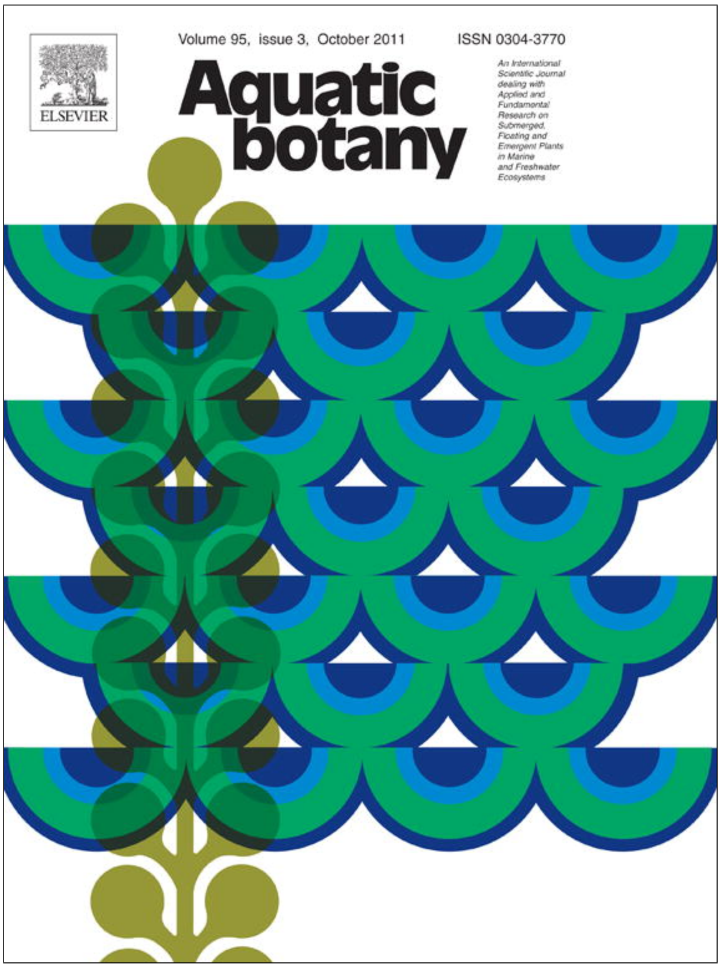
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Phenology, starch allocation, and environmental effects on *Myriophyllum aquaticum*

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ABSTRACT

Seasonal biomass and starch allocation patterns were determined from natural populations of *Myriophyllum aquaticum* that were sampled monthly from January 2006 to December 2007 in Mississippi. Water temperature, water depth, light irradiance, light transmittance, pH, and conductivity were also recorded during biomass harvests. Overall, few significant relationships were observed between the environmental factors tested and seasonal biomass. Submersed shoot biomass was negatively related ($p < 0.01$) with water temperature. Stolons accounted for 40–95% of total biomass followed by emergent shoot, submersed shoot, and root biomass. Percent starch in plant tissues was positively related to water temperature. Starch allocation was greatest in stolons where up to 16.3% of total starch was stored. Submersed shoots stored 0.6–11.0% of total starch followed by emergent shoots (0.4–7%). The roots of *M. aquaticum* stored less than 3.8% of total starch throughout the study period. Reduced biomass and starch storage occurred from October to March in both 2006 and 2007. Management strategies for this species could utilize an integrated approach to exploit times of low energy reserves (fall and winter), or to remove emergent shoots to gain access to the stolons and other submersed tissues.

1. Introduction

Phenology is the study of the seasonal timing of critical life stages in plants, and the allocation of biomass and other resources such as carbohydrates are fundamental aspects in the life history of plants. Plants in temperate regions typically store carbohydrates as starch in roots, rhizomes, and specialized structures for winter survival (Cyr et al., 1990). Plants allocate and store carbohydrates to support growth, photosynthesis, and maintenance throughout the growing season (Chapin et al., 1990; Spencer et al., 1997). Aquatic plants utilize many structures for storing starch, including roots (Madsen, 1997; Madsen and Owens, 1998), rhizomes (Gallagher et al., 1984), stems (Madsen, 1997; Madsen and Owens, 1998; Pennington and Sytsma, 2009), stembases (Tucker and DeBusk, 1981), tubers (Owens and Madsen, 1998), winter buds (Titus and Adams, 1979), and turions (Woolf and Madsen, 2003).

In most cases, aquatic plants will display distinct seasonal patterns in biomass (Wersal et al., 2006) and carbohydrate allocation (Woolf and Madsen, 2003); where storage peaks in summer or fall and is depleted in spring after plant growth has occurred (Madsen, 1991). Understanding these annual growth cycles will allow for the determination of seasonal reductions in energy reserves. Timing management to coincide with seasonal reductions in stored carbohydrates can exploit reduced energy reserves within the plant and possibly enhance efficacy of the management techniques; thereby reducing the ability of the target plant to re-grow, or survive times of seasonal dormancy (Madsen, 1997).

Herbicide treatments on alligatorweed (*Alternanthera philoxeroides* Mart. Griseb.) were found to be more effective when applied during times of low carbohydrate storage (Weldon and Blackburn, 1968). Mechanical harvesting of Eurasian watermilfoil (*Myriophyllum spicatum* L.) has been documented to reduce carbohydrate concentrations in affected populations (Perkins and Sytsma, 1987), and reduces overwintering survival (Kimbel and Carpenter, 1981). Harvesting has also been shown to reduce carbohydrates in hydrilla (*Hydrilla verticillata* L.f. Royle); and, if harvesting was maintained, tuber production was significantly reduced (Fox et al., 2002). The practical application of this strategy will be dependent upon knowing the phenological cycle of the target plant, and timing management to that cycle. However, management decisions are often dictated by practical reasons and not for maximizing treatment efficacy (Pennington and Sytsma, 2009).

Parrotfeather [*Myriophyllum aquaticum* (Vellozo) Verdecourt, synonymous with *M. brasiliense*] is a non-native invasive aquatic plant from South America that was introduced into the United States in 1890, likely near Haddonfield, New Jersey (Nelson and Couch, 1985). *M. aquaticum* is a common component of aquaria landscaping, which had undoubtedly served as the primary vec-

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tor of spread for this species (Sutton, 1985). Although it is not considered a major noxious aquatic weed throughout most of its range, it can cause severe localized problems in shallow ditches, streams, ponds, and shallow lakes. Dense populations can impede water movement in streams and ditches, resulting in increased flood duration and intensity (Timmons and Klingman, 1958). *M. aquaticum* poses a direct threat to drinking water supplies in South Africa (Jacot-Guillarmod, 1977). Furthermore, female *Anopheles* mosquitoes have increased oviposition rates when shoot densities reached approximately (1000thems m^{-2}), as *M. aquaticum* serves as a refuge from predation (Orr and Resh, 1989).

M. aquaticum can colonize a diverse range of habitats and tolerate disturbances to these habitats. Plants are not seriously affected by frost, and growth rate appears to be primarily affected by temperature and light availability (Sytsma and Anderson, 1993a; Moreira et al., 1999). Growth initiates when water temperatures reach 8 °C and displays a direct relationship with temperature (Moreira et al., 1999). In general, depths of less than 100 cm are optimal (Moreira et al., 1999); however, *M. aquaticum* has been observed growing in waters up to 2 m deep (Sutton, 1985). *M. aquaticum* can survive in coastal waters where frequent inundation of salt water occurs, promoting sediment root growth and establishment (Haller et al., 1974). Survival and spread of *M. aquaticum* depends solely on vegetative reproduction via fragmentation. Therefore, the objectives of this study were to: (1) document phenology (biomass allocation) over a 2-year period as it relates to environmental factors and plant tissues; and (2) quantify seasonal starch allocation patterns within the different plant tissues of *M. aquaticum*.

2. Materials and methods

2.1. Seasonal biomass collection

M. aquaticum biomass was harvested monthly from four locations in Mississippi from January 2006 to December 2007. Waterbody size ranged from approximately 0.1–15 ha however, samples were harvested from only 0.1–0.2 ha of each waterbody that contained *M. aquaticum*, to ensure consistency with sample area between sites. At each sample site, 30 biomass samples ($n = 1880$) were randomly harvested using a 0.018 m^2 PVC coring device as outlined in Madsen et al. (2007). Harvested biomass was rinsed to remove sediment and debris, and then divided into four categories: emergent shoots, submersed shoots, stolons, and sediment roots (here after referred to as roots) (Fig. 1). Emergent shoots were separated by cutting the shoots at approximately the third node below the last whorl of emergent leaves. Stolons were considered the horizontal growth below the emergent shoots as both emergent biomass and adventitious roots grew from the nodes along the stolons. By definition a stolon is a horizontal branch arising at or near the base of a plant and developing new plants at the nodes or apex (Gleason and Cronquist, 1963). Adventitious roots were left on stolons and were incorporated into stolon biomass; as previous reports suggest these roots do not function as storage tissues, but for water and nutrient acquisition (Sytsma and Anderson, 1993a,b). Plant parts were dried for at least 72 h at 70 °C in a constant temperature oven and then weighed. *M. aquaticum* total biomass as well as its constituent parts are expressed as g m^{-2} for each month.

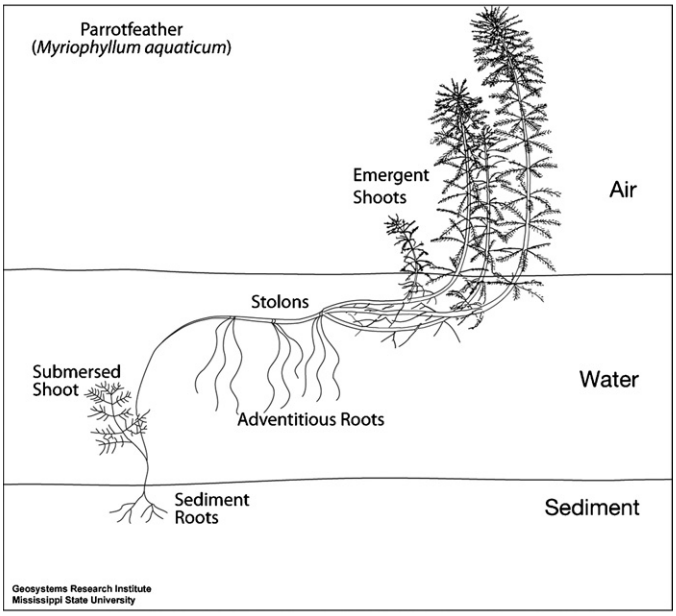

Fig. 1. A conceptualization of the growth form and plant structures of *Myriophyllum aquaticum*, including emergent shoots, submersed shoots, stolons, sediment roots, and adventitious roots (reproduction from Wersal and Madsen, 2011).

2.2. Environmental monitoring

During all harvest times water depth was recorded using a PVC rod with cm delineations for each sample, at all locations, prior to collecting a core. In 2006, site one contained moist soil from June to September with *M. aquaticum* present for sample collection, therefore water depth was recorded as 0 cm and then plants were harvested. In 2007, a similar situation occurred, however site three completely dried and had no plants present for harvesting. Therefore, water depth from site 3 was not collected and averages are based on only three sites for this time period. Sample location characteristics are summarized in Table 1.

In addition to water depth, pH, and conductivity were recorded once at each site every month with a Eureka Environmental Multi-Probe (Eureka Environmental, Austin, Texas). Measurements were made directly adjacent to plant stands. A HOBO temperature probe (Onset Computer Corporation, Pocasset, Maine) was deployed at

Table 1
Mean ($n = 24$ months, 2006–2007) site characteristics for the four biomass sample sites in Mississippi.

Characteristic	Site number			
	One	Two	Three	Four
Coordinates	32°20′45.859″N 89°20′43.939″W	32°40′34.715″N 89°38′56.758″W	33°26′30.332″N 88°54′13.453″W	33°16′24.641″N 88°47′33.994″W
Water temperature (°C)	18.38	17.74	20.62	19.22
Water depth (cm)	21.76	49.78	16.95	73.61
Incident light (μmol s^{-1} m^{-2})	769.46	531.71	710.96	506.88
Light transmittance (%)	25.55	16.51	20.76	18.62
pH	7.36	7.30	7.91	7.26
Conductivity (mS cm^{-1})	0.23	0.13	0.06	0.06

each of the four harvest locations to record water temperature in 1 h intervals for the 2 years of sampling. Light profiles in 25 cm increments from the water surface to the bottom sediment were determined monthly at each harvest location using a LI-1400 data logger with a LI-190 photometric sensor (incident light) and a LI-192 submersible sensor (400–700 nm) (LI-COR Biosiences, Lincoln, Nebraska). Light profiles were also recorded directly adjacent to plant stands. Incident and submersed light readings were used to calculate percent light transmittance through the water column (i.e. the amount of light from the water surface that reaches the sediment surface). This was accomplished by dividing the submersed irradiance by incident light and multiplying by 100 for each depth interval, and the mean of all depth intervals is reported.

2.3. Starch analysis

M. aquaticum biomass harvested during the life history evaluation was used to assess seasonal starch allocation in *M. aquaticum* tissues. For each set of 30 samples at each location in a given month, and for each tissue type, dried biomass was combined into 3 bulked samples comprising 10 samples each (i.e. life history biomass samples one through 10 were combined into tissue sample one, and so on). Combining samples ensured that adequate tissue mass was available for analytical techniques, and to reduce the number of tissue analyses required (Woolf and Madsen, 2003).

The bulked samples were ground using a Cyclone Sample Mill (UDY Corporation, Fort Collins, Colorado) to pass through #40 mesh screen (0.42 mm). Approximately 50 mg of the ground sample was transferred into plastic centrifuge tubes for storage and preparation for starch analysis. Starch extraction and determination was conducted using the STA20 starch assay kit (Sigma–Aldrich, St. Louis, Missouri). Wheat starch standards (84% pure starch) and two sets of duplicate *M. aquaticum* samples were also assayed to determine the reliability of our starch data. A total of 1178 samples were assayed for starch content. Standard curves ($n = 43$) were also developed to ensure that our starch data were within the range of what the kits could detect, and to assess the relative accuracy of our data. The precision of our assays as determined by the percent difference of our duplicate samples was 10.6% ± 0.8 SE. Accuracy as determined by our standard curves was ±2% ($r^2 = 0.98$). Starch recovery was 98.3% ± 1.9 SE which was determined using a known mass and purity of the wheat standard.

2.4. Data analyses

Monthly averages for biomass, percent starch, and environmental variables were computed for each site and analyzed together. Data were analyzed by fitting mixed models using the Mixed Procedure in SAS (SAS Institute, Inc., Cary, North Carolina) to determine potential relationships between environmental factors and *M. aquaticum* biomass and percent starch (Littell et al., 1996; Wersal et al., 2006). Total, emergent shoot, submersed shoot, stolon, and root biomass were included as dependent variables. Water temperature, water depth, incident light, light transmittance, pH, and year were included as the independent variables in all models. Site and site × year interaction term were included as random effects in the model to account for their influence on the results. All terms included in the analyses were linear. Data are reported as means (±1 SE) and analyses were conducted at a $p < 0.05$ significance level.

3. Results

3.1. Environmental factors

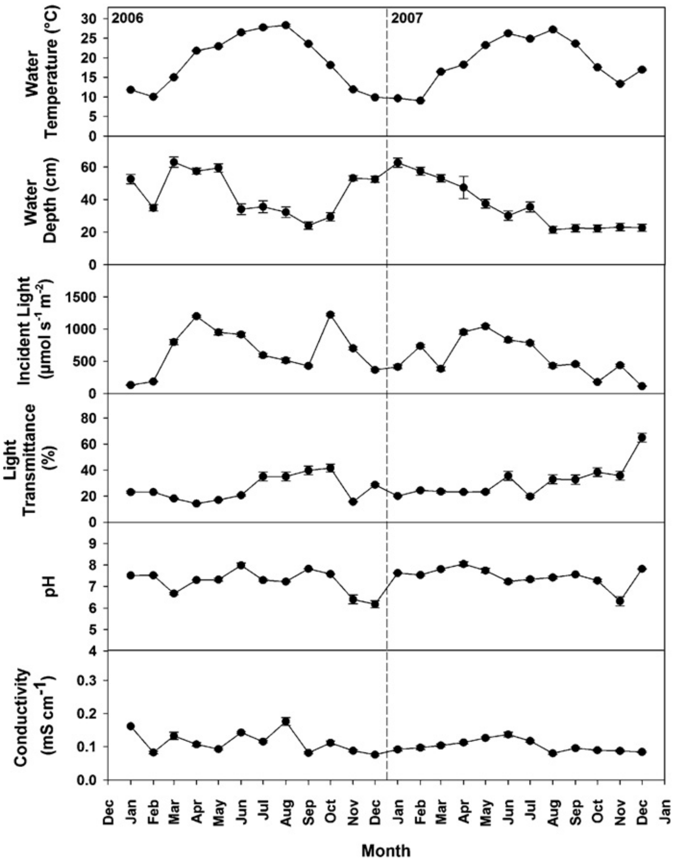

Fig. 2. Seasonal fluctuations in mean (±1 SE) environmental factors measured from four locations in Mississippi.

Seasonal changes in environmental factors are depicted in Fig. 2. Water temperature was greatest from June to August during both years and coincides with summer air temperatures. Mean water temperatures were 19.1 ± 1.0 and 18.8 ± 0.9 °C respectively for 2006 and 2007. Minimum and maximum water temperatures were 9.6 and 31.8 °C in 2006, and 8.5 and 31.5 °C in 2007. Water depths across the four sites declined during the summer months largely due to one site drying completely. Mean water depths were 44.1 ± 4.4 and 36.3 ± 4.4 cm respectively for 2006 and 2007. The maximum incident light recorded was 1432.8 and 1478.0 μmol s^{-1} m^{-2}. Light transmittance across all sites ranged from 5.2 to 65%, and was generally influenced by water depth. Mean pH for the four sample sites was 7.3 ± 0.1 and 7.6 ± 0.1 respectively for 2006 and 2007. Water pH generally remained between 6.0 and 8.6 throughout both years of the study. Conductivity fluctuated little across both years.

3.2. Seasonal biomass

Overall there were few significant relationships were observed between the environmental factors tested and *M. aquaticum* seasonal biomass (Table 2). There were no significant relationships observed between emergent shoot and root biomass with any of the environmental variables tested. There was a significant positive relationship between water temperature, total biomass ($p = 0.03$), and stolon biomass ($p = 0.02$). Submersed shoot biomass was negatively related to water temperature. The r^2 of the mixed models ranged from only 0.02–0.11, which indicates that other factors were influencing growth, relationships were not linear, or an additional approach is needed than relating plant growth to a “snap shot” of environmental factors.

Mean *M. aquaticum* biomass was greater in 2006 than in 2007 where maximum biomass was 510.7 g m^{-2} and 39.6 g m^{-2} respec-

Table 2
Solutions for fixed effects of the mixed procedures model analyzing *Myriophyllum aquaticum* biomass and environmental factors.

Tissue	Effect	*t* value	*p* value
Total biomass	Temperature	2.17	0.03
	Depth	1.06	0.29
	Incident light	1.05	0.29
	Transmittance	0.55	0.58
	pH	0.24	0.80
	Year	1.15	0.33
Emergent shoot biomass	Temperature	1.49	0.14
	Depth	1.71	0.09
	Incident light	0.97	0.33
	Transmittance	0.22	0.82
	pH	0.56	0.57
	Year	1.13	0.34
Submersed shoot biomass	Temperature	−2.71	<0.01
	Depth	−1.07	0.29
	Incident light	−0.98	0.33
	Transmittance	−0.55	0.58
	pH	0.48	0.63
	Year	1.97	0.17
Stolon biomass	Temperature	2.29	0.02
	Depth	0.41	0.68
	Incident light	1.10	0.27
	Transmittance	0.79	0.43
	pH	−0.25	0.80
	Year	1.13	0.34
Root biomass	Temperature	1.16	0.25
	Depth	1.49	0.14
	Incident light	0.78	0.43
	Transmittance	−0.43	0.66
	pH	0.77	0.44
	Year	1.10	0.35

tively for those years (Fig. 3). Data from 2006 and 2007 were presented in separate panels with different scales in order to better view the seasonal trends in biomass allocation. There was a drought in the summer of 2006 which caused site one to remain under moist soil conditions from June to September, though *M. aquaticum* was still present. In 2007, the same site again contained moist soil; however site three was completely dry from June to October and therefore resulted in reduced biomass yield in the fall of 2006 and all of 2007.

Stolons comprised the greatest proportion (40–95%) of total *M. aquaticum* biomass. Emergent shoots accounted for 6–43% of total biomass, followed by submersed shoots (0.2–23.1%), and roots (0.6–15.6%). Maximum total and stolon biomass was attained between May and July in both years. Maximum emergent shoot biomass was attained in March of 2006 and June of 2007. Maximum submersed shoot biomass was attained in February of both years. Seasonal biomass reductions occurred from October to March for both 2006 and 2007.

3.3. Starch allocation

Similar to biomass, few relationships were found between percent starch content and the environmental factors tested. Of the environmental factors, only temperature had a significant positive relationship for each plant tissue (Table 3); though the r^2 of the models used were only 0.02–0.11. *M. aquaticum* tissues varied in starch allocation over time however, starch allocation was greatest in stolons; where up to 16.3% of total starch was stored; this indicates that stolons are likely to be the primary storage location for carbohydrates (Fig. 4). Submersed shoots stored up to 10.8% of total starch from *M. aquaticum* followed by emergent shoots (up to 7.7%) and roots. The roots of *M. aquaticum* stored up to 3.8% of total starch, and for much of both years, starch content was less than 2%. In

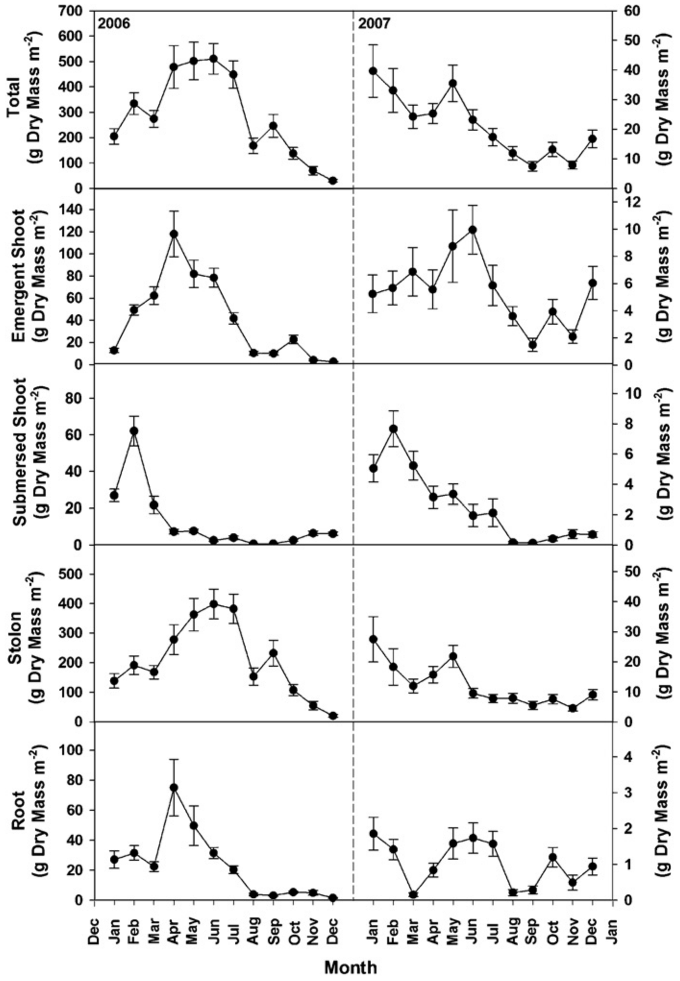

Fig. 3. Mean (±1 SE) total, emergent shoot, submersed shoot, stolon, and root seasonal biomass of *Myriophyllum aquaticum* from four populations in Mississippi. Data from 2006 and 2007 were presented in separate panels with different scales in order to view the seasonal trends in biomass allocation.

Table 3
Solutions for fixed effects of the mixed procedures model analyzing percent starch content of *Myriophyllum aquaticum* tissues with respect to environmental factors.

Tissue	Effect	*t* value	*p* value
Emergent shoot	Temperature	3.05	<0.01
	Depth	0.49	0.62
	Incident light	1.15	0.25
	Transmittance	−0.37	0.71
	pH	−0.82	0.41
	Year	0.19	0.85
Submersed shoot	Temperature	2.40	0.01
	Depth	0.40	0.68
	Incident light	0.28	0.78
	Transmittance	−1.20	0.23
	pH	−1.20	0.23
	Year	−0.27	0.80
Stolon	Temperature	2.97	<0.01
	Depth	−1.19	0.23
	Incident light	0.39	0.69
	Transmittance	0.66	0.51
	pH	−0.68	0.50
	Year	0.58	0.59
Root	Temperature	2.15	0.03
	Depth	−0.24	0.80
	Incident light	−0.24	0.81
	Transmittance	0.65	0.52
	pH	−0.66	0.51
	Year	−0.03	0.97

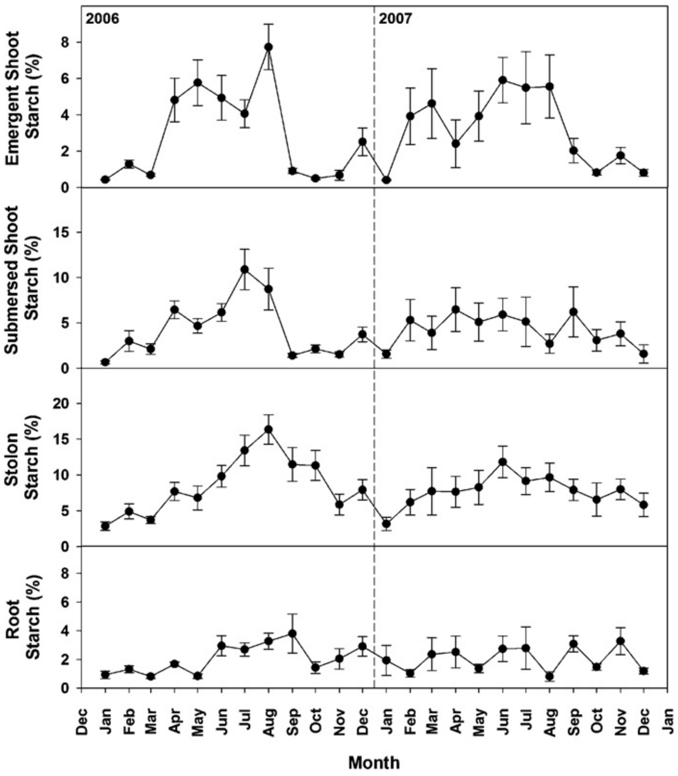

Fig. 4. Mean (±1 SE) seasonal percent starch (as % of dry weight) in individual tissues of *Myriophyllum aquaticum* from four populations in Mississippi.

general, total starch allocation followed a similar trend as biomass in both years. The greatest starch content (58.8–78.1 g m^{-2}) was observed between May and July 2006. Reductions in starch content (2.3–0.5 g m^{-2}) were observed between November and March each year.

4. Discussion

Maximum biomass observed in 2006 was within the range reported for *M. aquaticum* populations in California, where biomass ranged from 234 ± 74 g m^{-2} to 1001 ± 84 g m^{-2} depending upon the water depth in which plants were sampled (Sytsma and Anderson, 1993a). Biomass in 2007 was much lower than in previously reported populations. In Japan, *M. aquaticum* fresh weight was reported to be 13.3 kg m^{-2} (Shibayama, 1988), and in Portugal, fresh weight ranged from 22 to 26 kg m^{-2} (Monteira and Moreira, 1990). Sytsma and Anderson (1993a) reported a dry weight:fresh weight ratio of 0.21, therefore, fresh weight biomass in this study would have been approximately 2.4 kg m^{-2} in 2006 and 0.1 kg m^{-2} in 2007. The reduced biomass is attributed to a drought over the summer of 2006 and 2007. *M. aquaticum* survived at one site in remaining moist soil as small emergent shoots, though was killed in another site when the sediment dried. Maltchik et al. (2007) suggested that *M. aquaticum* is tolerant of drawdown events (complete removal of surface water) lasting 9 months if the sediment remains saturated. In 2006, standing water did not return to these sites until November when the rain season began and therefore subsequent biomass in the fall of 2006 and all of 2007 was reduced.

Although biomass was lower than in other populations, biomass allocation to specific tissues was comparable to previously reported populations. In California, stolon biomass accounted for 72–95% of the total biomass, followed by emergent shoots (≤24%), sediment roots (>12%) and submersed shoots (1–3%) (Sytsma and Anderson, 1993a). The Mississippi populations allocated more biomass to submersed shoots than roots. The allocation of biomass to submersed shoots was triggered by reductions in irradiance and temperature. In Mississippi, reductions in irradiance occurred during winter months and thus colder water temperatures were also present. Water temperature influences plant performance, especially photosynthetic rates, and can ultimately have a regulatory effect on phenology and resource allocation (Madsen, 1991). Biomass allocation to submersed shoots was over a short period of time beginning in January of both years; a peak in February, and declining in March when water temperatures and irradiance began to increase. The peak in submersed shoot biomass in February indicates that this growth form is adapted to shade environments (Salvucci and Bowes, 1982).

In contrast, the photosynthetic light saturation point is almost eight-fold higher in emergent leaves, approaching that of full sunlight (Salvucci and Bowes, 1982); and as light intensities increased beginning in March the allocation to emergent shoots also increased. Therefore, submersed shoot growth is transient and only utilized for short overwintering periods, times of reduced light and temperature, or to survive disturbances in the growing environment. *M. aquaticum* will rapidly reallocate biomass to emergent shoots when conditions are favorable and maintain emergent growth as long as energy stores are available. Although prolonged exposure to adverse growing conditions will result in reductions in biomass or plant mortality as observed after the summer droughts in this study; which may be an effective method of removing biomass and starch reserves and thus managing this species.

Aquatic plant species often produce specialized structures such as tubers, turions, and winter buds to store carbohydrates to survive exposure to adverse growing conditions (Madsen and Owens, 1998; Woolf and Madsen, 2003). *M. spicatum* and *Egeria densa* Planch. will store starch in root crowns and lower stems (Madsen, 1997; Pennington and Sytsma, 2009) However, *M. aquaticum* does not produce specialized structures for perennation or overwintering and therefore would have to store carbohydrates in other plant tissues. *M. aquaticum* utilizes stolons to store the majority of its starch. Stolons are brittle and fragment easily; therefore concentrating starch in stolon tissues would benefit *M. aquaticum* dispersal and colonization. When a plant is fragmented, the fragment would retain the starch concentrations in that segment and should have a greater chance of survival during dispersal, and increased colonization success if the fragment finds suitable habitat for growth.

Growth of *M. aquaticum* is largely influenced by water temperature as shown by both biomass and starch concentrations in this study, though other factors such as irradiance will also influence growth and effect water temperature. Starch was stored in all *M. aquaticum* tissues though stolons were the primary storage location. Knowing where starch is being stored and when lowest starch concentrations exist may offer insights into the efficacy of management options, and the potential regrowth capability of plants after management techniques have been implemented. Reductions in carbohydrate concentrations in aquatic plants in temperate regions typically occur during spring regrowth when plants are relying on stored energy to initiate growth of plant tissues until photosynthesis can begin (Madsen, 1997). Reductions in total biomass and starch concentrations of *M. aquaticum* in Mississippi occurred from October to March in both years. October to March are also times of reduced water temperatures and light transmittance which subsequently caused the senescence of emergent shoots and the reliance on stolons and submersed shoots for winter survival. Utilizing these results to time management activities during October to March, may result in increased efficacy of control techniques due to reductions in emergent shoot biomass and starch stores in stolon tissues.

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