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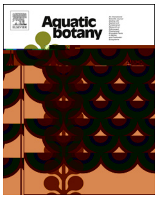

Does species richness affect the growth and water quality of submerged macrophyte assemblages?

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ABSTRACT

Biodiversity commonly plays important roles in ecosystem functioning. While many studies have tested effects of species diversity on productivity, carbon and nitrogen cycling and resistance to biological invasion, few have examined how diversity of submerged macrophytes affects the water quality of aquatic ecosystems. We assembled aquatic microcosms with 1, 2, 3 and 4 submerged macrophyte species (*Hydrilla verticillata, Ceratophyllum demersum, Myriophyllum verticillatum* and *Elodea nuttallii*), and measured growth of the macrophytes and physical and chemical properties of the water (total nitrogen and phosphorus, transparency, dissolved oxygen content, chemical and biochemical oxygen demand) in the microcosms after 36 days. Species diversity of submerged macrophytes did not significantly affect biomass and the vegetative reproduction of the macrophytes or the water factors such as total nitrogen and phosphorus, chlorophyll *a* content, chemical and biochemical oxygen demand of the aquatic ecosystems. Exceptionally, the 3-species treatment had higher light

world, however, the water quality of many freshwater lakes has degenerated due to remarkable loss of macrophytes caused by anthropogenic disturbance, e.g. fishery and pollution (Scheffer, 2004; Qin et al., 2006b). As a result, many of these lakes previously dominated by submerged macrophytes have been transformed into ecosystems dominated by phytoplankton, further deteriorating water quality (Qin et al., 2006a). Therefore, there is an urgent need to reveal the potential mechanisms that sustain aquatic vegetation growth and water quality in freshwater ecosystems.

One of such mechanisms may be that a diverse community of aquatic macrophytes can stably maintain high biomass production as well as good water quality. Bakker et al. (2010) found in an outdoor experiment that species composition of submerged macrophyte communities significantly affected plant biomass production, indicating potential effects of species diversity on aquatic vegetation growth. Moreover, in a microcosm study, Engelhardt and Ritchie (2001) showed that increasing species richness of submerged macrophytes significantly decreased phosphorus retention in the water. These findings suggest that increasing species diversity of submerged macrophytes may have beneficial effects on sustaining large aquatic vegetation production as well as on maintenance of good water quality of aquatic ecosystem and therefore likely limit water eutrophication. To date, however, under eutrophic conditions, whether increasing species diversity can enhance submerged macrophyte growth and water quality has not been widely studied in aquatic ecosystems (Engelhardt and Ritchie, 2001; Ostroumov, 2002).

Water eutrophication in lakes and ponds is a compound problem rather than only excessive nutrients (Scheffer et al., 1993). Many factors including e.g. phytoplankton content (measured by chlorophyll *a*), water transparency, dissolved oxygen, chemical and biochemical oxygen demands are also important parameters affecting and determining the health of the ecosystem. Studies have been shown that aquatic macrophytes can alter these physical and/or (bio)chemical factors (Carter et al., 1988). For instance, a field investigation of water quality inside and outside of the submerged macrophyte beds showed remarkable differences in dissolved oxygen, pH, temperature, chlorophyll *a* concentration and suspended particulate matter (Carter et al., 1988, 1991). However, it is still largely unknown whether the species richness of submerged macrophytes can affect these different processes.

We constructed aquatic plant microcosms consisting of 1, 2, 3 and 4 submerged macrophytes commonly found in freshwater lakes, and measured physical and chemical properties of the water in those microcosms. Specifically, we addressed the following questions: (1) Does species diversity affect the growth of the submerged macrophyte assemblage? (2) Does species diversity affect water quality (in terms of nutrients, chlorophyll *a* content, pH, dissolved oxygen content, light transmittance, and chemical and biochemical oxygen demand) in the aquatic microcosms?

2. Materials and methods

2.1. Macrophyte species collection

Four plant species were used for the construction of the experimental communities, and they were *Hydrilla verticillata* (L.) Royle, *Ceratophyllum demersum* L., *Myriophyllum verticillatum* L., and *Elodea nuttallii* (Planch.) H. St. John. All these species are perennial submerged macrophytes that are able to reproduce asexually via shoot fragments (Cortes-Lorenzo et al., 2014; Zhang et al., 2014). They can co-occur in freshwater lakes and rivers, but also show different preferences for specific habitats.

Ceratophyllum demersum (Ceratophyllaceae) grows in still or very slow-moving water. This species grows better in nutrient-rich water and can tolerate low light and high turbidity (Ceschin et al., 2010; Davidson et al., 2013). Both *H. verticillata* and *E. nuttalli* belong to the Hydrocharitaceae family (Davidson et al., 2013). Plants of *H. verticillata* can grow under a wide range of conditions from oligotrophic to eutrophic water, and reproduce asexually by shoot turions and subterranean tubers (Cortes-Lorenzo et al., 2014). The species *E. nuttalli* commonly has a thin branching stem, grows in lakes, rivers, and other freshwater bodies (Ha et al., 2013). Plants of *M. verticillatum* (Haloragaceae) have a high light requirement and a high photosynthetic rate (Street et al., 2013). This species commonly grows in still water and can grow vigorously in eutrophic water (Ceschin et al., 2010; Cortes-Lorenzo et al., 2014).

Shoots of the four species were collected from lakes in the Winter Palace in Beijing on 23 June 2014. All side branches of the shoots were removed, and each shoot fragment was 13 cm long with an apex. These shoot fragments were used for the experiment described below.

2.2. Experimental design

The experiment had four levels of species diversity (with 1, 2, 3 and 4 species). For the 1-species treatment, each pot (30 cm in diameter and 8 cm in height) was planted with 12 shoot fragments of the same species and there were five replicate pots. All the four species were used, making a total of 20 pots. For the 2-species treatment, each pot was planted with 6 shoot fragments of each of the two species. We used all the six types of the two-species mixture from the four species pool, and each type was replicated five times, making a total of 30 pots. For the 3-species treatment, each pot was planted with 4 shoot fragments of each of the three species. All the four types of the three-species mixture were used, and each type was replicated five times, making a total of 20 pots. For the 4-species treatment, each pot was planted with 3 shoot fragments of each of the four species, and there were ten replicate pots. Thus, there were totally 80 pots (plant assemblages), and plants in each pot were planted in four rows and three columns. The substrate in the pots was a layer of 5 cm quartz sand, and we used relatively large quartz (5–10 mm in diameter) to avoid binding too much nutrients from the water. Plants (with pots) were put in two tanks (100 cm in diameter and 70 cm in height) filled with 1/60 full strength of the modified Hoagland solution, and cultured in a greenhouse at Bajia in Beijing from June 24 to July 14, 2014.

After 20 days of recovery and growth, the 80 submerged macrophyte assemblages in the 80 pots were each sank in a bucket (40 cm long × 40 cm wide × 80 cm high) filled with artificially produced, eutrophic water. The water initially contained 7.62 nitrogen (N) mg L^{-1}, 0.52 phosphorus (P) mg L^{-1}, 0.09 chlorophyll *a* μg L^{-1} and 0.88 chemical oxygen demand (COD) mg L^{-1}, which was considered to be severe eutrophication (UNEP, 2013) and also within the range of the nutrients for the species (Tian et al., 2009). We also added to the water other necessary nutrients for the growth of the submerged plants, i.e. 1/60 concentrations of the modified Hoagland solution (Epstein, 1972). During the experiment, no additional nutrients were added to the buckets, and distilled water was added regularly to compensate for the water loss due to evaporation.

The experiment was performed in a greenhouse at Bajia experimental nursery in Beijing from 15 July to 20 August 2014. Buckets were placed randomly in a 5 m x 10 m area within the greenhouse, and were repositioned randomly every week. In the greenhouse, the temperature was 20.5 ± 0.1 °C (mean ± SE), relative humidity 80.0 ± 0.4% and light intensity 223.6 ± 6.5 μmol m^{-2} s^{-1} between 6:00 and 18:00, and 10.79 ± 0.26 μmol m^{-2} s^{-1} between 18:00 and 6:00 (measured every 20 min by an intelligent greenhouse control system, PH-WS, Xinpuhui Technology Co., Ltd, Wuhan, China).

2.3. Plant harvest

On 20–22 August 2014, we harvested all plants in each bucket and sorted them to species. As the plants were easily broken into numerous shoot fragments during harvest, it was impossible to count node number and measure shoot length for all shoot fragments. For each species, we therefore randomly selected eight shoots, measured their total length, and counted total number of nodes. These shoots were oven-dried at 85 °C for 48 h to determine their dry mass. The remaining plants of each species were also oven-dried and weighed.

2.4. *Water quality measurements*

The water quality was measured at 36 days after the experiment was started. From each bucket, we sampled 100 ml water at 20 cm depth below the water surface to determine the contents of total nitrogen, total phosphorus, chlorophyll *a*, COD and biochemical oxygen (BOD). Light transmittance at 5 depth under the water surface and dissolved oxygen were measured at 12:00 - 14:00 during the day with a universal light meter (ULM - 500, Walz GmbH, Effeltrich, Germany) and a Multi-parameter controller (Multi 350i, WTW GmbH, Weilheim, Germany), respectively, before the water samples were taken. To determine light transmittance at 5 depth under water, we measured light intensity both above the water surface and 5 under the water surface, and then divided the latter by the former.

All water samples were stored at 4 until analyses and the analyses were completed within 3 days after sampling. Total nitrogen and total phosphorus contents were measured with Autoanalyzer 3 system (Seal Analytical GmbH, Norderstedt, Germany), chlorophyll *a* content with PhytoPAM (WALZ004, Walz GmbH, Effeltrich, Germany), and dissolved oxygen content with. BOD_5 was determined using the dilution and seedling method and COD_{Cr} by the dichromate method.

2.5. *Data analysis*

For each species in each bucket, we calculated per unit, dry mass, shoot node number and shoot length based on total number of nodes, total shoot length and dry mass of the eight shoots. Then we calculated total number of shoot nodes and total shoot length of each species in a bucket by multiplying shoot node number per unit dry mass and shoot length per unit dry mass, respectively, by total dry mass of the species in the bucket. Dry mass, shoot node number and shoot length of the community in a bucket were the sum of dry mass, shoot node number and shoot length of the species in the bucket, respectively. As each shoot node is potentially able to develop into a new plant, total shoot node number and total shoot length are measures of potential vegetative (clonal) spread (Zhang et al., 2014).

All analyses were conducted in R (R Core Team, 2016). We fitted linear mixed-effects models using the *lme* function in the R package "*nlme*" to test the effect of species richness on the growth (total dry mass, total shoot length and total number of shoot nodes) of the submerged macrophyte assemblages, as well as contents of total nitrogen, total phosphorus, chlorophyll *a*, pH, BOD, COD, dissolved oxygen and light transmittance in the water. In all models, species richness was treatments (Fig. 3a, b & c).

3.2. Water quality

The establishment of the submerged macrophyte assemblages significantly contributed to nutrient removal from the eutrophic water. Approximately 1/3 of total nitrogen from initial concentration 7.62 mg L^{-1} to final concentration 5.09 mg L^{-1} and 2/3 of total phosphorus from initial concentration 0.52 mg L^{-1} to final concentration 0.15 mg L^{-1} were removed after 35 days of the treatments (Fig. 1a, b). However, increasing species richness of the submerged macrophyte assemblages did not significantly improve the capacity of nitrogen or phosphorus removal from the water in the aquatic microcosms (Fig. 1a, b). Species richness also did not significantly affect chlorophyll *a* content and pH in the water after 35 days of the treatments (Fig. 1c, d).

Species richness of submerged macrophytes significantly affected light transmittance and dissolved oxygen content in the water, but had no significant effect on COD and BOD (Fig. 2

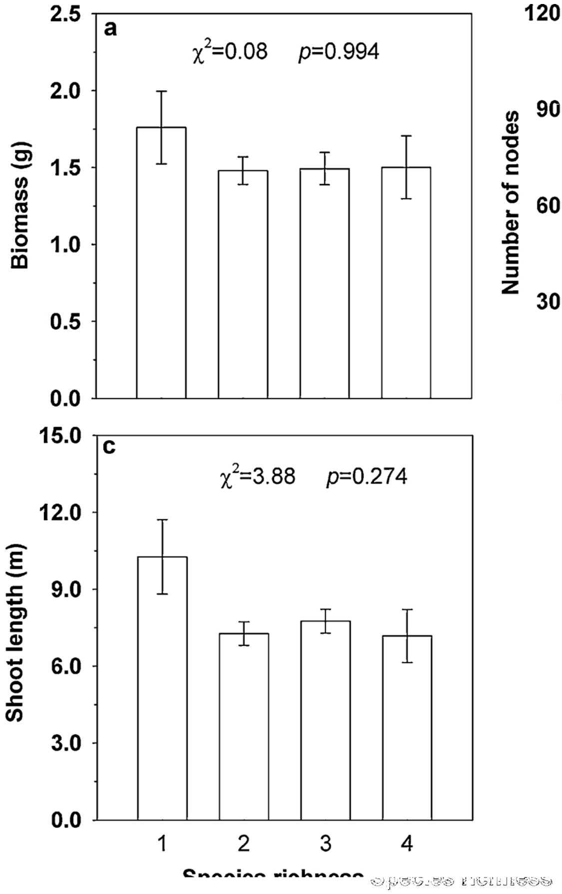

Fig. 3. Effects of species richness on (a) total biomass, (b) total number of nodes and (c) total shoot length of submerged plants. Bars and vertical lines represent means ± SE. Statistical results are also given. Different letters indicate significant difference among treatments.

The contrasting results of species diversity on community productivity between grassland and aquatic ecosystems might be attributed to different resource-partitioning levels of the two ecosystems (light, water, mineral nutrients). In grassland ecosystems, resource partitioning and thus complementary use of resources seem common among species, especially those from different functional groups (grasses, legumes and forbs) (Tilman et al., 1997b; Loreau, 2000). In grasslands, higher species richness commonly generates a stronger complementarity effect among plant species, resulting in a more complete use of resources and thus higher productivity (Shaver, 2002; von Felten et al., 2009; Brown and Rice, 2010). However, aquatic plant species are more similar in their resource use and functional roles compared to grassland plant species, especially when only one type (emergent, floating or submerged plants) of aquatic plant species is present (Mo et al., 2015). Moreover, in contrast to the patchy distribution of nutrients and water in grasslands, which potentially facilitates interspecific complementary interaction (von Felten et al., 2009; Wright et al., 2015), nutrients and water in aquatic ecosystem are distributed more evenly. Therefore, complementarity among submerged macrophyte species especially species of a similar type might be rather weak, resulting in the fact that species diversity had no effect on biomass or vegetative reproduction of certain types of submerged macrophyte assemblages. However, it is important to note that the types of species used in such experiments may result in different outcomes.

4.2. Effects of submerged plant diversity on water quality

Aquatic macrophytes can have significant effects on physical and chemical characteristics of water in aquatic ecosystems, including critical factors such as light transmittance and the availability of dissolved oxygen and mineral nutrients (Carter et al., 1988, 1991; Dierberg et al., 2002). In the current study, species richness significantly affected light availability in water, with the 3-species treatment having the higher light transmittance than monocultures. A higher light transmittance implies a higher water transparency and is usually associated with a smaller number of planktonic algae in the water (Gaiser et al., 2009; Kosten et al., 2009). However, in our study, light transmittance seems to have no clear relationship with the number of phytoplankton as chlorophyll *a* content kept stable in all four diversity treatments. Since light transmittance is affected by both the amount of suspended planktonic algae and small particles from the substrate (Engelhardt and Ritchie, 2001), it is likely that a certain combination of submerged macrophyte species (e.g. 3-species treatments) is more helpful for these particles to settle down. Further measurements are needed to test this hypothesis. In our study, the 1- and the 4-species treatments had significantly higher dissolved oxygen in water than the 2- and 3-species treatments, which is the opposite pattern of light transmittance. This surprising result might be related with the growing status of the submerged macrophytes during the experiment. We found that at the end of the experiment some leaves and/or shoots of the submerged macrophytes were old and yellowish, which may slow down the rates of photosynthesis and therefore the rates of oxygen production. It seems that this phenomenon was a little more obvious in the treatments of 2–3 species according to personal observations. Apparently, the more young, green and healthy shoots are more efficient in producing oxygen than the old and less green shoots, therefore leading to higher dissolved oxygen in the 1- and 4-species treatments. Notably, the old and yellowish shoots were not quantified during the experiment. Therefore, we should be cautious when explaining this result. In the future, it is advisable to monitor dissolved oxygen in a dynamic way to understand better its relationship with submerged plant richness and light transmittance. Overall, weak evidence is shown from our results that species richness of certain types of submerged macrophyte assemblages affects the water quality of the ecosystem.

Aquatic plants have long been used in constructed wetlands for nutrient removal (Dierberg et al., 2002; Nahlik and Mitsch, 2006; Gu, 2008). Similar to the results in previous studies, the submerged macrophyte assemblages in our study showed effective removal of nitrogen and phosphorus. However, increased species diversity of submerged macrophyte assemblages did not further enhance such nutrient removal. Nutrient removal from water could be due to variable processes, such as being retained by the substrate and macrophytes through physical filtration, taken up by the macrophytes and algae (Engelhardt and Ritchie, 2001) and transformed by micro-organisms. However, as the substrate was the same in all experimental treatments, the difference in nutrient removal would likely depend on plant and algae growth as well as the types of plant species (Engelhardt and Ritchie, 2001). Therefore, failure to detect a positive effect of species diversity on nutrient removal is likely because community biomass and phytoplankton content were maintained stable at all four levels of species richness in our study. This result contrasts with the finding of a mesocosm experiment where greater species richness of submerged macrophytes led to higher phosphorus retention (Engelhardt and Ritchie, 2001). The facilitated phosphorus removal in species-rich communities was primarily due to the type of species (sago pondweed and crisped pondweed) used in this study. In this experiment, due to its highly reticulate structure, sago pondweed is assumed to be important in physically filtering phosphorus. Crisped pondweed, on the other hand, is considered to facilitate algal growth to produce more biomass for phosphorus removal (Engelhardt and Ritchie, 2001). However, such a sampling effect due to the presence of certain species affecting ecosystem functions was not clear in our study, probably because similar functional species were used in our study. Therefore, it is not surprising that we did not find diversity effect on nutrient removal in our system. In addition to nutrient uptake by plants and algae, other important processes, e.g. nutrient recycling by microorganisms or nutrient binding to e.g. sediment or surface structures, also play a vital role in nitrogen and phosphorus removal. Due to some limitations of the current study, the mentioned mechanisms could not be investigated, but deserve further research.

5. Conclusions

In contrast to the beneficial effects of high species richness on community productivity and ecosystem functioning in grassland ecosystems, increasing species diversity of submerged macrophyte assemblages does not seem to directly influence the productivity and nutrient removal from eutrophic water in the current study. Despite the higher dissolved oxygen content in 2- and 3-species treatments compared with that in the other two treatments, a clear conclusion cannot be drawn. This is probably due to the use of functionally similar species. However, aquatic ecosystems commonly also consist of other types of aquatic plants, including emergent and floating plant species. Impacts of species diversity of aquatic plants may be different if emergent and floating plants species, or other submerged species, are involved. Further studies should consider different assemblages of different types of macrophytes to investigate the effects on ecosystem functions such as nutrient removal.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.aquabot.2018.11.006.

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