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NOTES AND COMMENTS

Effects of *Spirogyra arcta* on biomass and structure of submerged macrophyte communities

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Abstract

The presence of algae can greatly reduce the amount of light that reaches submerged macrophytes, but few experimental studies have been conducted to examine the effects of algae on biomass and structure of submerged macrophyte communities. We constructed communities with four submerged macrophytes (*Hydrilla verticillata*, *Egeria densa*, *Ceratophyllum demersum*, and *Chara vulgaris*) in three environments in which 0 (control), 50 and 100% of the water surface was covered by *Spirogyra arcta*. Compared to the control treatment, the 100% spirogyra treatment decreased biomass of the submerged macrophyte communities and of all the four macrophytes except *C. demersum*. Compared to the control and 50% treatments, the 100% treatment significantly increased relative abundance of *C. demersum* and decreased that of *E. densa*. Therefore, the presence of *S. arcta* can greatly affect the productivity and alter the structure of submerged macrophyte communities. To restore submerged macrophyte communities in conditions with abundant algae, assembling communities consisting of *C. demersum* or similar species may be a good practice.

Keywords: algae, aquatic plants, biotic factor, clonal plants, experimental communities, *Spirogyra*.

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Introduction

Submerged macrophyte communities are an important component of shallow lake and seashore ecosystems (Scheffer *et al*. 1993; Jeppesen *et al*. 1997; Xu *et al*. 2011). They contribute to the sustainability of such ecosystems by, for example, purifying water (Brix & Schierup 1989; Bunluesin *et al*. 2007), decreasing turbidity, absorbing nutrients and heavy metals (Hasler & Jones 1949; Scheffer 1999; Bakker *et al*. 2010), controlling the growth of algae (Reddy 1983), and providing food and refuge for some animals (Carpenter & Lodge 1986; Scheffer 1998).

Submerged macrophyte communities are sensitive to changes in both abiotic factors, such as light (Scheffer 1998; Cronk & Fennessy 2001; Karus & Feldmann 2012), and biotic factors, such as the abundance of algae (Sheldon 1987; van den Berg *et al*. 2002; Takamura *et al*. 2003). Currently, eutrophication of lakes and degradation of submerged macrophyte communities are important environmental problems worldwide, especially in developing countries (Harper 1992; Rast & Thornton 1996). In eutrophic lakes, proliferation and colonization of algae is a common phenomenon that can greatly affect the structure and functioning of the lake ecosystems (Scheffer 1998; Mulderij *et al*. 2009). One direct consequence is that proliferation of algae can sharply decrease light availability for submerged macrophytes (Sand-Jensen & Søndergaard 1981; Hill *et al*. 2009; Köhler *et al*. 2010; Liu *et al*. 2012). Studies have shown that decreasing light intensity can markedly decrease the growth of submerged macrophytes (Boardman 1977; Søndergaard & Bonde 1988; Middelboe & Markager 1997). Furthermore, proliferation of algae can reduce nutrients and oxygen in water (Eminson & Phillips 1978; Sand-Jensen *et al*. 1985; Sand-Jensen & Borum 1991) and decrease water temperature (Hansson 1990; Stevenson *et al*. 1996; Gupta & Rastogi 2008; Sun *et al*. 2010).

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Previous studies have revealed that the presence of algae such as *Spirogyra arcta* can greatly reduce the growth of submerged macrophytes such as *Littorella uniflora* (Sand-Jensen & Søndergaard 1981), *Zostera marina* (Sand-Jensen & Borum 1991) and *Ceratophyllum demersum* (Liu *et al*. 2012) when they grow alone. However, effects of algae on the growth of submerged plants may differ greatly among species. If different species respond to the presence of algae differently, then the presence of algae may greatly affect the interspecific interactions among submerged macrophytes and thus alter the structure of submerged macrophyte communities (Sand-Jensen & Borum 1991). To our knowledge, however, there is still little experimental evidence on how the presence of algae affects biomass and structure of submerged macrophyte communities.

In a greenhouse experiment, we constructed submerged macrophyte communities with four co-occurring submerged macrophytes (i.e. *Hydrilla verticillata*, *Egeria densa*, *Ceratophyllum demersum* and *Chara vulgaris*) in three environments where 0, 50 or 100% of water surface was covered by *S. arcta*. We hypothesized that the presence of *S. arcta* would affect the growth of the four submerged macrophytes differently, reduce the overall productivity of the community, and change its structure. We specifically asked: (i) how the different covers of *S. arcta* affect biomass and structure of submerged macrophyte communities and (ii) how they affect biomass and number of nodes of each of the four component species.

Materials and methods

Alga species

Spirogyra arcta K. (hereafter referred to as spirogyra) is a filamentous green alga of the Zygnemataceae family (John *et al*. 2002). It is widely distributed in pools, ditches, slow-flowing streams, and paddy field, and forms dense filamentous masses propagated by cell division and zygospores (Hu *et al*. 1980; John *et al*. 2002). On July 24, 2010, the spirogyra used in this experiment was collected in an artificial pond in the Botanical Garden of the Institute of Botany, the Chinese Academy of Sciences in Beijing.

Assembly of submerged macrophyte communities

The experimental aquatic communities were constructed with four co-occurring submerged macrophytes, that is, *Hydrilla verticillata* R. (Hydrocharitaceae), *Egeria densa* P. (Hydrocharitaceae), *Ceratophyllum demersum* L. (Ceratophyllaceae) and *Chara vulgaris* L. (Characeae). *Hydrilla verticillata* and *C. demersum* are native aquatic plants in China, but highly invasive in other counties such as America, South Africa, and Australia (Holm *et al*. 1977; Langeland 1996; Parsons & Cuthbertson 2001; Coetzee *et al*. 2009; Wu *et al*. 2011). *Chara vulgaris* is a native alga and widely distributed in China (Hu *et al*. 1980). *Egeria densa*, native to South America, is now naturalized in China (Yan *et al*. 2013). All four species can reproduce vegetatively from clonal fragments (e.g., stem fragments, tubers, or turions) and spread mainly via clonal dispersals (Holm *et al*. 1997; Parsons & Cuthbertson 2001; John *et al*. 2002). They can coexist in relatively enclosed aquatic conditions (e.g., ditches, ponds and lakes) where spirogyra may frequently occur (DiTomaso & Healy 2003; Zhang 2009). In mid-July 2010, stem fragments of the four species were collected in the lakes of the Winter Palace in Beijing, China, and subsequently cultivated for 20 days in a greenhouse at Forestry Science Co., Ltd, of Beijing Forestry University in Beijing. For each species 160 stem fragments were selected and all side branches were removed. To keep the fragment length similar (approximately 15 cm), each fragment of *C. demersum*, *H. verticillata*, and *E. densa* had eight nodes and each fragment of *C. vulgaris* contained five nodes. Of the 160 fragments of each species, 20 were randomly selected for initial measurements and 72 were used for the experiment. The average dry mass of the stem fragments of *C. demersum, H. verticillata*, *E. densa*, and *C. vulgaris* were 45.7, 24.4, 21.7, and 33.7 mg, respectively. Although *C. demersum* might have more initial mass than the other three species, there was no difference in the competitive hierarchy, that is, *C. demersum* could not be regarded as a dominant species at the start of the experiment.

The communities were assembled in 24 opaque plastic buckets (24 cm in diameter and 30 cm in height). Each bucket was filled at the bottom with a 10-cm-deep layer consisting of a mixture of yellow loam and sand at a volume ratio of 1 : 1 and then 20-cm-deep tap water (0.593 ± 0.161 mg total N/L and 0.011 ± 0.001 mg total P/L; mean ± SE) above the soil surface. Jing *et al*. (2008) investigated 21 lakes in Beijing where submerged macrophytes commonly inhabited, and found most of them were classified as "eutrophic lakes." The average values of total N and P in these lakes were, at least, more than five times higher than those in tap water (Jing *et al*. 2008; Yuan *et al*. 2009). However, Kosten *et al*. (2009) suggested that submerged macrophyte communities may be more stable and highly productive in the environments with total N concentrations below 1–2 mg/L, and thus the experimental condition may be also suitable for macrophyte growth. On August 15, three stem fragments of each species were planted in each bucket, making 12 fragments per bucket. This was the initial status of the submerged communities used in this experiment.

Experimental design

The experiment had three treatments: (i) control (the water surface of the submerged community in the bucket was not covered by spirogyra), (ii) 50% (50% of the water surface in the bucket was covered by spirogyra), and (iii) 100% (all the water surface in the bucket was covered by spirogyra). Before the start of the experiment, the water surface in each container was divided into two identical parts by a plastic divider placed vertically across the center of the container. For the control, the water surface was not covered by spirogyra; for the 50% treatment, one part of the container was completely covered by spirogyra and the other was not; for the 100% treatment, the container was completely covered. The divider was then removed after treatments were established and spirogyra randomly floated on the water surface during the experiment. We also checked and modified the coverage of spirogyra each week. Each treatment had eight replicates.

The experiment was conducted in the same greenhouse for cultivation and lasted 60 days from August 15 to October 14, 2010. During the experiment tap water was supplied to maintain the water depth at the same level. The temperature and relative humidity in the greenhouse were 21.8 ± 0.4°C and 77.0 ± 1.3% (mean ± SE), respectively, measured hourly by two Hygrochron temperature loggers (iButton DS1923, Maxim Integrated Products, USA). Photosynthetic photon flux density at noon (between 1100 h and 1400 h) was 273.1 ± 18.6 μmol/m^2/s (mean ± SE), measured by a Li-250A quantum sensor (LI-COR Biosciences, USA).

Measurements

Chara vulgaris is a green alga species, which does not produce real leaf, stolon, and root structures. However, to simplify the terminology in the study, we referred to the main axis and long branches of unlimited growth of *C. vulgaris* as "stems." At harvest, we measured the total stem length and counted the total number of stem nodes of each species in each bucket. Then all the plants were oven dried at 70°C for 72 h and weighed.

Data analysis

For each species, we calculated average internode length as stem length divided by number of stem nodes, and specific stem length as stem length divided by shoot biomass (leaf and stem biomass). Biomass and number of stem nodes of communities were the sum of the corresponding variables of all the four species. We also calculated the proportion of each species in the community as measures of relative abundance based on both biomass and number of nodes. We used non-parametric Kruskal–Wallis tests followed by Steel–Dwass multiple comparisons to examine effects of spirogyra cover on biomass and number of nodes at the community level. We conducted two-way ANOVAs to examine effects of spirogyra cover and species on the biomass, number of nodes, proportion of biomass, and node number of each species. Games–Howell post-hoc tests were followed to test the difference among spirogyra-cover treatments at the species level, because data did not meet the assumption of homogeneity of variances (SYSTAT 2009). We also performed two-way ANOVAs followed by Tukey's post-hoc tests for the effects of spirogyra cover and species on internode length and specific stem length. All analyses were conducted with SYSTAT 13.0 software (SYSTAT Software, Inc., Chicago, Illinois, USA).

Results

Growth of the submerged macrophyte communities

The presence of spirogyra significantly affected both total biomass and total number of stem nodes of the submerged macrophyte communities (Fig. 1). Biomass was largest in the control (no spirogyra), smallest in the 100% spirogyra treatment, and intermediate in the 50% spirogyra treatment ($\chi^2_2 = 16.35$, $P < 0.001$; Fig. 1A). Number of nodes was significantly smaller in the 100% spirogyra treatment than in the control and the 50% spirogyra treatment, but did not differ significantly between the control and the 50% spirogyra treatment ($\chi^2_2 = 19.28$, $P < 0.001$; Fig. 1B).

Growth of the four submerged macrophytes

Biomass and number of nodes of *C. vulgaris*, *E. densa*, and *H. verticillata* were smaller in the 100% spirogyra treatment than in the control and the 50% spirogyra treatment, but they did not differ significantly between the control and the 50% treatment (Table 1; Fig. 2A–C,E–G). Neither biomass nor number of nodes of *C. demersum* differed

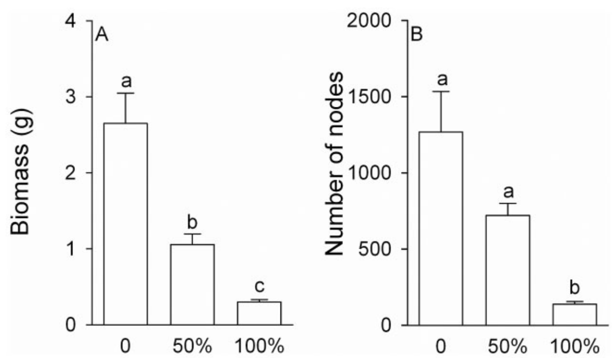

Fig. 1 (A) Total biomass and (B) total number of nodes of submerged macrophyte communities under three conditions where 0 (control), 50, and 100% of the water surface was covered by spirogyra. Bars sharing the same letters are not significantly different at $P = 0.05$. Means + 1 SE are given.

Table 1 Two-way ANOVA results for effects of spirogyra cover and species on biomass, number of nodes, proportion of biomass, proportion of node number, internode length, and specific stem length

	Cover (C)		Species (S)		C × S	
	$F_{2,84}$	P	$F_{3,84}$	P	$F_{6,84}$	P
Biomass	29.0	< 0.001	19.0	< 0.001	6.6	< 0.001
No. of nodes	14.4	< 0.001	10.6	< 0.001	4.7	< 0.001
Proportion of biomass	< 0.001	0.999	43.8	< 0.001	9.1	< 0.001
Proportion of node number	< 0.001	0.999	20.6	< 0.001	16.4	< 0.001
Internode length	6.9	0.002	99.2	< 0.001	7.7	< 0.001
Specific stem length	5.8	0.005	11.7	< 0.001	1.8	0.108

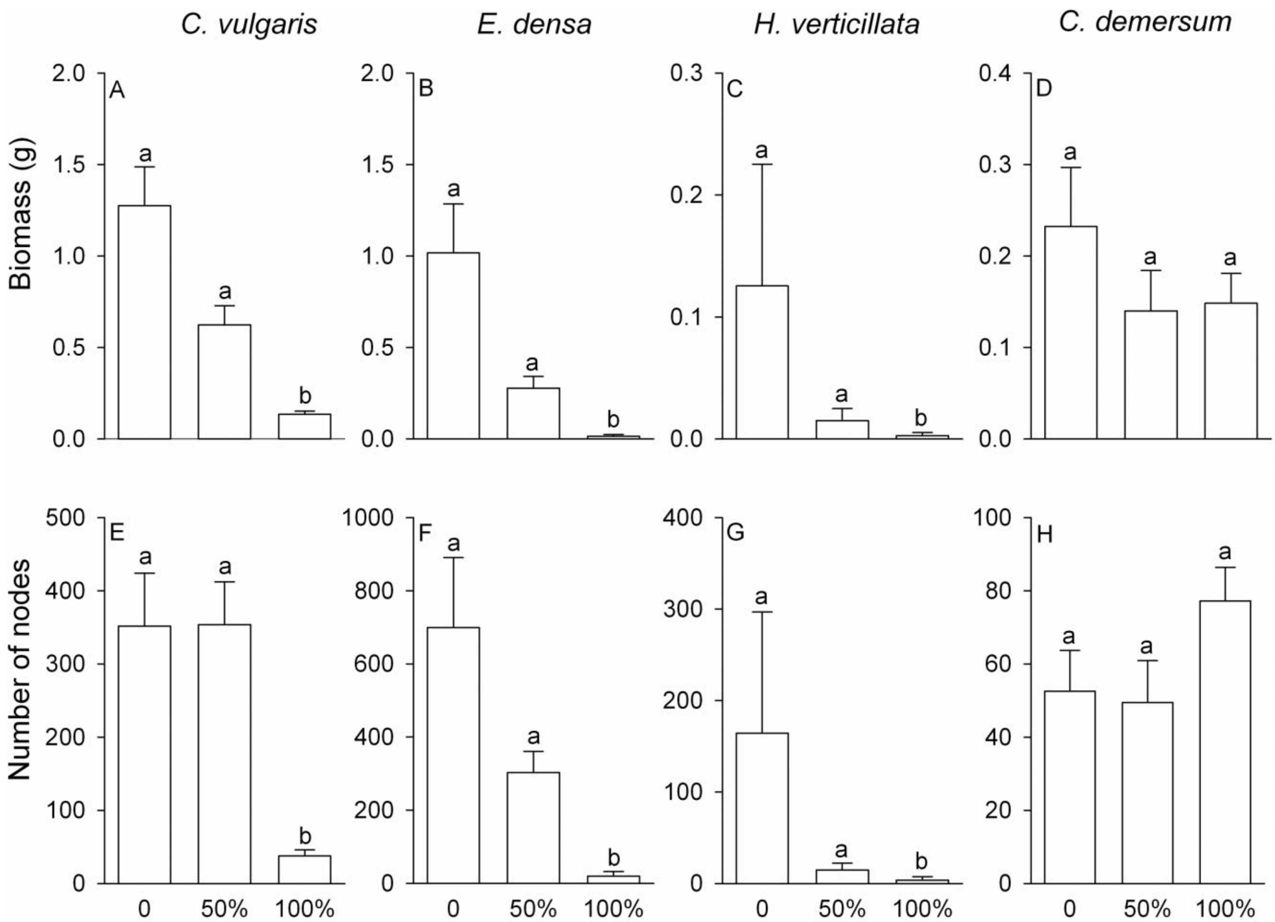

Fig. 2 (A–D) Biomass and (E–H) number of nodes of each of four submerged macrophytes under three conditions where 0 (control), 50, and 100% of the water surface was covered by spirogyra. Bars sharing the same letters are not significantly different at $P = 0.05$. Means + 1 SE are given.

significantly among the three spirogyra treatments (Fig. 2D,H).

Proportion of the four submerged macrophytes

The proportion of biomass or number of nodes of *C. vulgaris* or *H. verticillata* was not significantly affected by the spirogyra treatments (Table 1; Fig. 3). The proportions of biomass and number of nodes of *E. densa* were smaller in the 100% spirogyra treatment than in the control and the 50% spirogyra treatment, but they did not differ between the control and the 50% treatment (Fig. 3). In contrast, the proportions of biomass and number of nodes of *C. demersum* were greater in the 100% spirogyra treatment than in the control and the 50% spirogyra treatment (Fig. 3).

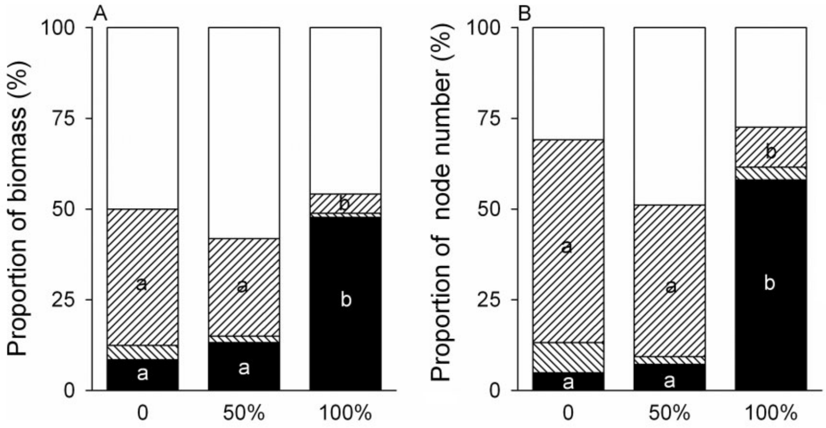

Fig. 3 The proportions of (A) biomass and (B) number of nodes of four submerged macrophytes in the communities under three conditions where 0 (control), 50, and 100% of the water surface was covered by spirogyra. For each species, different letters show significant differences among treatments; no letters suggest no significant difference among all three treatments. Means + 1 SE are given. □, *C. vulgaris*; ▨, *E. densa*; ▧, *H. verticillata*; ■, *C. demersum*.

Internode length and specific stem length of the four submerged macrophytes

Both internode length and specific stem length of *C. demersum* were greater in the 100% spirogyra treatment, smallest in the control, and intermediate in the 50% spirogyra treatment (Table 1; Fig. 4D,H). Internode length of *C. vulgaris* was larger in the 100% spirogyra treatment than in the control and 50% spirogyra treatment, but they did not differ between the control and the 50% spirogyra treatments (Fig. 4A). Specific internode length of *C. vulgaris* was not affected by spirogyra treatments (Fig. 4E). The presence of spirogyra significantly affected neither internode length nor specific stem length of *E. densa* or *H. verticillata* (Fig. 4B,C,F,G).

Discussion

The presence of spirogyra can cause complex changes influencing growth and structure of submerged communities, including changes in physical (e.g., light density, light quality, temperature) and chemical prosperities (e.g. status of nutrients) of water body and release of allelochemicals. Previous studies have indicated that spirogyra produced tannin compounds (Nishizawa *et al*. 1985), and changed the activity and growth of microalgae, such as *Microcystis aeruginosa*, *Chlorella vulgaris* and *Oscillatoria agardhii* (Mohamed 2002; Ma & Lei 2008). However, such an effect might be small on submerged macrophytes due to either the low tannin concentration or the strong tolerance of these plants to allelopathy (Gross 2003). Although the presence of spirogyra may alter physical and chemical characters in water, shading from spirogyra is very likely the main factor regulating responses of the individuals and communities (Irfanullah & Moss 2004; Fan *et al*. 2011). For instance, Zhang *et al*. (2012) found that the effects of spirogyra cover and shading were similar.

The growth of submerged macrophytes is commonly limited by light (Denny 1972; Cronk & Fennessy 2001). If light availability for them is too low, then their photosynthetic capacity and growth will be greatly reduced (Middelboe & Markager 2003; Mjelde *et al*. 2013). The presence of spirogyra, especially when the whole water surface is covered, can greatly decrease light that reaches the submerged macrophytes (Sand-Jensen & Søndergaard 1981; Huisman & Weissing 1994; Bakker *et al*. 2010). Consequently, we found that total biomass and number of stem nodes of the submerged macrophyte communities were markedly smaller in the 100% spirogyra treatment than in the control treatment.

The reduced growth of the submerged macrophyte communities was mainly due to the reduced growth of the two abundant species *E. densa* and *C. vulgaris*. Compared to the control, *E. densa* and *C. vulgaris* in the 100% spirogyra treatment reduced biomass by 99 and 89% and number of stem nodes by 97 and 89%. The less abundant species *H. verticillata* also contributed significantly to the reduced growth of the submerged macrophyte communities in the 100% spirogyra treatment. Therefore, these three species are “shade victims,” showing highly conservative utilization of resources and commonly accompanied by very low growth rates and low respiratory losses in the deep shade environment (Smith 1982) caused by, for example, the presence of spirogyra (De Fillippis & Pallaghy 1973; Spencer & Wetzel 1993; Hofstra *et al*. 1999).

In the present study, the presence of spirogyra had little effect on the growth of *C. demersum* when it grew together with the other three submerged macrophytes. In a previous study, 100% spirogyra cover significantly decreased the growth of *C. demersum* when it grew alone, whereas 50% spirogyra cover did not (Liu *et al*. 2012). Therefore, the effect of spirogyra on the growth of *C. demersum* is likely to depend on the interactions with other submerged macrophytes in the communities. The unresponsiveness to both 50% and 100% spirogyra cover when it grew with

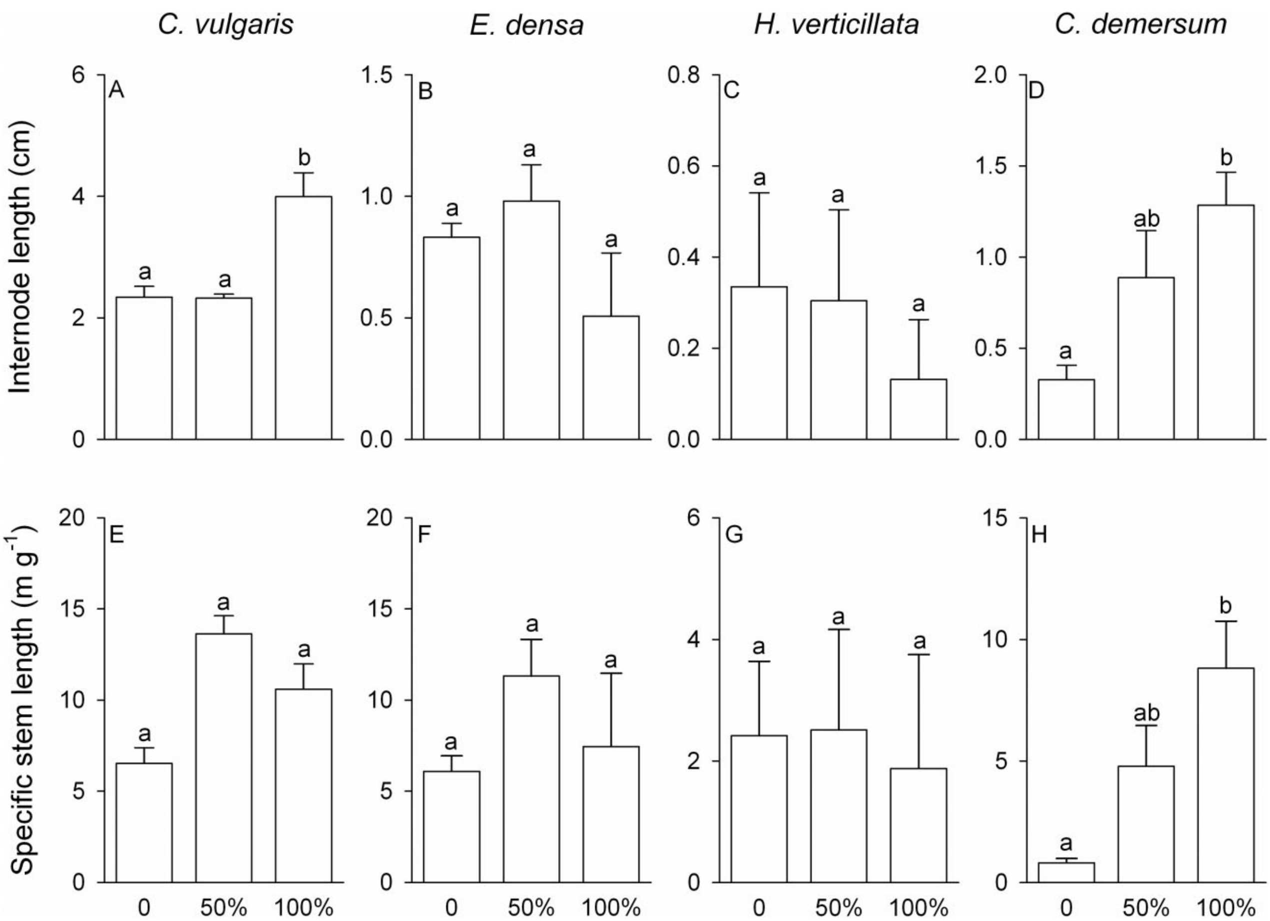

Fig. 4 (A–D) Internode length and (E–H) specific stem length of each of four submerged macrophytes under three conditions where 0 (control), 50, and 100% of the water surface was covered by spirogyra. Bars sharing the same letters are not different at $P = 0.05$. Means + 1 SE are given.

the other species and to the 50% spirogyra cover when it grew alone (Liu *et al*. 2012) is likely because *C. demersum* has a low light compensation point and takes an avoidance or escape strategy (Smith 1981, 1982; Spencer & Wetzel 1993). When the whole water surface was covered by spirogyra, stem internode length of *C. demersum* was markedly increased and stem thickness decreased (i.e., increased specific stem length). These morphological responses ensured that *C. demersum* could produce much longer stems so that its leaves and other photosynthetic tissues could be lifted to a much higher position in the water column in order to increase light harvest (Alpert & Stuefer 1997; Yu & Dong 2003; Svensson *et al*. 2005; Going *et al*. 2008). This may have counteracted the negative effects of shading by spirogyra and by other submerged macrophytes so that the growth (absolute abundance) of *C. demersum* was not significantly affected.

The presence of spirogyra, especially the 100% spirogyra treatment, markedly decreased the growth of *E. densa*, *C. vulgaris*, and *H. verticillata*, but did not affect that of *C. demersum*. Also the 100% spirogyra treatment greatly decreased the proportion of *E. densa* and increased that of *C. demersum*, so that the dominant species were shifted from *C. vulgaris* and *E. densa* in the control treatment to *C. demersum* in the 100% spirogyra treatment. These results confirm that the presence of spirogyra, especially when the cover of spirogyra is high, can greatly alter species composition of submerged macrophyte communities (Hansel-Welch *et al*. 2003). The results also confirm that different submerged macrophytes may show different patterns in both their absolute and relative abundances in response to the presence of spirogyra (Sand-Jensen & Søndergaard 1981; Hough *et al*. 1989). For *E. densa*, the 100% spirogyra treatment greatly decreased not only its absolute abundance (biomass and node number) but also its relative abundance (proportions of biomass and node number). For *C. vulgaris* and *H. verticillata*, the 100% spirogyra treatment decreased its absolute abundance but did not affect its relative abundance. In contrast, for *C. demersum*, the 100% spirogyra treatment did not affect its absolute abundance but sharply increased its relative abundance.

We conclude that, when the abundance/cover of spirogyra is high, the presence of spirogyra can greatly reduce the productivity and alter the structure of submerged macrophyte communities because different macrophytes differ greatly in their responses to the presence of spirogyra. To restore submerged macrophyte communities in conditions with low abundance of algae and better light supply, it would be more efficient to construct communities with *E. densa* and *C. vulgaris* or species with similar responses (Amoros *et al*. 2000; Burks *et al*. 2006; Wang *et al*. 2008). In contrast, to restore submerged macrophyte communities in conditions with abundant algae and low light, assembling communities consisting of *C. demersum* or similar species may be a better way (De Fillippis & Pallaghy 1973; Spencer & Wetzel 1993; Hofstra *et al*. 1999).

Furthermore, the above conclusions may not always hold in environments that differ from the experimental condition, where levels of nutrients in the water are higher. From meso-eutrophic to eutrophic lakes, the negative effects of algae on the community may become more severe so that the diversity of submerged macrophytes becomes less and the macrophyte community will be dominated by only one or a few species that have strong tolerance to the proliferation and blooming of algae (see, e.g., Yuan *et al*. 2009). In further studies we need to pay more attention to the influence of algae on submerged-macrophyte dynamics in different aquatic ecosystems.

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References

Alpert P. & Stuefer J. (1997) Division of labour in clonal plants. In: de Kroon H. & van Groenendael J. (eds). *The Ecology and Evolution of Clonal Plants*. Backhuys Publishers, Leiden, pp. 137–154.

Amoros C., Bornette G. & Henry C. P. (2000) A vegetation-based method for ecological diagnosis of riverine wetlands. *Environmental Management* **25**: 211–227.

Bakker E., Van Donk E., Declerck S., Helmsing N., Hidding B. & Nolet B. (2010) Effect of macrophyte community composition and nutrient enrichment on plant biomass and algal blooms. *Basic and Applied Ecology* **11**: 432–439.

Boardman N. K. (1977) Comparative photosynthesis of sun and shade plants. *Annual Review of Plant Physiology* **28**: 355–377.

Brix H. & Schierup H. H. (1989) The use of aquatic macrophytes in water-pollution control. *Ambio* **18**: 100–107.

Bunluesin S., Kruatrachue M., Pokethitiyook P., Upatham S. & Lanza G. R. (2007) Batch and continuous packed column studies of cadmium biosorption by *Hydrilla verticillata* biomass. *Journal of Bioscience and Bioengineering* **103**: 509–513.

Burks R. L., Mulderij G., Gross E., Jones J. I., Jacobsen L., Jeppesen E. & Van Donk E. (2006) Center stage: the crucial role of macrophytes in regulating trophic interactions in shallow lake wetlands. In: Bobbink R., Beltman B., Verhoeven J. T. A. & Whigham D. F. (eds). *Wetlands: Functioning, Biodiversity Conservation, and Restoration*. Springer-Verlag, Berlin and Heidelberg, pp. 37–59.

Carpenter S. R. & Lodge D. M. (1986) Effects of submersed macrophytes on ecosystem processes. *Aquatic Botany* **26**: 341–370.

Coetzee J. A., Hill M. P. & Schlange D. (2009) Potential spread of the invasive plant *Hydrilla verticillata* in South Africa based on anthropogenic spread and climate suitability. *Biological Invasions* **11**: 801–812.

Cronk J. K. & Fennessy M. S. (2001) *Wetland Plants: Biology and Ecology*. CRC Press, LLC, Boca Raton, FL.

De Fillippis L. & Pallaghy C. (1973) Effect of light on the volume and ion relations of chloroplasts in detached leaves of *Elodea densa*. *Australian Journal of Biological Sciences* **26**: 1251–1266.

Denny P. (1972) Sites of nutrient absorption in aquatic macrophytes. *Journal of Ecology* **60**: 819–829.

DiTomaso J. M. & Healy E. A. (2003) *Aquatic and Riparian Weeds of the West*. University of California Agriculture and Natural Resources Publication, Oakland, CA.

Eminson D. & Phillips G. (1978) A laboratory experiment to examine the effects of nutrient enrichment on macrophyte and epiphyte growth. *Verhandlungen Der Internationale Vereinigung Für Theoretische Und Angewandte Limnologie* **20**: 82–87.

Fan C.-M., Liu Y.-G., Guo Y.-M., Mao W.-J., Zheng N.-N. & Sai G.-N. (2011) Effects of *Spirogyra* on the cyanobacteria recruitment and phytoplankton community structure. *Acta Scientiae Circumstantiae* **31**: 2132–2137. (In Chinese with English abstract.).

Going B., Simpson J. & Even T. (2008) The influence of light on the growth of watercress (*Nasturtium officinale* R. Br.). *Hydrobiologia* **607**: 75–85.

Gross E. M. (2003) Allelopathy of aquatic autotrophs. *Critical Reviews in Plant Sciences* **22**: 313–339.

Gupta V. & Rastogi A. (2008) Biosorption of lead from aqueous solutions by green algae *Spirogyra* species: kinetics and equilibrium studies. *Journal of Hazardous Materials* **152**: 407–414.

Hansel-Welch N., Butler M. G., Carlson T. J. & Hanson M. A. (2003) Changes in macrophyte community structure in

Lake Christina (Minnesota), a large shallow lake, following biomanipulation. *Aquatic Botany* **75**: 323–337.
Hansson L. A. (1990) Quantifying the impact of periphytic algae on nutrient availability for phytoplankton. *Freshwater Biology* **24**: 265–273.
Harper D. (1992) *Eutrophication of Freshwaters: Principles, Problems and Restoration*. Chapman and Hall, New York.
Hasler A. D. & Jones E. (1949) Demonstration of the antagonistic action of large aquatic plants on algae and rotifers. *Ecology* **30**: 359–364.
Hill W. R., Fanta S. E. & Roberts B. J. (2009) Quantifying phosphorus and light effects in stream algae. *Limnology and Oceanography* **54**: 368–380.
Hofstra D., Clayton J., Green J. & Auger M. (1999) Competitive performance of *Hydrilla verticillata* in New Zealand. *Aquatic Botany* **63**: 305–324.
Holm L. G., Doll J., Holm E., Pancho J. V. & Herberger J. P. (1997) *World Weeds: Natural Histories and Distribution*. John Wiley and Sons, New York.
Holm L. G., Plucknett D. L., Pancho J. V. & Herberger J. P. (1977) *The World's Worst Weeds*. University Press, Honolulu, HI.
Hough R. A., Fornwall M. D., Negele B. J., Thompson R. L. & Putt D. A. (1989) Plant community dynamics in a chain of lakes: principal factors in the decline of rooted macrophytes with eutrophication. *Hydrobiologia* **173**: 199–217.
Hu H.-J., Li R.-Y., Wei Y.-X., Zhu H.-Z., Chen J.-Y. & Shi Z.-X. (1980) *The Freshwater Algae of China*. Science and Technology Press, Shanghai.
Huisman J. & Weissing F. J. (1994) Light-limited growth and competition for light in well-mixed aquatic environments: an elementary model. *Ecology* **75**: 507–520.
Irfanullah H. M. & Moss B. (2004) Factors influencing the return of submerged plants to a clear-water, shallow temperate lake. *Aquatic Botany* **80**: 177–191.
Jeppesen E., Jensen J. P., Søndergaard M., Lauridsen T., Pedersen L. J. & Jensen L. (1997) Top-down control in freshwater lakes: the role of nutrient state, submerged macrophytes and water depth. *Hydrobiologia* **342**: 151–164.
Jing H.-W., Hua L., Sun C.-H. & Guo J. (2008) Analysis on urban lakes' eutrophication status in Beijing. *Journal of Lake Sciences* **20**: 357–363. (In Chinese with English abstract.).
John D. M., Whitton B. A. & Brook A. J. (2002) *The Freshwater Algal Flora of the British Isles: An Identification Guide to Freshwater and Terrestrial Algae*. Cambridge University Press, New York.
Karus K. & Feldmann T. (2012) Factors influencing macrophyte metrics in Estonian coastal lakes in the light of ecological status assessment. *Hydrobiologia* **704**: 153–163.
Köhler J., Hachoł J. & Hilt S. (2010) Regulation of submersed macrophyte biomass in a temperate lowland river: interactions between shading by bank vegetation, epiphyton and water turbidity. *Aquatic Botany* **92**: 129–136.
Kosten S., Kamarainen A., Jeppesen E., van Nes E. H., Peeters E. T., Mazzeo N., Sass L., Hauxwell J., Hansel-Welch N. & Lauridsen T. L. (2009) Climate-related differences in the dominance of submerged macrophytes in shallow lakes. *Global Change Biology* **15**: 2503–2517.
Langeland K. A. (1996) *Hydrilla verticillata* (L.F.) Royle (Hydrocharitaceae), "The perfect aquatic weed". *Castanea* **61**: 293–304.
Liu R.-H., Dong B.-C., Li H.-L., Zhang Q. & Yu F.-H. (2012) Patchy distributions of *Spirogyra arcta* do not affect growth of the submerged macrophyte *Ceratophyllum demersum*. *Plant Species Biology* **27**: 210–217.
Ma J. & Lei G. Y. (2008) Characteristics of phosphorus removal and growth inhibition of micro-algal species by *Spirogyra*. *Acta Scientiae Circumstantiae* **28**: 476–483. (In Chinese with English abstract.).
Middelboe A. L. & Markager S. (1997) Depth limits and minimum light requirements of freshwater macrophytes. *Freshwater Biology* **37**: 553–568.
Mjelde M., Hellsten S. & Ecke F. (2013) A water level drawdown index for aquatic macrophytes in Nordic lakes. *Hydrobiologia* **704**: 141–151.
Mohamed Z. A. (2002) Allelopathic activity of *Spirogyra* sp.: stimulating bloom formation and toxin production by *Oscillatoria agardhii* in some irrigation canals, Egypt. *Journal of Plankton Research* **24**: 137–141.
Mulderij G., Mau B., de Senerpont Domis L., Smolders A. J. & Van Donk E. (2009) Interaction between the macrophyte *Stratiotes aloides* and filamentous algae: does it indicate allelopathy? *Aquatic Ecology* **43**: 305–312.
Nishizawa M., Yamagishi T., Nonaka G.-I., Nishioka I. & Ragan M. A. (1985) Gallotannins of the freshwater green alga *Spirogyra* sp. *Phytochemistry* **24**: 2411–2413.
Parsons W. T. & Cuthbertson E. G. (2001) *Noxious Weeds of Australia*. CSIRO Publishing, Collingwood.
Rast W. & Thornton J. A. (1996) Trends in eutrophication research and control. *Hydrological Processes* **10**: 295–313.
Reddy K. (1983) Fate of nitrogen and phosphorus in a wastewater retention reservoir containing aquatic macrophytes. *Journal of Environmental Quality* **12**: 137–141.
Sand-Jensen K. & Borum J. (1991) Interactions among phytoplankton, periphyton, and macrophytes in temperate freshwaters and estuaries. *Aquatic Botany* **41**: 137–175.
Sand-Jensen K., Revsbech N. P. & Barker Jörgensen B. (1985) Microprofiles of oxygen in epiphyte communities on submerged macrophytes. *Marine Biology* **89**: 55–62.
Sand-Jensen K. & Søndergaard M. (1981) Phytoplankton and epiphyte development and their shading effect on submerged macrophytes in lakes of different nutrient status. *Internationale Revue der Gesamten Hydrobiologie und Hydrographie* **66**: 529–552.
Scheffer M. (1998) *Ecology of Shallow Lakes*. Chapman and Hall, New York.
Scheffer M. (1999) The effect of aquatic vegetation on turbidity: how important are the filter feeders? *Hydrobiologia* **408**: 307–316.
Scheffer M., Hosper S., Meijer M., Moss B. & Jeppesen E. (1993) Alternative equilibria in shallow lakes. *Trends in Ecology and Evolution* **8**: 275–279.
Sheldon S. P. (1987) The effects of herbivorous snails on submerged macrophyte communities in Minnesota lakes. *Ecology* **68**: 1920–1931.
Smith H. (1981) Adaptation to shade. In: Johnson C. B. (ed.). *Physiological Processes Limiting Plant Productivity*. Butterworths, New York, pp. 159–173.
Smith H. (1982) Light quality, photoperception, and plant strategy. *Annual Review of Plant Physiology* **33**: 481–518.
Søndergaard M. & Bonde G. (1988) Photosynthetic characteristics and pigment content and composition in *Littorella uniflora* (L.) Aschers. in a depth gradient. *Aquatic Botany* **32**: 307–319.

Spencer W. E. & Wetzel R. G. (1993) Acclimation of photosynthesis and dark respiration of a submersed angiosperm beneath ice in a temperate lake. *Plant Physiology* **101**: 985–991.

Stevenson R. J., Bothwell M. L. & Lowe R. L. (1996) *Algal Ecology: Freshwater Benthic Ecosystems*. Academic Press, San Diego, CA.

Sun F.-F., Yin G.-P., Fan C.-X. & Cui G.-B. (2010) Influences of alga accumulation and wastewater discharge on content of aqueous nutrients in Taihu Lake. *Advances in Science and Technology of Water Resources* **30**: 24–28. (In Chinese with English abstract.).

Svensson B. M., Rydin H. & Carlsson B. (2005) *Clonal plants in the community*. In: van der Maarel E. (ed.). *Vegetation Ecology*. Blackwell, Oxford, pp. 129–146.

SYSTAT (2009) *SYSTAT Version 13 User's Manual*. Software Inc., Chicago, IL.

Takamura N., Kadono Y., Fukushima M., Nakagawa M. & Kim B. H. (2003) Effects of aquatic macrophytes on water quality and phytoplankton communities in shallow lakes. *Ecological Research* **18**: 381–395.

van den Berg M. S., Scheffer M., Coops H. & Simons J. (2002) The role of characean algae in the management of eutrophic shallow lakes. *Journal of Phycology* **34**: 750–756.

Wang H., Yu D. & Xiao K. (2008) The interactive effects of irradiance and photoperiod on *Chara vulgaris* L.: concerted responses in morphology, physiology, and reproduction. *Hydrobiologia* **610**: 33–41.

Wu Z.-Y., Raven P. H. & Hong D.-Y. (2011) *Flora of China*, Vol. 20–21. Science Press and Missouri Botanical Garden Press, Beijing and St. Louis, MO.

Xu N.-N., Tong X., Tsang P. K. E., Deng H. & Chen X.-Y. (2011) Effects of water depth on clonal characteristics and biomass allocation of *Halophila ovalis* (Hydrocharitaceae). *Journal of Plant Ecology* **4**: 283–291.

Yan X.-L., Shou H.-Y., Liu Q.-R., Zeng X.-F., Zhang Y., Chen L., Liu Y., Ma H. Y., Qi S. Y., Geng Y.-Y., Li Z.-Y. & Ma J.-S. (2013) The classification and grades of Chinese invasive plants. *Biodiversity Science* **21**: 1–17. (In Chinese with English abstract.).

Yu F.-H. & Dong M. (2003) Effect of light intensity and nutrient availability on clonal growth and clonal morphology of the stoloniferous herb *Halerpestes ruthenica*. *Acta Botanica Sinica* **45**: 408–416.

Yuan J., Cui G.-F. & Lei T. (2009) Major hydro environmental factors affecting the community composition of wetland submerged plants in Beijing. *Chinese Journal of Ecology* **28**: 2189–2196. (In Chinese with English abstract.).

Zhang Q., Dong B.-C., Li H.-L., Liu R.-H., Luo F.-L., Zhang M.-X., Lei G.-C. & Yu F.-H. (2012) Does light heterogeneity affect structure and biomass of submerged macrophyte communities? *Botanical Stuidies* **53**: 377–385.

Zhang S.-R. (2009) *Common Wetland Plants in China*. Science Press, Beijing.

