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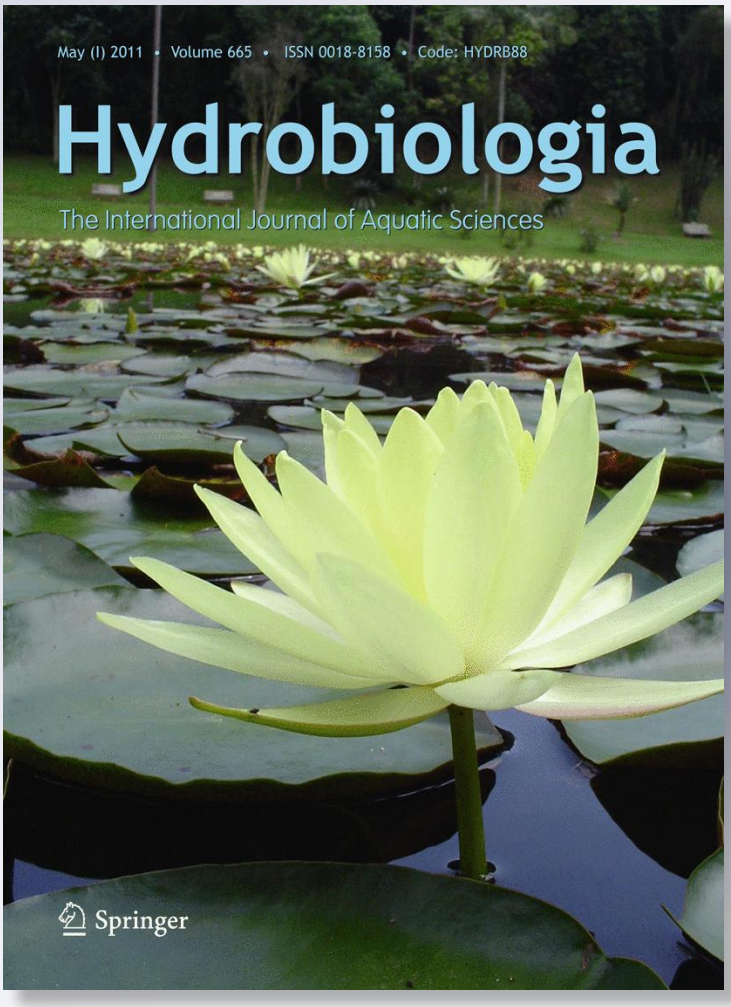

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PRIMARY RESEARCH PAPER

Influences of water column nutrient loading on growth characteristics of the invasive aquatic macrophyte *Myriophyllum aquaticum* (Vell.) Verdc.

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Abstract Nuisance growth of *Myriophyllum aquaticum* has often been attributed to high amounts of nutrients. The uptake of nitrogen and phosphorus from sediments and their allocation have been documented in both natural and laboratory populations. However, nutrient loading to surface water is increasingly becoming an important issue for water quality standards. Aquatic macrophytes that develop adventitious roots may be able to survive through the uptake of water column nutrients. Our objectives for this study were to assess *M. aquaticum* growth when combinations of nitrogen and phosphorus were added to the water column. Mesocosm experiments were conducted where nitrogen (1.8, 0.8, and 0.4 mg l^{-1}; high, medium, and low) and phosphorus (0.09, 0.03, 0.01 mg l^{-1}; high, medium, and low) concentrations were paired and added to the water column. After 12 weeks, the combination of 1.80:0.01 N:P resulted in greater ($P < 0.01$) total biomass and greater biomass for all plant tissues. Total biomass at the 1.80:0.01 N:P combination was 53% greater than biomass at all other combinations. The yield response of *M. aquaticum* was a quadratic function of tissue nutrient content. Yield was positively ($r^2 = 0.82$) related to increasing nitrogen content, whereas a negative ($r^2 = 0.89$) relationship was determined for increasing phosphorus content. We propose the negative relationship is due to increased nutrient competition and shading by algae resulting in reduced *M. aquaticum* growth. Tissue nutrient content indicated that critical concentrations (1.8% nitrogen and 0.2% phosphorus) for growth were not attained except for nitrogen in plants grown in the 1.80:0.01 N:P combination. These data provide further evidence that *M. aquaticum* requires high levels of nitrogen to achieve nuisance growth. Survival through uptake of water column nutrients may be a mechanism for survival during adverse conditions, a means of long distance dispersal of fragments, or may offer a competitive advantage over species that rely on sediment nutrients.

Keywords Nitrogen · Phosphorus · Aquatic plant · Parrotfeather · Non-native · Exotic

Introduction

Habitats around the world are experiencing an increasing number of invasions of non-indigenous species (Vitousek et al., 1997). Most species fail to successfully establish, but some species will colonize and grow to nuisance levels, often with negative consequences on the local plant community

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composition, ecosystem functions, and human uses and economic resources (Vitousek et al., 1996; Chapin et al., 2000; Pimentel et al., 2000). Environmental changes as a result of species invasions highlight the importance of understanding the factors that may limit a species ability to invade a particular habitat (Chadwell & Engelhardt, 2008). The theory of fluctuating resource availability implies that a plant community becomes more susceptible to invasion whenever there is an increase in unused resources (Davis et al., 2000). An increase in unused resources can occur from a decline in resource use from native species, or resource supply can increase at a faster rate than native species can sequester it (Davis et al., 2000). Whenever resource supply goes up, there are more resources available to invading species which makes a particular habitat more vulnerable to invasion (Davis et al., 2000).

A key resource that is often limiting in aquatic systems is the availability of nutrients for macrophyte growth. In recent years, the amount of nutrients of anthropogenic origin are increasingly finding their way into waterbodies worldwide, which has resulted in declines of macrophyte diversity and changes in community structure (Phillips et al., 1978; Vitousek et al., 1997; Bedford et al., 1999; Tracy et al., 2003). Increased nutrient availability may be a key component in the plant invasion process (Elton, 1958). Some invasive species are able to increase their growth rates in response to increases in nutrient availability and out-compete native species that cannot respond in a similar fashion (Burke & Grime, 1996; Vitousek et al., 1997; Kennedy et al., 2009). These new competitors that are capable of higher growth rates may have long-term negative impacts to native community composition (Kennedy et al., 2009).

Nutrient amendment studies for aquatic plants have typically focused on enrichment of sediment nutrients, as the sediment is often considered the most important source of nutrients for aquatic plants (Barko & Smart, 1981, 1986; Spencer & Ksander, 1995). However, as the amount of nutrients finding their way into waterbodies increases, understanding the effects of water column enrichment on macrophyte communities, invasive species, and the invasion process will become more important (Kennedy et al., 2009). One invasive aquatic macrophyte that is becoming problematic in shallow lakes, ponds, streams, rivers, and irrigation and drainage canals is *M. aquaticum*.

Myriophyllum aquaticum is not considered a major noxious aquatic weed throughout most of its range; however, it can cause severe localized problems (Sutton, 1985). Its reliance on high nutrient environments (Sutton, 1985; Sytsma & Anderson, 1993a, b) may be an important predictor as to where this species can colonize and the severity of the invasion. *Myriophyllum aquaticum* typically invades shallow wetlands, slow moving streams, irrigation reservoirs or canals, edges of lakes, ponds, sloughs, or backwaters (Sutton, 1985; Timmons & Klingman, 1958). These areas typically have frequent nutrient pulses and can support luxurious plant growth.

Previous studies of nutrient uptake by *M. aquaticum* indicate that the majority of nitrogen and phosphorus required for growth could be obtained from the sediment (Bristow & Whitcombe, 1971; Barko & Smart, 1981). However, Sytsma & Anderson (1993c) reported that only about 2% of water transpired by *M. aquaticum* originated in the sediment, and they concluded that mass flow did not enhance nutrient supply to or from sediment roots. The relative growth rate of sediments roots was similar to zero, further indicating a general lack of importance of sediment roots with respect to nutrient transport within the plant (Sytsma & Anderson, 1993c). Therefore, we conducted mesocosm experiments to determine how *M. aquaticum* would respond to the loading of different combinations of nitrogen and phosphorus to the water column representing oligotrophic to eutrophic water. Our objectives were to determine water column nutrient effects on whole plant biomass as well as each tissue type of *M. aquaticum*; and to determine the biomass yield response as nutrient content increased. These data should offer insights into habitat types in which *M. aquaticum* could be a successful invader and the potential importance of water column nutrients to invasive aquatic macrophyte growth.

Materials and methods

A mesocosm study was conducted at the R.R. Foil Plant Science Research Center, Mississippi State University, Starkville, MS (33°28′29.76″ N, 88°46′24.70″ W) for 12 weeks from September 20

to December 8, 2006 and repeated from September 7 to November 30, 2007. Both the studies were conducted in 36, 1100-l mesocosms (*L* 161 cm, *W* 175 cm, *H* 64 cm) with a 3 by 3 factorial arrangement of treatments arranged in a randomized complete block design with four repetitions per nutrient combination. Nutrient combinations consisted of all possible pairings of nitrogen (1.8, 0.8, and 0.4 mg l^{-1}; high, medium, low, as ammonium nitrate) and phosphorus (0.09, 0.03, 0.01 mg l^{-1}; high, medium, and low as potassium phosphate) to determine growth limitations of water column nutrients. Nitrogen and phosphorus concentrations were determined based upon concentrations found in eutrophic, mesotrophic, and oligotrophic waters (Wetzel, 2001).

Planting of *M. aquaticum* consisted of placing two apical shoots, approximately 20 cm in length, into each of 288, 3.78-l pots containing a washed pea gravel substrate. Pea gravel was used as a substrate to ensure there were no additional nutrients present that would otherwise occur in a soil substrate. Eight pots of planted *M. aquaticum* were placed into each mesocosm that were filled with 757 l of water. Water was supplied to each mesocosm from an irrigation reservoir adjacent to the mesocosm facility. Air was supplied to all mesocosms from a regenerative air blower using 2.5 cm stone diffusers and a PVC lift pipe.

After planting, pretreatment plant and water samples were collected to assess biomass and nutrient concentrations in the water column of each mesocosm prior to nitrogen and phosphorus amendments. Water samples were collected and transported to the Mississippi State University Forestry Soils and Hydrology Lab, where total nitrate and phosphate were determined using the APHA method 4110: determination of anions by ion chromatography (Eaton et al., 2005). Following pretreatment sampling, the total amount of nitrogen and phosphorus (mg) for use in treatment combinations was determined based on a water volume of 757 l. Appropriate amounts of nitrogen and phosphorus were measured using an analytical balance and added to appropriately labeled mesocosms at 0, 3, 6, and 9 weeks after start (WAS). Prior to any nutrient amendments at all treatment times, water samples were collected in a similar fashion to pretreatment samples and the water volume returned to 757 l in all mesocosms. In 2007, in vivo chlorophyll *a* was recorded in each mesocosm at 3, 6, 9, and 12 WAS using a handheld fluorometer (Turner Designs, Sunnyvale, CA) to estimate algal density for each nutrient combination.

Myriophyllum aquaticum biomass was assessed at 3, 6, 9, and 12 WAS by harvesting the plants from two pots in every mesocosm. Plants were washed and sorted to emergent shoots (2–3 nodes below the last green leaf), submersed shoots, stolon, and sediment roots. Plant tissues were dried at 70°C for 72 h then weighed; subsequent biomass is expressed as g DW pot^{-1} for each WAS and plant tissue. At 12 WAS, the dried emergent shoots were sent to the Mississippi State Chemical, Industrial and Agricultural Services Laboratory, Mississippi State University, where the percent nitrogen and phosphorus was determined using the AOAC Official Method 990.03, combustion method (AOAC International, 2000).

Statistical analyses were conducted using SAS software (SAS Institute, Inc., Cary, NC, USA). A Mixed procedures model was utilized to examine nutrient combination effects on total biomass, emergent shoot, submersed shoot, stolon, and root biomass of *M. aquaticum*; year, block, and their subsequent interactions were considered random effects in the model (Littell et al., 1996). Data were analyzed within WAS to account for a treatment by WAS interaction. If a significant main effect was observed, treatment means were separated using least squares means and grouped using the Least Significant Difference method. Relative growth rates (RGR) (ln log g DW pot^{-1} day^{-1}) were also calculated for each WAS and nutrient combination for total, emergent shoot, submersed shoot, stolon, and root biomass using the following equation outlined by Hunt (1982):

$$r = \frac{\ln(W_2) - \ln(W_1)}{t_2 - t_1} \quad (1)$$

where W_1 and W_2 are plant dry weights at times t_1 and t_2. A mixed procedures model was also utilized to determine differences in RGR, tissue nutrient content, and chlorophyll *a* across nutrient combinations.

Polynomial regression analysis was used to determine the relationship between total *M. aquaticum* biomass yield and nutrient content in tissues. Regression models were sequentially fit beginning with a linear model. Polynomial terms were then added one at a time and lack of fit determined using partial

t-tests. Regression analysis would also allow the estimation of a critical nutrient content for plant tissues. All analyses were conducted at a $P < 0.05$ level of significance.

Results

Mean (±1 SE) water column nutrient data are summarized in Table 1. Pretreatment (0 WAS) nutrient concentrations were 0.02 ± 0.01 mg l^{-1} for nitrate and 0.00 mg l^{-1} for phosphate, indicating there were very little nutrients present in the water column prior to amendments and all nutrients available for plant growth would come from our treatment combinations. Overall, there was very little nitrate or phosphate detected in the water across nutrient combinations. The exceptions being the medium:low and high:low N:P combinations which had an accumulation of nitrate by 12 WAS. Relative growth rates for each tissue component and nutrient combinations across WAS ranged from 0.0 to 0.02 for total biomass, −0.10 to 0.03 for emergent shoot biomass, −0.15 to 0.05 for submersed shoot biomass, −0.01 to 0.02 for stolon biomass, and −0.19 to 0.07 for root biomass. The large negative values are indicative of the planting technique used in the study. The emergent fragments used for planting did not have submersed shoots, stolons, or roots attached and, therefore, the calculation of RGR for the time interval from planting to 3 WAS would always be negative when using a natural logarithm approach because the weight at time two is subtracted (most often a negative number) from the weight at time one which is 0 for the above-mentioned tissues. Analyses of RGR resulted in no significant differences ($P > 0.05$) between nutrient combinations and all *M. aquaticum* biomass (total and plant parts) across WAS which is likely a result of nutrient deficiency, therefore, there will be no further discussion of these data.

Total *M. aquaticum* biomass was significantly greater at the high:low N:P combination by 6 WAS than biomass at all other nutrient combinations (Fig. 1). Biomass was on average 42% greater at the high:low N:P combination during this time. At 12 WAS, biomass was 53% greater at the high:low N:P combination, significantly higher than all other nutrient combinations. When nitrogen was held constant at 1.80 mg l^{-1} and phosphorus increased from 0.01 to 0.09 mg l^{-1}, there was a significant decrease in *M. aquaticum* biomass beginning at 6 WAS and continued to 12 WAS.

Myriophyllum aquaticum stolon biomass was slower to respond to water column nutrient amendments as differences were not observed until 9 WAS (Fig. 2). Stolon biomass in the high:high N:P combination at 9 WAS was significantly lower (43 and 36%, respectively) than the high:low and high:-medium N:P combinations. At 12 WAS, the only difference in stolon biomass occurred at the high:low N:P combination where biomass was on average 43% greater than biomass in other nutrient combinations.

Table 1 Summary of mean (±1 SE) nitrate and phosphate concentrations for each water column nutrient combination

Target concentration N:P (mg l^{-1})	Weeks after start							
	3		6		9		12	
	NO_3	PO_4	NO_3	PO_4	NO_3	PO_4	NO_3	PO_4
0.40:0.01	0.17 ± 0.06	0.02 ± 0.01	0.03 ± 0.02	0.00 ± 0.00	0.02 ± 0.01	0.03 ± 0.03	0.04 ± 0.01	0.00 ± 0.00
0.40:0.03	0.17 ± 0.07	0.05 ± 0.02	0.01 ± 0.00	0.01 ± 0.01	0.01 ± 0.00	0.00 ± 0.00	0.01 ± 0.00	0.01 ± 0.00
0.40:0.09	0.17 ± 0.06	0.18 ± 0.05	0.01 ± 0.01	0.02 ± 0.01	0.00 ± 0.00	0.04 ± 0.02	0.03 ± 0.01	0.19 ± 0.06
0.80:0.01	0.30 ± 0.11	0.02 ± 0.01	0.02 ± 0.01	0.00 ± 0.00	0.18 ± 0.07	0.05 ± 0.02	0.25 ± 0.06	0.00 ± 0.00
0.80:0.03	0.30 ± 0.11	0.05 ± 0.02	0.01 ± 0.00	0.01 ± 0.01	0.01 ± 0.00	0.01 ± 0.01	0.06 ± 0.02	0.00 ± 0.00
0.80:0.09	0.31 ± 0.11	0.14 ± 0.05	0.02 ± 0.01	0.02 ± 0.01	0.01 ± 0.00	0.05 ± 0.01	0.06 ± 0.03	0.11 ± 0.04
1.80:0.01	0.92 ± 0.14	0.02 ± 0.01	0.59 ± 0.23	0.00 ± 0.00	3.39 ± 0.32	0.01 ± 0.01	5.95 ± 0.33	0.00 ± 0.00
1.80:0.03	0.53 ± 0.22	0.04 ± 0.02	0.03 ± 0.01	0.01 ± 0.01	0.12 ± 0.06	0.04 ± 0.03	0.47 ± 0.17	0.00 ± 0.00
1.80:0.09	0.63 ± 0.24	0.14 ± 0.05	0.01 ± 0.01	0.03 ± 0.01	0.04 ± 0.03	0.05 ± 0.02	0.27 ± 0.11	0.03 ± 0.02

Pretreatment (0 WAS) nutrient concentrations were 0.02 ± 0.01 mg l^{-1} for nitrate and 0.00 mg l^{-1} for phosphate

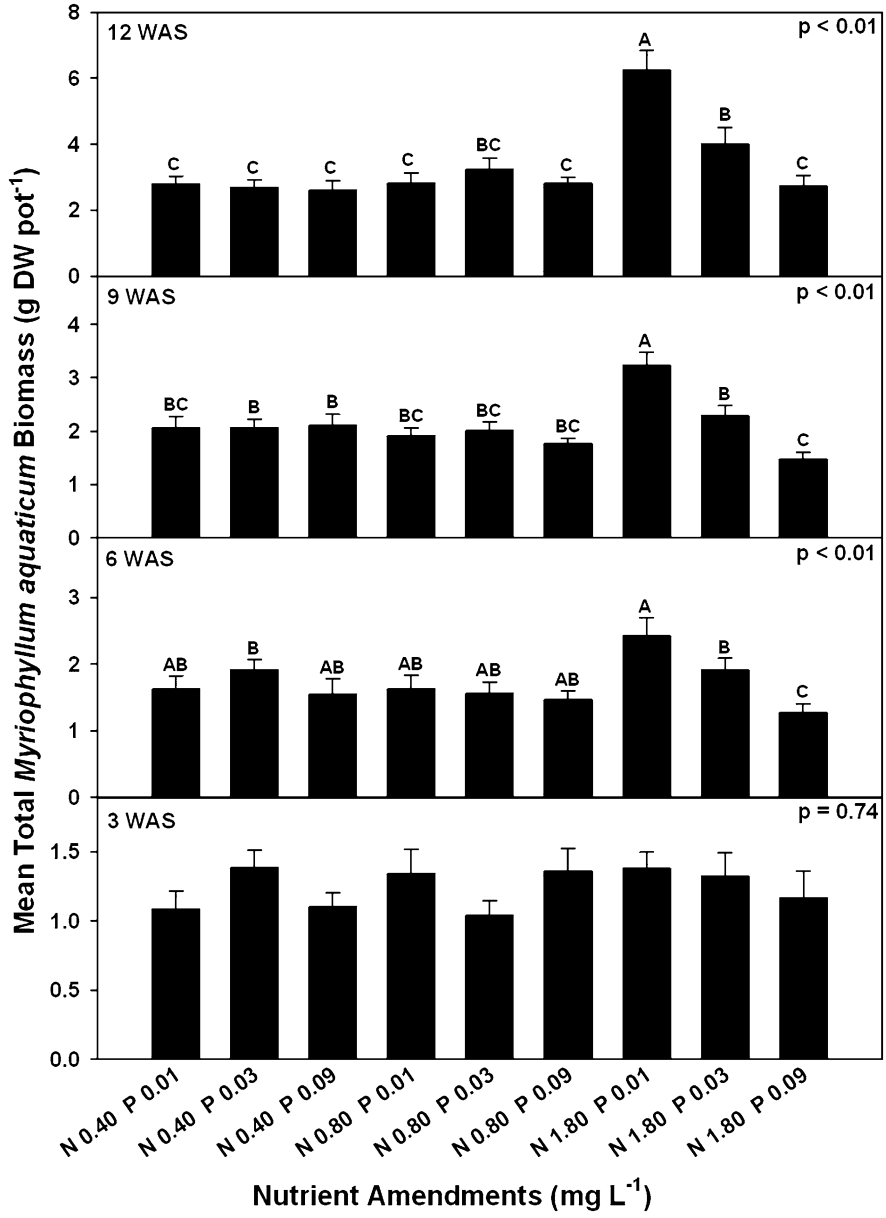

Fig. 1 Mean (±1 SE) total biomass of *Myriophyllum aquaticum* grown in varying nitrogen and phosphorus combinations to the water column. Analyses were conducted within WAS and *bars* sharing the *same letter* are not significantly different at a $P < 0.05$ level of significance

Root biomass was greatest at the high:low N:P combination at 6 WAS (Fig. 3). However, at 9 and 12 WAS root biomass was similar between the high:low and high:medium N:P combinations. When phosphorus was supplied at 0.09 mg l^{-1} root biomass was reduced when compared to the high:low N:P combination.

Submersed shoots constituted the smallest proportion of total biomass and was generally similar across nutrient combinations and WAS with the exception of the high:low N:P combination. Submersed shoot biomass was greatest at the high:low N:P combination by 9 WAS (Fig. 4). When phosphorus was increased to 0.03 and 0.09 mg l^{-1} it resulted in reductions in submersed shoot biomass when nitrogen was fixed at 1.80 mg l^{-1}, although there was no difference in biomass between the medium and high phosphorus combinations.

Emergent shoot biomass of *M. aquaticum* was also significantly higher at the high:low N:P combination

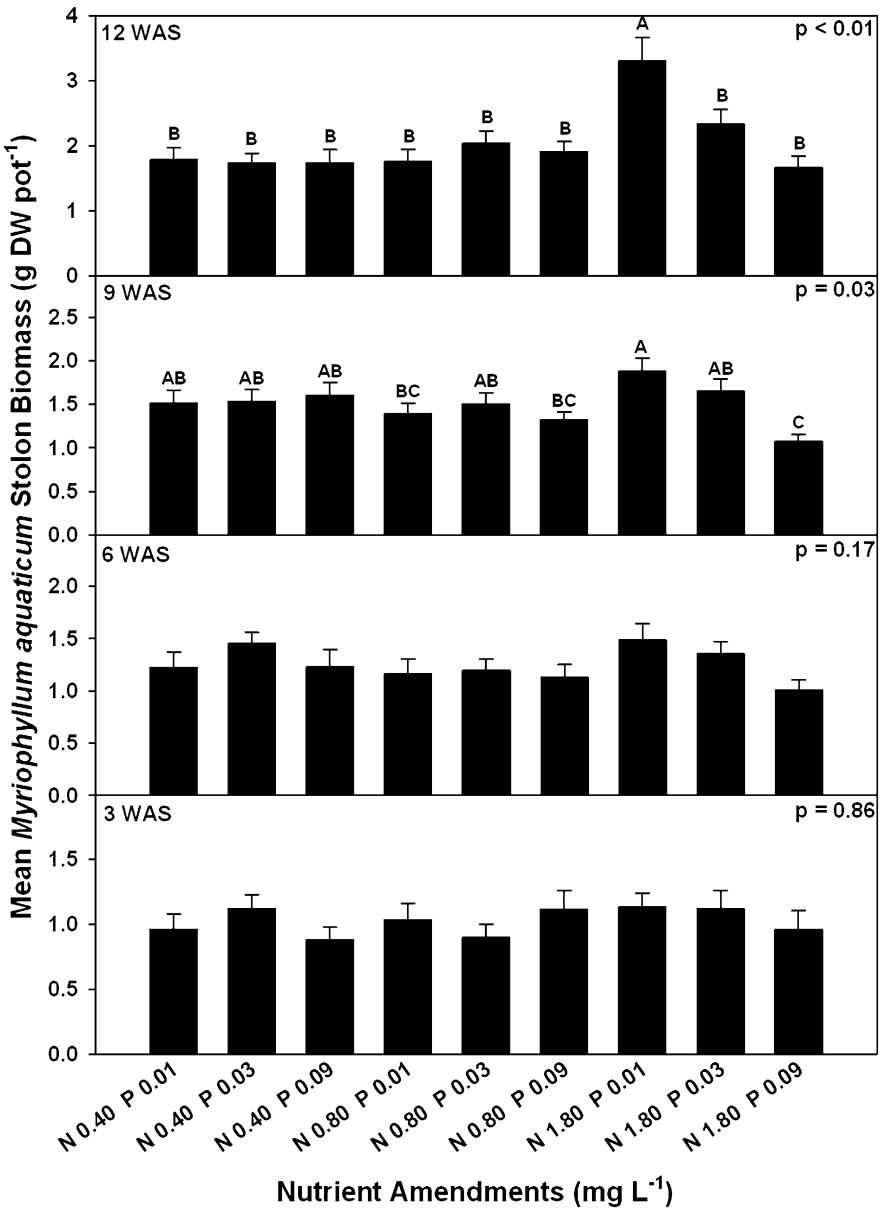

Fig. 2 Mean (±1 SE) stolon biomass of *Myriophyllum aquaticum* grown in varying nitrogen and phosphorus combinations to the water column. Analyses were conducted within WAS and *bars* sharing the *same letter* are not significantly different at a $P < 0.05$ level of significance

(Fig. 5). Emergent shoot biomass was on average 53, 68, and 76% greater at the high:low N:P combination than biomass at all other nutrient combinations at 6, 9, and 12 WAS, respectively. Similar to total biomass, emergent shoot biomass decreased as phosphorus concentration increased when nitrogen was fixed at 1.80 mg l^{-1}.

Yield response of *M. aquaticum* was a quadratic function of both nitrogen ($r^2 = 0.82$) and phosphorus ($r^2 = 0.78$) content in plant tissues; however, the relationship was positive for nitrogen and negative for phosphorus (Fig. 6). As the nitrogen content increased, total yield increased only after nitrogen content rose above 1.80% of plant tissue, indicating a growth limiting nitrogen level. Conversely, as phosphorus content increased, biomass decreased. The decrease in biomass is evident after phosphorus content exceeded 0.20% (Fig. 6). Overall, *M. aquaticum* was nutrient-limited as all combinations were at or near critical nutrient levels with the

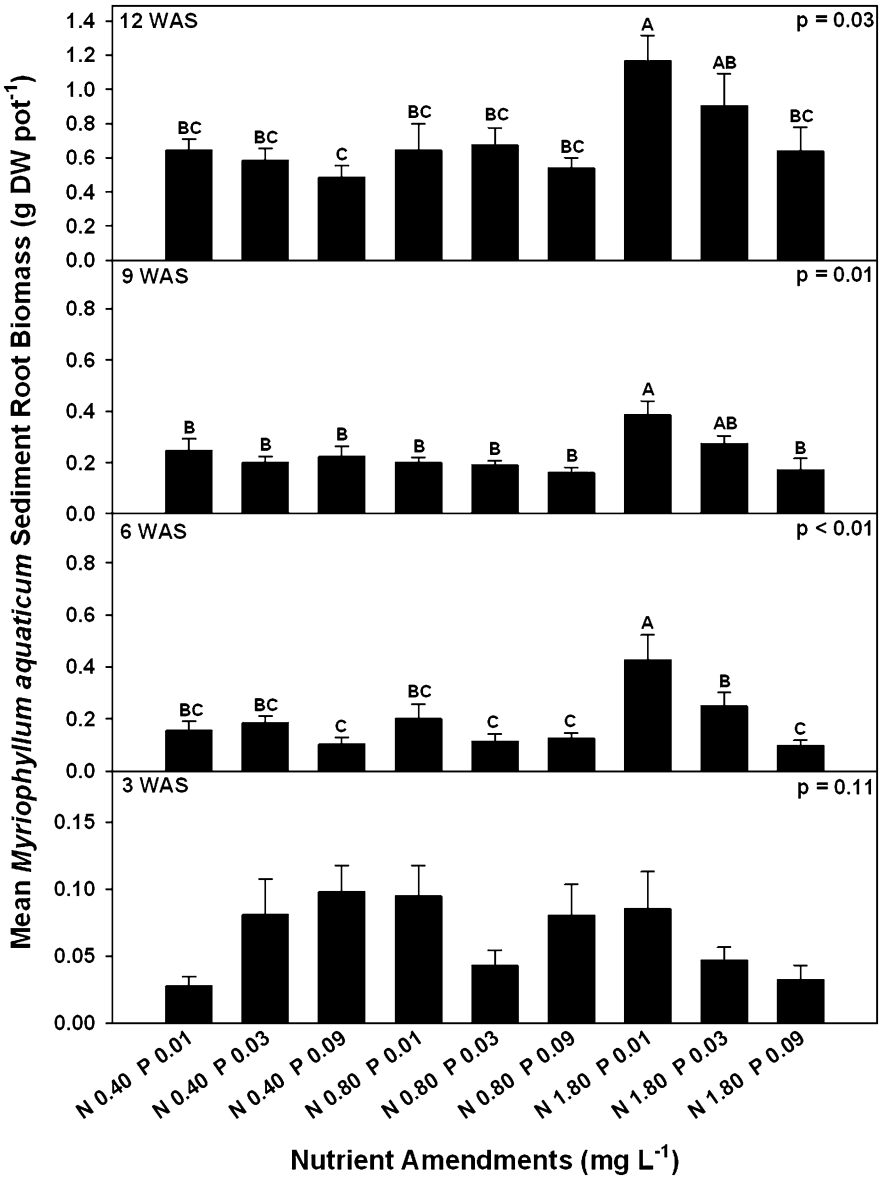

Fig. 3 Mean (±1 SE) root biomass of *Myriophyllum aquaticum* grown in varying nitrogen and phosphorus combinations to the water column. Analyses were conducted within WAS and *bars* sharing the *same letter* are not significantly different at a $P < 0.05$ level of significance

exception of the high:low N:P combination where nitrogen content was above the critical threshold (Fig. 7).

The addition of nutrients to the water column resulted in the growth of algae as determined by chlorophyll *a* measurements in all nutrient combination treatments (Fig. 8). However, only the high:high N:P combination resulted in significantly more algae by 12 WAS. Visually, there was an increase in filamentous algae as the phosphorus concentration increased, suggesting that algae were responding to phosphorus additions to the water column.

Discussion

Myriophyllum aquaticum growth was limited by nitrogen when concentrations in the water were supplied below 1.80 mg l^{-1}, and by phosphorus concentrations in the water column throughout this study. *Myriophyllum aquaticum* yield increased with increasing nitrogen content after 1.8%, which suggests that nutrient uptake was in fact occurring from the water column. We estimated the critical limiting nutrient threshold to be 1.80% nitrogen and 0.20% phosphorus in plant tissues. These values support

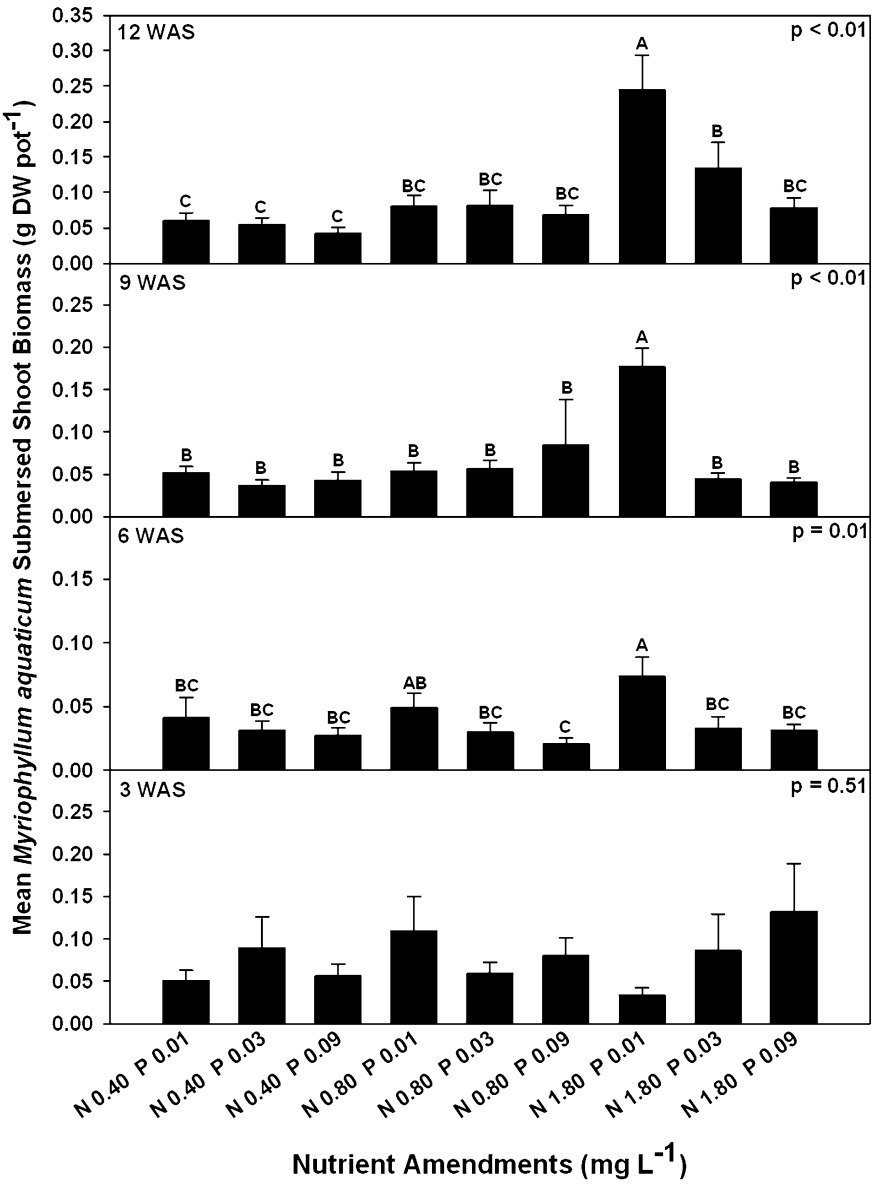

Fig. 4 Mean (±1 SE) submersed shoot biomass of *Myriophyllum aquaticum* grown in varying nitrogen and phosphorus combinations to the water column. Analyses were conducted within WAS and *bars* sharing the *same letter* are not significantly different at a $P < 0.05$ level of significance

previously published data for emergent shoots where critical values were estimated at 1.54 and 0.19% for nitrogen and phosphorus, respectively, for shoots grown in nutrient solutions (Sytsma & Anderson, 1993a). Tissue concentrations of nitrogen and phosphorus were close to or below the critical thresholds established in this and previous studies. Nutrient limitation is further supported in that biomass did not differ across nutrient combinations until nitrogen increased to 1.80 mg l^{-1}. This suggests that plants grown at the lower nutrient combinations were not acquiring sufficient amounts of nutrients from the water column to initiate or sustain high biomass production. The combination of high:low N:P had tissue nitrogen above the critical threshold, but phosphorus was below the critical threshold which may suggest that nitrogen has a larger role in *M. aquaticum* growth than phosphorus when supplied to the water column at concentrations at or above 1.80 mg l^{-1}.

Uptake of both nitrogen and phosphorus is likely from the water column primarily, and is facilitated

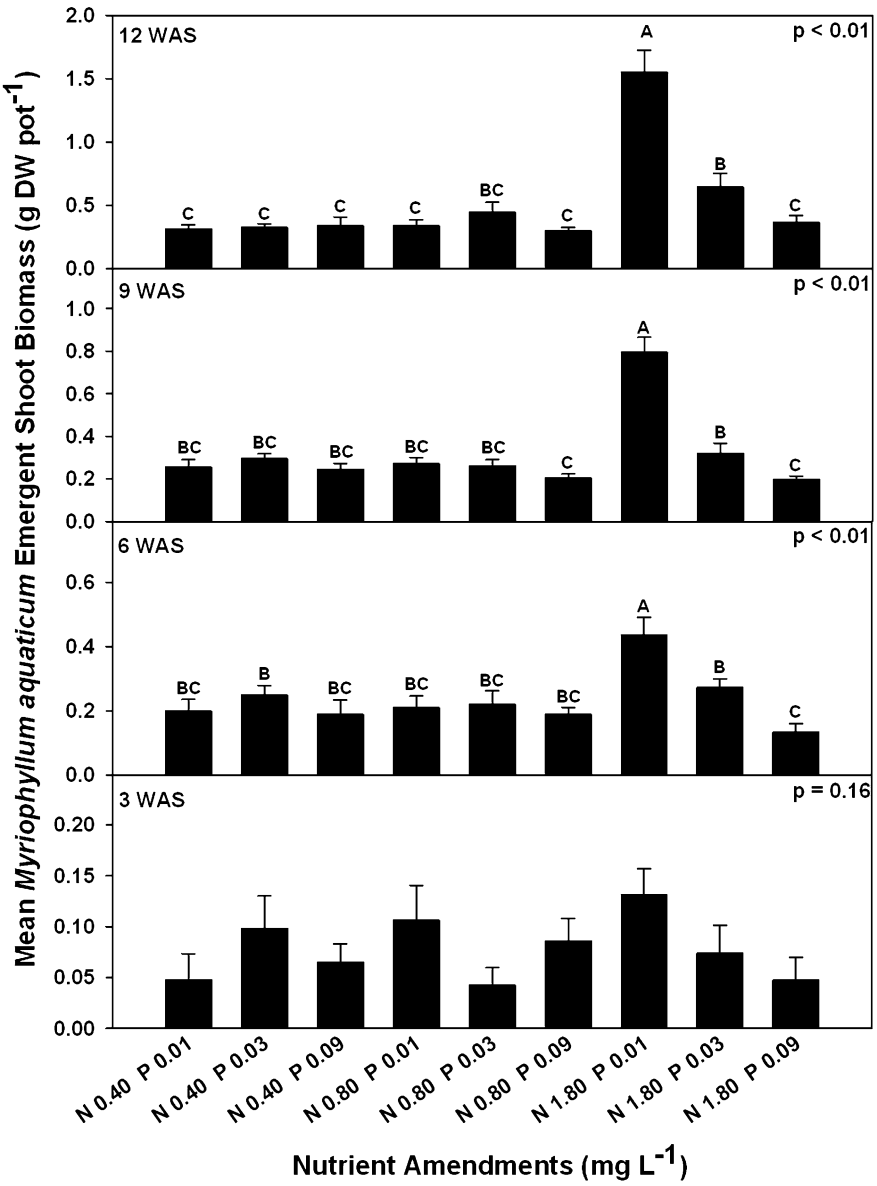

Fig. 5 Mean (±1 SE) emergent shoot biomass of *Myriophyllum aquaticum* grown in varying nitrogen and phosphorus combinations to the water column. Analyses were conducted within WAS and *bars* sharing the *same letter* are not significantly different at a $P < 0.05$ level of significance

via adventitious roots. These roots grow from each node of the stolon where growth will begin as soon as old emergent shoots are submersed in the water column. Adventitious roots can grow to lengths of approximately 30–50 cm giving greater access to water column nutrients than other macrophyte species. Adventitious roots generally have a higher RGR than even total RGR (Sytsma & Anderson, 1993c). A dense population of *M. aquaticum* with adventitious roots along each stolon of every plant would have increased access to water column nutrients. However, more research is needed to determine the real function of adventitious in the growth of *M. aquaticum*, although our data and previous studies suggest they may be the primary site of nutrient uptake, especially for plants growing in deeper water (Sytsma & Anderson, 1993d).

Myriophyllum aquaticum does have sediment roots; however, they are highly cuticularized which may limit nutrient uptake from the sediment (Sutton & Bingham, 1973). *Myriophyllum aquaticum* has a low sediment root:shoot ratio further reducing the

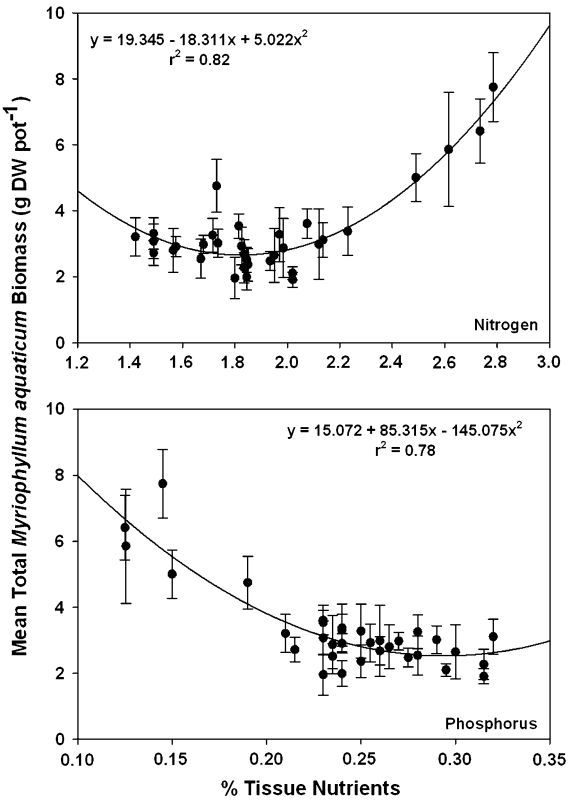

Fig. 6 Mean (±1 SE) total yield response of *Myriophyllum aquaticum* to nitrogen (*top*) and phosphorus (*bottom*) concentrations in plant tissues. The regression line represents the best fit of a polynomial regression analysis. Total yield response is a quadratic function of tissue nutrient concentration

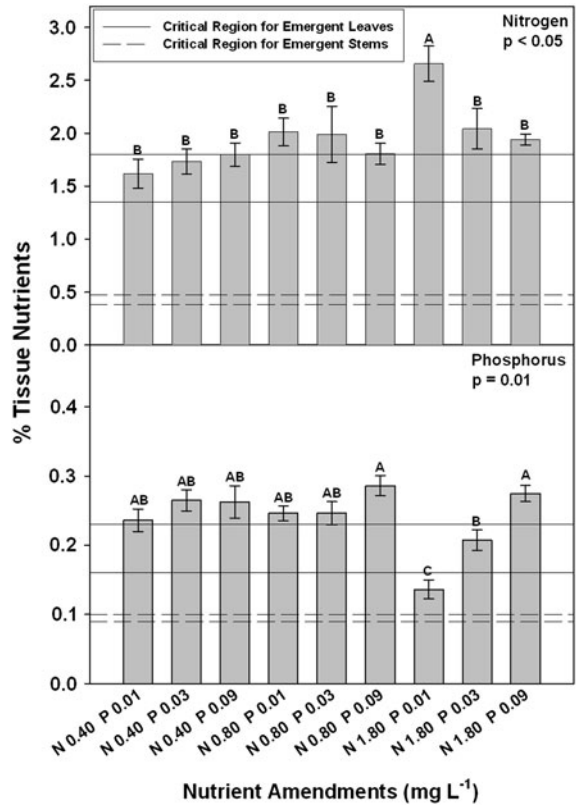

Fig. 7 Mean (±1 SE) nitrogen (*top*) and phosphorus (*bottom*) content in emergent shoots of *Myriophyllum aquaticum* grown in varying nitrogen and phosphorus combinations to the water column. Critical concentration lines were established from values reported by Sytsma & Anderson (1993c). *Bars* sharing the *same letter* are not significantly different at a $P < 0.05$ level of significance

ability of sediment roots to contribute to the total nutrient supply for plants. Plant growth did not reduce sediment nutrient concentrations over the course of a laboratory study due to a shift in allocation patterns from sediment roots to adventitious roots after the development of emergent shoots (Sytsma & Anderson, 1993c). In natural populations, stolons and emergent shoots of natural populations were the sink for nitrogen where allocation was >80% throughout the year with the majority of nitrogen stored in stolon tissues (Sytsma & Anderson, 1993b). Nitrogen allocation to sediment roots never exceeded 18% and was below 10% the majority of the time (Sytsma & Anderson, 1993b). Emergent shoots comprised >80% of the total phosphorus pool in these same natural populations with no annual accumulation of phosphorus in other tissues, suggesting that *M. aquaticum* relies on phosphorus uptake from the water column (Sytsma & Anderson, 1993b).

An inverse relationship was observed between *M. aquaticum* yield and increasing phosphorus content. In general, increasing or decreasing phosphorus availability typically affects root growth as is indicated in agricultural plants (Cassman et al., 1980; Linkohr et al., 2002); though in this study root biomass did not respond to changes in phosphorus concentration. Therefore, we attribute the negative relationship in yield response and phosphorus availability to competition for light and nutrients with algae; given that *M. aquaticum* relies on the water column for its phosphorus supply. Algae assimilate phosphorous at rates more rapid than what is actually used for growth; and if other conditions are adequate, enrichments of phosphorus in the water often result in

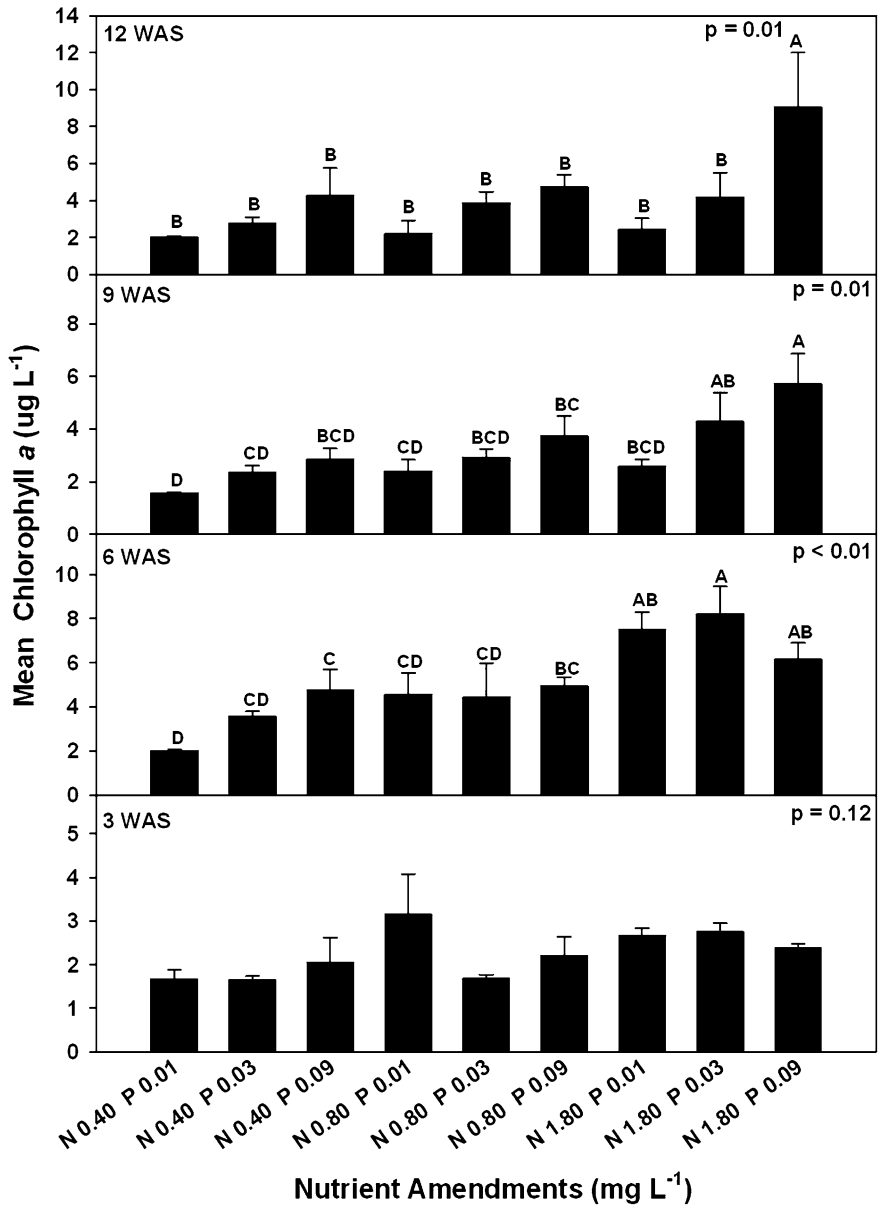

Fig. 8 Mean (±1 SE) chlorophyll *a* concentration for each nutrient combination. Chlorophyll *a* was only measured in 2007. Analyses were conducted within WAS and *bars* sharing the *same letter* are not significantly different at a $P < 0.05$ level of significance

immediate increases in algal photosynthesis and growth rates (Wetzel, 2001).

This would also be a plausible explanation for the reduction in total and emergent shoot biomass at the high:medium and high:high N:P combinations. There was a significant increase in chlorophyll *a* in the high:high N:P combination after 12 weeks. By 9 WAS, mats of filamentous algae were floating on the water surface and growing on *M. aquaticum* plants at the highest phosphorus concentration with little to no filamentous algae growing in the lowest phosphorus combinations. The filamentous algae coated the surface of emergent stems, stolons, and adventitious roots when phosphorus was increased.

Aquatic macrophytes are often attaching points for filamentous algae and other epiphytic organisms or serve to cycle nutrients within a waterbody. Phosphorus uptake from the water column by rooted macrophytes is often much less than by attached algae (Wetzel, 2001). Epiphytes may reduce macrophyte growth by intercepting light and nutrients that would have otherwise been absorbed through leaf

surfaces (Phillips et al., 1978; Ruesink, 1998). Epiphyte production was found to be higher on *Myriophyllum spicatum* L. than native or plastic plants in a controlled study (Cattaneo & Kalff, 1979). The authors attributed the greater epiphyte production to the highly dissected leaves that is characteristic of *Myriophyllum* spp., which may have allowed epiphytes to better utilize light and dissolved nutrients in the water. In natural macrophyte communities, 3.4–8.9% of phosphorus present in epiphytes was contributed by macrophytes (Carignan & Kalff, 1982). Furthermore, *M. spicatum* alone was estimated to increase total phosphorus load to the water column by 2.2%, of which more than half of this amount is readily available to epiphytes and algae (Carignan & Kalff, 1982).

Myriophyllum aquaticum has both an emergent and submersed leaf form as well as adventitious roots offering more attachment points for algae. As reported earlier >80% of total phosphorus is located in the emergent shoots of *M. aquaticum* (Sytsma & Anderson, 1993b); meaning that a large source of phosphorus for algal growth is concentrated at or near the water surface and readily accessible by free floating or epiphytic algae. Therefore, as phosphorus was added to the mesocosms over the course of the current study, algae densities increased and could directly uptake nutrients more quickly than *M. aquaticum*; or, filamentous algae directly inhibited nutrient uptake from the water column by growing on *M. aquaticum* plants. Although we did not specifically measure phosphorus content of algae in our mesocosms, we did document concentrations of phosphorus or nitrogen in the water column during regular water sampling events where very little NO_3 and PO_4 were recorded. Furthermore, tissue nutrient concentrations of *M. aquaticum* indicated that nutrients were often below critical limits. The low water column nutrient concentrations and low tissue nutrient concentrations offer further support for algal interference with nutrient uptake by *M. aquaticum*; although a mass balance of total nitrogen and phosphorus would be needed to confirm this. Pursuant to this, additional research is needed to test for interference effects of algae on *M. aquaticum* growth by regulating algal densities through the use of copper-based algaecides in a replicated study; this would in fact determine if algae interfered with *M. aquaticum* growth. Chelated copper had no impact on the growth of *M. aquaticum* in replicated studies as compared to untreated reference plants, and therefore, could be used in such an experiment (Wersal & Madsen, 2010).

Understanding the relationships between nutrient loading and invasive plant growth is becoming more important as anthropogenic nutrient sources increase. Our data provide further evidence to support previous claims that *M. aquaticum* growth and distribution are controlled in large part by environmental nutrient supply (Sutton, 1985; Sytsma & Anderson, 1993a, b); and in habitats where eutrophication is occurring *M. aquaticum* may become very problematic through increased nutrient uptake from the water column. Fragments of *M. aquaticum* have been shown to have higher growth rates, rooting efficiency, and root growth in response to nutrient enrichment when compared to native species (Xie et al., 2010). Characteristics such as these would be advantageous in areas that are subject to increased disturbance, which would result in fragmentation and thus increased propagule formation and spread of *M. aquaticum*. Therefore, data from this study provide basic ecological information and, when combined with other growth limiting data, predictive models can be developed to identify which habitats are most prone to invasion by *M. aquaticum*. Our results suggest that *M. aquaticum* could invade a range of habitats including oligotrophic lakes; however, colonization success and nuisance growth would likely be limited to eutrophic habitats or areas where nutrient competition with algae or other macrophytes is low.

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