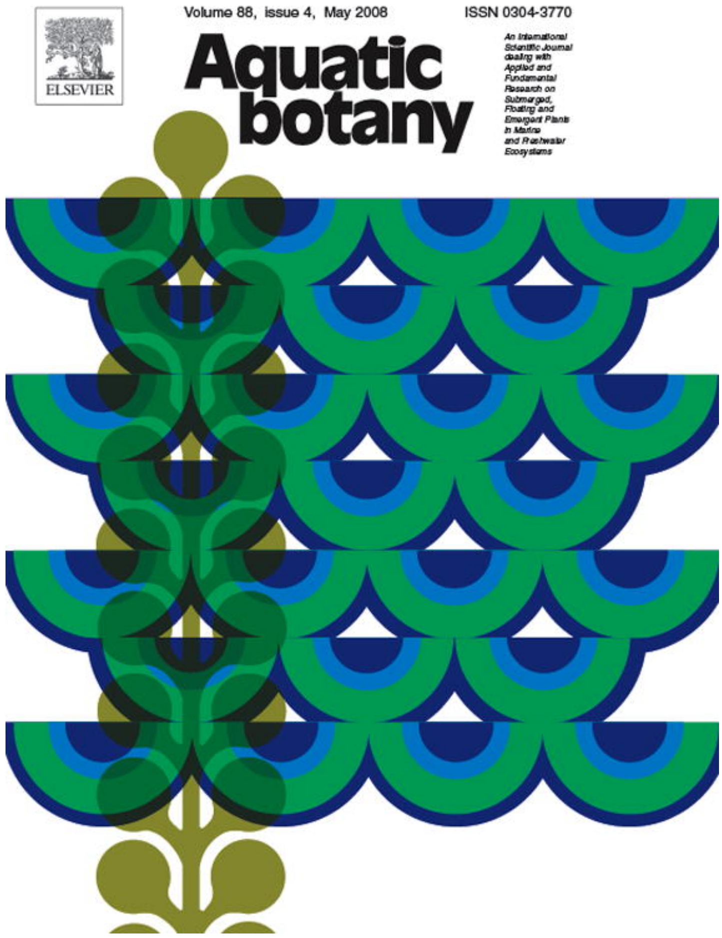
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Short communication

A comparison of irradiance and phosphorus effects on the growth of three submerged macrophytes

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Abstract

A fully factorial pond experiment was designed using two irradiance levels and two phosphorus concentrations to investigate irradiance and phosphorus effects on the growth of three submerged macrophytes: common waterweed (*Elodea canadensis*), Eurasian water milfoil (*Myriophyllum spicatum*), and water stargrass (*Zosterella dubia*). Results revealed that higher irradiance (230 μmol s^{-1} m^{-2} vs. 113 μmol s^{-1} m^{-2} at 2 m depth) had significant positive effects on submerged macrophyte growth: increasing the number of individuals (seven-fold), the number of species surviving (two-fold), aboveground biomass (11-fold), belowground biomass (10-fold), and total biomass (11-fold), whereas elevated sediment phosphorus (2.1–3.3 mg g^{-1} vs. 0.7 mg g^{-1} dry sediment) did not have any significant impact. However, responses to irradiance differ among macrophyte species due to their morphology and physiology. Waterweed increased in numbers of individuals and total biomass under high irradiance while biomass per individual remained the same (~0.02 g). The other species increased both in numbers and biomass per individual. These results suggest that increased irradiance rather than decreased phosphorus loading is the main driver of changes in submerged macrophytes in North American temperate lake ecosystems.

Keywords: Submerged macrophyte; Dreissenid mussel; Water clarity; Species richness; Phosphorus; Irradiance

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1. Introduction

Often invasive species are associated with human impacts and environmental degradation (Mills et al., 1994). However, increased filtering by invasive dreissenid mussel increased water clarity, thereby altering ecosystem function in many North American lakes during the last several decades (Skubinna et al., 1995; Zhu et al., 2006). At the same time, phosphorus (P) loading was reduced in many lakes, especially following the Great Lakes Water Quality Agreement (GLWQA) of 1972. Both changes are likely to affect macrophyte communities by increasing species richness and altering community composition (Chambers, 1987; Chambers and Kalff, 1987; Rørslett, 1991; Toohey et al., 2004; Wernberg et al., 2005). However, field observations cannot separate the relative importance of dreissenid mussels and P reduction as a cause for the observed changes in macrophyte communities in North American lakes. Natural systems often experience multiple environmental changes; understanding the combined impact of these changes, such as the mussel invasion and the decline in nutrients, is essential for predicting ecosystem responses and developing management strategies (Lauridsen et al., 2003; Chu et al., 2004).

We conducted an experiment to test the separate effects of irradiance (mimicking dreissenid invasion) and changes in P concentration on submerged plant communities. We chose three common species with different growth forms in this study. Erect common waterweed (*Elodea canadensis*) usually grows as a tangled mat on the sediment, tolerates low irradiance, and can continue some photosynthesis under ice (Stodola, 1967). Unlike waterweed, erect water stargrass (*Zosterella dubia*) retains long stems in water column. Eurasian water milfoil (*Myriophyllum spicatum*) generally forms canopies and shades other plants (Smith and Barko,

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1990). Both Eurasian milfoil and water stargrass absorb nutrients through roots from the sediments (Carignan and Kalff, 1980). Therefore, we expect these three species to respond differently to changes in irradiance and P: canopy-forming species should be less affected by an irradiance decrease than erect species and the response to P-addition in the sediments should be positively correlated with the degree these species depend on nutrients from roots. Our objective was to assess the response of submerged macrophytes to high and low irradiance and high and low sediment P with special attention to species surviving, numbers of individuals, and biomass.

2. Methods

2.1. Experimental setup

The experiment was conducted in a research pond (area = 30 m × 30 m and depth = 2 m) at the Cornell Experimental Ponds facility, Ithaca, NY from June 18 to September 13, 2004. We used a completely randomized factorial design with two irradiance levels (shade simulated pre-dreissenid irradiance and ambient irradiance represented current irradiance) and two P concentrations (P-addition simulated pre-GLWQA and ambient P represented current P concentration). Twenty-four plastic containers (56 cm in diameter and 50 cm in height) were randomly assigned to four different treatments: (1) ambient irradiance/P-addition (Light + P), (2) ambient irradiance/ambient P (Light), (3) shade/P-addition (Shade + P), and (4) shade/ambient P (Shade). Each container was filled with 25 kg of previously dried and well-mixed soil, which was collected from the nearby pond bank and therefore did not contain propagules of submerged macrophyte species. Containers were evenly spaced at a distance of 4 m on the bottom of the pond. Dissolved triple phosphate (100 g, 46%, Espoma Co., Millville, NJ) was added to the P-addition treatments and 70% shade cloth (1.5 m × 1.5 m, International Greenhouse Company, Georgetown, IL) was secured by ropes and stakes on the water surface for shade treatments. Common waterweed, Eurasian water milfoil, and water stargrass were collected in nearby natural ponds and three 10 cm long individuals of each species were planted in each container.

2.2. Irradiance in water and total phosphorus (TP) concentration in the sediments

Irradiance (400–700 nm) was measured at water depths of 0, 1, 1.5, and 2 m using a LI-193 spherical quantum sensor coupled with a LI-COR 1400 data logger (LI-COR, Lincoln, NE). Sediment samples were collected from each container at the beginning and the end of the experiment. Samples were dried at 65 °C until a constant weight was achieved. They were homogenized and 5 mg sub-samples were dissolved with 5% (w/v) potassium persulfate. The samples were analyzed for P content using a Beckman DU® 640 Spectrophotometer (Beckman Coulter, Inc., Fullerton, CA) following the procedures of APHA (2000).

2.3. Submerged macrophyte measurement

Whole plants were harvested after all water was pumped out of the pond. Plants were separated by species and counted; stem segments were counted for common waterweed because this species reproduces short stems from stem fragmentation. Stems (including leaf) and roots were separated. Aboveground and belowground biomass were weighed after drying at 65 °C until a constant weight was achieved. Total biomass was calculated as the sum of aboveground and belowground biomass.

2.4. Statistical analysis

Measured variables were shown as mean ± S.E. We used two-way ANOVA to compare TP content in sediments with P-addition and time as the independent factors as well as plant species surviving and total number of individuals (all species combined) with irradiance and P concentration as the independent factors. We also used ANOVA for split-plot designs (irradiance and P treatments were whole-plot factors, and macrophyte species was sub-plot factor) to compare irradiance and P effects on several measures of growth of the three plant species, including number of individuals, aboveground biomass, belowground biomass, and total biomass (Kuehl, 2000). No transformations were needed following tests for heteroscedasticity. All ANOVA was followed by the least significant difference (LSD) analysis to compare different treatments at the level $\alpha = 0.05$ and all statistical analyses were conducted by using the GLM procedure of SAS 9.0 (SAS Institute, Cary, NC).

3. Results

3.1. Irradiance in water and TP concentration in the sediments

Irradiance at 1, 1.5, and 2 m depths was reduced by 51–71% by the shade cloth compared with ambient irradiance, but the water surface irradiance (above the shade cloth) was similar across all treatments (1240–1350 μmol s^{-1} m^{-2}). Thus, the shade cloth produced a substantial shading effect in the shade treatments.

Mean TP concentration of the sediment in the P-addition treatments was higher than in the ambient P treatments (average 2.7 mg g^{-1} vs. 0.8 mg g^{-1} dry sediment) throughout the experiment even though there was a decline of TP of approximately 30% in the P-addition treatment over the course of the experiment (d.f. = 1, $F = 86.80$, $p < 0.001$). Sediment TP was initially higher in the Shade + P (3.3 ± 0.3 mg g^{-1} dry sediment) than the Light + P treatment (2.1 ± 0.3 mg g^{-1} dry sediment), probably due to the difficulty in homogenizing sediments in the containers.

3.2. Abundance and species surviving

Total number of individual plants (abundance) summed over all three species differed among treatments (Fig. 1A, ANOVA,

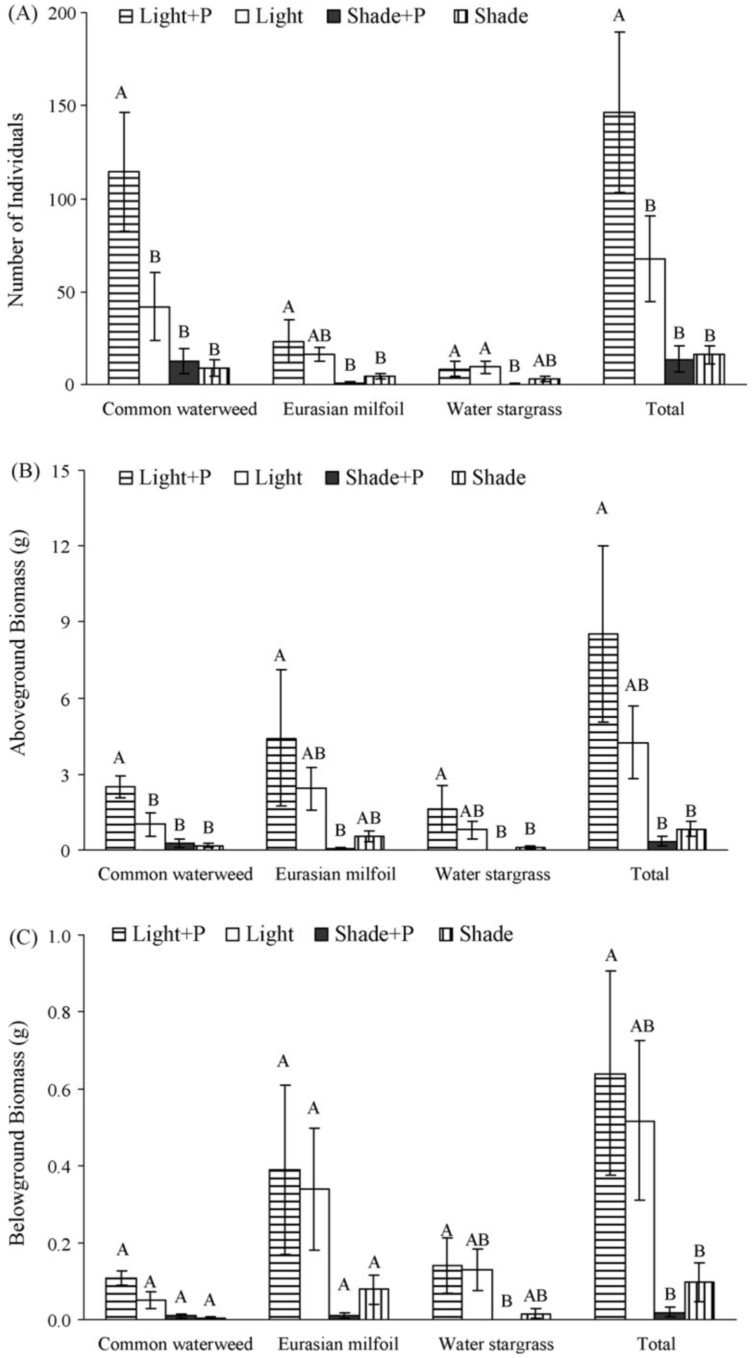

Fig. 1. Growth of three submerged macrophytes in response to changes in irradiance and phosphorus in the pond experiment: (A) number of individuals; (B) aboveground biomass; and (C) belowground biomass. Light + P means ambient irradiance and P-addition; Light means ambient irradiance and ambient P; Shade + P means shade and P-addition; and Shade means shade and ambient P. Different letters denote significant differences among treatments within species at $\alpha = 0.05$ level using the LSD analysis in ANOVA.

d.f. = 3, $F = 6.29$, $p = 0.004$); it was significantly higher (146 ± 48) in the Light + P treatment than in the other three treatments (14–68). Abundance was seven-fold higher, on average in the light vs. shade treatments (d.f. = 1, $F = 13.84$, $p = 0.001$). There was no significant P effect nor was there an interaction effect between irradiance and P on abundance (P effect: d.f. = 1, $F = 2.36$, $p = 0.140$; interaction: d.f. = 1, $F = 2.66$, $p = 0.119$).

The three macrophyte species responded differently to irradiance and P (Fig. 1A, d.f. = 31, $F = 5.11$, $p < 0.001$; species effect: d.f. = 2, $F = 18.49$, $p < 0.001$). Abundance of common waterweed was significantly higher in the Light + P treatment with no differences among the other three treatments. Abundance of Eurasian water milfoil and water stargrass was similar in the Light and Light + P treatments and higher than in both shade treatments (Fig. 1A). There was no difference in abundance between Shade and Shade + P treatments for any species.

The average number of species at the end of the experiment (species surviving) differed among the four treatment combinations (d.f. = 3, $F = 4.90$, $p = 0.010$). Nearly 50% more species survived in the light treatments compared to the shade groups (2.5 ± 0.1 vs.1.7 ± 0.3; d.f. = 1, $F = 12.25$, $p = 0.002$), whereas adding P did not affect species surviving (d.f. = 1, $F = 1.81$, $p = 0.193$). In addition, there was no significant interaction between irradiance and P on species surviving (d.f. = 1, $F = 0.65$, $p = 0.429$).

3.3. Submerged macrophyte biomass

Macrophyte aboveground, belowground and total biomass for all the three species combined paralleled the results for abundance and was significantly higher in the Light + P treatment (Fig. 1B and C). The light treatments contained 11-fold more aboveground biomass, 10-fold more belowground biomass, and 11-fold more total biomass than the shade treatments. P-addition had no significant effect (Table 1). The response in belowground biomass of individual plant species differed significantly, and the differences in responses in aboveground biomass and total biomass were marginally significant (Table 1).

4. Discussion

Our experiment investigated macrophyte growth under two irradiance levels comparable to before and after the dreissenid invasion, and two sediment P concentrations similar to those occurring due to P abatement dictated by the GLWQA. The results showed that submerged macrophyte growth, abundance, and diversity responded more strongly to irradiance increases than to lower sediment P. Therefore, we concluded that the irradiance is the primary controlling factor for these submerged macrophytes. We contend that water clarity is mainly driven by the invasion of dreissenid mussels and, if true, that dreissenid invasion is the main driving force for recent changes in submerged macrophytes in North American lakes. In contrast, P reduction may have minimal or no impacts on macrophyte communities. This is consistent with findings from available observational studies in freshwater lakes (Skubinna et al., 1995; Mayer et al., 2002; Chu et al., 2004; Zhu et al., 2006, 2007).

Our results demonstrated that P concentration in the sediments had no significant impact on either plant diversity (species surviving) or growth and reinforce earlier studies that indicated a lack of temporal association between P reduction and expansion of macrophytes (Mayer et al., 2002; Lauridsen et al., 2003; Zhu et al., 2006). Sediment TP in this study (0.74–3.3 mg g^{-1} dry sediment) was somewhat high compared to temperate mesotrophic–eutrophic North American lakes (0.3–1.2 mg g^{-1} dry sediment) (Carignan and Kalff, 1980; Chambers, 1987; Rooney et al., 2003). However, a decrease in sediment P to at least 0.7 mg g^{-1} dry sediment should have little effect on macrophytes. Consequently, a reduction in P in the sediments following the implementation of the GLWQA should have minimal effects on submerged macrophytes.

Submerged macrophyte species exhibited different responses to irradiance and P both in our study as well as elsewhere (e.g., Chambers and Kalff, 1987). This is likely due to plant morphology and growth forms. For example Eurasian water milfoil and water stargrass can succeed in a range of sediment types and grow relatively tall because they depend on roots to obtain nutrients from the sediment (Carignan and Kalff, 1980). Conversely, waterweed has minimal roots and nutrients from the water column may be more important for this species. Thus, we expected a larger effect of P-addition on the two species with higher dependency on roots. This was not the case. The higher biomass of waterweed in the Light + P treatment compared to the Light treatment may have been due to increased TP in the water column in the P-addition treatment as there was a 30% loss of sediment TP during the experiment. The lack of a P effect in the plants more dependent on roots indicates that TP in the sediments was not limiting to these species. Another example of differences in macrophyte species is their responses in changes in total number of individuals or biomass. Waterweed increased in total number of individuals to gain more biomass in the light treatments while its individual mass remained the same (~0.02 g). Other species changed both the number and individual mass in their responses. The difference in response to irradiance and P among species is associated with their reproductive strategy and morphology (Stodola, 1967; Smith and Barko, 1990) and may also be affected by competition (Chambers and Prepas, 1990; Toohey et al., 2004). We could not quantify competition in this study due to the relatively short experimental period. Chambers and Kalff (1987) found erect species to be primarily regulated by sediment TP (0.22–0.86 mg g^{-1} dry sediment) and bottom-dwelling species largely regulated by irradiance (17–39% surface irradiance). Irradiance range in this study was similar to that in our study (29–49%) whereas TP was lower than in our study and therefore more likely limiting to the macrophytes tested by Chambers and Kalff (1987). This difference in sediment P concentrations may explain the differences between Chambers and Kalff's results and ours.

Many temperate lakes have been experiencing both P reduction and water clearing due to dreissenid grazing,

Table 1
Summary of *p*-values from ANOVA for measured variables from the pond experiment to test irradiance and phosphorus (P) effects on three submerged macrophyte species

Variables	ANOVA model	Irradiance effect	P effect	Interaction (irradiance × P)	Species effect
Species surviving	0.010	0.002	0.193	0.429	–
Total individuals	<0.001	0.001	0.140	0.119	<0.001
Aboveground biomass (g)	0.004	0.006	0.326	0.218	0.074
Belowground biomass (g)	0.010	0.006	0.898	0.562	0.009
Total biomass (g)	0.004	0.006	0.359	0.236	0.063

subsequent changes in submerged macrophyte communities, and associated alteration of ecosystem structure and function (Skubinna et al., 1995; Chu et al., 2004; Zhu et al., 2006, 2007). Because the increased irradiance, independent of changes in P, is coupled with the arrival of dreissenid mussels in many ecosystems, our study suggests the increase in dreissenid grazing is likely to have a larger impact on submerged macrophytes than P reduction. The observed responses varied among species, probably associated with differences in their morphology and physiology (Chambers, 1987; Toohey et al., 2004; Wernberg et al., 2005). In addition, their response can be affected by the presence of other species (e.g., Toohey et al., 2004). Predictions of macrophytes community responses to increased irradiance based on a mechanistic understanding of the multitude of species-specific responses and interactions is a formidable task. But experiments such as ours, when directed by observational studies, help us understand current processes in nature and predict future changes in submerged macrophyte communities.

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