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Seasonal and environmental factors affecting growth of Illinois pondweed

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ABSTRACT

Illinois pondweed (*Potamogeton illinoensis* Morong) is a native submersed plant that is widely distributed throughout North America and occurs in about 15% of Florida lakes. These experiments evaluated the effects of season, salinity, water flow, and substrate on biomass accumulation and seed production by Illinois pondweed. Seasonal growth studies conducted over a 1-yr period revealed that maximum growth occurred in the summer when water temperatures were between 26 and 30 C. Seed production by 8-wk-old plants was highest in summer, but seeds developed in spring and fall as well. Growth was reduced when water salinity was 5.02% and plants died at salinities ≥8.57%. Greatest weight of plants cultured in 660-L mesocosms was achieved when water flowed at ≥9.1 L min^{-1}. Growth in substrates with 2.7% organic matter (OM) was about three times greater than growth in sand only, but additions of organic matter (OM) to 73% elicited no additional growth. Illinois pondweed grew well in coarse to very coarse silica sand particle sizes, whereas hydrilla [*Hydrilla verticillata* (L.f.) Royle] produced minimal growth. These data suggest that substrate particle size may have a more important effect on the distribution of submersed plants in waterways than other hydrosoil characteristics such as nutrients and OM content.

Key words: hydrilla, organic matter, particle size, *Potamogeton*, salinity, substrate, water flow.

INTRODUCTION

Illinois pondweed is a North American native submersed plant that occurs from Puerto Rico to the Arctic Circle (U.S. Department of Agriculture–Natural Resources Conservation Service [USDA-NRCS] 2016). In Florida, Illinois pondweed has been reported in 47 of 322 lakes surveyed by the Florida Lakewatch program (Hoyer et al. 1996) and often co-occurs with other common submersed plants such as hydrilla, eelgrass (*Vallisneria americana* Michx.) and southern naiad [*Najas guadalupensis* (Spreng.) Magnus].

The environmental factors that determine why a particular submersed species grows in one location in a waterbody but not another in close proximity is poorly understood, but factors that may play a role include water flow, salinity, and substrate composition. For example, hydrilla and hygrophila [*Hygrophila polysperma* (Roxb.) T. Anderson] accumulated more weight when plants were grown in mesocosms with flowing water vs. static water (Van Dijk et al. 1986). Excessive growth of Illinois pondweed in irrigation and drainage canals in South America (Armellina et al. 1996) may be due in part to water flow. Salinity also influences growth and distribution of aquatic plants, and growth rates typically decline as salinity increases (Haller et al. 1974). This is particularly problematic in Florida, which has an increased risk of saltwater intrusion because of the state's flat topography and extensive system of irrigation and drainage canals. Substrate composition could influence submersed plant growth and distribution as well. Barko and Smart (1983) reported that growth of three submersed aquatic species was reduced when plants were cultured in fertilized substrate amended with OM vs. the same substrate without OM. This could be true for Illinois pondweed as well, because this species most commonly occurs in sandy substrates in Florida (M. Netherland, pers. comm.). In contrast, Wetzel (1976) stated that growth of aquatic macrophytes was generally higher on organic-rich substrates than on sandy substrates, and Spencer et al. (1993) reported that sago pondweed (*Potamogeton pectinatus* L.) weight and tuber production was higher when plants were grown in substrate amended with peat.

Despite its widespread occurrence in North America, little is known regarding the influence of water flow, seasonality, salinity, and substrate composition on growth of Illinois pondweed. Therefore, the objective of these experiments was to evaluate the effects of these factors on growth of Illinois pondweed in northern Florida.

MATERIALS AND METHODS

These experiments were conducted at the University of Florida IFAS Center for Aquatic and Invasive Plants (CAIP) in Gainesville, FL between 2014 and 2016. Plants used in these studies were originally collected from Rodman Reservoir (Putnam County, FL) and maintained in culture at CAIP. Well water used in these studies contained 20 to 50 ppb total phosphorus, 2,500 to 3,500 ppb total nitrogen, conductivities of 200 to 400 μS/cm and pH of 7.4 to 7.8 (M. Hoyer, pers. comm.). Unless otherwise noted, washed masonry sand with no organic matter (OM) (hereafter "CAIP sand") was used in these studies and had the following particle size distribution (USDA and Soil Conservation Service 1987): 6.8% very coarse, 30.8% coarse, 44.8% medium, 17.4% fine, and 0.2% very fine sand. All plants were cultured in 3.5-L plastic pots without holes that were

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filled to a depth of 10 cm with substrate amended with 18N–6P_2O_5–12K_2O Osmocote® Classic controlled-release fertilizer[1] (690 mg nitrogen and 115 mg phosphorus pot^{-1}) and capped with a 3-cm-deep layer of unfertilized sand. Osmocote Classic does not contain micronutrients and is formulated to release nutrients in terrestrial use over an 8 to 9–mo period. At the conclusion of each study, plant material was harvested, separated into roots and shoots, and washed to remove sand and debris. Harvested material was oven[2] dried at 80 C until a constant weight was achieved, and then the material was weighed. Treatment means were separated with the use of a single-factor analysis of variance (ANOVA) and Tukey's honestly significant differences (HSD) in SAS.[3] This experimental design, harvest protocol, and data analysis was used in all studies unless otherwise noted.

Seasonal growth and seed production

Growth of Illinois pondweed was determined over a 1-yr period from July 2015 to August 2016. These experiments were conducted outdoors under full sun in a circular high-density polyethylene (HDPE) tank (diameter 3 m) that was filled with well water to a depth of 0.6 m, and water temperature was monitored with a Hobo® temperature data logger.[4] Ten pots (replicates), each with three 15-cm-long apical shoots of Illinois pondweed planted in amended CAIP sand as described above, were established on the first day of every month. After 2 mo of culture, the number of infructescences (fruiting spikes) pot^{-1} was recorded and plant material was harvested and processed as described above. Water-temperature data were used to develop a growing-degree-day (GDD) model for Illinois pondweed with the use of the following formula:

$$GDD = (T_{\max} + T_{\min})/2 - T_{\text{base}},$$

where $T_{\max}$ = maximum daily temperature, $T_{\min}$ = minimum daily temperature (set to 17 C if water temperature was $\leq$17 C), and T_{base} = 17 C (because very little growth of Illinois pondweed occurs when water temperature is $\leq$17 C; W. Haller, pers. comm.). The accumulated GDD value for each 8-wk culture period was the sum of the daily GDD values for that period. Accumulated GDDs are widely used in ornamental and vegetable production for tracking plant development as a function of temperature (McMaster and Wilhelm 1997).

Water flow

The effect of water flow rate on growth of Illinois pondweed was evaluated in summer (July through September) 2016. Thirty-six pots, each with three 15-cm-long apical shoots of Illinois pondweed planted in amended CAIP sand as described above, were prepared. Twelve fiberglass mesocosms (1.75 by 0.75 m) were filled with well water to a depth of 0.5 m (660 L), and three planted pots were randomly placed in each mesocosm. Four flow rates—static (no flow), low (1.9 L min^{-1}), medium (9.1 L min^{-1}), and high (21.3 L min^{-1})—were studied, with three replicates (mesocosms) for each rate. Flow rates were established with the use of SunSun® submersible powerhead pumps[5] directed down the center of the mesocosm, and pump intakes were cleaned of debris two or three times each week to ensure consistent flow throughout the experiments. After 8 wk of culture, plants were harvested and processed as described above.

Salinity

Response of Illinois pondweed to salinity was also evaluated in summer 2016. Ninety-six pots, each with three 15-cm-long apical shoots of Illinois pondweed planted in amended CAIP sand, were prepared and allowed to grow in well water for 4 wk. Two planted pots were then randomly placed in each of 48 mesocosms (95 L) that were filled to a depth of 0.5 m and maintained in a shadehouse. Salinity levels were induced with the use of Instant Ocean® Sea Salt,[6] which was added to the mesocosms at 0, 1, 2.5, 5, 7.5, 10, 12.5, and 15 g L^{-1} of water, and six replicates (mesocosms) were prepared for each salinity level. A Mettler-Toledo AG® conductivity meter[7] was used to measure salinity (%) biweekly during these experiments; after 8 wk of culture, plants were harvested and processed as described above.

Substrate OM content

Substrate mixes with one of six OM contents were prepared in summer 2016 by mixing CAIP sand and an organic histosol (73.8% OM) obtained from the University of Florida IFAS Research and Education Center, Belle Glade, Palm Beach County, FL to achieve final OM contents of 0 (sand only), 2.3, 5.6, 16.1, 27.9, or 73.8% (histosol only). Uniform distribution of OM in the final substrate mixes was achieved by placing dry sand in a cement mixer, adding a small amount of water to slightly moisten the sand, and then adding the lightweight histosol. This technique was difficult but produced the most consistent blend of substrate materials. These OM contents were selected to simulate the 0.8 to 84.2% OM range reported for substrates in 97 Florida lakes reported by Brenner and Binford (1988). All mixes were then amended with Osmocote Classic, placed in pots to a depth of 10 cm and capped with a 3-cm layer of masonry sand. Six replicates (pots) were prepared for each mix, and each pot was planted with three 15-cm-long apical shoots of Illinois pondweed. Planted pots were randomly placed in a circular HDPE tank (diameter 3 m) that was filled with well water to a depth of 1 m. Plants were cultured for 10 wk outside in full sun, then harvested and processed as described above.

Nine unfertilized samples (replicates) of each sand/histosol mix were dried to a constant weight and ca. 4 g of each sample was placed in clean, dry 50-ml beakers. These were then placed in a Thermolyne® 1400 electric muffle furnace[8] at 550 C for 5 h, removed from the furnace, cooled, and weighed to determine postignition soil mass. Weight loss between initial soil weight and soil weight following ignition was then used to calculate percent soil organic matter by weight for each mixture.

Table 1. Particle size composition of five commercial sandblasting silica products. Product is the commercial product name assigned by the manufacturer (Edgar Minerals, Inc., Edgar, FL). Micron ranges are the mean percent of each particle size of three 100-g dry samples of each product processed using U.S. standard soil sieves. Particle size categories are those described in the U.S. Department of Agriculture Soil Textural Classification Guide (1987) as follows: VC = very coarse; C = coarse; M = medium; F = fine; VF = very fine; S/C = silt/clay.

Product	Micron Range	VC	C	M	F	VF	S/C
EGS	0–250	0	0	14.5	78.5	5.5	1
30/65	50–1,000	0	32	36	31.5	0.5	0
30/45	250–1,000	0	83	17	0	0	0
20/30	250–2,000	12.5	84	3.5	0	0	0
4/9	1,000–2,000	100	0	0	0	0	0

Substrate particle size

The influence of substrate particle size on growth of Illinois pondweed and hydrilla was compared in summer 2016 with the use of five commercial silica sandblasting sands[9] ranging from fine to coarse (EGS, 30/65, 30/45, 20/30, 4/9) (Table 1). Each sand was amended with Osmocote Classic and placed in pots to a depth of 10 cm. In contrast to the experiments described above, these pots were not capped with masonry sand, because using a masonry-sand cap could "contaminate" the particle-size treatments in these studies. Twelve pots were prepared of each sand, and pots were then planted with three 15-cm-long apical shoots of either Illinois pondweed or hydrilla to create six replicates of each species/sand combination. Planted pots were randomly placed in a circular HDPE tank (diameter 3 m) that was filled with well water to a depth of 1 m. Plants were cultured for 8 wk, then harvested and processed as described above.

RESULTS AND DISCUSSION

Seasonal growth and seed production

The purpose of this experiment was to characterize seasonal growth of Illinois pondweed in Florida, because its distribution in North America extends to nearly the Arctic Circle, which suggests the species may grow well at colder water temperatures. However, root weight and infructescence production was greatest when plants were grown for 8 wk in midsummer (during July and August), when water temperature was >28.1 C (Table 2). Shoot weight was lowest during winter (i.e., November through March) and greatest when plants were cultured between March and September, although growth was reduced in plants grown during June and July (Table 2). The factors responsible for reduced shoot growth in June and July in these experiments is unknown; Nachtrieb et al. (2011) reported that growth of Illinois pondweed could be reduced due to herbivory, but we did not observe faunal feeding on plants in these experiments.

The effects of average water temperature were evaluated with the use of cumulative GDD values to determine whether high temperatures could be responsible for the reduced shoot growth noted in June, August, and September (Table 2). GDDs and shoot weight (mg pot^{-1} d^{-1}) were regressed for each growth period and these analyses revealed a linear relationship (r^2 = 0.87), but the analysis did not provide evidence that high temperature reduced growth of Illinois pondweed. Greatest shoot weight was achieved in plants grown in July and August, April and May, and May and June (6.2, 5.9 and 5.6 g pot^{-1}, respectively; GDD 833, 527, and 723, respectively; mean water temperature 29.3, 25.5, and 28.8 C, respectively), but low shoot growth (2.4 g pot^{-1}) occurred when plants were cultured during June and July (GDD 851, mean water temperature 30.9 C). Based on these observations, it seems unlikely that the slightly higher GDD and water temperature values recorded during June and July are responsible for the drastic reduction in growth noted in these studies. Regression analyses of GDD and shoot weight provides no evidence that Illinois pondweed grows well at lower water temperatures, despite reports that the species' distribution extends far north. Growth of Illinois pondweed

Table 2. Dry weights and infructescence production by Illinois pondweed over 8-wk culture periods. Culture period indicates the first day of the 8-wk culture period. GDDs = cumulative growing degree days; daily values were calculated with the use of the formula GDD = $(T_{MAX} + T_{MIN})/2 - T_{BASE}$, where T_{MAX} = maximum daily temperature, T_{MIN} = minimum daily temperature (set to 17 C if water temperature was ≤17 C), and T_{BASE} = 17 C. The GDD values presented are the sum of all daily GDD values in the 8-wk culture period. Shoot biomass, root biomass, and number of infructescence values are the mean of 10 replicates (pots). Values in the same column that are coded with the same letter are not significantly different as determined by Tukey's honestly significant difference test at $\alpha = 0.05$.

Culture Period	GDDs	Mean Water Temperature (C)	Shoots (g pot^{-1})	Roots (g pot^{-1})	No. Infructescences
July 1	833	29.3	6.2 a	3.7 a	3.5 a
August 1	749	28.1	4.0 b	2.2 bc	0.2 b
September 1	544	25.9	2.8 bc	1.9 bc	0.2 b
October 1	367	22.6	2.3 cd	1.6 bc	0.1 b
November 1	252	20.4	1.3 d	1.2 c	0 b
December 1	114	16.6	0.3 d	0.2 d	0 b
January 1	29	14.9	0.1 d	0.1 d	0 b
February 1	142	18.6	1.2 d	0.7 cd	0 b
March 1	327	22.5	3.5 bc	1.2 c	0 b
April 1	527	25.5	5.9 a	2.5 b	0.6 b
May 1	723	28.8	5.6 a	2.0 bc	0.7 b
June 1	851	30.9	2.4 cd	1.4 c	1.3 b

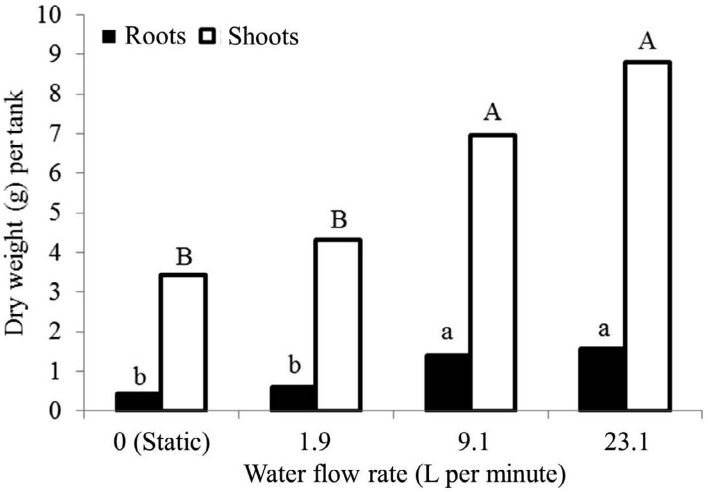

Figure 1. Dry weights of Illinois pondweed grown under different water flow rates for 8 wk during summer 2016. Bars are the mean of three replicates (tanks) of each treatment. Treatments labeled with the same letter are not significantly different within a species as determined by Tukey's honestly significant difference test at $\alpha = 0.05$.

collected in Florida was greatly reduced in December through February, when water temperatures were 14.9 to 18.6 C and GDD was <200; also, no seed production occurred during this period. It is likely that photoperiod influences growth of Illinois pondweed, but evaluation of that factor was beyond the scope of these studies. These experiments provide baseline growth data for Illinois pondweed, but further investigations are needed to evaluate temperature : photoperiod effects on this species. It would also be interesting to conduct similar annual growth experiments to compare the growth response of Illinois pondweed collected from northern North America to plants collected in Florida.

Water flow

Plants accumulated the greatest root and shoot weights when cultured with medium (9.1 L min^{-1}) or high (21.3 L min^{-1}) water flow, but there was no difference between these two treatments (Figure 1). There was also no difference in root and shoot weight of plants grown under static and low-flow (1.9 L min^{-1}) conditions. The twofold increase in growth of Illinois pondweed in our studies is similar to that reported for hydrilla by Van Dijk et al. (1986). The Van Dijk et al. study evaluated growth of hydrilla and hygrophila in circular tanks equipped with pumps to provide flow volumes resulting in complete water volume turnover times of 0, 5, 2, and 1 h. Hydrilla growth over a 6-wk period increased twofold in the two highest water flow treatments (i.e., 2 and 1 h), but hygrophila growth was increased 4 to 5 times at all flow rates compared to plants grown under static conditions. Flow rates in our Illinois pondweed studies had similar turnover times (0, 4.5, 1, and 0.4 h) and produced 2 times as much shoot growth in tanks with the highest water flow rates, similar to the results reported by van Dijk et al. (1986) for hydrilla.

Table 3. Shoot dry weights of Illinois pondweed cultured under different salinity levels for 8 wk during summer 2016. Salt was applied as Instant Ocean Sea Salt. Conductivity and salinity values are the mean of six replicates measured five times during the 8-wk culture period; SD = standard deviation. Shoot biomass values are the mean of six replicates (pots). Values coded with the same letter are not significantly different as determined by Tukey's honestly significant difference test at $\alpha = 0.05$.

Salt Applied (g^{-1} L)	Conductivity (mS^{-1} cm)	Salinity (%) (1 SD)	Shoots (g)
0	0.16	0.10 (0.02)	11.1 a
1	1.50	0.90 (0.03)	10.6 a
2.5	3.38	2.03 (0.13)	11.1 a
5	5.83	3.50 (0.41)	9.3 a
7.5	8.37	5.02 (0.41)	6.9 b
10	11.32	6.79 (0.51)	4.2 c
12.5	14.28	8.57 (0.39)	1.0 d
15	16.71	9.92 (0.84)	0.1 d

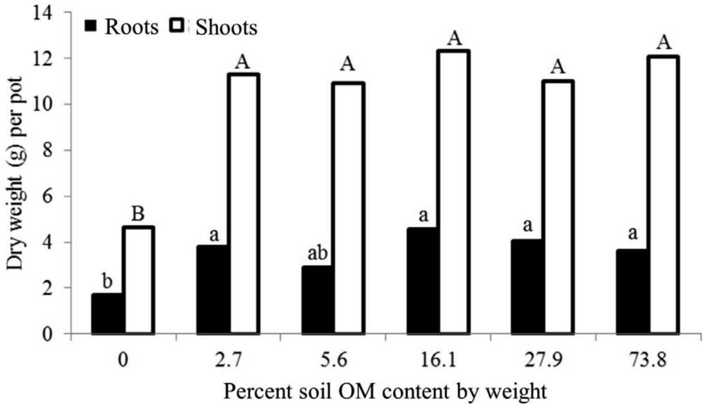

Figure 2. Dry weights of Illinois pondweed grown in substrates with different OM contents for 10 wk during summer 2016. Bars are the mean of six replicates of each treatment. Treatments labeled with the same letter are not significantly different within a species as determined by Tukey's honestly significant difference test at $\alpha = 0.05$.

Growth of both hydrilla and Illinois pondweed increases ca. twofold when plants are cultured in flowing water with a 1 to 2–h turnover time. Van Dijk et al. (1986) suggested that increased growth of these submersed plants in flowing water could be due to increased CO_2 availability in flowing vs. static water. Others (e.g., Smith and Walker 1980, Crossley et al. 2002) have postulated that increased flow reduces the thickness of the boundary layer at the leaf surface, which increases nutrient and gas availability, thus increasing photosynthesis and spurring greater plant growth.

Salinity

Salinity levels remained constant throughout these 8-wk-long experiments, which were conducted during summer 2016 (Table 3). Dry weights at harvest were greatest when Illinois pondweed was grown in water with salinities that were $\leq$3.50%, with no differences in growth in 0.10, 0.90, 2.03, or 3.50% salinities. Growth was reduced at salinities $\geq$5.02% and continued to decline as salinity increased. Leaves cultured in a salinity of 5.02% became dark and lost buoyancy, and those grown with salinity levels $\geq$6.79% turned brown and sank to the bottom of the mesocosms after 3 to 4 wk of exposure. These results suggest that Illinois pondweed is as salt-tolerant as hydrilla and eelgrass (both 6.66%), but is less tolerant of salinity than are southern naiad

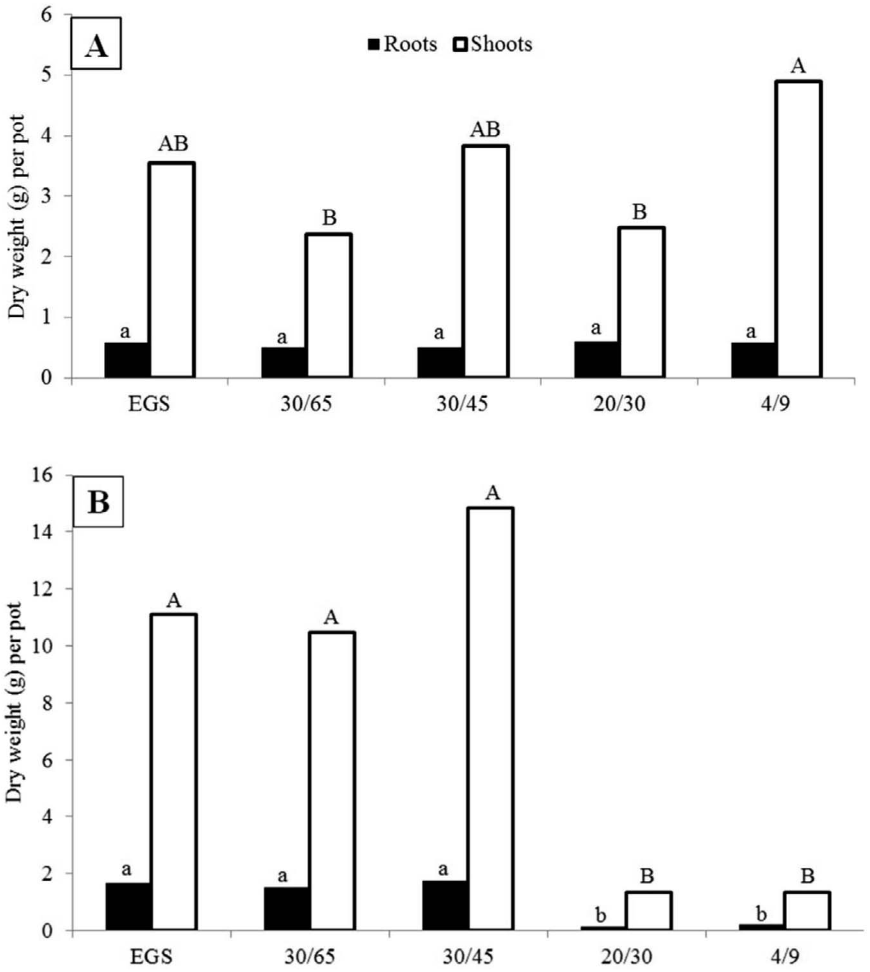

Figure 3. Weight of Illinois pondweed (A) and hydrilla (B) grown in one of five commercial sands with different particle sizes for 8 wk during summer 2016. Sands are arranged on the x-axis from finest-grained (EGS; left) to coarsest-grained (4/9; right). Bars are the means of six replicates (pots) of each treatment. Treatments labeled with the same letter are not significantly different within a species as determined by Tukey's honestly significant difference test at $\alpha = 0.05$.

and Eurasian watermilfoil (*Myriophyllum spicatum* L.) (10.00 and 13.32%, respectively) (Haller et al. 1974).

Substrate OM content

Root and shoot growth of Illinois pondweed increased two- to threefold when grown in substrates with 2.7 to 73.8% OM compared to plants grown in OM-free sand (Figure 2). This level of growth in treatments with higher OM contents was unexpected, because field observations indicate that this species most commonly occurs in sandy substrates (M. Netherland, pers. comm.; the authors, pers. obs.). These results conflict with those of Barko and Smart (1983), who reported that growth of submersed aquatic plants typically decreased when OM was added to rooting substrates, but support those of Wetzel (1976), who noted that growth of aquatic macrophytes was generally higher on OM-rich substrates than on sandy substrates.

Field studies conducted concurrently with these experiments characterized substrate composition of discrete beds of hydrilla and Illinois pondweed in four Florida lakes (Gosselin 2016). Substrate OM in 21 Illinois pondweed beds was 3.4 ± 5.5%, whereas substrate OM in hydrilla beds was 11.6 ± 16.6%. Although Illinois pondweed most commonly occurs in sandy substrates in Florida, the controlled and field studies we present here provide evidence that OM levels in most Florida lakes are not likely to adversely impact growth of this species. However, additional field studies are needed to verify these findings.

Substrate particle size

Shoot dry weights of Illinois pondweed grown in sands with different particle sizes ranged from 2.5 to 5.0 g pot^{-1} and there was no clear trend between particle size and shoot weight (Figure 3A). Root dry weight was not affected by particle size in the five silica sands evaluated in these experiments (Figure 3A).

In contrast, hydrilla root and shoot growth was greatly reduced in plants cultured with the two most coarse sands (20/30 and 4/9) with particle sizes of 250 to 2,000 microns (Table 1; Figure 3B). Hydrilla growth was much higher when plants were grown in the three finer-grained sands (EGS, 30/65 and 30/45) with particle sizes of 0 to 1,000 microns (Figure 3B). Growth of hydrilla was limited in coarse sand, but root and shoot weights of hydrilla grown in finer sands were 3 to 4 times greater than those of Illinois pondweed.

These results suggest that Illinois pondweed may grow best—and may have an advantage over hydrilla—in coarse substrates with large particle sizes. However, the limited substrate sampling reported by Gosselin (2016) does not support this hypothesis, because fine to medium-fine sand comprised 92 and 79% of the substrates from several monotypic beds of hydrilla and Illinois pondweed, respectively, collected from four lakes in Florida.

Hoyer et al. (1996) reported that hydrilla and Illinois pondweed occur in 49% and 15%, respectively, of 322 lakes surveyed in Florida. Although these two species often occur together, they are usually found in separate but adjacent areas of the same lakes. It seems likely that this spatial distribution is due to differences in substrate characteristics, but the specific factors that influence establishment and persistence of these species in discrete locations in Florida lakes are unclear.

SOURCES OF MATERIALS

[1] Osmocote® Classic controlled-release fertilizer, Everris, Dublin, OH 43041.

[2] Power-O-Matic 60® oven, Blue M Electric Company, Blue Island, IL 60406.

[3] SAS Software Version 9.3, SAS Institute, Cary, NC 27513.

[4] Hobo® Pro V2 temperature data logger, Onset Computer Corporation, Bourne, MA 02532.

[5] SunSun® submersible powerhead pumps, SunSun, Dinghai, Zhoushan, Zhejiang, China.

[6] Instant Ocean® Sea Salt, Spectrum Brands Inc., Blacksburg, VA 24060.

[7] Conductivity meter, Mettler-Toledo Group, Schwerzenback, Switzerland 8603.

[8] Thermolyne® 1400 electric muffle furnace, Barnstead Thermolyne, Dubuque, IA 52001.

[9] Commercial silica sandblasting sands, Edgar Minerals, Inc., Edgar, FL 32640.

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