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Seasonal Biomass and Carbohydrate Allocation in Dioecious Hydrilla

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ABSTRACT

The phenology of dioecious hydrilla (*Hydrilla verticillata* (L.f.) Royle) was studied to discern seasonal low points in the carbohydrate storage of this nonindigenous weedy aquatic plant. Hydrilla was sampled monthly from two outdoor ponds (0.3 ha each) at the Lewisville Aquatic Ecosystem Research Facility (LAERF) in Lewisville, Texas, from January 1994 through July 1995. Monthly samples were dried to obtain biomass dry weight (g m^{-2}) and analyzed for total nonstructural carbohydrates (TNC), free sugars, and starch. Results indicated the lowest amount of stored TNC occurred in July for 1994 and in June for 1995, with stolon (6%), upper stem (6%), root crown (10%) and lower stem (11%). Tubers (65%) and turions (60%) exhibited their lowest TNC concentrations when the total plant stores of TNC were at their lowest point. Biomass increased from May through September, regrowing from overwintering shoots and root crowns, but not tubers. In addition to the hydrilla pond sampling, containers planted with hydrilla were harvested from January 1995 through December 1996. Monthly samples were likewise analyzed for carbohydrate storage. The lowest concentrations of stored carbohydrates occurred in June for both growing seasons. These studies provide more insight into the timing of major allocation shifts in the hydrilla seasonal growth cycle for the purpose of optimizing management techniques.

Key words: *Hydrilla verticillata*, total nonstructural carbohydrates, starch, phenology.

INTRODUCTION

Hydrilla is an invasive, nonindigenous submersed aquatic plant which was first discovered in the United States in the 1960's (Pieterse 1981). A native of Southeast Asia and Australia, hydrilla exhibits aggressive growth strategies, rapidly expanding to the surface and forming a dense canopy. Due to this dense canopy formation, native vegetation cannot compete for available light, therefore diversity is reduced (Barko et al. 1991, Sutton 1990). Two distinct biotypes (monoecious and dioecious) exist in the United States (Spencer and Anderson 1986). Monoecious hydrilla has both staminate and pistillate flowers on the same plant while dioecious biotypes produce staminate and pistillate flowers on separate plants. Currently, only the pistillate flower-forming plants are found within the United States, therefore sexual reproduction of dioecious hydrilla does not occur. Thirteen states (AL, AZ, CA, CT, FL, GA, LA, MS, NC, OK, SC, TN, TX) have confirmed populations of dioecious hydrilla, while monoecious hydrilla can be found in six states (CA, DE, MD, NC, VA, and WA) (Les et al. 1997, Steward et al. 1984).

Once hydrilla invades an aquatic ecosystem, the plant spreads rapidly, either from the root crowns, stolon growth, drifting fragments or turions. The production of the dense canopy can impede navigation, destroy habitat, degrade water quality, and interfere with recreational activities[3]. A number of control methods are available for management including aquatic herbicides, biocontrol, harvesting, and triplod grass carp (Gallagher and Haller 1990).

Phenology is the study of the seasonal timing of critical stages in the life of plants and animals. By understanding the phenology of the target plant, the implementation of management techniques can be applied at the most effective time period in the seasonal or phenological cycle. Previous research has successfully demonstrated that timing the control technique with the target plant's low point in carbohydrate storage can increase the effectiveness of management. For instance, a knowledge of carbohydrate allocation patterns was used to improve the management of quackgrass (*Agropyron repens* (L.) Beau., Schirman and Buchholtz 1966). Phenological studies have also been demonstrated to improve the control of cattail (*Typha latifolia* L.)[4]. Previous studies have also examined carbohydrate allocation in waterhyacinth (*Eichhornia crassipes* (Mart.) Solms) and Eurasian watermilfoil (*Myriophyllum spicatum* L.) (Madsen et al. 1993, Madsen 1997).

Many aquatic plants have specialized storage organs for carbohydrate reserves, such as tubers in sago pondweed (*Potamogeton pectinatus* L.), winter buds in American pondweed (*P. nodosus* Poiret), turions in curly-leaved pondweed (*P. crispus* L.), rhizomes in cattail (*Typha* spp.) and yellow pond-lily (*Nuphar advena* (Ait.)), and stembases in waterhyacinth (Luu and Getsinger 1990). Hydrilla has a number of organs for carbohydrate storage, including the root crowns, stolons, tubers and turions. The upper shoots perform photosynthe-

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[2]AscI Corporation, Lewisville Aquatic Ecosystem Research Facility, RR #3 Box 446, Lewisville, TX 75056-9720. Received for publication May 14, 1998 and in revised form September 18, 1998.

[3]Langeland, K.A. 1990. Hydrilla (*Hydrilla verticillata* (L.f.) Royle), a continuing problem in Florida waters. Center for Aquatic Plants, IFAS, University of Florida, Gainesville, Fl. Circular No. 884.

[4]Linde, A. F., T. Janisch, and D. Smith. 1976. Cattail—The significance of its growth, phenology and carbohydrate storage to its control and management. Technical Bulletin #94, Wisconsin Department of Natural Resource, Madison, WI.

sis, exporting excess carbohydrates to storage organs for use during overwintering or environmental stress. In the spring, when the plant requires energy to regrow, stored carbohydrates are remobilized to the growing shoots.

During the early growing season, high levels of stored carbohydrates from the previous year provide nutrients for growth in the spring. When photosynthesis exceeds the plant's immediate growth requirements, carbohydrates are transported to the storage organs and stored total nonstructural carbohydrates (TNC) increase (Madsen 1991). When the stored carbohydrates and consequent ability to regrow are at minimum levels, some management techniques may be most effective. As the growing season progresses, carbohydrates from photosynthesis are shuttled to the storage organs until the carbohydrates have reached high levels for a prolonged overwintering period. Since the plant is dormant throughout the winter, the stored carbohydrates remain available for the new spring growth. The goal of this study was to describe dioecious hydrilla's seasonal growth and carbohydrate allocation patterns in relation to the timing of tuber and turion production and germination.

METHODS

Pond Study

This study was conducted at the Lewisville Aquatic Ecosystem Research Facility (LAERF), in Lewisville, Texas (latitude 33°04'45"N, longitude 96°57'30"W) during 1994 through 1996. Two experimental ponds (0.3 ha) were employed, with an average depth of 1.0 m and a maximum depth of 1.5 m. Both ponds had been planted with dioecious hydrilla obtained from within the State of Texas one growing season before the initiation of the study. Daily water temperature was monitored adjacent to the hydrilla research ponds using the Omnidata Easy Logger™ Field Data Recording System (Omnidata Corp, Logan, UT). Missing temperature data was obtained from the National Oceanic and Atmospheric Administration (NOAA) monthly summary for the Dallas-Ft. Worth Regional Airport[5].

From January 1994 through July 1995, twelve biomass samples were collected monthly from each of the two experimental ponds, between the hours of 10:00 am and 12:00 pm. Using a computer-generated random sampling design, the above and below ground portions of the rooted plants were collected employing a 0.1 m^2 quadrat (Madsen 1993). Each biomass sample was separated into upper and lower shoots, root crowns, stolons, tubers and turions. Upper and lower shoots were obtained by cutting the individual hydrilla plant at 50% of their length. The number of inflorescences, root crowns, stolons, tubers and turions was counted. All samples were dried at 55 C using a Blue M forced air oven (General Signal, Atlanta, GA) for a minimum of 48 hours before weighing. After obtaining a dry weight, samples were ground using a Cyclone Sampling Mill (UDY Corp, Ft. Collins, CO), then analyzed for free sugars, starch and total nonstructural carbohydrates (TNC).

Plant samples were analyzed for TNC according to a modified procedure by Swank et al. (1982). TNC (starch, hydrolyzable sugars, reducing sugars) extracts were incubated at 55 C for fifteen minutes with one unit of amyloglucosidase (Sigma A-3042) per milliliter to completely hydrolyzed starch before assaying for reducing sugars (Nelson 1944, Madsen 1997). Free sugars were determined on extracts not incubated with amyloglucosidase and starch content was calculated from TNC and sugar content (Madsen 1997). Total TNC storage (g m^{-2}) was calculated by multiplying the biomass dry weight (g m^{-2}) by the percent TNC for each sampling period.

In addition, twenty sediment core samples per pond were collected monthly from January 1994 through July 1995 using a Wildco sediment sampler (Saginaw, MI; model #2424-L15) with a 4.5 cm diameter cylinder. Samples were washed, tubers counted and processed as above to obtain dry weight, TNC, free sugar, and starch content.

Plant tissue samples from the hydrilla pond sampling portion of the study were analyzed for nitrogen, phosphorus and potassium according to standard methods (APHA et al.1989). All plant samples were digested and 250 mg of the ground plant material were mixed with reagents and heated at 250 C for 15 min, then at 380 C for approximately 3 h (Allen et al. 1974). After cooling, samples were prepared for the specific macronutrient analysis (APHA et al. 1989). Nitrogen samples were analyzed on an Orion ion analyzer Model 940 with a Orion selective ion electrode, (Boston, MA); phosphorus samples were examined using a Shimadzu 1201 UV-VIS Spectophotometer (Columbia, Maryland) and potassium samples were analyzed using a Varian AA-10 Atomic Absorption Spectophotometer (Melbourne, Australia). All instruments were calibrated daily prior to analysis.

Container Study

In addition to the above mentioned hydrilla pond biomass samples, 300 containers (5 L) of LAERF pond sediment were planted with two apical sprigs of hydrilla (15 cm) and placed into one of the study ponds. Each container was amended with one slow-release fertilizer briquet (14N, 3P, 3K; Woodace Briquets, Vigoro Industries Inc., Fairview Heights, IL). The hydrilla was allowed to grow for a complete growing season (1994) before sampling was initiated. Each month, starting in January 1995 through December 1996, twelve containers were harvested, processed, then analyzed for carbohydrates as mentioned above. Containers were used to overcome the inability to adequately sample underground plant organs (roots, stolons and tubers) of hydrilla in ponds.

RESULTS AND DISCUSSION

Pond Study

Biomass and Density. Hydrilla biomass was allocated principally to the aboveground shoots with a maximum dry weight of approximately 1200 g m^{-2} occurring between July and October 1994 (Figure 1C, 1D). Other studies indicate maximum hydrilla biomass to range from 52 g m^{-2} for Big

[5]National Oceanic and Atmospheric Administration (NOAA), 1994-1995, Local Climatological Data Monthly Summary, P.O. Bx 610086, Dallas-Ft.Worth, TX.

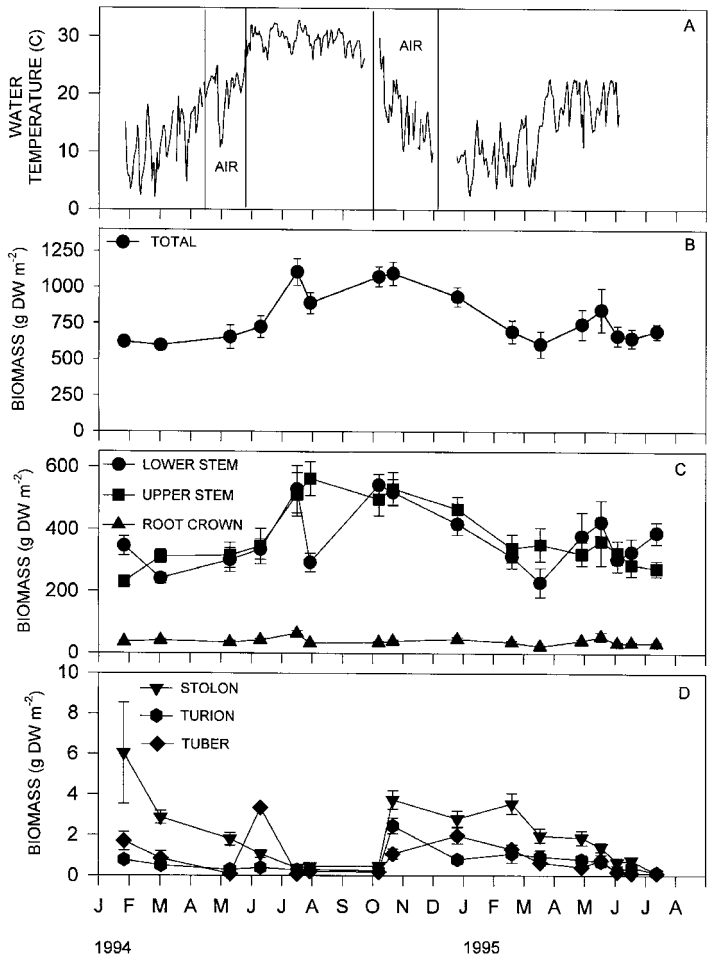

Figure 1. Hydrilla populations in experimental ponds in Lewisville, Texas, during 1994-1995. (A) Average daily water temperature in research ponds. The portions between the dotted lines indicate air temperature to replace missing water temperature data. (B) Total biomass (g DW m^{-2}) of hydrilla; (C) Biomass (g DW m^{-2}) of hydrilla lower shoots, upper shoots and root crowns; (D) Biomass (g DW m^{-2}) of hydrilla stolons, turions and tubers. Bars indicate ± 1 standard error of the mean.

Lake, NC (Harlan et al. 1985) to 890 g m^{-2} for Lake Trafford, FL (Bowes et al. 1979). Maximum total biomass for the LAERF was approximately 1000 g m^{-2} occurring in July 1994 (Figure 1B). Since hydrilla is a canopy producer, during the warmer months (May through October), hydrilla rapidly elongated to the surface to maximize photosynthetic capabilities. As the water temperature increased, the biomass in the upper and lower stems increased (Figure 1A, 1B). Biomass of root crowns, stolons, tubers and turions was relatively low throughout the summer months before increasing in October as new storage organs were produced (Figure 1C).

Hydrilla did not undergo complete dormancy throughout the winter months, although biomass decreased. As the water temperature dropped, the upper canopy of hydrilla senesced, although biomass remained within 50% of maximum summertime biomass (Figure 1). During the summer months, over 90% of the plant biomass occurred in the aboveground shoot regions. Since hydrilla allocates most biomass to the aboveground material, especially with the formation of a dense surface canopy, the plant can maximize photosynthetic capabilities (Madsen 1991). Alkalinity levels at the LAERF average 100 mg L^{-1} annually (Smart et al. 1995), therefore indicating sufficient dissolved inorganic carbon should be available for photosynthesis.

During the fall months, starting in October 1994, stolon, tuber and turion densities increased (Figure 2A, 2B, 2C, 2D). Flowering hydrilla was observed in late September, just prior to tuber and turion formation. Increases in tuber density were also evident in the core data (Figure 2C). Other experiments have indicated that undisturbed hydrilla tubers will germinate in the latter part of July through August in Texas (unpubl. data). Evidence for this timing of tuber germination can be seen in the decrease in tuber numbers before new tubers are produced in the fall (Figure 2C, 2D). At the LAERF, hydrilla regrows in the spring from stolon and root crowns, rather than from tubers. The optimum temperature for tuber germination has been shown to occur between 15 and 35 C (Haller et al. 1976), but temperature is not the only

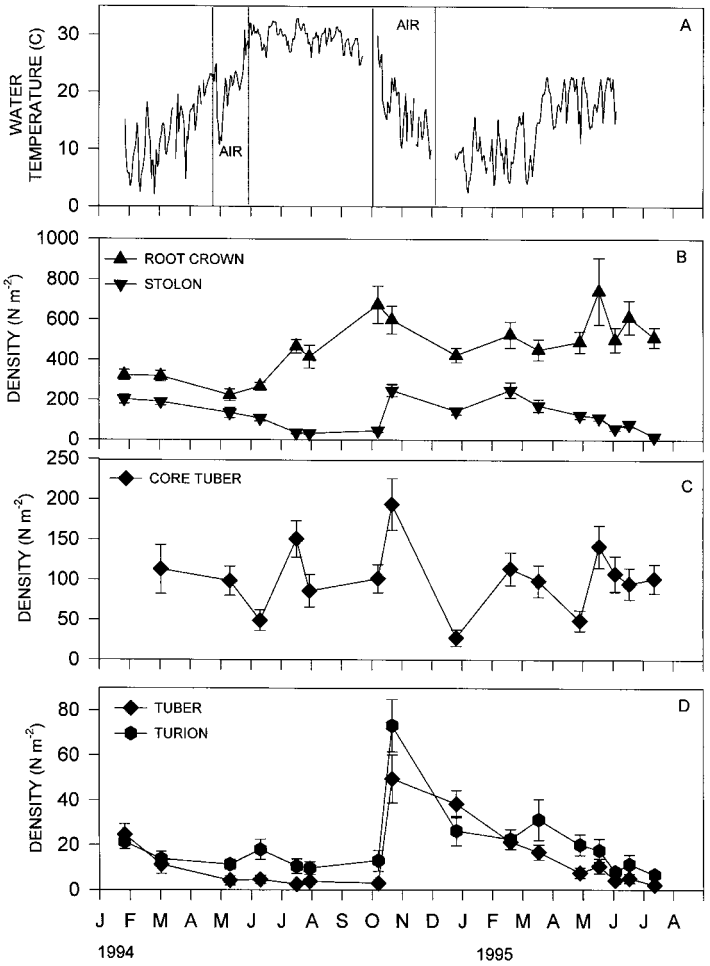

Figure 2. Hydrilla populations in experimental ponds in Lewisville, Texas, during 1994-1995. (A) Average daily water temperature in research ponds. The portions between the dotted lines indicate air temperature to replace missing water temperature data. (B) Density (N m^{-2}) of hydrilla root crowns and stolons; (C) Density (N m^{-2}) of hydrilla tubers from sediment core data; and (D) Density (N m^{-2}) of hydrilla tubers and turions from quadrat data. Bars indicate ± 1 standard error of the mean.

controlling factor. For example, tubers are stimulated to germinate after drawdown (Netherland 1997). Following a drawdown in Rodman Reservoir, Florida, 80% of the hydrilla tubers were found to germinate (Haller et al. 1976). Tubers provide a survival strategy for the primary plant, and turions allow the primary plant a means of long distance dispersal, depending on water movement.

An apparent disparity between tuber densities in core data (Figure 2C) and quadrat data (Figure 2D) occurs because plants produce tubers at the end of positively-geotropic underground shoots, and tubers remain in the sediment after these shoots senesce. Tubers remain in the sediment, accumulating over time and, unless disturbed, can remain viable in the sediment for up to four years, with several million being produced per hectare (Netherland 1997, Haller and Sutton 1975); loosely attached or detached tubers were not detected. Tuber densities (up to 200 m^{-2}) observed in our experimental ponds as sampled by coring are comparable to densities cited in the literature, though possibly at the low end of the range (Netherland 1997). Tuber density can be affected by sediment type and organic components. According to one study (Spencer et al. 1992), addition of straw or peat to six different sediments resulted in tuber density increases. Therefore the Lewisville pond sediment, which is composed of 28% sand, 33% silt and 38% clay (Smart et al. 1995) could affect tuber density, as could the age of the hydrilla population, depth, nutrient inflows and light.

Nutrient Content. Plant allocations of nitrogen, phosphorus and potassium were performed for the hydrilla pond sampling study from January 1994 through June of 1995. Previous research determined sediment N availability was limiting to plant growth in the LAERF ponds. Further, this study established average hydrilla biomass on unfertilized and fertilized LAERF pond sediment to attain approximately 300 g m^{-2} dry shoot weight and 700 g m^{-2} dry shoot weight, respectively, over a ten-week time frame (Barko and Smart 1981, Smart et al. 1995). Hydrilla biomass in the upper shoots ranged from 200 g m^{-2} dry shoot weight during the winter months to nearly 600 g m^{-2} dry shoot weight during the summer months (Figure 1B). Although nitrogen was established as the limiting element for plant growth at LAERF, nitrogen is available for spring growth from senescence of hydrilla plant material and recycling of nutrients to the sediment (Smart et al. 1995). Therefore, when hydrilla was increasing in biomass during the early to mid-summer months, nitrogen was available for uptake. Nitrogen levels in the plant tissues were similar for upper and lower shoots (22-25 mg g^{-1}) during the mid-summer months and 20 mg g^{-1} for the winter months. The root crown levels (15-20 mg g^{-1}) were within 5 mg g^{-1} of the aboveground levels (Figure 3A).

The shoot nitrogen levels (22-25 mg g^{-1}) found were midway between levels found by Barko et al. (1988). These researchers found shoot nitrogen levels of hydrilla in previously unplanted sediment of approximately 32 mg g^{-1} while levels for plants grown on previously planted sediment were approximately 12 mg g^{-1}. Hydrilla tissues are composed of as much as 95% water, therefore hydrilla can produce large quantities of biomass with limited supplies of nutrients, including nitrogen[3]. Although the Lewisville pond sediment could be nitrogen limited (Smart et al. 1995), sufficient

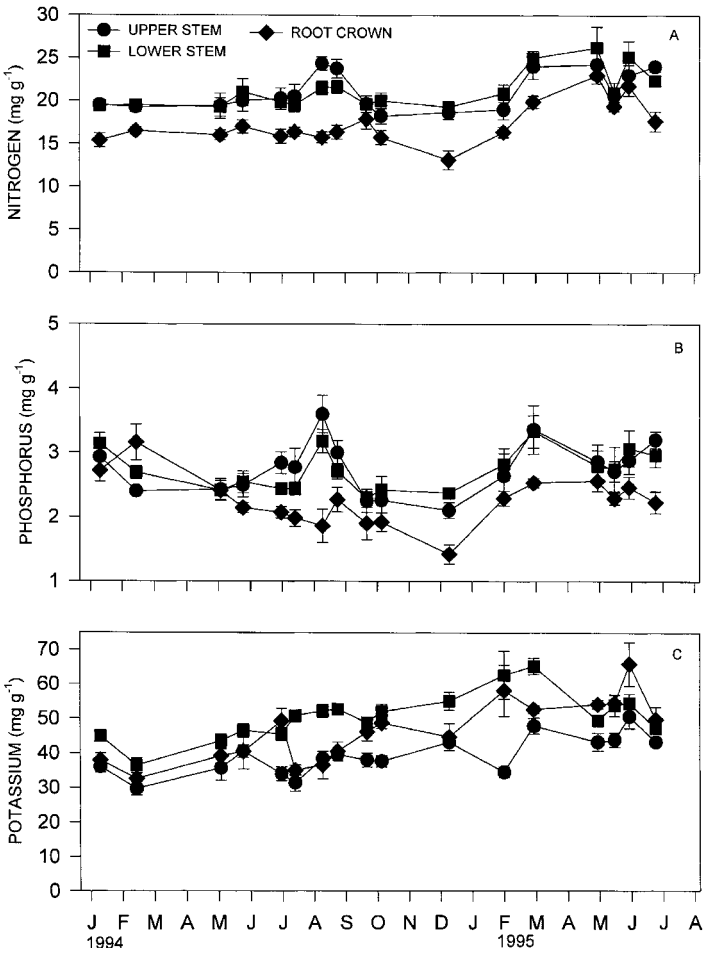

Figure 3. Tissue nutrient concentration for *Hydrilla verticillata* harvested from research ponds from 1994 through July 1995. (A) Nitrogen (mg g^{-1}) allocation for upper stems, lower stems and root crowns; (B) Phosphorus (mg g^{-1}) allocation for upper stems, lower stems and root crowns; (C) Potassium (mg g^{-1}) allocation for upper stems, lower stems and root crowns. Bars indicate ± 1 standard error of the mean.

nitrogen was available for hydrilla growth within these research ponds.

Mean phosphorus levels, a macronutrient taken up by the roots, is translocated to the aboveground biomass (Barko et al. 1988). Phosphorus levels for samples of upper and lower stems ranged from 2.1-3.9 mg g^{-1} with higher levels occurring during the mid-summer months, and low levels during winter. The root crown levels averaged from to 1.7-2.5 mg g^{-1}, showing the same seasonal trend as the stems (Figure 3A,3B). Smart et al. (1995) determined phosphorus levels at the LAERF to be adequate for plant growth.

Hydrilla shoot phosphorus levels from this study were comparable to shoot phosphorus levels on previously planted sediment (2.7 mg g^{-1}) and lower levels than for unplanted sediments at 7.4 mg g^{-1} (Barko et al 1988). Barko and Smart (1980) determined plant shoot phosphorus levels for five different sediments ranging from 3.4-6.7 mg g^{-1}.

Normally, potassium is not limited in aquatic ecosystems (Wetzel 1975), and most submersed plants can readily obtain this element out of the water column (Barko and Smart

1981). Potassium levels for the upper stems, lower stems, and root crowns averaged from 30-60 mg g^{-1}, while levels in the roots were from 2 to 4 mg g^{-1} (Figure 3C). These shoot potassium levels are comparable to levels found for unplanted sediments, while previously planted sediment values were about 22 mg g^{-1} (Barko et al. 1988).

Carbohydrate Allocation. The different hydrilla plant components were found to vary seasonally as well as by specific plant part. Tubers and turions had maximum concentrations of stored TNC and starch, ranging from approximately 50 to 70% DW seasonally. Stored TNC and starch levels for these storage organs were consistently high throughout the year with a small drop occurring in July 1994 and June 1995. The free sugars averaged approximately 5% over the year (Figure 4E, 4F).

Stolons and root crowns had a maximum stored TNC in March for both years, with maxima of approximately 40% (stolon) and 25% (root crown) with similar concentrations of starch, and minima at 5% (stolon) and 10% (root crown)

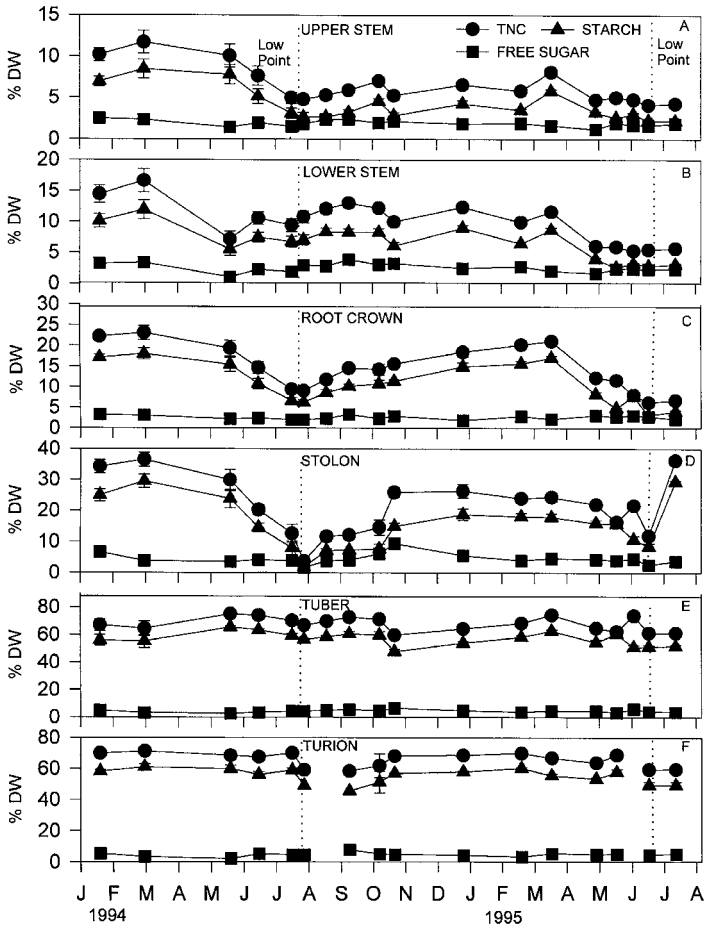

Figure 4. Hydrilla populations in experimental ponds in Lewisville, Texas, during 1994-1995. Dashed lines indicate TNC seasonal low points. (A) TNC, starch and free sugar concentrations (% DW) of hydrilla upper stems; (B) TNC, starch and free sugar concentrations (% DW) of hydrilla lower stems; (C) TNC, starch and free sugar concentrations (% DW) of hydrilla root crowns; (D) TNC, starch and free sugar concentrations (% DW) of hydrilla stolons; (E) TNC, starch and free sugar concentrations (% DW) of hydrilla tubers and (F) TNC, starch and free sugar concentrations (% DW) of hydrilla turions. Bars indicate ± 1 standard error of the mean.

in July 1994 and June 1995. Root crowns are the major storage organs used by the primary hydrilla plant to overwinter or survive a significant environmental event. Tubers and turions are survival strategies in the event that the aboveground portion of the plant senesces. Free sugars were also low within the stolons and root crowns, ranging from 0 to 5% (Figure 4C, 4D).

The upper stems are not typically considered a region of storage (due to exposure to temperature fluctuations, herbivory, and potential breakage), and the plant rapidly shifts carbohydrates approximately 12% in February 1994 and 8% in March of 1995 and starch levels were 8% and 6% at the same times (Figure 4A). These are well below TNC and starch for the more typical storage organs (Figure 4C, 4D, 4E, 4F). The lower stem also contained the highest stored TNC (16%) and starch (11%) in February 1994, and approximately 9% TNC and 5% starch in March 1995.

Minimum TNC and starch for all hydrilla plant organs occurred in July 1994 and June 1995 (Figure 4), when most stored carbohydrates had been utilized by the plant for spring regrowth. From April through June, a steady increase in aboveground biomass was observed (Figure 1B) as plants rapidly employed stored carbohydrates to develop a canopy. The low point in carbohydrate storage may vary between years and sites. The carbohydrate low point may represent an optimal time for the utilization of some management techniques.

The upper and lower stems were found to contain the greatest amount of total TNC storage (g m^{-2}) among the various plant components. The levels ranged from less than 100 g m^{-2} total TNC storage for the upper stem in August for 1994 to the maximum amount total TNC storage of 700 TNC g m^{-2} for the lower stem, occurring in October 1994 (Figure 5A, 5B). This maximum storage (October) for the stem regions occurred after the culmination of the active growing season, with a gradual decrease over the winter months due to metabolic utilization. Other weedy aquatic plant species exhibit similar total TNC storage (g m^{-2}) allocation patterns of the aboveground biomass. Madsen (1997) and Madsen et al. (1993) found similar allocation patterns occurring in Eurasian watermilfoil and waterhyacinth, respectively. The photosynthetic capabilities of these plants allows for increased levels of total TNC storage in the aboveground regions to support rapid growth and expansion.

Total TNC storage increased in the specialized storage organs (root crown, stolon, tuber, and turion) of the hydrilla plant, starting in October and November. As winter progressed, levels in these storage organs stayed relatively consistent, before decreasing in the early to mid-summer time period as new plant growth was initiated. Levels for root crowns ranged from least total TNC storage in August (20 g m^{-2}) to almost 100 g m^{-2} in March. Stolon levels ranged from 1 g m^{-2} to 20 g m^{-2} with tuber and turion levels from 2.5 g m^{-2} to 15 g m^{-2} (Figure 5C, 5D, 5E, 5F).

Typically, studies of carbohydrate allocation and storage patterns have focused only on the concentration of TNC, rather than on whole-plant quantities of stored carbohydrates. This has lead to the presumption that storage organs, such as tubers and turions, were the critical component for overwintering storage of carbohydrates. While other plant

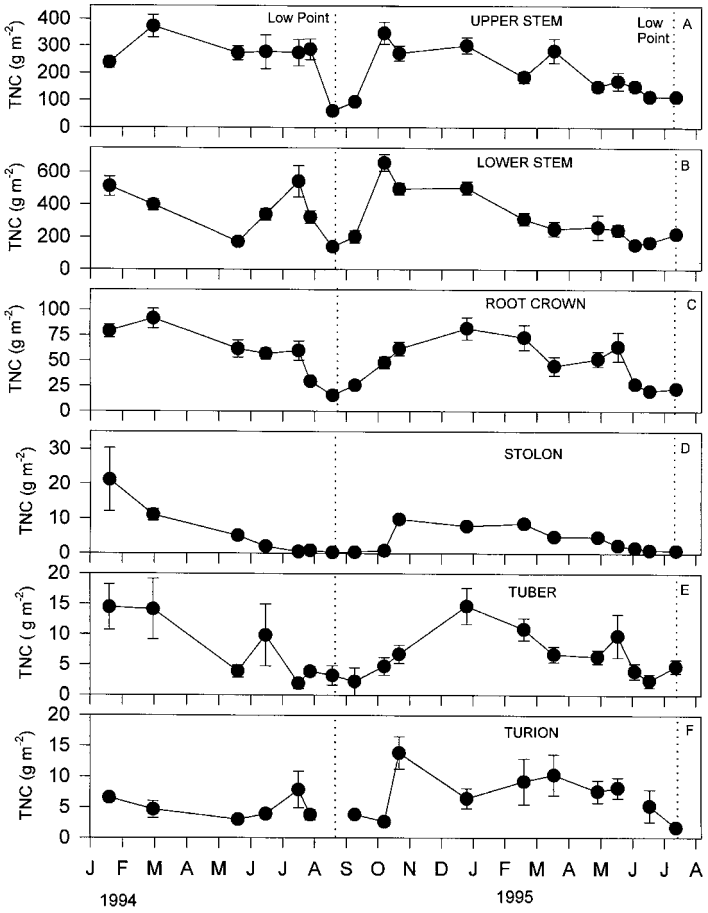

Figure 5. Hydrilla populations in experimental ponds in Lewisville, Texas, during 1994-1995. Dashed lines indicate total TNC storage seasonal low points. (A) Total TNC storage (g TNC m^{-2}) concentrations of hydrilla upper stems; (B) Total TNC storage (g TNC m^{-2}) concentrations of hydrilla lower stems; (C) Total TNC storage (g TNC m^{-2}) concentrations of hydrilla root crowns; (D) Total TNC storage (g TNC m^{-2}) concentrations of hydrilla stolons; (E) Total TNC storage (g TNC m^{-2}) concentrations of hydrilla tubers; (F) Total TNC storage (g TNC m^{-2}) of hydrilla turions. Bars indicate ± 1 standard error of the mean.

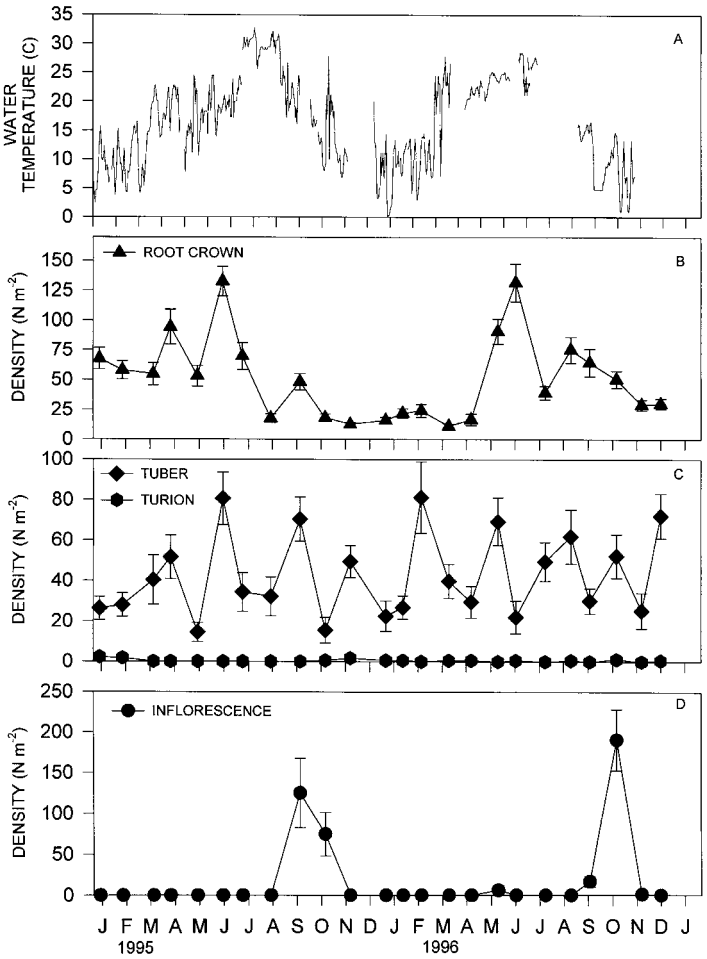

Figure 6. Hydrilla container study conducted in Lewisville, Texas, during 1995-1996. (A) Average daily water temperature in research ponds. (B) Density (N m^{-2}) of hydrilla root crowns; (C) Density (N m^{-2}) of hydrilla tubers and turions and (D) Density (N m^{-2}) of hydrilla inflorescence. Bars indicate ± 1 standard error of the mean.

parts are typically lower in stored carbohydrates, their higher biomass in fact makes tissues such as stems and root crowns larger pools of stored carbohydrates than tubers and turions. As with waterhyacinth (Madsen et al. 1993) and Eurasian watermilfoil (Madsen 1997), this data suggests this to be true of hydrilla.

Container Study

Density. In spring, hydrilla regrows from root crowns (Figure 6A, 6B). As temperatures increased, starting in April for both years, root crown densities increased as new growth was initiated. Root crown density decreased over winter. Tuber densities were variable throughout the two year time frame of this study; however, seasonal tuber densities can increase or decrease due to environmental effects, such as light and temperature on the parent plant, as well as tuber germination following exposure of the tuber bank in sediment (Netherland 1997, Spencer and Ksander 1991, Sutton and Portier 1985, Thakore et al. 1997). Turion densities were consistently low throughout the container study. Flowering occurred in September and October of 1995 and September of 1996.

Carbohydrate Allocation. Aboveground stems, root crowns and tubers were analyzed for TNC, free sugars, and starch for the two years of this study. On a dry weight basis, tubers contained the greatest concentrations of TNC and starch, ranging from 50 to 70% seasonally. The quantity of tuber free sugar averaged approximately 5% annually (Figure 7C). The root crown, also another major storage organ for hydrilla, had maximum levels of TNC (20%) and starch (17%) occurring in January 1996 and 1997. The minimum storage level occurred in June for both years, with TNC ranging from 5 to 10% and starch at approximately 5%. As fall progressed, more carbohydrates were translocated from the stems to the storage organs, as evidenced by the gradual increase of TNC and starch (Figure 7B).

The maximum level of TNC in the aboveground biomass occurred in January for both years with levels ranging from 15 to 20% and 10 to 15% for starch. Free sugars ranged from 1 to 3% (Figure 7A).

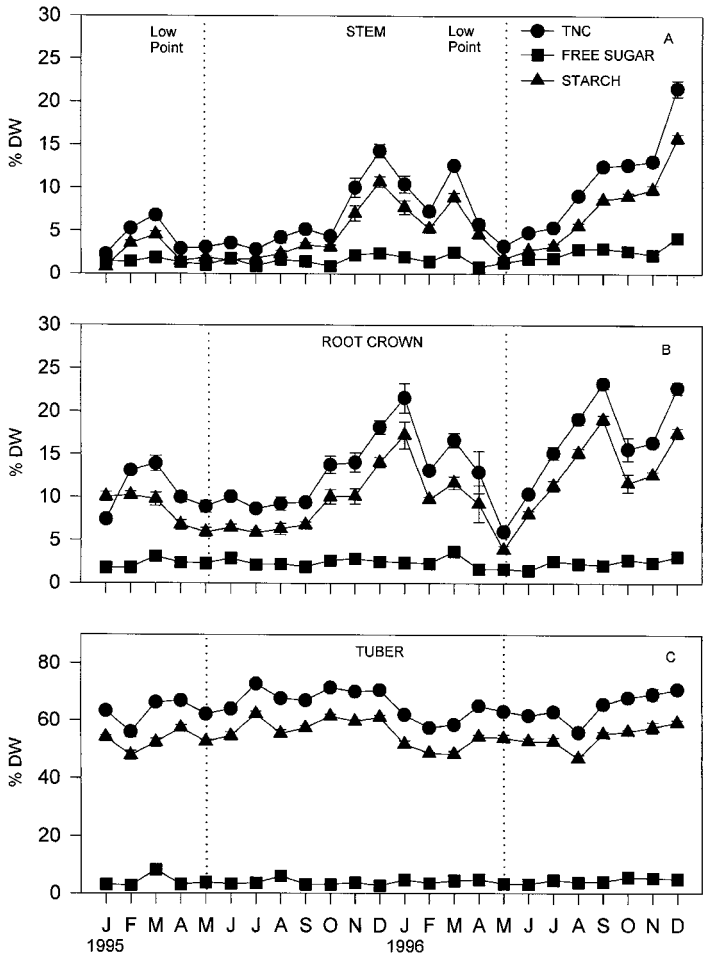

Figure 7. Hydrilla container study conducted in Lewisville, Texas, during 1995-1996. Dashed lines indicate TNC seasonal low points. (A) TNC, starch and free sugar concentrations (% DW) of hydrilla stems; (B) TNC, starch and free sugar concentrations (% DW) of hydrilla root crowns and (C) TNC, starch and free sugar concentrations (% DW) of hydrilla tubers. Bars indicate ± 1 standard error of the mean.

Minima of TNC and starch concentrations for all plant components occurred in June for both years (Figure 7). This is consistent with the timing of low points for the pond sampling in 1994 and 1995 (Figure 4). Values for both the hydrilla pond and container study for TNC, starch and free sugar were comparable. Results from both studies indicate TNC values for the aboveground biomass ranged from a low point of less than 5% DW TNC to maxima over the winter months of 15 to 20% DW TNC. Root crown values ranged from 5% DW TNC during the mid-summer to 25% DW TNC in January while tuber values were concurrent, ranging from 50 to 65% DW TNC for both studies.

Hydrilla biomass was allocated to the aboveground shoots from May through September for the three years of these combined studies. As water temperatures increased, hydrilla elongated to the surface to maximize photosynthetic capabilities and increase biomass. Root crowns in the pond study remained consistent in biomass annually but the hydrilla container study found an increase from May through June, as the aboveground shoots initiated regrowth. Turion and tuber densities in the pond study were constant or decreased during the summer months. Turion densities were consistently low for the container study.

Both studies found an increase in storage organ densities occurring in the fall months as the primary plant translocated excess carbohydrates to the root crown, stolons, tubers and turions for overwintering. Flowering occurred in September and October for both studies over the three years.

Low points in carbohydrate storage for the three year time period occurred from June through July. Although hydrilla populations will vary in timing of low points from year to year, these mid-summer low storage levels can be exploited for management purposes to prevent excessive summer growth and to control above ground biomass before production of new tubers in the fall.

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