Comparative effects of water level variations on growth characteristics of *Myriophyllum aquaticum*

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Summary

Myriophyllum aquaticum is a non-native aquatic plant that has invaded a range of habitats in the United States and Europe. *Myriophyllum aquaticum* reduces native species richness at local scales, water quality, habitat quality for fish and wildlife and impacts on human uses. Despite the submersed leaf form, *M. aquaticum* is not typically a weed problem as water level increases, although little data exist describing basic biological and ecological mechanisms affecting growth. The objective of this study was to quantify changes in *M. aquaticum* growth as water levels increase from 0 (representing shoreline habitat) to 137 cm under controlled mesocosm conditions. Total biomass at 0 cm was 96% greater than plants grown at a depth of 137 cm. Biomass of emergent shoots, stolons and roots were also greater when *M. aquaticum* was grown at the 0 cm water level. Submersed shoot biomass was on average 99% greater between 37 and 77 cm. Submersed shoots comprised a small fraction, 0.1–12% of total biomass, depending on water level. Total plant length was 25% greater when plants were grown at water levels from 0 to 77 cm, compared with plants grown at 97, 117 or 137 cm. Nuisance growth is dependent upon plants emerging from the water column; as water levels increase, this becomes more difficult for plants, as a result of the reduced photosynthetic ability of submersed leaves. These results can be used to identify optimal areas for *M. aquaticum* growth and possibly predict areas of new infestations.

Keywords: Parrot's feather, light transmittance, non-native, aquatic macrophyte, exotic species, alien species, invasion, environmental factors.

Introduction

Hydrologic variations within wetlands and shallow lakes often determine patterns of plant zonation and community structure (Casanova & Brock, 2000; van Geest *et al.*, 2005). The water regime of a given habitat is often characterised by the depth, duration and frequency of flood and drawdown events (Casanova & Brock, 2000). Sustained or frequent flooding can lead to a more stable environment and a shift in species dominance and ultimately species composition (van der Valk, 2005). More stable environments created by flooding often inhibit emergent macrophyte growth (Casanova & Brock, 2000) and favour submersed aquatic macrophytes, such as evergreen perennial species. Water level fluctuations can be viewed as disturbance to the plant community and disturbance is often the primary mechanism that facilitates invasions through removing native species and opening niche space for colonising species (Davies *et al.*, 2005; Lockwood *et al.*, 2005; Capers *et al.*, 2007).

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 colonise and grow to nuisance levels, often with negative consequences on the local plant community composition, ecosystem functions and human uses (Chapin *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).

Myriophyllum aquaticum (Vell.) Verdc. (Parrot's feather) is an herbaceous perennial aquatic plant that is native to South America and is increasingly becoming problematic in shallow streams, irrigation ditches, ponds and shallow lakes of the United States. *Myriophyllum aquaticum* typically invades shallow waterbodies that are prone to disturbances, such as repeated and frequent water level fluctuations. Once established, disturbances that can fragment plants, such as harvesting, mowing, chaining, or the rapid rise and fall of water level, will favour the growth and spread of this species. *Myriophyllum aquaticum* is tolerant to mechanical disturbances and the repeated occurrence of these events favours dominance in canals (Sabbatini *et al.*, 1998). Survival and spread of *M. aquaticum* depends solely on vegetative reproduction via fragmentation, as this species does not produce any specialised reproductive structures, such as seeds, tubers or turions, in its introduced range (Sutton, 1985). *Myriophyllum aquaticum* is heterophyllous, meaning it has a distinct submersed and emergent leaf form that can be viewed as phenoplasticity, or the change in growth form as a response to extreme environmental changes (Winn, 1999; Trémolières, 2004). An inundation gradient can be a major factor which induces plasticity in plants (Trémolières, 2004). Having two distinct growth forms may give *M. aquaticum* the ability to overcome extreme disturbances in the water regime and impart a competitive advantage over macrophytes that are more sensitive to changes in their environment.

The impact of water level and duration of flooding on wetland macrophyte communities, particularly emergent and submersed species, are well documented at the field scale (van der Valk *et al.*, 1994; Casanova & Brock, 2000; Richardson *et al.*, 2002; van der Valk, 2005; Maltchik *et al.*, 2007), with some effects reported for amphibious species (Casanova & Brock, 2000; Maltchik *et al.*, 2007). Casanova and Brock (2000) reported on the influence of water depth on macrophyte establishment; however, the deepest depth in their study was 60 cm. Hussner *et al.* (2009) reported differences in *M. aquaticum* total shoot length, shoot biomass, root biomass and total biomass, over a limited range of water levels. *Myriophyllum aquaticum* is capable of growing in deeper water depths; however, the direct effects of deeper water levels on growth characteristics are unknown. Therefore, the objective of this study was to determine the growth response, particularly of biomass and plant length, of *M. aquaticum* and its individual structures under increasing water depths.

Materials and methods

Plant description

Godfrey and Wooten (1981) describe *M. aquaticum* as 'stout, stems moderately elongate, partially submersed but with portions of leafy branches emergent. Leaves are whorled, stiff, usually with 20 or more linear filiform divisions, appearing feather-like and greyish green'. Vegetative reproduction occurs solely by fragmentation of emergent and submersed shoots. Submersed shoots are comprised of whorls of 4–6 filamentous, pectinate leaves arising from each node (Mason, 1957). When the submersed shoot emerges, the stem morphology changes so that emergent shoots become denser and contain more structural tissues than submersed shoots (Sytsma, 1992). After plants reach the water surface, plant growth changes from vertical to horizontal (stolons) to facilitate the rapid covering of the water surface (Fig. 1). Once stolon formation begins, extensive lateral branching occurs as the growth of new emergent shoots (Moreira *et al.*, 1999).

Experimental design and growing conditions

Studies were conducted in a mesocosm facility located at the R.R. Foil Plant Science Research Center, Mississippi State University, Starkville, MS (33°28′29.76″N, 88°46′24.70″W) from 8 June to 4 September 2008 and repeated from 2 June to 28 August 2009. Both studies were conducted in 28, 1900 L mesocosms (137 cm diameter by 157 cm deep) arranged in a randomised complete block design with four repetitions per water level treatment for 12 weeks. Water level treatments were 0 (pots just below the water surface, which represents shoreline habitat), 37, 57, 77, 97, 117 and 137 cm.

Platforms were constructed from sheets of galvanised metal to reduce rust formation when submersed and to maximise platform strength when potted plants were placed on them. The platforms were 130 cm long by 30.5 cm wide with grooves to hold pots from falling off the platforms. Platforms were suspended at the appropriate water level using vinyl coated chain. Water levels were determined based upon the total height of the planting containers (pots were 16.5 cm diameter by 20 cm deep), and the depth from the top of the pot to the water surface was considered the treatment depth. Therefore, when pots were placed on
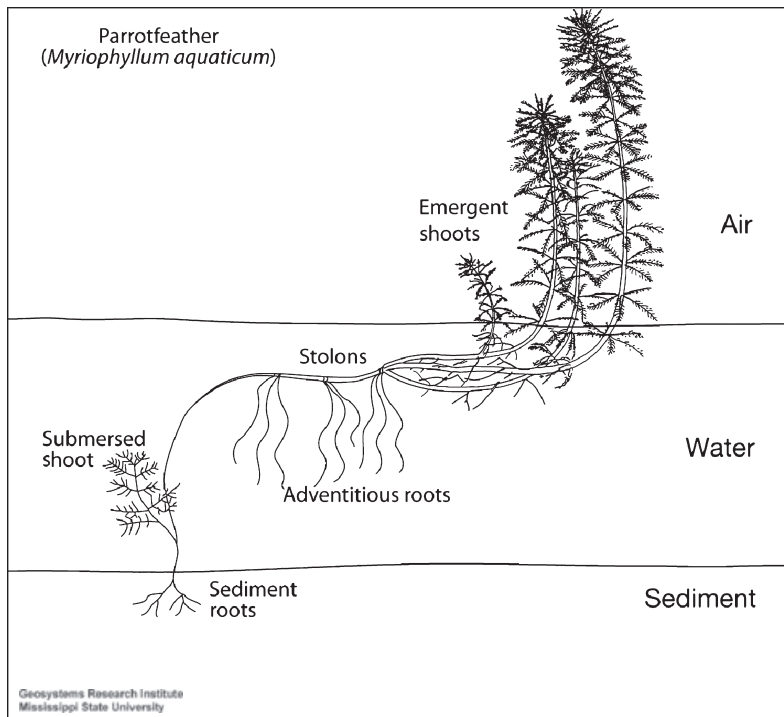
Fig. 1 A conceptualisation of the growth form and plant structures of *Myriophyllum aquaticum*, including emergent shoots, submersed shoots, stolons, sediment roots and adventitious roots.

the bottom of the mesocosms, the treatment level was 137 cm. Platforms were then suspended at appropriate depths within designated mesocosms to achieve the treatment water levels from the top of the pot to the water surface. The 0 cm water level was achieved by immersing the pots just below the water surface so that the top of each pot was just below the water line to maintain moist soil.

Water was supplied to each mesocosm from an irrigation reservoir adjacent to the mesocosm facility. Additional water was added from the irrigation reservoir to every mesocosm 2–3 times per week to offset losses from evaporation, to keep the water level stable, and aid in water circulation. Very little planktonic algae were observed over the course of the study, as water remained clear enough to see the bottom of each mesocosm. Some epiphytic algae were observed growing on the sides of the mesocosms and on the platform, although little algal growth was observed on plants. We did not attempt to remove or control the epiphytic algae on the sides of the mesocosms, as the methods to do so would likely have a greater impact on *M. aquaticum* growth than leaving the algae in place.

Myriophyllum aquaticum was harvested from a local water body and transported to Mississippi State University for planting. Planting consisted of placing two emergent apical shoots of *M. aquaticum*, 20 cm in length, into each of 168, 3.78 L pots (16.5 cm diameter by 22.5 cm high) containing a top soil, loam and sand mixture (3:2:1) (10 mg NO_3-N kg^{-1} soil, 26 mg P_{tot} kg^{-1} soil). Sediment was placed to within 2 cm from the top of each pot and amended at a rate of 2 g L pot^{-1} using Osmocote 19-6-12 fertiliser to maintain growth throughout the study (The Scotts Company, Marysville, OH, USA). Six pots of planted *M. aquaticum* were placed onto the platforms in each tank, with the exception of the 137 cm water level when pots were placed directly on the bottom. A 30% shade cloth was installed over the top of all mesocosms to mediate heat effects, as *M. aquaticum* biomass is not affected by shade cloth up to 50% when compared with plants grown in full sunlight (Wersal, 2010).

Light intensity, both incident and submersed, was recorded at each water level in each mesocosm using a LI-1400 data logger with a LI-190 photometric sensor (incident light) and a LI-192 submersible sensor (LI-COR Biosciences, Lincoln, NE, USA). Light data were recorded approximately twice per week for 12 weeks during both studies. After 12 weeks, all pots were removed from the tanks, total plant length was determined from the sediment to the longest apical tip for each plant and all biomass was harvested including roots. Plants were washed and sorted into 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. Biomass is expressed as g dry weight (DW) pot^{-1}.

Statistical analysis

Statistical analyses were conducted using SAS software (SAS Institute, Cary, NC, USA). A mixed procedures

model using year as a random effect was utilised to examine water level effects on total biomass, emergent shoot, submersed shoot, stolon and root biomass of *M. aquaticum*, as well as total plant length (Littell *et al.*, 1996). 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 calculated for total biomass at each water depth 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 utilised to determine differences in RGR.

Light transmittance was calculated by dividing the submersed values by incident values for each mesocosm and is presented as a percentage. Polynomial regression analysis was used to determine the relationship between water depth and percent light transmittance. Regression models were sequentially fitted, beginning with a linear model. Polynomial terms were then added one at a time and lack of fit determined using partial *t*-tests. There was no block effect ($P = 0.85$) for biomass or plant length ($P = 0.07$). All analyses were conducted at a $P < 0.05$ level of significance.

Results

Relative growth rates of *M. aquaticum* were greatest (0.053 g DW day^{-1}; $P < 0.001$) when plants were grown in the 0 cm water level (Fig. 2A). The RGR of plants grown at 97, 117 and 137 cm were lower than RGRs of all other water level treatments and these data correspond with biomass data. Total biomass of *M. aquaticum* decreased by 96% when plants were grown at 137 cm (5.4 ± 0.9 g DW pot^{-1}), compared with plants grown at 0 cm (140 ± 7.1 g DW pot^{-1}) (Fig. 2B). Biomass at 37 cm was 58% less than plants grown at 0 cm. In fact, *M. aquaticum* biomass at the 0 cm water level was significantly ($P < 0.01$) greater than biomass at all water levels.

Emergent shoot biomass was 35.9 ± 1.9 g DW pot^{-1} at the 0 cm water level, which was 96% greater than emergent shoot biomass of plants grown at the 137 cm water level (1.6 ± 0.4 g DW pot^{-1}) (Fig. 3). Stolon biomass of *M. aquaticum* was also greater at the 0 cm water level (91.6 ± 5.6 g DW pot^{-1}) and overall, stolon biomass accounted for approximately 45–70% of total biomass across all water levels (Fig. 4). Root biomass was 6.5 ± 0.5 g DW pot^{-1} at the 0 cm water level and was also greater than root biomass at any other water

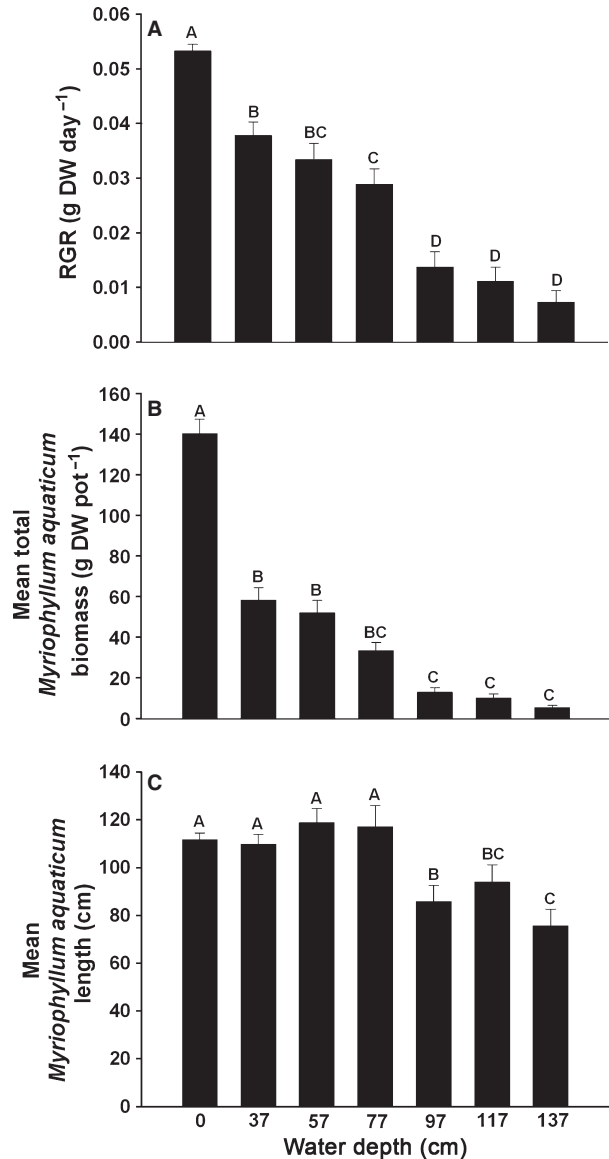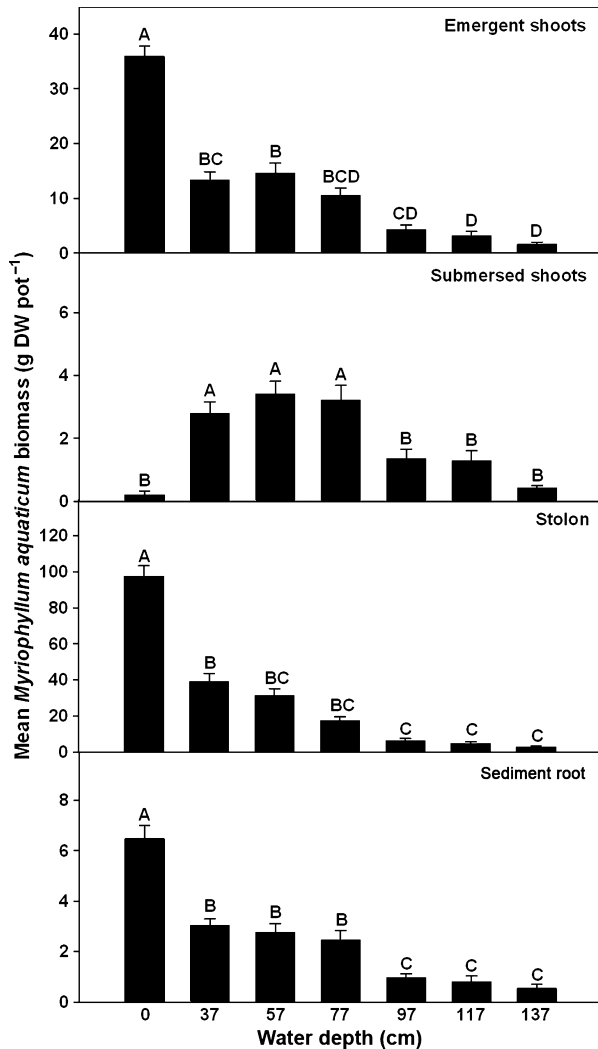**Fig. 2** Mean (±1 SE) *Myriophyllum aquaticum* RGR (A), mean (±1 SE) biomass (g DW pot^{-1}) (B), and mean (±1 SE) total plant length (cm) (C) at increasing water levels under controlled conditions. Bars sharing the same letters are not significantly different according to the LSD procedure using a Mixed Procedures Model at $P < 0.05$ significance level.

level. Root biomass comprised 4.5–9% of total biomass across water levels, with a larger proportion of root biomass relative to total biomass as water levels increased.
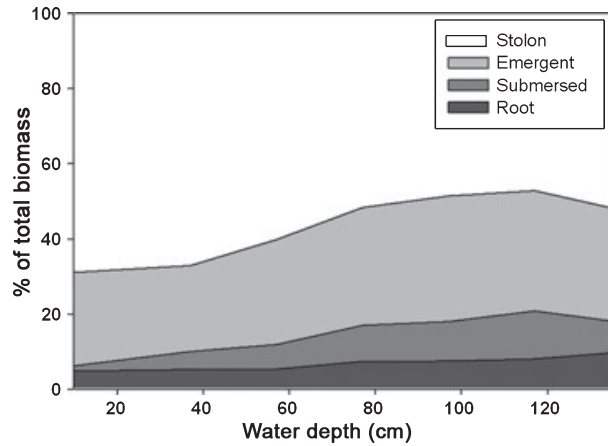
Submersed shoot biomass was greatest when *M. aquaticum* was grown at the 33, 57 and 77 cm water levels (Fig. 3). Average submersed shoot biomass across these levels (33, 57 and 77 cm) was 3.1 ± 0.4 g DW pot^{-1}, which was 90% greater than all other water levels combined and where biomass was only 0.8 ± 0.2 g DW pot^{-1}. Submersed shoot biomass never accounted for

Fig. 3 Mean (± 1 SE) emergent shoot, submersed shoot, stolon and root biomass (g DW pot^{-1}) of *Myriophyllum aquaticum* at increasing water levels under controlled conditions. Bars sharing the same letters are not significantly different according to the LSD procedure using a Mixed Procedures Model at $P < 0.05$ significance level.

Fig. 4 Biomass allocation (as % of total biomass) patterns of individual plant tissues for *Myriophyllum aquaticum* across a water depth gradient under controlled conditions.

$$y = 59.03 - 0.43x + 0.001x^2$$
$$r^2 = 0.99$$
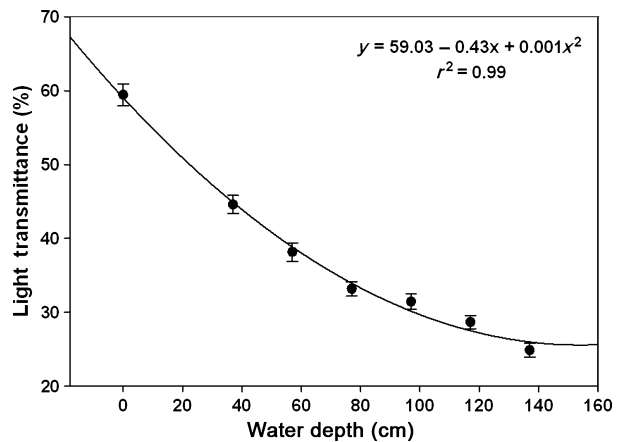
Fig. 5 Polynomial regression analysis of mean (± 1 SE) light transmittance (% of total irradiance) calculated for each water level under controlled conditions over the course of 12 weeks.

more than 12% of total biomass for a given water depth (Fig. 4).

Although total biomass is generally a good metric to evaluate plant response under controlled conditions, we also wanted to determine water level effects on the other distinct plant tissues of *M. aquaticum*, namely emergent shoots, submersed shoots, stolons and sediment roots. *Myriophyllum aquaticum* plant length was similar across the 0, 37, 57 and 77 cm water levels and was greater ($P < 0.01$) than plants grown at the 97, 117 and 137 cm levels (Fig. 2C). Plant lengths were 111.7 ± 2.8, 109.7 ± 4.1, 118.8 ± 5.9, 117.2 ± 8.8 cm for the 0, 37, 57 and 77 cm water levels, respectively, and 85.8 ± 6.8, 93.9 ± 7.2 and 75.7 ± 6.9 cm for the 97, 117 and 137 cm levels respectively. Plants had reached

the water surface in less than seven days in the 37 and 57 cm water levels and in less than 14 days when water level was at 77 cm. *Myriophyllum aquaticum* had difficulty reaching the water surface in deeper water levels between 14 and 21 days for plants growing at levels of 97, 117 and 137 cm, and therefore plant lengths are lower than the treatment level.

Incident light was similar ($P = 0.52$) across all water level treatments, indicating the same amount of light was reaching the surface of each mesocosm. However, light transmittance through the water column was negatively ($R^2 = 0.99$) related as a quadratic function to increasing water depth, meaning light attenuation was rapidly occurring as water levels increased, even though the bottom of all mesocosms could be observed (Fig. 5). We contend that this trend in light availability corresponds with the observed decreases in *M. aquaticum* biomass, as there is a similar trend in biomass data.

Discussion

Relative growth rates and biomass of *Myriophyllum aquaticum* were negatively affected as water levels increased, with the exception of submersed shoot biomass that increased at intermediate water levels. The RGRs in this study are comparable with rates reported in previous studies (Sytsma & Anderson, 1993a,b; Hussner, 2009), although the rates reported for deepest water levels are slightly lower than in other studies. In natural populations, total *M. aquaticum* biomass was 1001 g m^{-2} when plants were harvested from water depths < 0.5 m. This represented a 77% increase in biomass from plants collected at sites (234 g m^{-2}) that were 0.5–1.5 m in depth (Sytsma & Anderson, 1993c). Biomass allocation to emergent shoots is also greater when plants grow in water depths < 0.5 m (Sytsma & Anderson, 1993c). We attribute these results to the heterophyllous growth of *M. aquaticum* and the response to light intensity in its growing environment. *Myriophyllum aquaticum* grown at the 0 cm water level did not have to switch growth forms, as evidenced by the increased RGR, and could allocate energy to horizontal growth over the water surface, growth of stolons and growth of adventitious roots.

Adventitious roots have been suggested as an important site for water and nutrient uptake that result in a reduced reliance upon sediment roots. *Myriophyllum aquaticum* growth did not reduce sediment nutrient concentrations over the course of a controlled study when adventitious roots were present and the water column provided 98% of water utilised by plants (Sytsma & Anderson, 1993b). In the current study, root biomass increased as water levels decreased, which is similar to observations reported by Hussner *et al.* (2009). Sediment roots are typically heavily cuticularised, thick, stiff and lack root hairs (Sutton & Bingham, 1973; Sytsma & Anderson, 1993b), which may limit nutrient uptake from sediments. However, *M. aquaticum* also increases rooting depth with decreasing water level (Hussner *et al.*, 2009), which would allow greater access to sediment pore water. The increased access to sediment pore water may give this species a competitive advantage in drawdown situations over aquatic plants that have shallow rooting depths.

When *M. aquaticum* becomes submersed, the leaf form rapidly changes from emergent tissues to submersed tissues; in the current study, this switch occurred in a matter of days. Plants in the intermediate water levels were able to reach the water surface and begin emergent shoot growth, as well as promoting new growth from root crowns, which accounted for the increase in submersed shoot biomass in these water level treatments. The submersed shoots in the deepest water levels were responsible for maintaining plant growth and for plant elongation to the water surface. Light transmittance was ≥25% in all treatments, which is sufficient to promote submersed plant growth (Chambers & Kalff, 1985). However, we observed significant declines in biomass and plant length as water levels increased, suggesting that submersed leaves alone cannot sustain *M. aquaticum* growth for long periods of time.

Optimal photosynthetic rates of *M. aquaticum* occur in the emergent form and therefore *M. aquaticum* will not remain as a submersed plant for long periods of time; the photosynthetic rate of submersed leaves may not be sufficient to support plant growth (Salvucci & Bowes, 1982). *Myriophyllum aquaticum* has a relatively high temperature optimum and gas exchange, with a photosynthetic light saturation point that is approximately threefold higher in emergent leaves (900 µE m^{-2}·s; Hussner, 2009) than in submersed leaves (250–300 µ E m^{-2}·s; Salvucci & Bowes, 1982). Light levels in this study were sufficient to promote plant growth, based upon the light saturation values even under shade cloth. The lower photosynthetic rate of submersed leaves suggests that this growth form is adapted to a shade environment (Salvucci & Bowes, 1982). However, a low light saturation point could also be caused by a CO_2 limitation, rather than a physiological difference in response to light (Maberly & Spence, 1989).

In the current study, there could have been potential growth limitations because of the availability of dissolved inorganic carbon (DIC) and CO_2 to submersed shoots, especially if pH rose above 8.0 thereby reducing free CO_2 in the water column (Maberly & Spence, 1989). If this occurred, it would have only been for a short period, because once plants emerged from the water column, typically 5–21 days depending upon depth, the reliance on CO_2 in the water column is greatly reduced. Maberly and Spence (1989) reported that access to air by amphibious plants probably enhances rates of photosynthesis by alleviating limitations in supply of DIC underwater. In the case of *M. aquaticum*, once emergent leaves were formed, there would likely be little photosynthetic input from submersed leaves, especially after canopy formation and possible self-shading.

The congeneric Eurasian watermilfoil (*Myriophyllum spicatum* L.), which grows completely submersed, will undergo self-shading when a surface canopy is produced; leaves below 1 m of the surface canopy begin to senesce, because of the light attenuation of the surface canopy (Madsen *et al.*, 1991). The light levels recorded in this study may have been enough to mimic the self-shading effect of a surface canopy at the deeper water depths; when plants reached the surface and began emergent growth, this would have created a self-shading environment for plants still in the water column. This

may explain the reduced submersed shoot biomass at the 0 cm water depth and the overall reduction in biomass at the deeper water depths. We contend that submersed growth is transient and only utilised for short overwintering periods, times of reduced light and temperature (Sytsma & Anderson, 1993a), or to survive disturbances in the growing environment. Prolonged exposure to adverse growing conditions will result in reductions in growth or plant mortality.

Myriophyllum aquaticum is described as responding to hydrological fluctuations and a species that grows in a variety of habitats and conditions, such as flooded conditions, damp or drawdown conditions. It has morphological plasticity (heterophylly) in response to water level variations (Casanova & Brock, 2000). In a study conducted in a 2-ha palustrine wetland in the Sinos River Basin, Brazil, *M. aquaticum* was collected during both a flooded period and a drawdown period, but was more associated with wet growing conditions (Maltchik *et al.*, 2007). These authors also suggest that *M. aquaticum* may be tolerant of drawdown events (complete removal of surface water) lasting 9 months, if the sediment remains saturated. It was also reported that near-permanent wetland and flooded wetland conditions were dominated by amphibious fluctuation-responder plant species under mesocosm conditions (Casanova & Brock, 2000). These studies show that *M. aquaticum* is well adapted to survive both drawdown and flooding events of various durations. Shorter flooding durations allow for amphibious species to recover between flooding events and survival at intermediate durations required plants to tolerate both immersion and emergence (Casanova & Brock, 2000). Casanova and Brock (2000) concluded that flood duration would determine if there is sufficient time for amphibious plants to respond by changing leaf morphology or elongation of stems.

In this study, *M. aquaticum* was subjected to different water levels and one flood duration of 12 weeks. The plants responded quickly to immersion, by changing leaf morphology. However, plants in deeper water levels were unable to grow to the water surface and begin emergent growth. *Myriophyllum aquaticum* may have responded differently, if the duration of flooding was reduced. Our data suggest that this species does not grow well under sustained deep flood conditions. The reduced biomass and plant length observed in this study, along with evidence of reduce photosynthetic rates of the submersed leaves from previous studies, may offer some evidence that there is an energetic cost associated with heterophylly. Aquatic plant populations that experience frequent changes in the water regime also exhibit the greatest degree of heterophylly (Cook & Johnson, 1968), and a reduction in heterophylly in populations from more stable environments also suggests that there

may be costs associated with heterophylly (DeWitt *et al.*, 1998). Heterophylly is a trait that must have some adaptive value, otherwise it would not be found in nature (Trémolières, 2004). In its native habitat, *M. aquaticum* is often found growing in palustrine habitats, or areas that are prone to frequent water level variations (Rolon & Maltchik, 2006). Therefore, heterophylly allows *M. aquaticum* to survive in its native palustrine habitats.

The objective then would be to predict the growth of *M. aquaticum* and other non-native species based upon life history traits (Trémolières, 2004). Often however, basic biological and ecological data are overlooked and the focus is placed solely on management of the problematic species. Based on results from the current study, the establishment and growth *M. aquaticum* is going to be limited to shallow areas where fragments can root and plants can grow rapidly to the water surface and establish an emergent canopy and adventitious roots. In deeper water, growth is going to be limited or inhibited by light availability, fragment establishment and the ability of submersed plants to grow to the water surface and establish an emergent canopy, unless flood duration is reduced to allow plant growth to the water surface. Other studies are needed to address flood duration effects on *M. aquaticum*. Additional experiments are also needed to determine effects of environmental variability and resources availability on specific attributes of non-native plant growth in aquatic systems (Trémolières, 2004), thereby allowing the identification of optimal areas for invasion and the development of early detection and rapid response programmes.

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