Interspecific competition effects on phosphorus accumulation by *Hydrilla verticillata* and *Vallisneria natans*

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\textbf{Abstract}

The competition between submersed plants has been recognized as an important factor influencing the structure of plant communities in shallow lakes. The ability of different species to take up and store nutrients from the surrounding ambience varies, and hence plant community structure might be expected to affect the cycling of nutrients in lake ecosystems. In this study, the uptake of phosphorus by *Hydrilla verticillata* and *Vallisneria natans* was studied and compared in monoculture and competitive mixed-culture plantings. Results showed that for both studied species the phosphorus concentrations of different tissues and of whole plants was unaffected by competition. However, the quantity of phosphorus accumulated by whole plants of *H. verticillata* was significantly higher in mixture culture than in monoculture, while that of *V. natans* was lower in the mixed culture. The results indicated that *H. verticillata* has a competitive advantage over *V. natans*, when the two species are grown in competition, and is able to accumulate a greater quantity of phosphorus.

\textbf{Key words}: interspecific competition; submersed plants; phosphorus storage

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\section*{Introduction}

Submersed plants play an important role in the cycling of phosphorus through aquatic systems. The uptake and accumulation of nutrients for growth, maintenance, and reproduction during the growing season facilitate the exchange between sediment, water column and plant tissues (Carpenter and Lodge, 1986; Qiu et al., 2001). Furthermore, it is known that nutrient utilization by submersed plants can significantly affect the trophic status and ecosystem functions of shallow lakes (Blindow et al., 2002). Because of these important effects, submersed plant communities have been the subject of numerous investigations in aquatic ecology (Hofstra et al., 1999; Mony et al., 2007).

Competition between submersed plants is a common phenomenon in nature (Tilman, 1987), and is recognized as one of the most important factors determining species dominance in aquatic ecosystems, impacting on many aspects of lake ecosystem function (Gopal and Goel, 1993; Vitousek et al., 1997; Doyle et al., 2007). The competitive abilities of particular plant species may vary with environmental conditions. For example, in mixed cultures at high fertility, *Hydrilla verticillata* has been shown to be a stronger competitor than *Vallisneria americana*; however, under nutrient limited conditions, the growth and competitive abilities of *H. verticillata* were depressed and *V. americana* became the dominant species (Van et al., 1999).

The variable rates of nutrient uptake and release observed for different plant species can have distinct effects on ecosystem nutrient cycling (Knops et al., 2002). Phosphorus concentrations in tissue in 41 different plant species varied from 0.13\% to 1.1\% of plant biomass in dry weight (McJannet et al., 1995). The ability to extract and retain nutrients from the environment may be one of the important factors that influence the general distribution pattern of the competing plant species (Grime and Hodgson, 1987; Garbey et al., 2004). For example, plants with high storage capacities should occur over a broader ecological range than those species with low storage capacities (Thiébaut, 2005).

Although competitive interactions between submersed plant species are very important for the structure and function of ecosystems and may have particularly profound effects on processes such as the phosphorus cycle, few studies have simultaneously investigated the growth and...
biomass allocation effects of competition between aquatic plants with dissimilar growth forms (Wu and Yu, 2004; Larson, 2007). Similarly, few studies have directly examined the competitive abilities of submerged plants with respect to phosphorus uptake. Consequently, the effects of competition between macrophytes, particularly those with dissimilar growth forms, on uptake and storage of phosphorus, are as yet poorly understood (Zhang et al., 2007). Notwithstanding this lack of information, the impact of submerged plant competition in aquatic situations may be of significant ecological significance (Wu and Yu, 2004) and ought to be more thoroughly investigated.

In this study, two aquatic macrophytes with significantly different growth forms were selected for an investigation of competitive effects on phosphorus assimilation. *Hydrilla verticillata* (L.f.) Royle and *Vallisneria natans* (Lour.) Hara are the dominant plant species in many natural aquatic ecosystems in China and are commonly used in the restoration of eutrophic shallow lakes (Qu et al., 2001). The waterweed *H. verticillata* is a rooted submerged species with typically high rates of reproduction and growth (Shearer et al., 2007). It often forms a dense mat, or canopy, at the water surface, reducing the penetration of sunlight to the zones beneath. It exhibits C4-type photosynthesis, resulting in lowered photorespiration, and produces various types of vegetative propagules including stem fragments, axillary turions, and tubers (subterranean turions). The root system is relatively underdeveloped and a significant proportion of nutrient requirement can be absorbed exclusively from the water (Langeland, 1996).

The cosmopolitan eelgrass *V. natans*, is also widespread and highly adaptable (Xie et al., 2007), but typically occurs in the same freshwater habitats to *H. verticillata* (Xie et al., 2006). *V. natans* produces a basal rosette of leaves, but does not form a canopy. The plant therefore depends more on light being available near the sediment for growth and survival. The roots are adventitious without laterals.

In the present study, *H. verticillata* and *V. natans* were grown separately in single-species monocultures and together in mixed-species plantings to investigate their competitive abilities with respect to phosphorus uptake. The results shed light on the role of submerged plants on phosphorus cycling in aquatic ecosystems.

1 Materials and methods

1.1 Plant materials

Specimens of *H. verticillata* and *V. natans* were collected from Huizhou West Lake in Huizhou, Guangdong Province, South China and were pre-incubated in the laboratory of Jinan University for about five months. Apical shoots of *H. verticillata* measuring 20 cm in length were separated from the mother plant, weighed to determine initial fresh weight, and then washed with distilled water before experiments. Whole plants of *V. natans*, each also about 20 cm length, were selected, weighed and washed before experimentation.

1.2 Experimental set-up

The experiments were carried out in nine aquaria with same dimensions (40 cm length × 30 cm width × 50 cm height), each containing sediments and water. The sediments used were obtained from an abandoned rice field in a suburb of Guangzhou City. The sediment was air-dried, then passed through a 0.5 mm mesh sieve to remove coarse debris. The sediment was homogenized and used to cover the bottom of each aquarium to about 10 cm depth. The aquaria were then filled with 55 L lake water taken from Lake Ming in Guangzhou and filtered by plankton net (mesh size: 0.064 mm).

Three treatments were performed in triplicates: monocultures of *H. verticillata* and *V. natans*, respectively, and a mixed culture of both species. The nine experimental aquaria were exposed to natural sunlight from above and the sides were covered by insulating material to prevent light entering laterally. Nutrients were supplied to each aquarium as analytical grade anhydrous NaH$_2$PO$_4$ amounting to a phosphorus load of 100 µg/(L-week); and KNO$_3$ equating to a nitrogen load of 2 mg/(L-week) (expressed as N). In the event of rain, a plastic greenhouse was brought in to shelter the experimental setup and was moved away immediately when rain ceased.

1.3 Sampling and analyses

Plants were harvested on October 1, 2007, after eight weeks' growth in the experimental aquaria. Material harvested from the mixed culture treatments was separated according to species. The plants were washed over a 1 mm mesh sieve to remove attached sediment, debris, and epiphytes. Plant tissues from all nine aquaria were separated into two parts: aboveground and belowground. The plant tissues were oven-dried at 80°C to constant weight for about 12 hr and their dry mass recorded. The plant material was then ground into fine powder in a pestle and mortar for chemical (P) analysis. All samples were digested with a mixture of H$_2$SO$_4$; H$_2$O$_2$ and tissue phosphorus concentrations were analyzed by colorimetry. The phosphorus concentration was expressed as mg phosphorus per gram dry weight and total stored phosphorus was calculated by multiplying concentration (mg P/g) by plant biomass (g).

1.4 Statistical analyses

The means of plant biomass, phosphorus concentrations and storage values for different treatments were compared using an Independent-Sample T Test performed with SPSS Version 16.0 software.

2 Results

2.1 Biomass

The biomass of *H. verticillata* was not significantly different in mixed culture and monoculture (*P > 0.05*, Fig. 1). In contrast, both the aboveground and belowground biomasses of *V. natans* in mixed culture were significantly lower (*P < 0.05*) than that in monoculture. The total
reduction in V. natans biomass under competition from H. verticillata was about 77%.

2.2 Phosphorus concentration

Under monoculture conditions, the concentration of phosphorus in whole plants of H. verticillata was (3.48 ± 0.48) mg P/g. For the aboveground part biomass it was (3.51 ± 0.55) mg P/g and for belowground biomass was (3.22 ± 0.20) mg P/g. For H. verticillata grown in mixed culture, phosphorus concentration was (3.99 ± 0.16) mg P/g for whole plants, (4.03 ± 0.18) mg P/g for aboveground biomass and (3.51 ± 1.02) mg P/g for belowground biomass. There was no significant difference in phosphorus concentration for total, aboveground or belowground biomasses of H. verticillata grown in monoculture (P > 0.05). For V. natans grown under monoculture, phosphorus concentration in whole plants was (4.41 ± 0.46) mg P/g, in aboveground biomass was (4.43 ± 0.29) mg P/g and in belowground biomass was (4.34 ± 1.42) mg P/g. In the mixed planting, phosphorus levels were (4.83 ± 0.73) mg P/g for whole plants, (5.28 ± 0.89) mg P/g in aboveground biomass and (3.40 ± 1.71) mg P/g in belowground biomass. Differences in phosphorus levels observed between the monoculture and mixed culture were not significant (P > 0.05) for whole plants or for the above- and belowground components (Fig. 2).

2.3 Phosphorus storage

Phosphorus storages in both total and aboveground biomass components of H. verticillata in plants grown in mixed culture were much higher than in monoculture (P < 0.05) (Fig. 3). The mean storage of phosphorus in aboveground biomass was 60.18 mg P per plant in monoculture, and 76.72 mg P in mixed plant with an increase of about 27%. The mean phosphorus content of the total biomass was 66.34 mg P in monoculture compared to 83.48 mg P in mixed planting. However, there was no significant difference in the amount of phosphorus stored in belowground tissues between monoculture and mixed culture (P > 0.05).

3 Discussion

Interspecific competition results from mutual exploitation of limiting resources (Tilman, 1987). When more than one species occupy the same habitat and require the same limited resources simultaneously, competition occurs. In shallow lakes, two sources of phosphorus are potentially available to submersed plants: water and sediment (Carignan and Kalff, 1980). However, the relative importance of roots and shoots for nutrients uptake may vary (Barko and James, 1998; Eugelink, 1998). Moreover, submersed
plants can alter their resource allocation to aboveground and belowground tissues, thus optimizing their uptake potential when interspecific competition occurs (Stuart et al., 1999; Zhang et al., 2007). The present study shows that the phosphorus concentration of different tissues (aboveground and belowground biomass) and the whole plant (total biomass) of both species was not significantly altered by the competition. Previous studies have yielded similar results, for example, under the competition between Canna indica and Schoenoplectus validus at low and high nutrient conditions, the phosphorus contents in the aboveground, rhizome and root of both plants (except that in the root of S. validus in high nutrient) were not significantly different to those achieved in monoculture (Zhang et al., 2007).

Aquatic plant species may differ in their capacity to assimilate nutrients from the environment (Kadlec and Knight, 1996). For instance, the nutrient uptake capacity of Phragmites australis was seen to be higher than that of Cyperus pyrus (Brix, 1994). The capacity of submersed plants for nutrient storage depends on both the requirement for nutrients used in rapid growth and the plant’s ability to accumulate nutrient (Garbey et al., 2004). Plants with high nutrient storage capacities in nature should be able to occur over a broader ecological range than those with low storage capacities, and therefore be highly competitive (Grime and Hodgson, 1987; Garbey et al., 2004). In the present study, phosphorus storage in H. verticillata was observed to be higher in mixed culture than in monoculture, suggesting that in the presence of V. natans, H. verticillata has an enhanced capacity for accumulating phosphorus. In contrast, for V. natans, the amount of phosphorus stored in both aboveground and belowground biomass was lower in mixed culture, apparently as a result of the large reduction in overall biomass caused by the presence of H. verticillata (Fig. 1). This result suggests that competition between H. verticillata and V. natans decreases the ability of V. natans to thrive and accumulate phosphorus and therefore that the former species may affect phosphorus cycling in aquatic ecosystems more profoundly than the latter.

In conclusion, when competition exists between H. verticillata and V. natans, the former has a competitive advantage in terms of accumulating phosphorus.

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References


