated agricultural reservoirs (Kim and Hwang,

2004; Lee *et al.*, 2007) (Fig. 4). Lower chlorophyll *a* levels in our study support the notion that water bodies with submerged plants usually have lower chlorophyll *a* levels or turbidity than those without submerged plants (Scheffer *et al.*, 1993; Rooney and Kalff, 2003; Takamura *et al.*, 2003).

Our results show that two species may have potential to suppress phytoplankton biomass among studied submerged macrophytes. In both spatial and temporal surveys, *M. spicatum* and *H. verticillata* showed tendency of decreasing chlorophyll *a*/TP ratios with increases of their biomass while *P. maackianus* and *C. demersum* showed somewhat ambiguous patterns (Figs. 4,

Table 2. List of submerged macrophytes collected in only one site, their biomass, total phosphorus concentration, chlorophyll *a* (Chl. *a*) concentration, and Chl. *a*/TP ratio. From the patch of *Potamogeton distinctus* in Uirim Reservoir, we did not measure total phosphorus concentration and chlorophyll *a* concentration

Site	Species	Biomass (g m ⁻²)	TP (µg P L ⁻¹)	Chl. <i>a</i> (µg L ⁻¹)	Chl. <i>a</i> /TP
Uirim Reservoir	<i>Potamogeton distinctus</i>	18.8			
Gakgi Reservoir	<i>Potamogeton crispus</i>	24.0	37.70	5.65	0.15
Eouipond	<i>Potamogeton malaiianus</i> var. <i>latifolius</i>	44.0	33.26	1.38	0.04
Gosam Reservoir	<i>Ottelia alismoides</i>	25.6	48.80	1.08	0.02
Sewol Reservoir	<i>Limnophila sessiliflora</i>	3.8	39.92	5.64	0.14
Dogok Reservoir	<i>Potamogeton berchtoldii</i>	25.8	33.26	4.21	0.13

5). *Chara* sp. showed that they are living in waters with lower chlorophyll *a*/TP ratios. Although additional 5 submerged plants lowered phytoplankton biomass (Fig. 4, Table 2), they were observed at only one site in this study indicating that they are not common species. Based on our field survey results, *M. spicatum*, *H. verticillata* and *Chara* sp. were expected to be as candidates capable of producing allelopathic substances. Our selection of *M. spicatum* and *Chara* sp. support many previous studies that showed *M. spicatum* and *Chara* sp. had a potential to release allelopathic substances (Crawford, 1979; Planas *et al.*, 1981; Jasser, 1995; Gross, 1999; Nakai *et al.*, 2005).

Our study did not include phytoplankton composition for water bodies we sampled. A recent study report that 36% of total variation in phytoplankton communities were explained by the presence or absence of submerged macrophytes (Takamura *et al.*, 2003). Phytoplankton composition with and without submerged macrophytes would provide valuable insight on species specific suppression of phytoplankton by submerged macrophytes. We would investigate the interactions between submerged macrophytes and phytoplankton community dynamics in further studies.

Our results suggest only possibility of production of allelopathic substances from the chosen submerged macrophytes. Other factors such as competition for light may have caused such effects on phytoplankton biomass. Another aspect to consider is periphytic algae on submerged plants. Submerged plants can provide substrates for periphyton thus indirectly affect phytoplankton growth through competition between periphyton and phytoplankton (Jones *et al.*, 2002). Also inorganic carbon may be an important factor in

competition among phytoplankton and submerged macrophytes (Maberly and Spence, 1983). To show more direct evidence of allelopathic inhibition on phytoplankton by submerged macrophytes, it is necessary to control other factors such as light, temperature, carbon/nutrient conditions and periphytic growth (Gross *et al.*, 2007). One possible approach would be conducting phytoplankton growth experiments using waters collected from patches of submerged macrophytes. Phytoplankton growth experiments with extracts from submerged macrophytes would be another direct examination for allelopathic interactions between phytoplankton and submerged macrophytes. Results of our successive study showed that extracts and waters from the patches of *M. spicatum* indeed suppressed *M. aeruginosa* growth (Nam and Park, 2007).

In conclusion, our results showed that phytoplankton biomass levels in waters with submerged macrophytes were much lower than those predicted from total phosphorus concentrations based on relationships found in other water bodies in Korea. In addition, we found that *M. spicatum* and *H. verticillata* exhibited patterns of lowering phytoplankton biomass according to their biomass both spatial and temporal surveys. It will be necessary to further investigate whether these plants are actually capable of releasing allelopathic substances to inhibit phytoplankton growth.

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LITERATURE CITED

- Coveney, M.F., D.L. Stites, E.F. Lowe, L.E. Battoe and R. Conrow. 2002. Nutrient removal from eutrophic lake water by wetland filtration. *Ecological Engineering* **19**: 141-159.
- Crawford, S.A. 1979. Farm pond restoration using *Chara vulgaris* vegetation. *Hydrobiologia* **62**: 17-31.
- Dierberg, F.E., T.A. DeBusk, S.D. Jackson, M.J. Chimney and K. Pietro. 2002. Submerged aquatic vegetation-based treatment wetlands for removing phosphorus from agricultural runoff: response to hydraulic and nutrient loading. *Water Research* **36**: 1409-1422.
- Gross, E.M. 1999. Allelopathy in benthic and littoral areas: case studies on allelochemicals from benthic cyanobacteria and submerged macrophytes, p. 179-199. *In: Principles and Practices in Plant Ecology: Allelochemical Interactions* (Innderjit Dakshini, K.M.M. and C.L. Foy eds.). CRC Press, Boca Raton.
- Gross, E.M. and R. Sütfield. 1994. Polyphenols with algicidal activity in the submerged macrophyte *Myriophyllum Spicatum* L. *Acta Horticulturae* **381**: 710-716.
- Gross, E.M., S. Hilt, P. Lombardo and G. Mulderij. 2007. Searching for allelopathic effects of submerged macrophytes on phytoplankton-state of the art and open questions. *Hydrobiologia* **584**: 77-88.
- Jasser, I. 1995. The influence of macrophytes on a phytoplankton community in experimental conditions. *Hydrobiologia* **306**: 21-32.
- Jones, J.I., J.O. Young, J.W. Eaton and B. Moss. 2002. The influence of nutrient loading, dissolved inorganic carbon and higher trophic levels on the interaction between submerged plants and periphyton. *Journal of Ecology* **90**: 12-24.
- Kim, H.-S. and S.-J. Hwang. 2004. Analysis of eutrophication based on chlorophyll-*a*, depth and limnological characteristics in Korean reservoirs. *Korean J. Limnol.* **37**: 213-226.
- Lee, J.-Y., J.-H. Lee, K.-H. Shin, S.-J. Hwang and K.-G. An. 2007. Trophic state and water quality characteristics of Korean agricultural reservoirs. *Korean J. Limnol.* **40**: 223-233.
- Maberly, S.C. and D.H.N. Spence. 1983. Photosynthetic inorganic carbon use by freshwater plants. *Journal of Ecology* **71**: 705-724.
- Nakai, S., S. Yamada and M. Hosomi. 2005. Anti-cyanobacterial fatty acids released from *Myriophyllum spicatum*. *Hydrobiologia* **543**: 71-78.
- Nakai, S., Y. Inoue, M. Hosomi and A. Murakami. 2000. *Myriophyllum spicatum*-released allelopathic polyphenols inhibiting growth of blue-green algae *Microcystis aeruginosa*. *Water Research* **34**: 3026-3032.
- Nam, S. and S. Park. Inhibition of aquatic vascular plants on phytoplankton growth. II. Algal growth experiments with water and plant extracts from submerged macrophytes. *Korean J. Limnol.* **40**(4): 520-526.
- Planas, D., F. Sarhan, L. Dube, H. Godmaire and C. Cadieux. 1981. Ecological significance of phenolic compounds of *Myriophyllum spicatum*. *Verh. Int. Verein. Limnol.* **21**: 1492-1496.
- Romero, J.A., F.A. Comin. and C. Garcia. 1999. Restored wetlands as filters to remove nitrogen. *Chemosphere* **39**: 323-332.
- Rooney, N. and J. Kalff. 2003. Interactions among epilimnetic phosphorus, phytoplankton biomass and bacterioplankton metabolism in lakes of varying submerged macrophyte cover. *Hydrobiologia* **501**: 75-81.
- Scheffer, M., S.H. Hopper, M.-L. Meijer, B. Moss and E. Jeppesen. 1993. Alternative equilibria in shallow lakes. *Trends in Ecology and Evolution* **8**: 275-279.
- Strickland, J.D.H. and T.R. Parsons. 1972. A practical handbook of seawater analysis. Bulletin 167. Fisheries Research Board of Canada, Ottawa, Ontario.
- Takamura, N., Y. Kadono, M. Fukushima, M. Nakagawa and B.-H.O. Kim. 2003. Effects of aquatic macrophytes on water quality and phytoplankton communities in shallow lakes. *Ecological Research* **18**: 381-395.
- Turner Designs. 2006. Trilogy Laboratory Fluorometer User's Manual. Turner Designs, Sunnyvale.
- Van Donk, E. and W.J. de Bund. 2002. Impact of submerged macrophytes including charophytes on phyto- and zooplankton communities: allelopathy versus other mechanisms. *Aquatic Botany* **72**: 261-274.
- Vollenweider, R.A. and J. Kerekes. 1982. Eutrophication of waters. Monitoring, assessment and control. OECD Cooperative programme on monitoring of inland waters (Eutrophication control), Environment Directorate, OECD, Paris.

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