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Effects of N and P additions to water column on growth of *Vallisneria natans*

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ABSTRACT

We examined the effects of adding nitrogen (N) and phosphorus (P) to the water column of aquatic mesocosms in which the freshwater eelgrass *Vallisneria natans* was growing. Total nitrogen (TN) and total phosphorus (TP) concentrations in the water column, biomasses (measured as Chl *a*) of phytoplankton and periphyton, light intensity, and dry biomasses of plant material were measured. Ramet count, biomass/ramet, and ratio of belowground/aboveground biomass were calculated. Compared to controls, mesocosms with added N exhibited increased TN, periphyton Chl *a*, and biomass ratio, but showed reductions in ramet counts, biomass, total biomass/ramet, and aboveground biomass/ramet of *V. natans*. The addition of P resulted in increased ramet counts, biomass, and biomass ratio compared to controls, but reduced total biomass/ramet and aboveground biomass/ramet. The addition of combined N + P resulted in higher concentrations of TP and Chl *a* of phytoplankton, but lower light intensity, ramet counts, and biomasses compared with controls. Biomass (total and aboveground)/ramet and biomass ratio remained unaltered after N + P addition. Our study demonstrates that growth of *V. natans* is significantly affected by addition of N and P in the water column, which has important implications for plant management in aquatic ecosystems because decline or enhancement of the growth of submersed plants can markedly alter many aspects of aquatic ecosystem. In light of our findings, both N and P loading to aquatic ecosystems should be controlled to restore the degraded aquatic ecosystem or protect aquatic ecosystems with submerged plants.

Key words: nutrient, growth, submerged plant, aquatic ecosystem.

INTRODUCTION

Submerged plants have significant effects on the trophic character of aquatic ecosystems (Blindow et al. 2002) and play an important role in the cycling of nutrients within shallow lakes (Carpenter and Lodge 1986). They compete with microalgae for nutrients, thereby limiting phytoplankton growth (Blindow et al. 1993), absorb nutrients directly from the water column, and contribute to the oxygenation of the water (Wetzel 1964, Carpenter and Lodge 1986, Barko and James 1998). These effects have been the subject of numerous investigations and much discussion in aquatic ecology.

Although most aquatic macrophytes growing below the water level rely heavily on sediment nutrients (Carignan and Kalff 1980), nutrient levels in the water column also affect their growth (Harlin and Thorne-Miller 1981). Numerous studies have confirmed that growth of submerged plants correlates positively with nutrient concentrations in water columns (Cronin and Lodge 2003, Xie et al. 2005), although others have indicated that such enrichment can have a negative effect on growth (Wang and Li 2002, Irfanullah and Moss 2004). These effects are commonly attributed to light limitation resulting from shading by periphyton and phytoplankton (Phillips et al. 1978, Larned 2010).

Nutrient availability in natural habitats is heterogeneous in both space and time, even on a small scale (Xie et al. 2004). In freshwater systems, concentrations of specific nutrients such as nitrogen (N), phosphorus (P), or N and P together, often vary temporally and spatially in the water column (Smith et al. 1999), and in the context of shallow lakes these variations may have significant effects on growth of submerged plants (Madsen and Cedergreen 2002, Guo et al. 2008). In addition, nutrients can affect resource allocation of individual plants, influencing belowground/aboveground biomass ratios (Cronin and Lodge 2003, Xie et al. 2004). However, these observations are based on relatively few studies, and the effects of N and P additions to the water column on submerged plants are not well understood. Further research is required to shed light on the role of these nutrients in lake ecosystems.

We conducted experiments in 12 aquatic ecosystems in order to evaluate the effects of additional N and P in the water column on growth of *Vallisneria natans* (Lour.) Hara, a freshwater eelgrass with a clonal growth habit. *Vallisneria natans* is widely distributed and highly adaptable (Xie et al. 2007), and is the dominant species in most natural aquatic ecosystems in China. It is also commonly used in the restoration of eutrophicated lakes (Qiu et al. 2001, Xie et al. 2005).

MATERIALS AND METHODS

Experimental setup

Experiments were carried out in mesocosms (upper diameter = 54 cm, bottom diameter = 40 cm, and height = 60 cm; i.e., 100-L volume) containing sediments and water. Sediments (total N [TN], 1.13 ± 0.04 mg · g^{-1} DW; total P [TP], 0.56 ± 0.01 mg · g^{-1} DW) obtained from Ming Lake (Zhang and Mei, 2013), a eutrophic shallow water body in

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Guangzhou City, were air dried, powdered, and sieved through a sieve (mesh size 0.5 mm) to remove coarse debris and clumps. The homogenized sediment was added as a ~10-cm-thick layer to each mesocosm. These mesocosms were then filled with Ming Lake water (100 L), filtered through a plankton net (mesh size 0.064 mm) to remove zooplankton and coarse phytoplankton. Other parameters for the filtered water were as follows: TN, 2.15 mg · L^{-1}; TP, 0.06 mg · L^{-1} (Zhang and Mei, 2013). The mesocosms were exposed to natural sunlight and allowed to acclimatize for 2 wk. Nutrient concentrations in the mesocosms after acclimatization were TN, 2.41 ± 0.42 mg · L^{-1}; and TP, 0.14 ± 0.01 mg · L^{-1}.

At the end of the acclimatization period, nine rooted clonal individuals (ramets) of *V. natans* (18.2 ± 1.2 cm in length and 0.041 ± 0.010 g in dry weight), originating from stock collected from the Huizhou West Lake in Huizhou, Guangdong Province, South China but subsequently grown in outdoor tanks at Jinan University for several years, were planted in each mesocosm and permitted to grow for 8 wk before they were harvested. Mesocosms were then separated into three treatment groups: three replicates received additional N, three replicates were supplemented with P, and a further three received extra N + P (Wolfe and Lind 2010). An additional group of three replicate mesocosms to which no nutrients were added served as controls. The calculated doses of 1.5 mg N L^{-1} wk^{-1} (as sodium nitrate), and 0.1 mg P L^{-1} wk^{-1} (as sodium dihydrogen phosphate) were added as solutions, prepared by dissolving nutrient compounds in distilled water. Nutrient solutions were stirred into the mesocosms to ensure complete mixing. Filtered lake water was added periodically to each mesocosm in order to maintain the water levels during the experiment.

In order to assess the colonization of periphyton, single identical strips of artificial grass (Liboriussen and Jeppesen 2006) measuring 32.1-cm length by 1.5-cm width were set on the sediment surface of each mesocosm 2 wk before the end of the experiment.

SAMPLING AND ANALYSIS

Samples of mesocosm water for analysis of total nitrogen (TN) and total phosphorus (TP) concentrations were collected every 2 wk during the experiment (8 wk) before the addition of nutrients. 500 ml of water was obtained from each mesocosm with the use of a clean bottle. TN and TP were analyzed spectrophotometrically after persulfate digestion according to American Public Health Association [APHA] (1992).

Five hundred milliliter samples of water for phytoplankton biomass (chlorophyll *a*, i.e., Chl *a*) analyses were collected from each mesocosm at the end of the experiment. Chl *a* was determined spectrophotometrically after ethanol extraction at room temperature, as described by Jespersen and Christoffersen (1987). The artificial grass strips were removed from the mesocosms at the end of the experiment and the accumulated biomass (Chl *a*) of periphyton was determined spectrophotometrically after ethanol extraction at room temperature, as above. Meanwhile, light intensity above the sediment surface was also measured between 0900 and 1200 h with the use of an underwater irradiance meter (ZDS-10W).

Plants were harvested at the end of the experiment (after 8 wk) and washed over a 1-mm mesh sieve to remove attached sediments, debris, and epiphytes. The number of plants in each tank was recorded. Plant tissues were separated into aboveground and belowground biomass and oven dried overnight at 80° C to constant weight, so that dry masses could be recorded. The number of *V. natans* ramets present in each mesocosm was divided by the original number (nine).

Statistical analyses

Repeated-measurement ANOVAs were used to test for significant differences in TN and TP under different enrichment regimes. Where a significant difference was determined, an LSD test was used to detect treatments that differed. One-way ANOVA was performed to detect differences between treatments on each sampling occasion. If a significant difference emerged, LSD test was used to detect the differing treatments. One-way ANOVA was also performed to detect differences in Chl *a* levels of phytoplankton and periphyton, light intensity, ramet count, biomass ratio, and biomass/ramet, as well as biomasses of plants under different nutrient enrichment treatments. Where a significant difference was determined, an LSD test was used to detect treatments that differed. Results are presented as means ± standard deviation (SD).

RESULTS AND DISCUSSION

Studies have shown that plant growth may respond to changes in nutrient levels with alterations in ramet number (Guo et al. 2008) and growth rate (Cronin and Lodge 2003, Xie et al. 2004), which are regarded as plastic responses to nutrient availability (Grime et al. 1986). N and P are the most frequently cited factors affecting the growth of submerged plants (Phillips et al. 1978, González Sagrario et al. 2005). In this study, TN concentrations in the water column varied dramatically between treatments (repeated-measurements ANOVAs, treatment effect; Figure 1), being higher in the N-added treatments (1.36 ± 0.11 mg · L^{-1}) than in the control group throughout the trial (0.76 ± 0.39 mg · L^{-1}; $P < 0.05$). No significant difference in TN concentrations was observed between the controls and the P-added (0.81 ± 0.26 mg · L^{-1}) groups, or in the N + P–added (0.92 ± 0.29 mg · L^{-1}; $P > 0.05$) groups. TP concentrations in the water column also varied dramatically with additions of N and P (repeated-measurements ANOVAs, treatment effect; Figure 1). TP concentrations in the water column did not differ significantly between the controls (0.06 ± 0.02 mg · L^{-1}) and groups with additions of either N (0.06 ± 0.02 mg · L^{-1}) or P alone (0.08 ± 0.03 mg · L^{-1}; $P > 0.05$) (Figure 1). However, TP was significantly elevated in treatments with N + P added together (0.12 ± 0.03 mg · L^{-1}) compared to the controls ($P < 0.05$).

Opinions on the nature of the response under different nutrient conditions vary. Some researchers perceive that

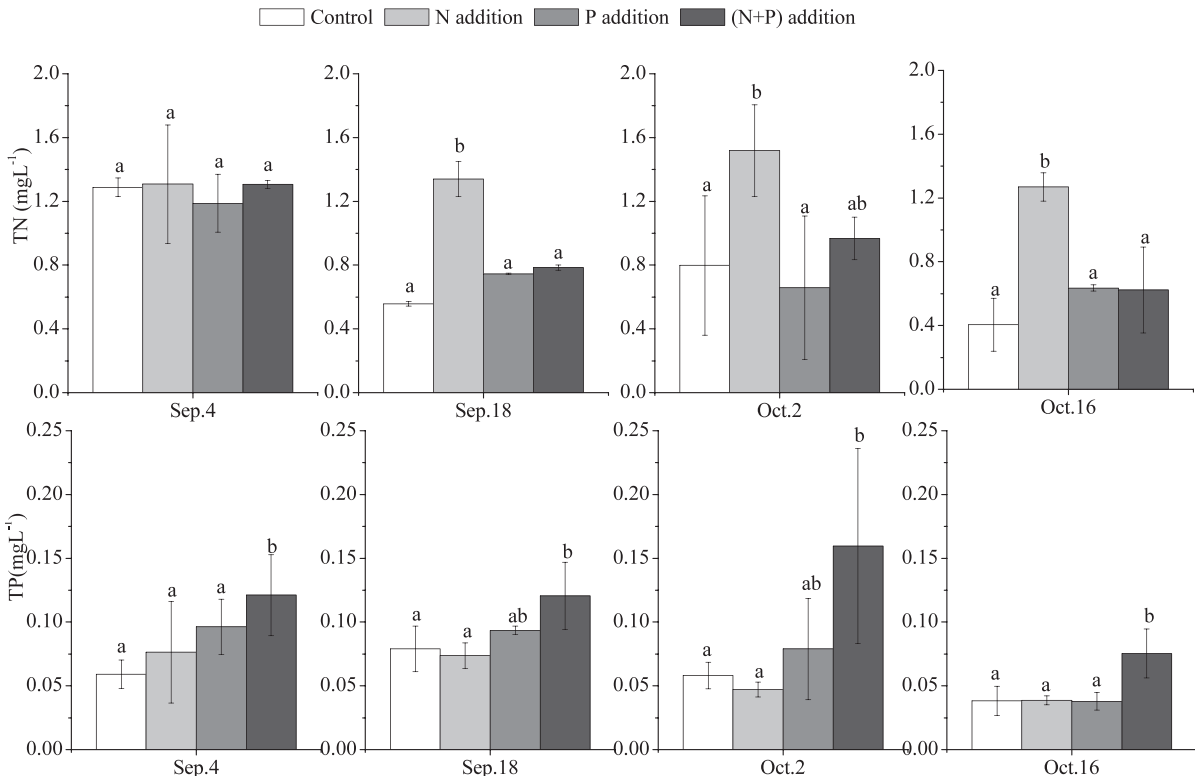

Figure 1. Total nitrogen (TN) and total phosphorus (TP) (mean ± SD) in different treatment groups. Letters (a), (b), and (c) indicate significant ($P < 0.05$) differences in TN. Statistically equal TN levels share a common letter.

the addition of N to water columns increases growth of submerged plants (Ye et al. 2007), whereas others find evidence for an inhibitory effect (Best 1980, Cao and Ni 2004). Similarly, increased levels of N and P in the water column have been linked with reduced growth of submerged plants (Jeppesen et al. 1998), but this is not always the case (Cronin and Lodge 2003). In the current study, ramet counts of *V. natans* were found to be lower in groups receiving additional N and N + P than in the controls (one-way ANOVA, treatment effect, $P < 0.05$; Figure 2). In the controls, the average number of ramets was 5.6 ± 0.6 plant^{-1}. In groups receiving supplementary N and N + P, counts averaged 4.4 ± 0.3 and 3.1 ± 0.7 plant^{-1}, 22 and 44% lower than in controls, respectively. In addition, total and tissue (belowground and aboveground) biomasses, as well as total biomass/ramet, aboveground biomass/ramet were lower in the N- and N + P–added treatments than in the controls (one-way ANOVA, treatment effect, $P < 0.05$; Figures 3 and 4). Compared with controls (3.30 ± 0.27 g), total biomass was about 40% lower by the addition of N (1.99 ± 0.16 g) and 46% lower with added N + P (1.77 ± 0.13 g). Belowground biomass was 17% lower in N-added treatments (0.37 ± 0.00 g) and 51% lower in N + P–added groups (0.22 ± 0.00 g). Aboveground biomass was 43% lower with N added (1.62 ± 0.15 g) and 46% lower in N + P treatments (1.55 ± 0.12 g). These results indicate that growth rates of *V. natans* decrease in the presence of additional N and N + P.

Previous studies have shown that addition of N stimulates the growth of periphyton on the leaves of submerged plants (Smith and Lee 2006) and excessive periphyton can inhibit the growth of macrophytes (Lauridsen and Peder 2003). In the current study, periphyton biomass was significantly increased by the addition of N (Figure 5), suggesting a likely mechanism for the reduced growth of *V. natans*.

The reduction in submerged plant growth in the N + P– treatment group can best be explained by the shading effect of increased phytoplankton (Jeppesen et al. 1998). The addition of N + P together has been previously reported as a strong promoter of phytoplankton growth (Smith et al. 1999, Smith et al. 2006). Growth of phytoplankton leads to increased light attenuation, so that light becomes a limiting resource for submerged plants, leading to poor growth rates and low ramet number. In this study, the Chl *a* of phytoplankton increased (Figure 5) and light intensity decreased (Figure 6) upon addition of both N + P. However, ramet formation was increased in the group receiving additional P (one-way ANOVA, treatment effect, $P < 0.05$; Figure 2). Ramet numbers increased to 10.6 ± 0.8 plant^{-1} in the P-added treatment, an increase of about 92% over controls. Total biomass increased by 39% (4.57 ± 0.65 g), belowground biomass by 66% (0.74 ± 0.12 g), and aboveground biomass by 34% (3.83 ± 0.56 g) in treatments with added P (Figure 3). These data suggested that the addition of P stimulates the growth of *V. natans*. The natural availability of P is often limited in aquatic ecosystems (Richardson et al. 1999). Many studies have shown strong correlations between water column P concentration and growth of submerged plants (Thiébaut and Muller 2003,

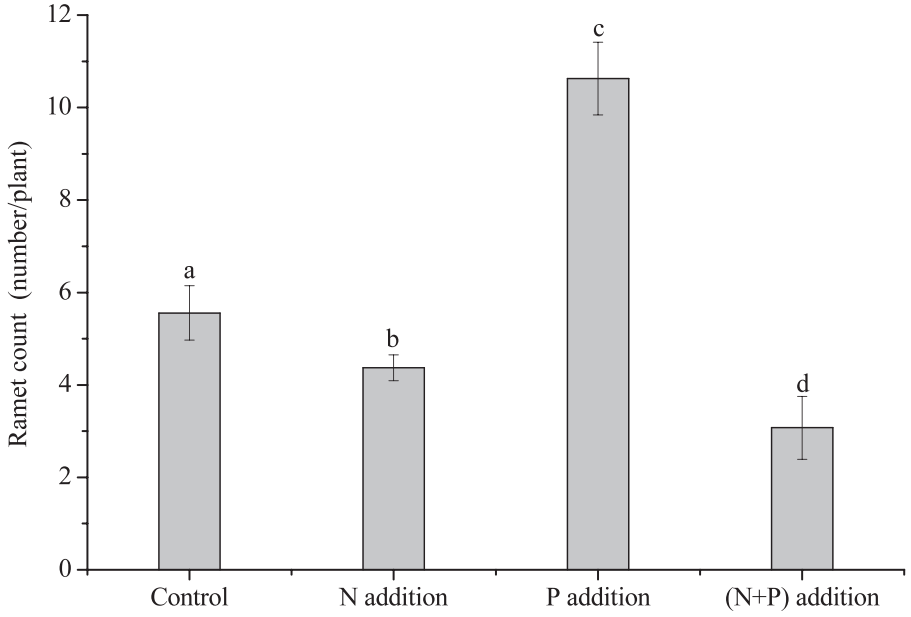

Figure 2. Ramet number under different treatment conditions (mean ± SD). Letters (a), (b), (c), and (d) indicate significant ($P < 0.05$) differences in ramet number.

Zhang et al. 2007). Our finding that added P increases growth of *V. natans* in experimental mesocosms is consistent with these studies.

Biomass allocations were found to vary under different treatment conditions (Figure 7). These changes may reflect the mechanism whereby submerged plants regulate resource capture under variable conditions. Generally, when nutrient levels in water are low, plants allocate more resource to the growth of roots, resulting in an increased ratio of belowground/ aboveground biomass (Grime et al.

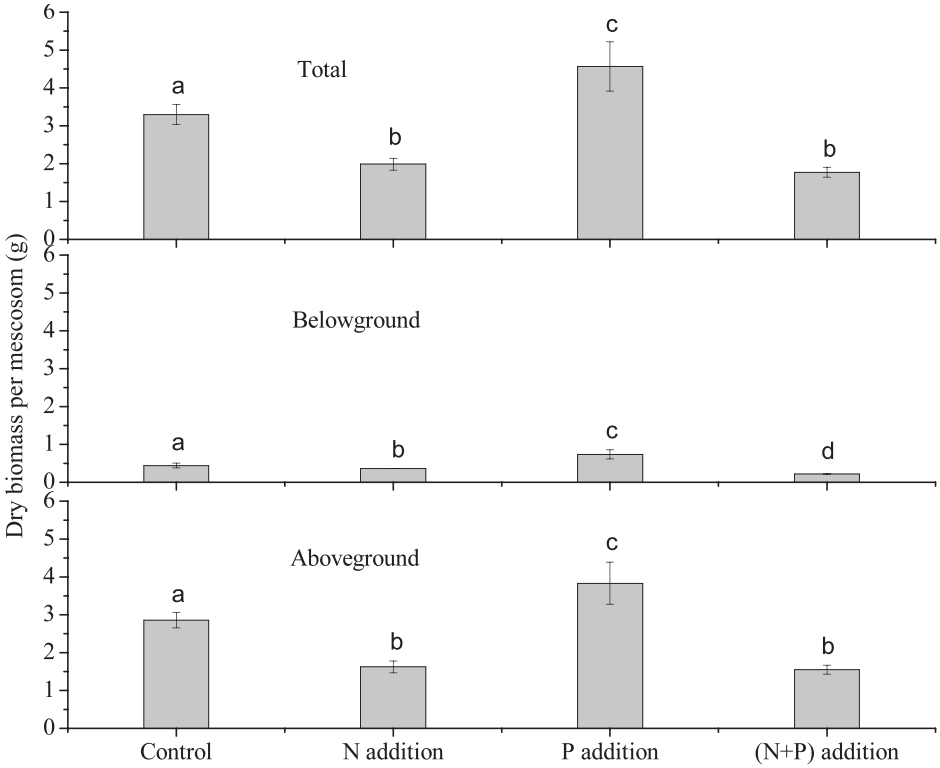

Figure 3. Dry biomass of *Vallisneria natans* under different treatment conditions (mean ± SD). Letters (a), (b), (c), and (d) indicate significant ($P < 0.05$) differences in the dry biomass. Statistically equal biomasses share a common letter.

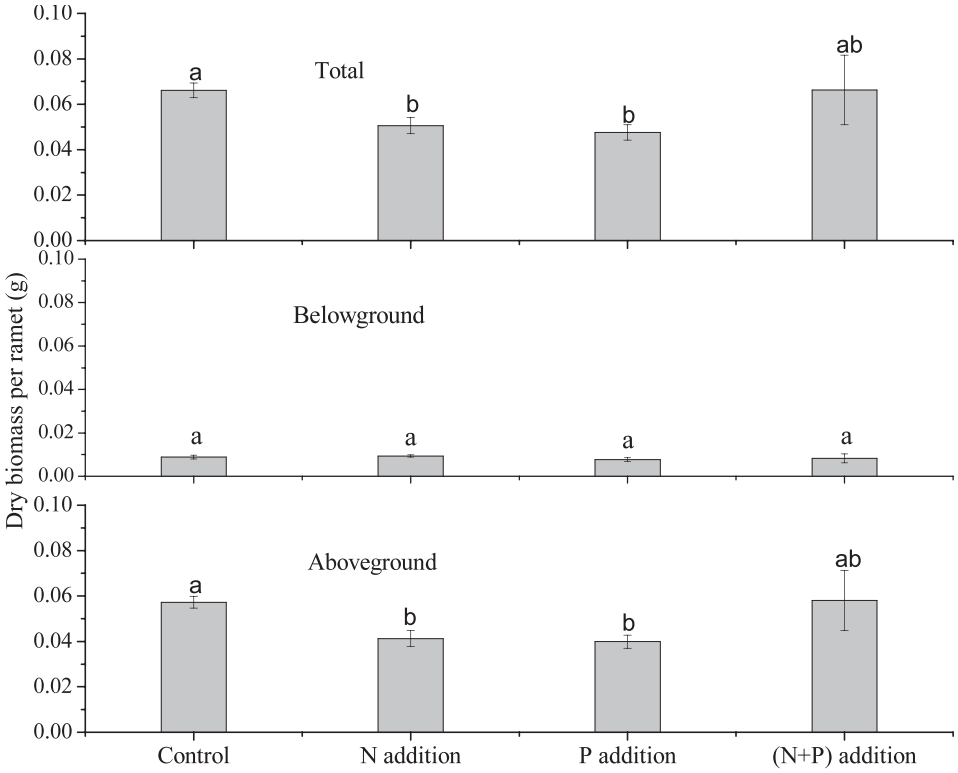

Figure 4. Dry biomass per ramet of *Vallisneria natans* under different treatment conditions (mean ± SD). Letters (a), (b), and (c) indicate significant ($P < 0.05$) differences in the dry biomass. Statistically equal biomasses share a common letter.

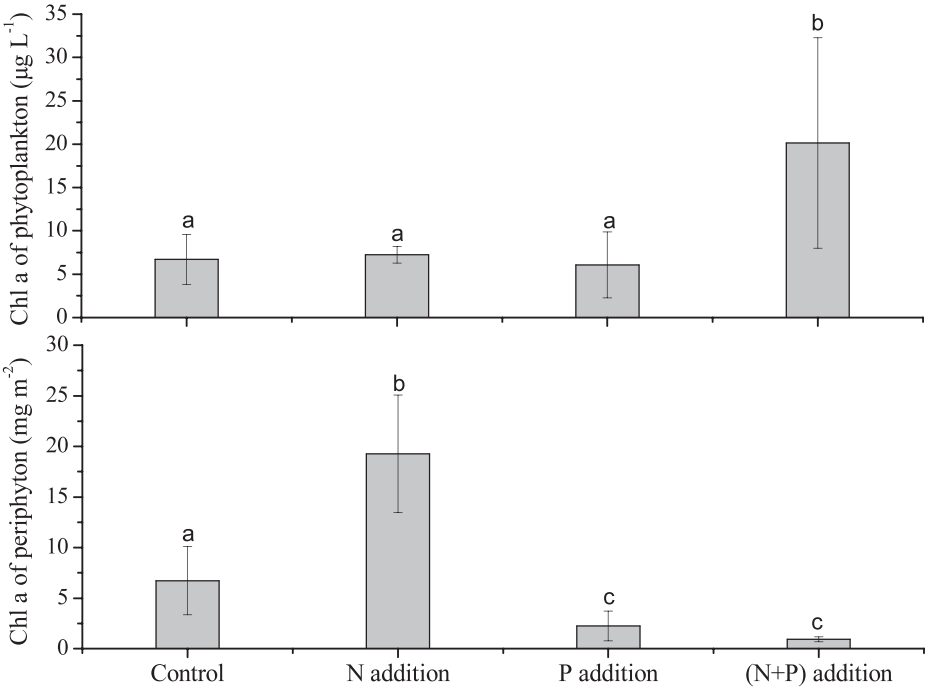

Figure 5. Phytoplankton and periphyton biomasses under different treatment conditions (mean ± SD). Letters (a), (b), and (c) indicate significant ($P < 0.05$) differences in biomasses of phytoplankton and periphyton. Statistically equal biomasses of phytoplankton and periphyton share a common letter.

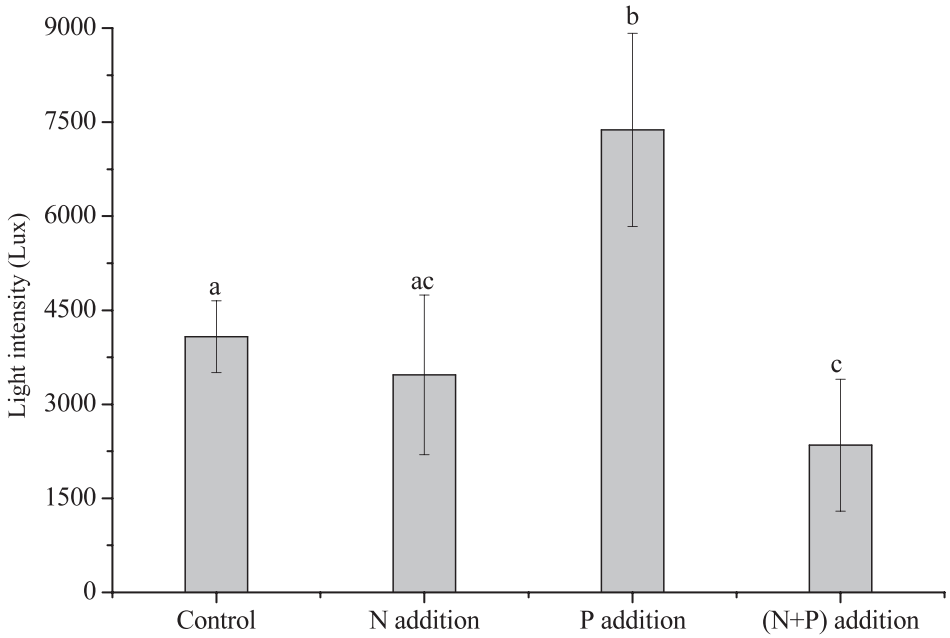

Figure 6. Light intensity (mean ± SD) in different treatments. Letters (a), (b), and (c) indicate significant ($P < 0.05$) differences in the light intensity. Statistically equal light intensities share a common letter.

1986). Conversely, when water nutrient levels are high, more resources are directed to the growth of shoots, resulting in lower belowground/aboveground ratios (Denny 1972). Interestingly, however, examples of the opposite effect or no effect on the root biomass ratio in response to water column nutrients have also been reported (Chambers et al. 1989). In the present work, belowground/aboveground biomass ratios of *V. natans* increased in treatment groups where N and P were added separately (one-way ANOVA, treatment effect, $P < 0.05$). However, in the combined N + P–addition group, biomass ratios remained stable as biomass accumulation was similarly reduced both belowground and aboveground.

It is well known that human activities have profound effects on global biogeochemical cycles of both N and P (Galloway et al. 1995, Vitousek et al. 1997, Ashley et al. 2011). Excessive nutrients delivered to aquatic ecosystems through human activities can inhibit or enhance the

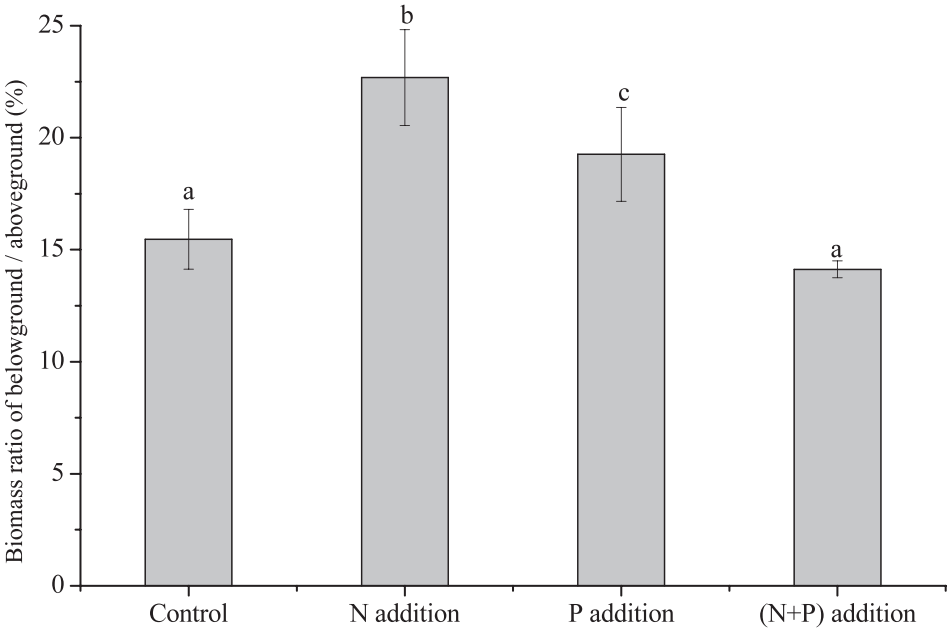

Figure 7. Biomass ratio of *Vallisneria natans* under different treatment conditions (mean ± SD). Letters (a), (b), and (c) indicate significant ($P < 0.05$) differences in the biomass ratio. Statistically equal biomass ratios share a common letter.

growth of submerged plants, with marked knock-on effects on many aspects of freshwater ecosystem functioning. For example, enhanced growth of submerged plants can contribute to decreased phytoplankton biomass, resulting in clear water. Conversely, inhibition of growth and even loss of submerged plants due to excessive nutrient loading may promote phytoplankton production and lead to a turbid state in shallow lakes. Thus, submerged plants play important roles in aquatic ecosystems (Carpenter and Lodge 1986), and their restoration and protection are thus of key importance for plant management. This study is helpful in understanding the basic biology of the native plant known to be an important measure in restoring the degraded aquatic ecosystems because of nutrient loading. In such degraded aquatic ecosystems, the reduction of external nutrients loading of both N and P would be useful for the growth of the plant, thereby enhancing the plant restoration in these degraded aquatic ecosystems. In addition, to protect plants in aquatic ecosystems with submerged plants, both N and P loading to such ecosystems should be controlled.

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