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**Editor's Choice Article**

# Influences of light intensity variations on growth characteristics of *Myriophyllum aquaticum*

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*Myriophyllum aquaticum* is a heterophyllous plant that is native to South America and has been introduced to the United States. The reallocation of resources to emergent or submersed growth forms likely allows *M. aquaticum* to overcome changes in light availability and to invade different habitats. Our objective was to determine the effects of light availability on plant length, biomass allocation, and relative growth rate through replicated mesocosm experiments. *Myriophyllum aquaticum* was grown in full sunlight, 30%, 50%, and 70% shade in replicated treatments. Total plant length, emergent shoot length, submersed shoot length, and the total of number of emergent and submersed shoots were recorded. Plants were harvested and sorted into emergent shoots, submersed shoots, roots, and stolons, then dried and weighed to assess biomass allocation. After 12 weeks, biomass was different among shade treatments. Differences in plant mass were a result of greater plant growth in the 30% shade treatment. Total plant length was greatest in the 50% shade treatment with a reduction in plant length observed in full sunlight. Emergent shoot length was reduced in full sunlight, while an increase in submersed shoot length occurred in 70% shade. Our data suggest that intermediate light availability is optimal for *M. aquaticum* growth and that the growth of two leaf forms is a physiological response to changes in environmental conditions.

**Keywords:** exotic species; aquatic plants; biomass allocation; plant ecology; environmental factors

## Introduction

The presence and spread of invasive species is often associated with human activities and the subsequent habitat degradation from these activities (Mills et al. 1994). Wetlands and shallow lakes are often prone to invasion due to the increased frequency at which disturbances occur. Disturbances that can alter the light environment, such as changes in water quality, can cause a shift in species dominance and species composition within a water body (van der Valk 2005). If native species are removed, the open niche space may facilitate invasions by creating more access to resources for invading species (Davies et al. 2005; Lockwood et al. 2005; Capers et al. 2007). In light of the negative impacts often associated with species invasions, it is

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important to gain an understanding of the factors that may limit a species' ability to invade a particular habitat (Chadwell and Engelhardt 2008).

In aquatic habitats, light is thought to be the most important factor limiting the growth of aquatic macrophytes (Barko et al. 1986) and it can determine community composition as well as zonation within a water body (Spence 1967; Seabloom et al. 1998). Those species that have morphological adaptations to optimize the capture of light will most often be successful in colonizing and establishing populations in low-light environments (Barko et al. 1986). Such adaptations include changes in whole plant morphology, specific leaf morphology, the ability of stem elongation, and canopy production (Barko et al. 1982). Submersed aquatic plants such as Eurasian watermilfoil (*Myriophyllum spicatum* L.) will produce fewer, longer shoots with longer leaves that have increased surface areas in response to low-light conditions. However, some plant species have adapted alternate growth forms to survive environmental fluctuations.

Parrotfeather, *Myriophyllum aquaticum* (Vell.) Verdc., is a heterophyllous herbaceous perennial plant from South America that is not native to the United States. *Myriophyllum aquaticum* has two distinct leaf forms that can grow together on the same plant or, more commonly, the growth form will be dictated by growing conditions (Figure 1). Emergent leaves are feather-like and grayish green, stiff, and grow in whorls around the emergent shoot (Godfrey and Wooten 1981). These leaves have stomata, a thick waxy cuticle, and short cylindrical leaflets (Sutton and Bingham 1973). Submersed leaves are typically orange to red, lack both stomata and a leaf cuticle, and grow in whorls around submersed shoots (Mason 1957). The anatomical and morphological differences in the submersed and emergent form of parrotfeather may result from physiological adaptations to conditions in their respective environments (Sculthorpe 1967).

Having two distinct growth forms may give *M. aquaticum* the ability to overcome changes in water level and convey a competitive advantage over macrophytes that are more sensitive to changes in their growing environment. In the Sinos River Basin, Brazil, *M. aquaticum* growth occurred during both a flooded period and a drawdown period (Maltchik et al. 2007), thereby causing plants to rapidly change growth forms

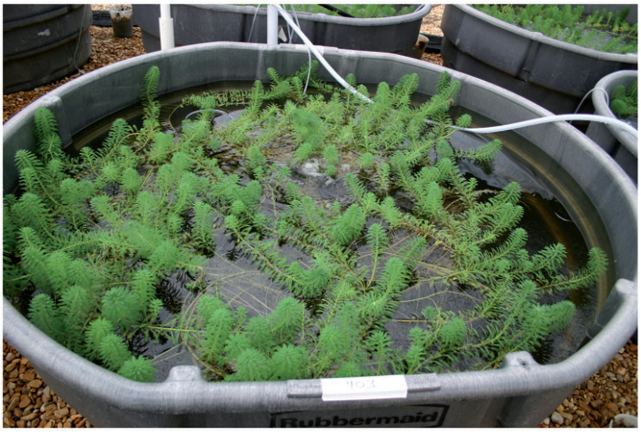

Figure 1. Photograph of emergent *M. aquaticum* in an experimental mesocosm.

to survive changing light profiles. The reallocation of resources to emergent or submersed growth likely allows *M. aquaticum* to overcome changes in light availability and to optimize the use of light in their respective environments. Therefore, our objective was to determine the direct effects of light intensity on growth characteristics of *M. aquaticum* and to determine growth-limiting levels. Understanding the environmental constraints posed by light intensities will indicate what environments *M. aquaticum* can colonize and exploit to establish new infestations. These areas can be targeted for more aggressive monitoring to identify infestations at their onset before plants become firmly established.

## Methods

A mesocosm study was conducted at the R.R. Foil Plant Science Research Center, Mississippi State University, Starkville, MS (N 33°28′29.76″, W 88°46′24.70″) for 12 weeks from 5 June to 30 August 2006 and repeated from 6 June to 27 August 2007. Both studies were conducted in twenty-four 1100 L mesocosms ($161 \times 175 \times 64\,\mathrm{cm}^3$) with six replications per light treatment: full sun, 30%, 50%, and 70% shades. Shade cloth of desired percentage was suspended above and on all four sides of a grouping of six tanks with the exception of the full sun treatment. Water was supplied to each mesocosm from an irrigation reservoir adjacent to the mesocosm facility. All mesocosms were filled to a water depth of approximately 50 cm. Air was supplied to all mesocosms from a regenerative air blower using 2.5 cm stone diffusers and a PVC lift pipe to circulate water within tanks and to provide a source of $CO_2$. Incident light intensity measurements were recorded once per day in each light treatment between the hours of 12:00 and 2:00 using a LI-1400 datalogger with a LI-190 photometric sensor (LI-COR Biosiences, Lincoln, NE, USA). A HOBO$^{\mathrm{TM}}$ temperature probe (Onset Computer Corporation, Pocasset, ME, USA) was deployed in each mesocosm to record temperature in 1 h intervals for the duration of the study.

Planting of *M. aquaticum* consisted of placing two emergent apical shoots, approximately 20 cm in length, into each of 336 pots (3.78 L) containing a top soil, loam, and sand mixture (3 : 2 : 1; $10\,\mathrm{mg NO_3{-}N\,kg^{-1}}$ soil, $26\,\mathrm{mg}\, P_{\mathrm{tot}}\,\mathrm{kg^{-1}}$ soil; Wersal and Madsen 2011). Sediment was amended at a rate of $2\,\mathrm{g\,L^{-1}}$ in each pot using Osmocote 19-6-12 fertilizer (Scotts-Sierra Horticultural Products Company, Marysville, OH, USA). After planting, 14 pots of *M. aquaticum* were placed into each mesocosm. *Myriophyllum aquaticum* biomass was measured at 0, 2, 4, 6, 8, 10, and 12 weeks after start (WAS) by removing two pots from each tank. Plants were removed from the pots and rinsed to remove sediment, debris, and algae growing on the plants. After rinsing, total plant length (cm) was recorded for each plant by measuring from the roots (sediment line) to the longest emergent tip. Plants were then separated into emergent shoots, submersed shoots, stolons, and sediment roots. Total emergent and submersed shoot length were recorded (cm) for each shoot as well the total number of each shoot type. Plant tissues were then placed into a forced air oven and dried at 70°C for 72 h. *Myriophyllum aquaticum* biomass is expressed as gram dry weight (DW) $\mathrm{pot}^{-1}$ for total biomass and each plant tissue.

Statistical analyses were conducted using SAS software (SAS Institute, Inc., Cary, NC, USA). A mixed procedures model was utilized to examine main effects of light treatments on biomass, plant length, and shoot number of *M. aquaticum*. Year and subsequent interactions with year were considered random effects in the model to account for their influence on the results (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 (RGRs; $\ln \mathrm{g\,DW\,pot^{-1}\,day^{-1}}$) were calculated for each WAS and light treatment for total, emergent shoot, submersed shoot, stolon, and root biomass using the following equation outlined by Hunt (1982)

$$\mathrm{RGR} = \frac{\ln(W_2) - \ln(W_1)}{t_2 - t_1} \tag{1}$$

where $W_1$ and $W_2$ are plant DWs at times $t_1$ and $t_2$, respectively. A mixed procedures model was also utilized to determine differences in RGR within WAS for each biomass tissue type. All analyses were conducted at $\alpha = 0.05$ significance level.

## Results

On average, incident light was reduced by 35.8 ± 9.1%, 59.4 ± 7.2%, and 78.8 ± 4.1% of full sunlight for the 30%, 50%, and 70% shade treatments, respectively (Figure 2). These data indicate that the shade cloth offered the desired

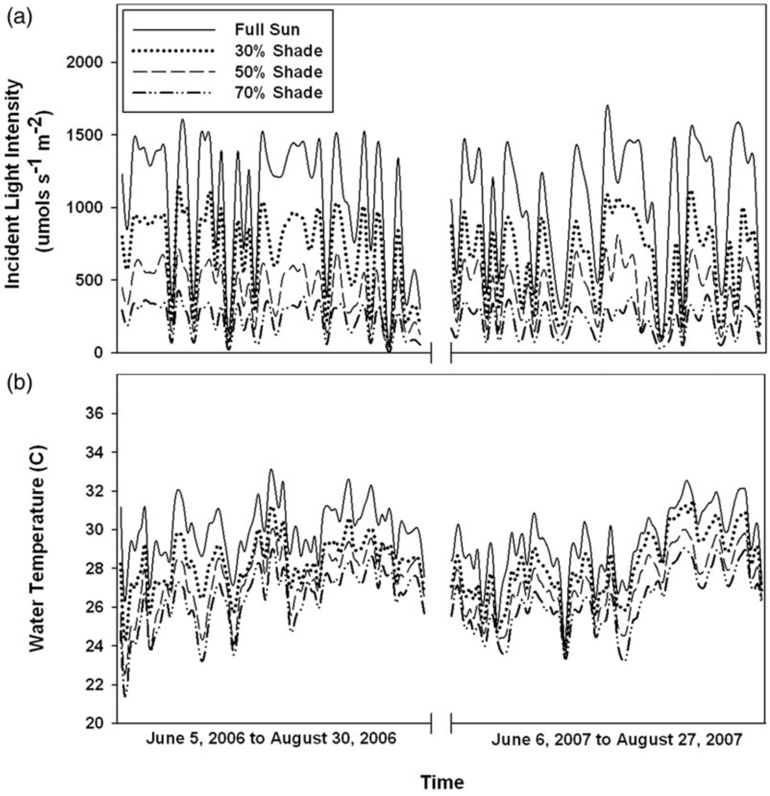

Figure 2. Instantaneous light intensity measurements (a) and mean daily water temperatures (b) collected throughout both the studies in 2006 and 2007.

levels of light attenuation for the study. Daily water temperatures were on average 29.6 ± 0.03°C, 28.2 ± 0.01°C, 27.2 ± 0.01°C, and 26.3 ± 0.04°C for the full sun, 30%, 50%, and 70% shade treatments, respectively, and were significantly different ($p < 0.01$) among treatments.

The variation in light levels did not result in a difference in the total number of emergent shoots ($p = 0.48$) or submersed shoots ($p = 0.96$) produced by *M. aquaticum* over 12 weeks of plant growth. Total plant length, however, was affected by light levels as early as 4 WAS when plants were grown in 50% shade; where on average, these plants were 15% longer than plants in the other light treatments (Figure 3).

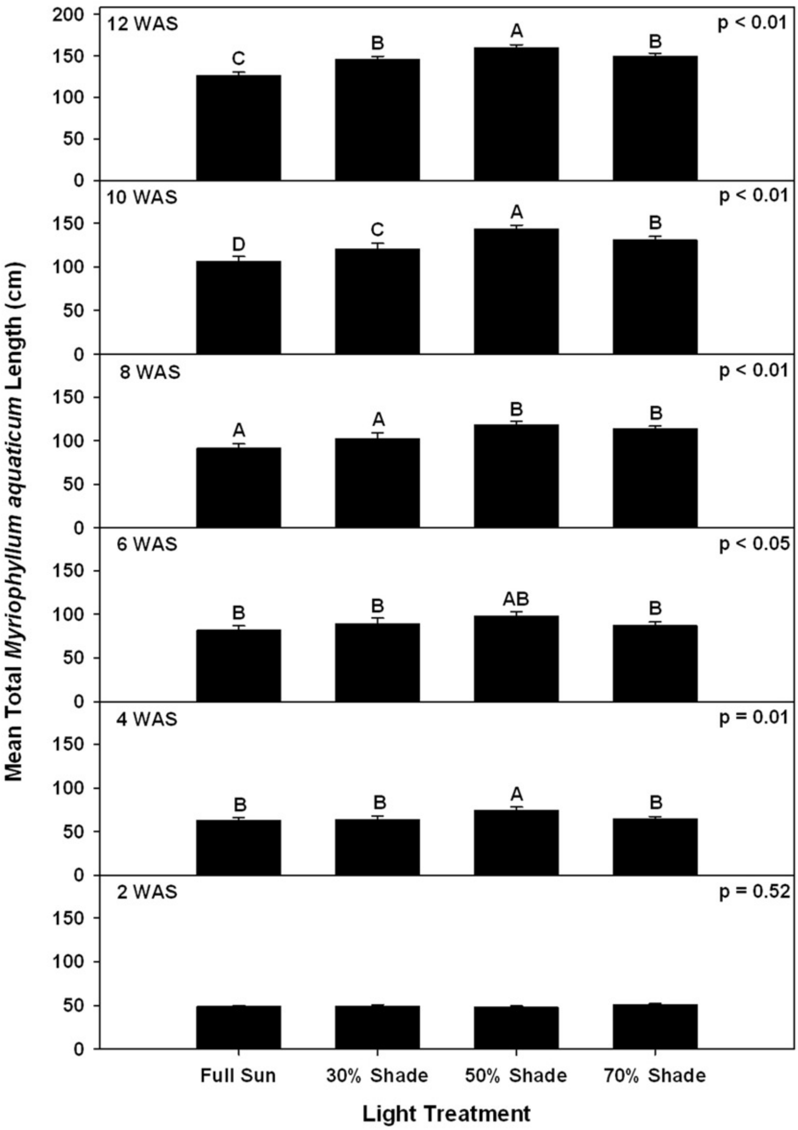

Figure 3. Mean (±1 SE) total plant length of *M. aquaticum* at each harvest interval (WAS). Bars sharing the same letter are not significantly different at $p < 0.05$ as determined by the least-squares means method.

By 12 WAS, *M. aquaticum* length was still greater when plants were grown in 50% shade. Plant length was 159.7 ± 3.7 cm pot$^{-1}$ when grown in 50% shade at 12 WAS, whereas plant lengths were 126.3 ± 3.9, 145.5 ± 4.1, and 149.6 ± 3.4 cm pot$^{-1}$ for the full sunlight, 30% and 70% shade treatments, respectively.

Differences in emergent shoot length were not as well defined as with total plant length by 12 WAS (Figure 4). However, from 6 WAS to the conclusion of the study, emergent shoot length was always greater when plants were grown in 30–70% shade

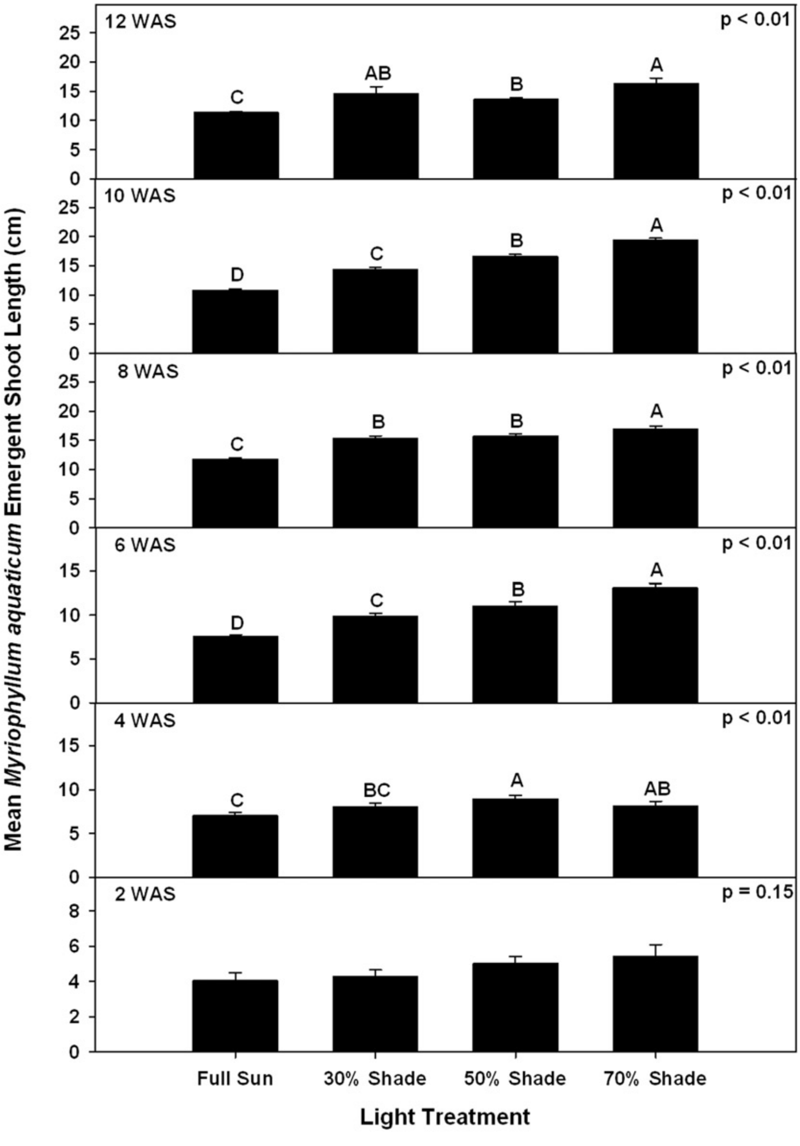

Figure 4. Mean (±1 SE) emergent shoot length of *M. aquaticum* at each harvest interval (WAS). Bars sharing the same letter are not significantly different at $p < 0.05$ as determined by the least-squares means method.

as opposed to full sunlight. By 12 WAS, *M. aquaticum* grown under shaded conditions had emergent shoots that were on average 24% longer than plants grown in full sunlight. Submersed shoot length of *M. aquaticum* was greatest when plants were grown in 70% shade as early as 2 WAS (Figure 5). However at 6, 8, and 10 WAS, submersed shoot length was similar to plants grown at 30% and/or 50% shade. By 12 WAS, submersed shoot length was significantly greater (18%) when plants were grown in 70% shade versus plants grown in the other light treatments.

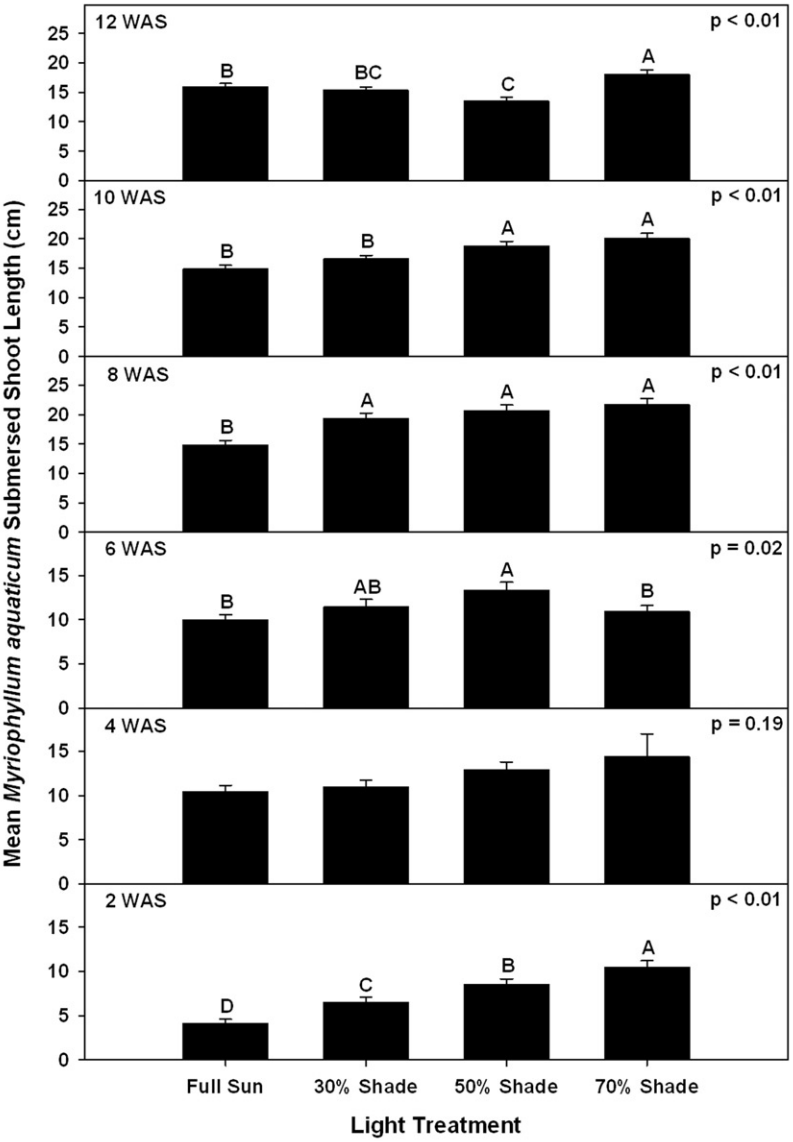

Figure 5. Mean (±1 SE) submersed shoot length of *M. aquaticum* at each harvest interval (WAS). Bars sharing the same letter are not significantly different at $p < 0.05$ as determined by the least-squares means method.

Pretreatment biomass was 1.5 ± 0.9 g DW $pot^{-1}$. At the conclusion of the study, biomass was > 40.0 g DW $pot^{-1}$ which indicates that plants were actively growing in all light treatments throughout the study. Total biomass was greater when plants were grown in 30% and 50% shade at 8 and 10 WAS; however, by 12 WAS, total biomass was greatest in the 30% shade treatment (Figure 6). At the conclusion of the study, total biomass was reduced in the 70% shade treatment when compared to all the other light treatments. Total biomass after 12 weeks in the 30% shade treatment

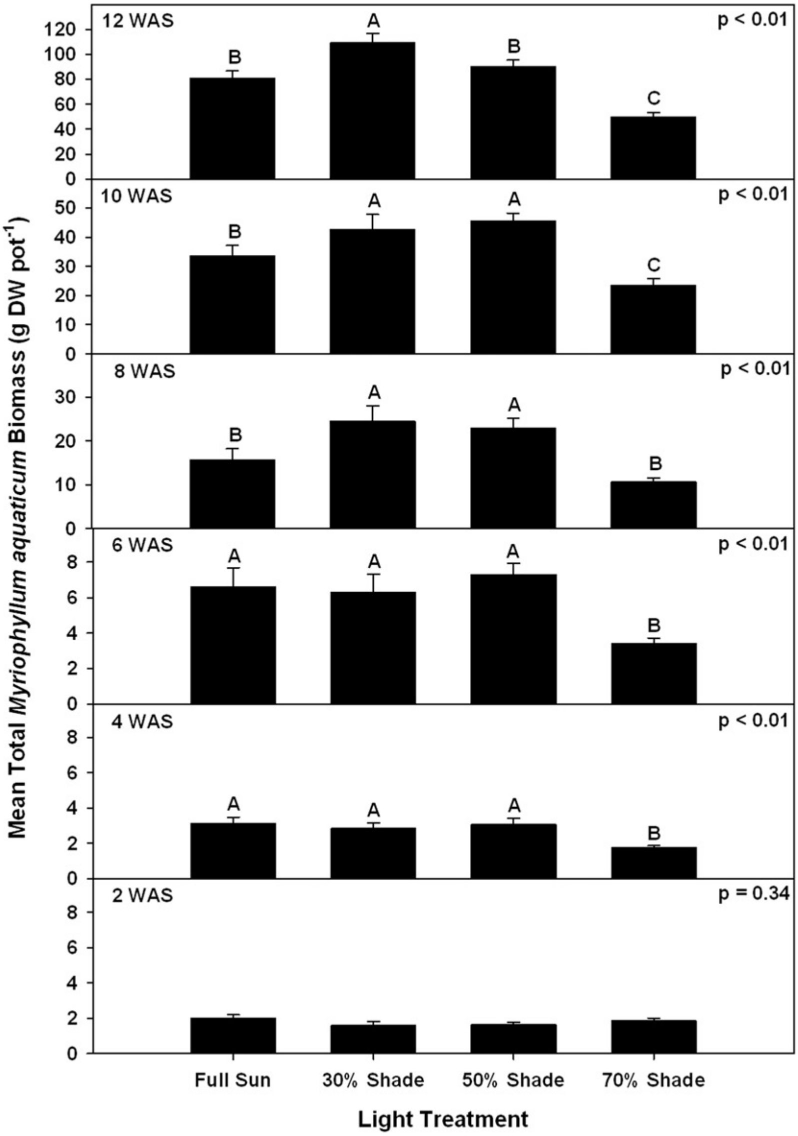

Figure 6. Mean (±1 SE) total plant biomass of *M. aquaticum* at each harvest interval (WAS). Bars sharing the same letter are not significantly different at $p < 0.05$ as determined by the least-squares means method.

was 109.1 ± 7.4 g DW pot$^{-1}$, whereas biomass in the 70% shade treatment was 49.6 ± 3.6 g DW pot$^{-1}$, a 55% decrease in biomass. Total biomass of *M. aquaticum* grown in full sunlight was 80.5 ± 6.0 g DW pot$^{-1}$ at 12 WAS.

Emergent shoot biomass followed a similar pattern as total biomass when *M. aquaticum* responded more favorably to the 30% and 50% shade treatment at 8 and 10 WAS (Figure 7). Biomass was 27.0 ± 1.4 g DW pot$^{-1}$ 12 WAS when plants were grown in 30% shade, whereas emergent shoot biomass was 16.2 ± 1.1 and 19.7 ± 1.1 g DW pot$^{-1}$ for plants in the 70% and full sunlight treatments, respectively.

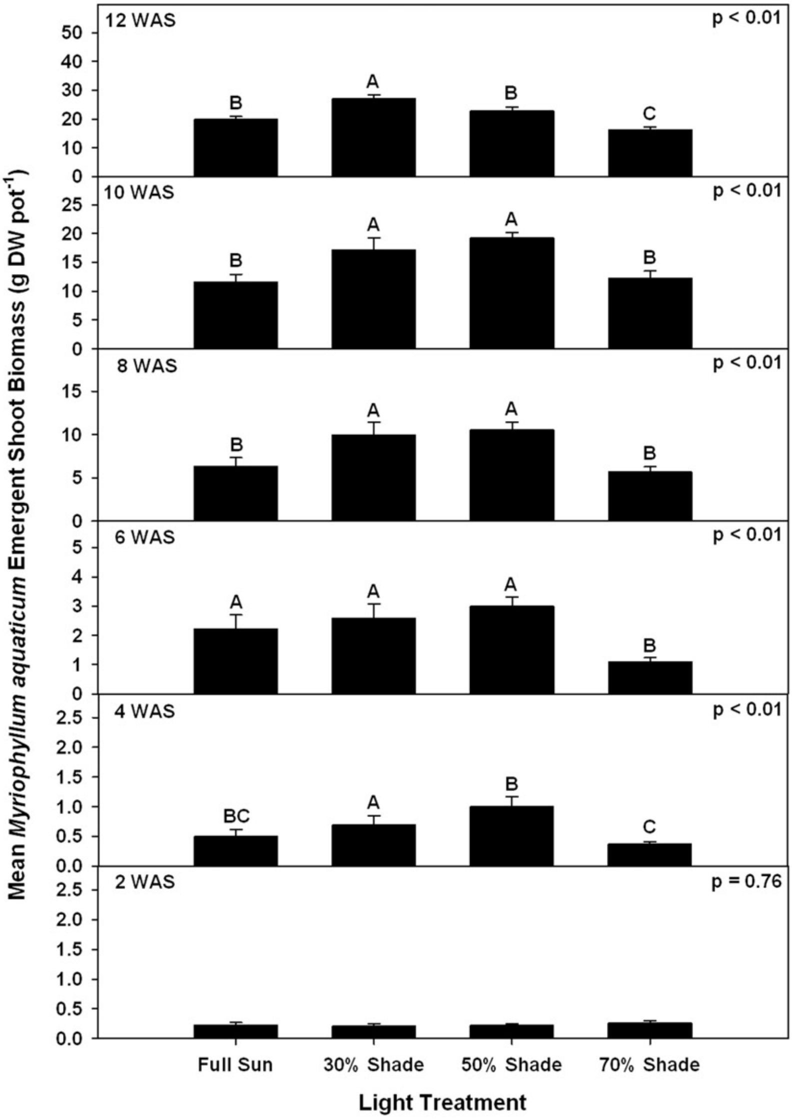

Figure 7. Mean (±1 SE) emergent shoot biomass of *M. aquaticum* at each harvest interval (WAS). Bars sharing the same letter are not significantly different at $p < 0.05$ as determined by the least-squares means method.

Emergent shoot biomass at 12 WAS was greater when plants were grown in 30% shade when compared to the other light treatments. Emergent shoot biomass comprised 12–45% of total biomass across light treatments and WAS. Submersed shoot biomass comprised the smallest proportion of total biomass throughout the study, in that it never exceeded 2% of total biomass. At the conclusion of the study, submersed biomass only accounted for 1.8%, 1.1%, 1.3%, and 1.6% of total biomass for the full sunlight, 30%, 50%, and 70% light treatments, respectively. Submersed shoot biomass was not different ($p = 0.05$) between light treatments at 12 WAS (Figure 8).

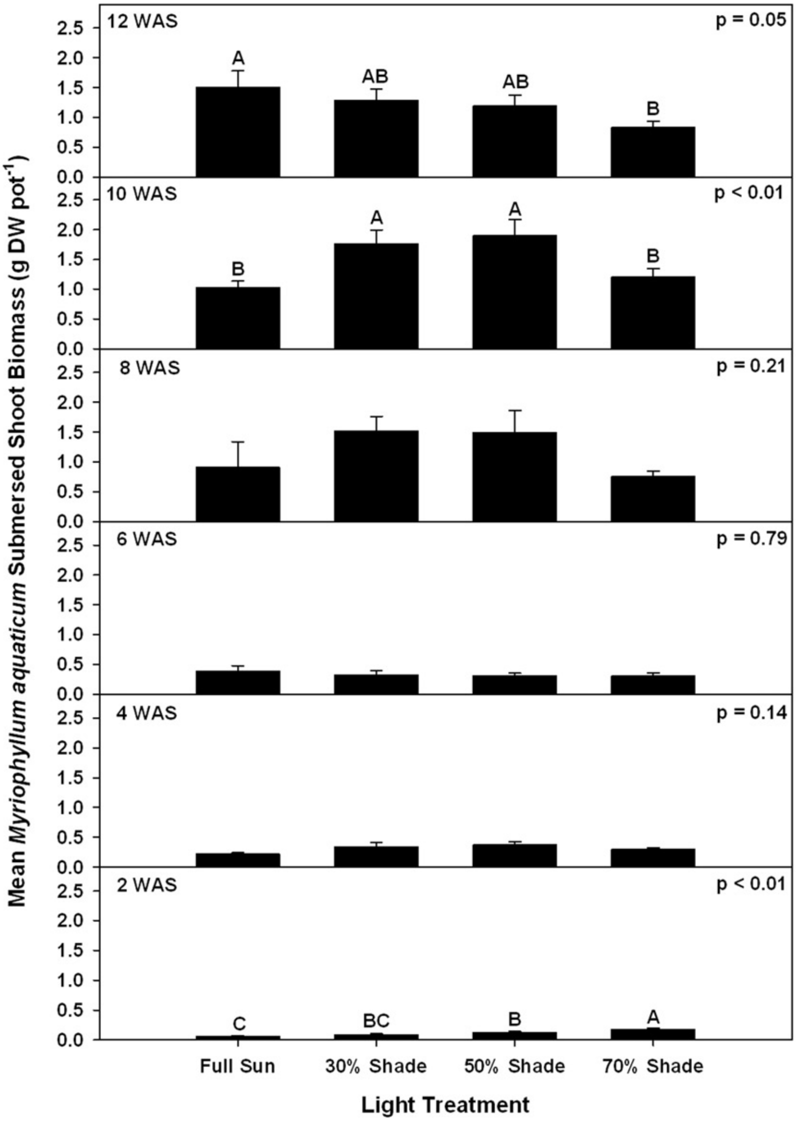

Figure 8. Mean (±1 SE) submersed shoot biomass of *M. aquaticum* at each harvest interval (WAS). Bars sharing the same letter are not significantly different at $p < 0.05$ as determined by the least-squares means method.

Stolon biomass consistently comprised the greatest proportion of total biomass. Stolon biomass ranged from 34% to 81% across light treatments and WAS. Biomass was lower ($p < 0.01$) for plants grown in 70% shade from 4 WAS to the conclusion of the study (Figure 9). Stolon biomass was similar between the full sunlight, 30%, and 50% treatments from 6 to 12 WAS. On average, stolon biomass was 50% greater in the 30% and 50% shade treatments than stolon biomass in the 70% shade treatment.

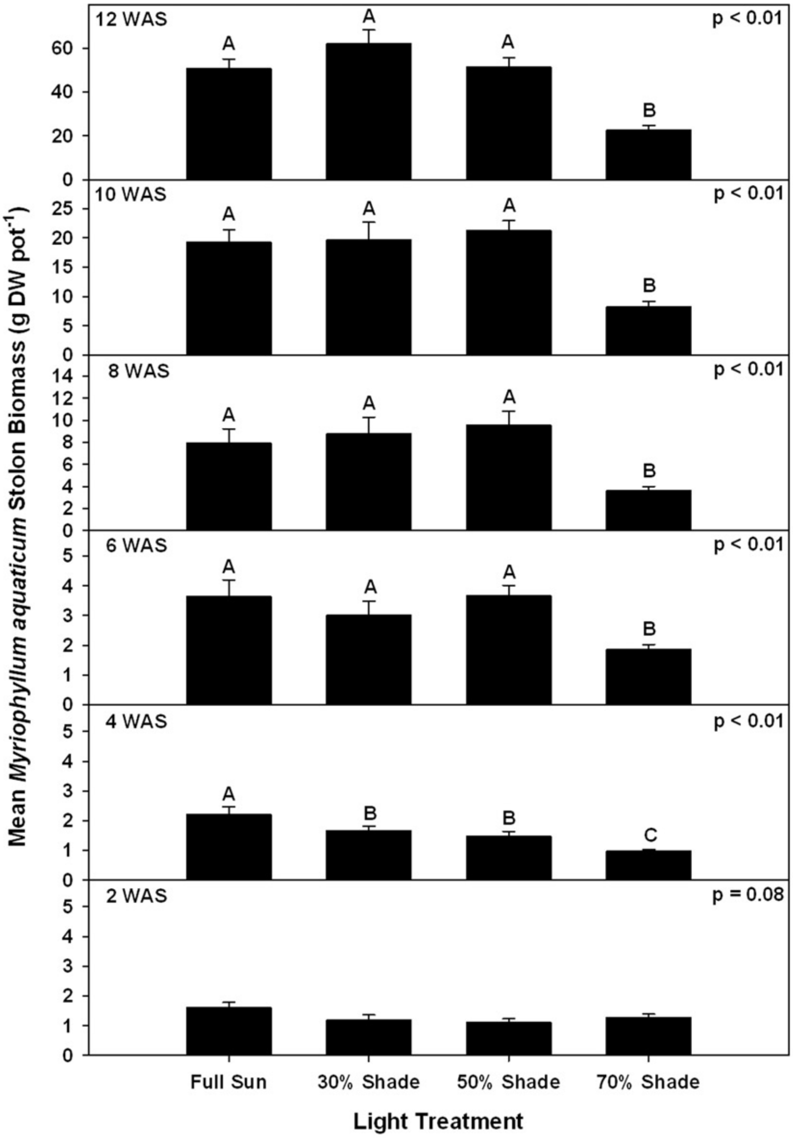

Figure 9. Mean (±1 SE) stolon biomass of *M. aquaticum* at each harvest interval (WAS). Bars sharing the same letter are not significantly different at $p < 0.05$ as determined by the least-squares means method.

Root biomass was greatest in the 30% shade treatment at 8 WAS (Figure 10). However at 12 WAS, biomass was similar between the plants grown in 30% and 50% shade, and root biomass was similar between plants grown in 50% and 70% shade. Root biomass of plants grown in 30% was always greater than plants grown in full sunlight which reflects the pattern observed for total biomass and emergent shoot biomass. Root biomass comprised 6–20% of total biomass across light treatments and WAS.

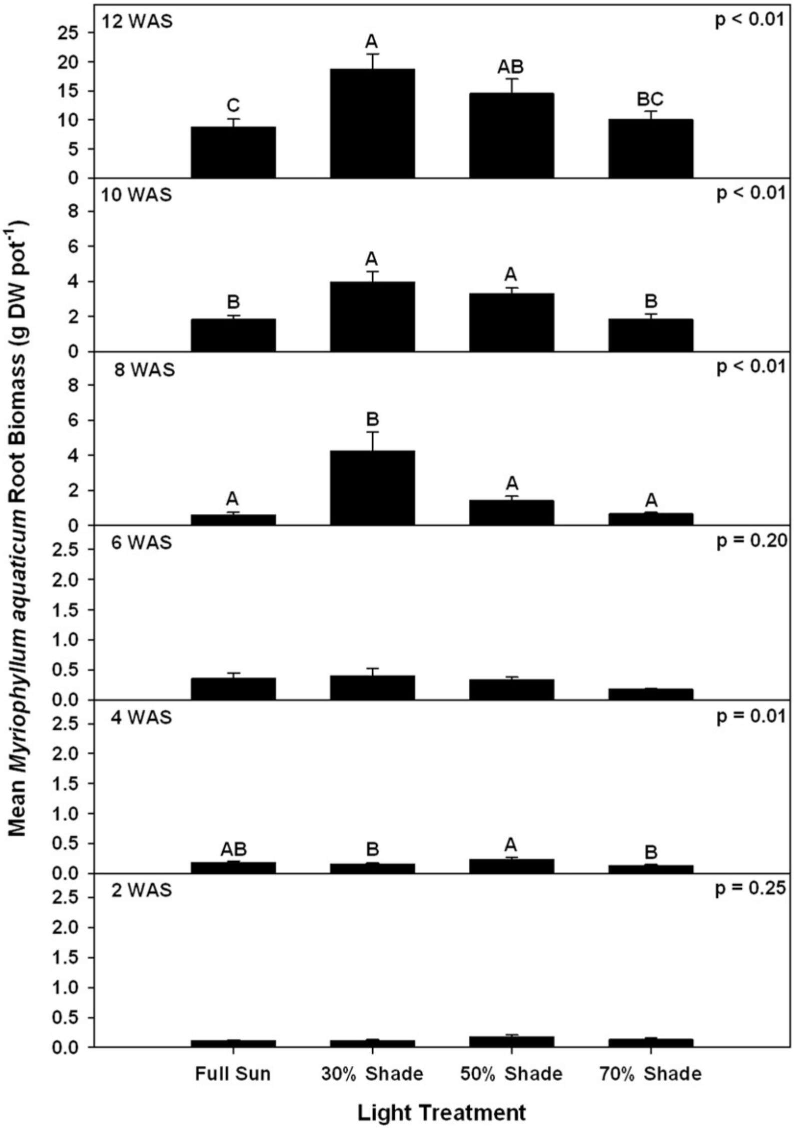

Figure 10. Mean (±1 SE) root biomass of *M. aquaticum* at each harvest interval (WAS). Bars sharing the same letter are not significantly different at $p < 0.05$ as determined by the least-squares means method.

The RGRs of *M. aquaticum* tissues varied greatly throughout the study (Table 1). However, a general pattern is visible with respect to RGR, tissue type, and when significant differences were observed. Significant effects were apparent for total biomass, emergent shoot biomass, and stolon biomass between 2 and 6 WAS, which represent times of increased growth and canopy production. Submersed shoot RGR was only affected by light intensity after 6 weeks when plants had reached the water surface and new shoot production began from root crowns, or in response to self-shading. Similarly, root RGR effects were observed at 8 and 10 WAS, which would correspond to the time when plants had emerged from the water column, formed a canopy and additional root biomass would be needed to anchor increasing emergent biomass.

Table 1. Mean RGRs ($\ln \mathrm{g\,DW\,d^{-1}}$) for *M. aquaticum* biomass.

| | WAS | | | | | |
|---|---|---|---|---|---|---|
| Light treatment | 2 | 4 | 6 | 8 | 10 | 12 |
| *Total biomass* | | | | | | |
| Full sun | 0.01ab | 0.02ab | 0.04 | 0.06 | 0.07 | 0.07 |
| 30% shade | −0.02b | 0.04a | 0.04 | 0.09 | 0.05 | 0.07 |
| 50% shade | 0.01a | 0.05a | 0.06 | 0.09 | 0.05 | 0.05 |
| 70% shade | 0.02a | 0.00b | 0.04 | 0.08 | 0.06 | 0.06 |
| *p* | **0.02** | **0.01** | 0.34 | 0.17 | 0.49 | 0.10 |
| *Emergent shoot* | | | | | | |
| Full sun | −0.10 | 0.05bc | 0.07 | 0.09 | 0.05 | 0.05a |
| 30% shade | −0.13 | 0.12a | 0.05 | 0.11 | 0.05 | 0.04a |
| 50% shade | −0.12 | 0.10ab | 0.10 | 0.09 | 0.05 | 0.01b |
| 70% shade | −0.10 | 0.01c | 0.08 | 0.13 | 0.05 | 0.03ab |
| *p* | 0.18 | <**0.01** | 0.31 | 0.16 | 0.88 | **0.02** |
| *Submersed shoot* | | | | | | |
| Full sun | −0.17 | 0.06 | 0.05 | 0.00b | 0.07 | 0.02a |
| 30% shade | −0.15 | 0.05 | 0.01 | 0.08a | 0.03 | −0.03b |
| 50% shade | −0.17 | 0.09 | 0.00 | 0.09a | 0.02 | −0.03b |
| 70% shade | −0.13 | 0.04 | 0.00 | 0.07a | 0.03 | −0.03b |
| *p* | 0.23 | 0.44 | 0.16 | <**0.01** | 0.24 | **0.02** |
| *Stolon biomass* | | | | | | |
| Full sun | 0.02 | 0.02a | 0.03b | 0.05 | 0.08 | 0.07 |
| 30% shade | 0.00 | 0.04a | 0.02b | 0.07 | 0.06 | 0.08 |
| 50% shade | 0.00 | 0.02ab | 0.07a | 0.07 | 0.06 | 0.06 |
| 70% shade | 0.01 | −0.02b | 0.04ab | 0.05 | 0.06 | 0.08 |
| *p* | 0.15 | **0.02** | **0.01** | 0.29 | 0.45 | 0.39 |
| *Root biomass* | | | | | | |
| Full sun | −0.16 | 0.03 | 0.01 | 0.06b | 0.09 a | 0.10 |
| 30% shade | −0.17 | 0.02 | 0.05 | 0.15a | 0.02 b | 0.12 |
| 50% shade | −0.15 | 0.04 | 0.02 | 0.09ab | 0.08 a | 0.09 |
| 70% shade | −0.17 | 0.01 | 0.03 | 0.09b | 0.07 a | 0.12 |
| *p* | 0.66 | 0.76 | 0.29 | **0.02** | <**0.01** | 0.64 |

Notes: Standard error is $\leq$0.01 for all RGR estimates.
Analyses were conducted within tissue type and WAS.
Within a column, entries sharing the same letter are not statistically different according to the least squares method at a $\alpha < 0.05$ significance level.

## Discussion

Increasing light availability did not result in increased growth of *M. aquaticum*. Results indicate that optimal growth occurred at intermediate light intensities, particularly 30% shade. *Myriophyllum aquaticum* did thrive in full sunlight and survive in 70% shade through adaptations to optimize its capture and use of light; however, biomass was reduced when *M. aquaticum* was grown in 70% shade. In the shaded treatments, submersed shoots elongated to reach the water surface to maximize light acquisition which is evident by the increased shoot length in the 70% treatment. However, once the submersed shoots of *M. aquaticum* reached the water surface, growth changed back to the emergent leaf form, an observation reported previously when plants were grown in varying water depths (Hussner et al. 2009; Wersal and Madsen 2011).

Optimal photosynthetic rates of *M. aquaticum* occur in the emergent form (Hussner 2009) and, therefore, *M. aquaticum* will not remain as a submersed plant for long periods of time as the photosynthetic rate of submersed leaves may not be sufficient to support plant growth (Salvucci and Bowes 1982). We contend that the submersed leaf form is an intermediate growth form, at least in the United States, and is only utilized for short overwintering periods, times of reduced light and temperature (Sytsma and Anderson 1993; Wersal et al. 2011), or to survive disturbances in the growing environment. Prolonged exposure to adverse growing conditions such as reduced light intensity will result in reductions in growth or plant mortality. *Myriophyllum aquaticum* grown in 70% shade had reduced total biomass, emergent shoot biomass, and stolon biomass when compared to the other treatments.

Overall, *M. aquaticum* has a light saturation point that approaches full sunlight and, therefore, it would be expected that plants exposed to full sunlight would have increased growth (Salvucci and Bowes 1982; Hussner 2009). However, based on our data of reduced biomass and shoot length in full sunlight as compared to 30% shade, full sunlight light may not be optimal for this species even with the emergent leaf form. Increased light availability is often correlated with increases in water temperature, which may result in water stress of *M. aquaticum*, where transpiration from emergent shoots exceeded water uptake. In fact, water temperature was higher in the full sunlight treatment throughout the study and in some instances daily maximum temperatures approached or exceeded 32°C. The increased temperature may have caused periodic reductions in photosynthesis and increased rates of photorespiration resulting in greater energy use in full sunlight and an overall reduction in plant growth (Salvucci and Bowes 1982). Although the direct effects of temperature cannot be determined in this study as our light treatments were causing the observed temperatures in the shade treatments, temperature is a major factor in plant growth and life history strategies. In a study of naturally occurring *M. aquaticum* populations, it was observed that seasonal water temperatures significantly influenced total plant biomass, submersed shoot biomass, stolon biomass, and starch allocation patterns (Wersal et al. 2011). One way to offset potential costs associated with variability in abiotic factors is to have alternative growth forms that can adapt to current growing conditions.

*Myriophyllum aquaticum* displays a high level of morphological plasticity (heterophylly) in response to changes in its growing environment (Casanova and Brock 2000). There have been many factors cited for having a role in inducing heterophylly in aquatic plants including temperature (Kane and Albert 1982; Deschamp and Cooke 1984; Goliber and Feldman 1990), photoperiod (Cook 1969), and light intensity (Goliber 1989). We observed a general increase in submersed shoot biomass in the 30% and 50% shade treatment 6 WAS, and an increase 10 WAS followed by a switch to emergent shoots when plants reached the water surface. *Myriophyllum aquaticum* was likely maximizing growth under reduced light conditions by growing submersed shoots. When plants reached the water surface and had access to more light, the growth form changed to emergent shoots to maximize photosynthesis.

*Myriophyllum aquaticum* is adapted to habitats that have frequent short periods of inundation where plants survive by growing submersed shoots. It was observed that the duration of flooding was an important factor controlling the growth and establishment of amphibious plant species (Casanova and Brock 2000). Flood duration will determine whether there is sufficient time for plants to respond, by changing morphology or elongation of stems, to flood conditions (Casanova and Brock 2000). Under sustained flooding of 12 weeks, *M. aquaticum* biomass was reduced when water depths were $>30$ cm (Wersal and Madsen 2011). It was concluded that reduced light availability in deeper water depths and the low photosynthetic rate of the submersed shoots limited shoot elongation to the water surface and the subsequent growth of an emergent canopy, ultimately resulting in reduced biomass. The light treatments utilized in this study had light intensities similar to those that *M. aquaticum* would experience under prolonged flooded conditions. *Myriophyllum aquaticum* had greater shoot elongation under shaded conditions, which would be similar to shoot elongation to the water surface in deeper water. However, prolonged exposure to low-light conditions reduced biomass.

Unlike plant length and biomass, RGR was much less sensitive to light effects although a few interesting patterns were observed that may highlight life history traits and allocation patterns of *M. aquaticum*. Changes in RGRs were only observed for total biomass and stolon biomass prior to 8 WAS. Changes in RGRs were observed for emergent shoot biomass at 4 WAS. We speculate that the time period from planting to 8 WAS represented rapid shoot production, elongation to the water surface, and the initiation of an emergent canopy to sustain plant growth. The rapid growth of stolons and emergent shoots contributed to the higher RGR for total plant biomass between 2 and 4 WAS. In contrast, submersed shoot RGR and root RGR was only significant after 8 weeks. This may suggest that *M. aquaticum* had sufficiently established an emergent canopy and was reallocating energy to the formation of a root crown and the growth of new submersed shoots that would in turn grow to the water surface to fill in gaps in the emergent shoot canopy. By 12 WAS, the emergent canopy covered the water surface resulting in self-shading of new submersed shoots in the water column. The congeneric *M. spicatum* will undergo self-shading when a surface canopy is produced; leaves below 1 m of the surface canopy begin to senesce and slough due to the light attenuation of the surface canopy (Madsen et al. 1991). Leaf morphology of submersed *M. aquaticum* is such that self-shading could be a plausible explanation for the observed negative RGR of submersed shoots during this time period.

Aquatic plants are generally very plastic in their response to environmental factors. Usually in reduced light environments, plant and leaf morphology will change, in general producing fewer, longer shoots and leaves (Barko and Smart 1981; Barko et al. 1982). The anatomical and morphological differences in the emergent and submersed form of *M. aquaticum* likely result from physiological adaptations to conditions in their respective environments (Sculthorpe 1967; Salvucci and Bowes 1982). Being able to adapt to changing environmental conditions is an important determinant for success in plants, especially in low-light environments (Barko et al. 1986). Species such as *M. aquaticum* that are capable of elongating to the water surface and forming a canopy may have a competitive advantage over other species (Haller and Sutton 1975; Barko and Smart 1981). *Myriophyllum aquaticum* not only can produce a surface canopy, it can survive as a submersed plant at reduced light intensities for short durations and survive drawdown conditions for up to 9 months (Maltchik et al. 2007). This suggests that *M. aquaticum* could possibly invade a wide range of habitats through shifts in its growth form and annual life history characteristics. However, to fully understand the invasion potential of *M. aquaticum*, more experiments are needed to determine direct effects of environmental variability, resource availability, resource use, and resource allocation on specific attributes of plant growth (Trémolières 2004). The ability to predict potential habitats suitable for invasion would be invaluable for monitoring and management programs of invasive species. In order to gain predictability, we need more information on plant response to environmental factors and resource availability across a landscape.

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