J. Aquat. Plant Manage. 36: 40-44

Phenological Studies of Carbohydrate Allocation in Hydrilla

CHETTA S. OWENS[1] AND JOHN D. MADSEN[2]

ABSTRACT

Hydrilla (*Hydrilla verticillata* (L.f.) Royle), a nonindigenous submersed aquatic plant, was first introduced into the United States in the 1960's. Hydrilla exhibits aggressive growth, forming dense canopies of biomass at the surface of the invaded aquatic systems, affecting fisheries, water quality, transportation and recreational usage. Studies of the phenological seasonal cycles of invasive plants indicate optimal timing to apply management techniques. Biomass and total nonstructural carbohydrate (TNC) allocation of dioecious hydrilla were studied in outdoor ponds in Texas between January 1994 through July 1995. Biomass increased from May through September, growing from overwintering shoots and root crowns, not tubers. Tuber germination occurred in August. Tuber and turion production occurred from October through April. A carbohydrate storage minimum was observed in late July for 1994 and June for 1995, with storage generally split between stolon (7% TNC), root crown (10% TNC) and lower stem (16% TNC). Tubers and turions ranged from 58 to 68% TNC. These studies provide more insight into the timing of major allocation shifts in the hydrilla seasonal growth cycle.

Key words: Hydrilla verticillata, total nonstructural carbohydrates, Hydrocharitaceae, dioecious hydrilla.

INTRODUCTION

Most native aquatic plants enhance their ecosystems. Some of the derived benefits include fish and waterfowl habitat, sediment stabilization and improved water quality (Madsen 1997a). However, many introduced species, including hydrilla, can have negative impacts. Invaded aquatic ecosystem are impacted by increased biomass and dense canopy production which affects water quality, especially dissolved oxygen. Further, dense canopy production shade out native vegetation, thereby leading to a loss of native diversity.

Hydrilla is native to Southeast Asia and Australia. The first discovery of hydrilla in the United States was in the state of Florida during the 1960's (Pieterse 1981). Two distinct biotypes (monoecious and dioecious) exist in the United States (Spencer and Anderson 1986). Monoecious hydrilla has both staminate and pistillate floral components on the same plant while dioecious biotypes produce staminate and pistillate on separate plants. Currently, within the United States, dioecious hydrilla is pistillate producing only; therefore, indicating that no seeds are produced. Dioecious hydrilla is found throughout the southeastern United States and as far north as Connecticut (Les et al. 1997).

Phenology is the study of the seasonal cycle of plants and animals. Previous plant phenology research has successfully demonstrated optimal timing for control of cattails[3]. The utility of herbicide application timing to carbohydrate depletion to improve weed management has also been demonstrated for the terrestrial weed quackgrass (Schirman and Buchholtz 1966). At the Lewisville Aquatic Ecosystem Research Facility (LAERF), phenology studies have been conducted on waterhyacinth (*Eichhornia crassipes* (Mart.) Solms) (Luu and Getsinger 1990) and Eurasian watermilfoil (*Myriophyllum spicatum* L.) (Madsen 1997b).

Many aquatic plants have specific organs for storage of carbohydrates, such as tubers in sago pondweed (*Potamogeton pectinatus* L.), turions in curly-leaf pondweed (*P. crispus* L.) and stembases in waterhyacinth (Madsen 1991). Hydrilla has a number of different storage organs for carbohydrates, including tubers, turions, stolons and root crowns. Upper shoots perform photosynthesis, exporting carbohydrates to these storage organs for use during periods of overwintering or environmental stress. In the spring, these stored carbohydrates provide energy to the plant for regrowth. The goal of this study was to document seasonal changes in the storage of total nonstructural carbohydrates (TNC), expressed as percent TNC of dry weight and observe low points in carbohydrate storage which might be exploited for management of this species.

METHODS

This study was conducted at the LAERF, in Lewisville, Texas (latitude 33°04'45"N, longitude 96°57'30"W), from January 1994 through July 1995. Two experimental ponds (0.3 ha) were utilized, with an average depth of 1.0 m and a maximum depth of 1.5 m. Daily water temperature were continuously monitored using an Omnidata Easy Logger™ Field Data Recording System adjacent to the hydrilla research ponds. Missing temperature data was obtained from the NOAA (National Oceanic and Atmospheric Administration) monthly summary for the Dallas-Ft. Worth Regional Airport[4].

From January 1994 through July 1995, 12 biomass samples were collected monthly from each of the two ponds, using a

---

[1] AscI Corporation, Lewisville Aquatic Ecosystem Research Facility, RR#3, Box 446, Lewisville, TX 75056-9720.

[2] U.S. Army Engineer, Waterways Experiment Station, ATTN: CEWES-ES-P, 3909 Halls Ferry Road, Vicksburg, MS 39180-6199. Received for publication December 9, 1997 and in revised form January 2, 1998.

[3] Linde, A. F., T. Janisch and D. Smith. 1976. Cattail-The significance of its growth, phenology and carbohydrate storage to its control and management. Tech. Bull. 94, WI Dept. Nat. Resourc., Madison, WI. 27 p.

0.1 m^2 quadrat. Biomass samples were separated into upper and lower shoots, root crowns, stolons, tubers and turions. Inflorescences, root crowns, tubers and turions were counted. All samples were dried at 55 C in a Blue M forced air oven (General Signal, Atlanta, GA) for a minimum of 48 hours, then weighed. After obtaining a dry weight, samples were finely ground using a Cyclone Sampling Mill (UDY Corp, Ft. Collins, CO), for carbohydrate analysis.

Plant samples were analyzed for TNC using a modified procedure by Swank et al. (1982). Total nonstructural carbohydrate (starch, hydrolyzable sugars, reducing sugars) extracts were incubated at 55C for 15 minutes with one unit of amyloglucosidase (Sigma A-3042) per milliliter of completely hydrolyzed starch before assaying for reducing sugars (Nelson 1944, Madsen 1997b).

Additional core tuber samples (40) were collected monthly from January 1994 through July 1995 using a Wildco sediment sampler (Saginaw, MI; model # 2424-L15) with a 4.5 cm wide cylinder. Samples were washed, tubers counted and then processed as above to obtain dry weight and TNC content.

RESULTS AND DISCUSSION

Hydrilla exhibited an aggressive growth strategy as water temperatures increased. This is evident in the expansion in root crown density (Figure 1A, 1B) during the summer months. Flowering of hydrilla was observed in late September through October, just prior to tuber and turion formation (Figure 1C).

During the fall months, starting in October 1994, an increase in stolon, tuber and turion densities occurred as these storage organs were produced for winter (Figure 1B, 1E). Increases in tuber density were also evident in the core data (Figure 1D). Other experiments (unpubl. data) have indicated that undisturbed hydrilla tubers will germinate in the latter part of July through August at this location. 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 1D, 1E). At the LAERF, hydrilla regrows in the spring from stolon and root crowns, rather than tuber germination. 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 controlling factor. Following a drawdown in Rodman Reservoir, Florida, 80% of the hydrilla tubers were found to germinate (Haller et al. 1976). Tubers, as well as turions, are backup survival strategies for the primary plant. Thus all reproductive activities (sexual and asexual) occurred in the fall preceding plant senescence for winter.

An apparent disparity between tuber densities in core data (Figure 1D) and quadrat data (Figure 1E) occurs because plants produce tubers at the end of stolons, then stolons senesce and the tuber is left in the sediment. Tubers remain in the sediment, accumulating over time. The only tubers detected through quadrat sampling were those still firmly attached to stolons, which were removed with the biomass samples. 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).

Hydrilla biomass was allocated principally to the aboveground shoots with a maximum dry weight of approximately 1200 g m^{-2} occurring in June through August 1994 (Figure 2A, 2B). Since hydrilla is a canopy producer, during the warmer months, hydrilla effectively obtained sufficient light to extend carbohydrate production. As the water temperature increased, the biomass in the upper and lower stems increased (Figure 2A, 2B). Stolon, tuber and turion biomass decreased throughout the summer months before increasing in October as new storage organs were produced (Figure 2C).

The minimum for total nonstructural carbohydrate (% TNC) for all plant organs occurred in July 1994 and June 1995 for this study (Figure 2), when most reserve carbohydrates had been utilized by the plant for spring regrowth. From April through June, a steady increase in aboveground biomass was detected (Figure 2B) as the hydrilla rapidly utilized stored carbohydrates to reach the surface. Additional data at the LAERF (unpubl. data) have shown a low point for carbohydrate storage occurred in June, indicating that hydrilla populations can vary the point of low carbohydrate storage throughout a mid-summer time frame. A similar variation in the primary low point for carbohydrate storage was observed for Eurasian watermilfoil (Madsen 1997b). The time when hydrilla is expected to be most susceptible to a management technique is at the point in the seasonal cycle when the stored carbohydrates are at the lowest (Figure 2D, 2E). Without sufficient stored carbohydrates, the plant will recover more slowly, and the management technique may provide more effective control. In addition, mid-summer management of hydrilla may eliminate the formation of tubers and turions in the fall.

These phenological studies indicate that hydrilla utilizes carbohydrates stored in the root crown to promote rapid new spring growth. Carbohydrate storage in hydrilla is at its lowest point during the seasonal cycle in late June to mid-July, with storage predominantly in root crowns, stolons, and lower shoots. Tubers and turions are also storage organs, but provide for dispersal (turion) and long-term survival if the plant dies. These low points in carbohydrate storage may enable the aquatic resource manager to utilize specific timing of control for improved management of this weedy species.

ACKNOWLEDGMENTS

This research was conducted under the US Army Corps of Engineers Aquatic Plant Control Research Program, Environmental Laboratory, US Army Engineer Waterways Experiment Station (WES). Permission was granted by the Chief of Engineers, HQUSACE, to publish this information. Field assistance at LAERF was provided by Nicole Flint, Dian Smith, Melissa Smith, and Nathan Standifer. Laboratory analyses were performed at WES by Anne Stewart, under the supervision of Dr. Susan Sprecher. Mr. John Skogerboe and Dr. Susan Sprecher reviewed the manuscript for WES.

---

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

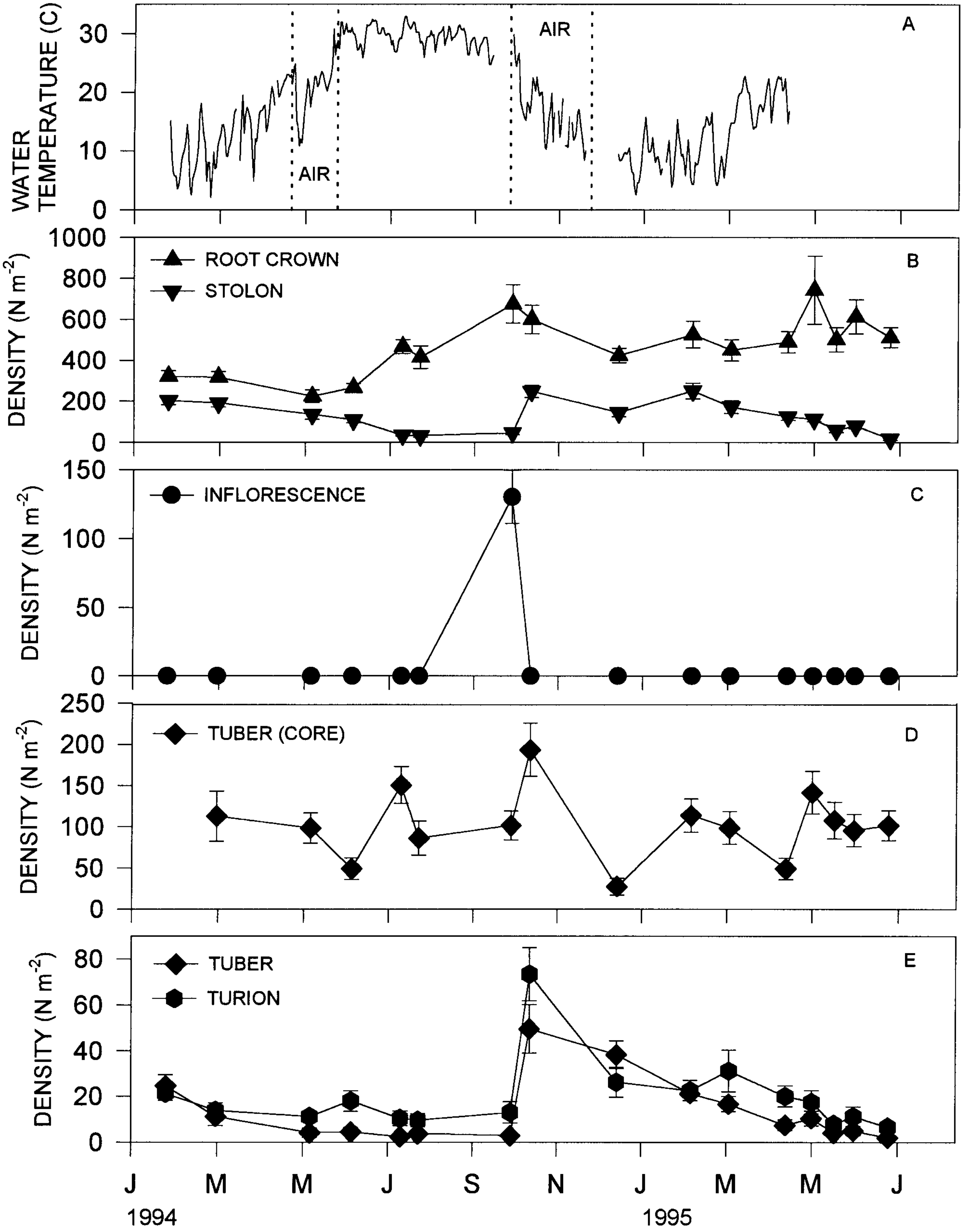

Figure 1. Hydrilla populations in experimental ponds in Lewisville, Texas, during 1994-1995. (A) Average daily water temperature in research ponds. The portions between the dotted lines indicate air temperature to replace missing water temperature data. (B) Density (N m^{-2}) of hydrilla root crowns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

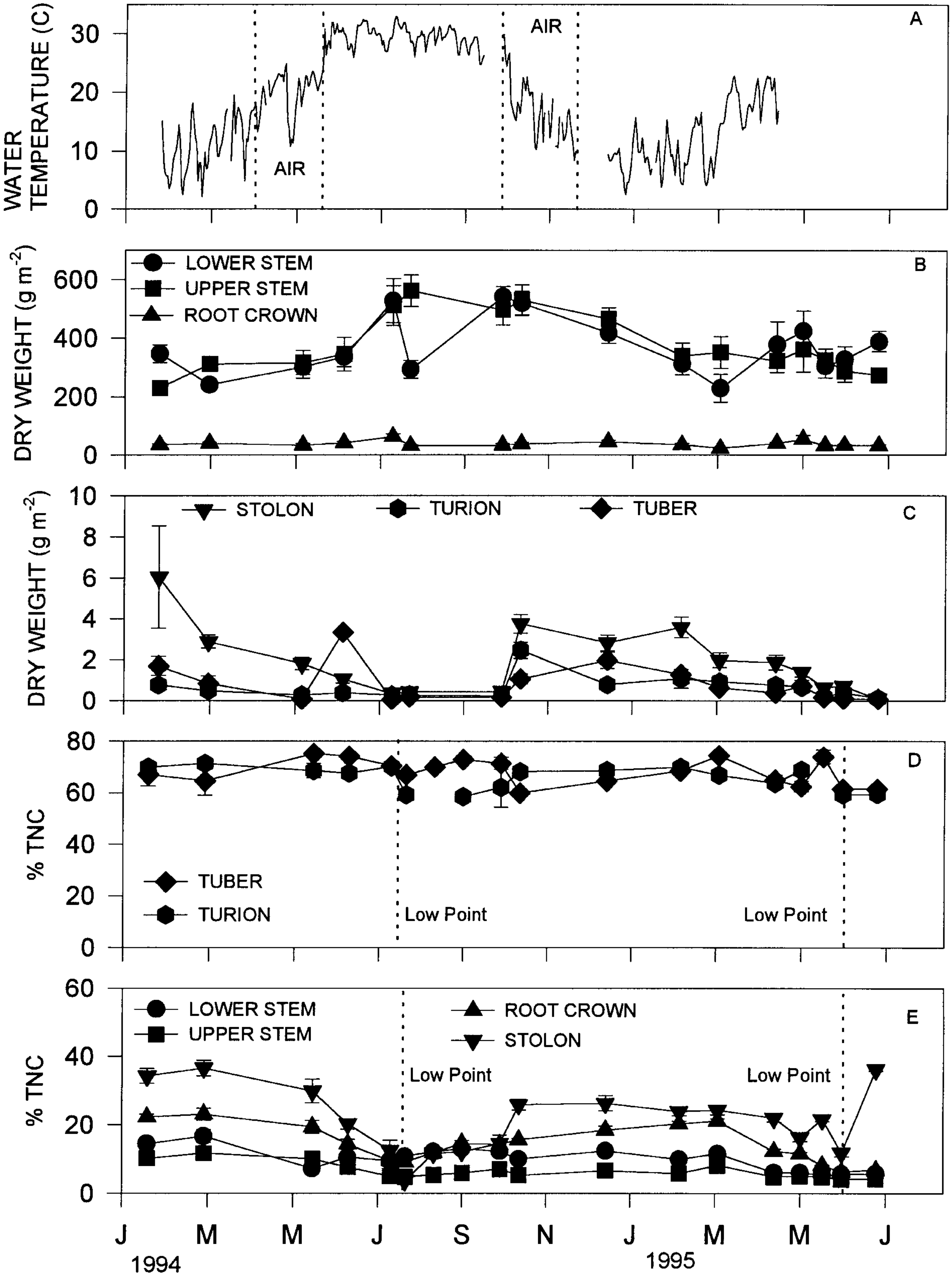

Figure 2. Hydrilla populations in experimental ponds in Lewisville, Texas, during 1994-1995. (A) Average daily water temperature for research ponds. The portions between dotted lines indicate air temperature to replace missing water temperature data. (B) Biomass (g m^{-2}) of hydrilla lower stems, upper stems and root crowns; (C) Biomass (g m^{-2}) of hydrilla stolons, turions and tubers; (D) TNC concentrations (% dry weight) of hydrilla tubers and turions. Dashed line indicates TNC seasonal low point; (E) TNC concentrations (% dry weight) of hydrilla root crowns, stolons, lower stems and upper stems. Dashed line indicates TNC seasonal low point. Bars indicate ± stand error of the mean.

LITERATURE CITED

Haller, W. T., J. L. Miller, and L. A. Garrard. 1976. Seasonal production and germination of hydrilla vegetative propagules. J. Aquat. Plant Manage. 14: 26-29.

Les, D. H., L. H. Mehroff, M. A. Cleland, and J. D. Gabel. 1997. *Hydrilla verticullata* (Hydrocharitaceae) in Connecticut. J. Aquat. Plant Manage. 35: 10-14.

Luu, K. T. and K. D. Getsinger. 1990. Seasonal biomass and carbohydrate distribution in waterhyacinth. J. Aquat. Plant Manage. 28:3-10.

Madsen, J. D. 1991. Resource allocation at the individual plant level. Aquat. Bot. 41: 67-86.

Madsen, J. D. 1997a. Method for Management of Nonindigenous Aquatic Plants. In: J. O. Luken and J. W. Thieret (eds). Assessment and Management of Plant Invasions. Springer, New York. pp. 145-171.

Madsen, J. D. 1997b. Seasonal biomass and carbohydrate allocation in a southern population of Eurasian watermilfoil. J. Aquat. Plant Manage. 35: 15-21.

Nelson, N. 1944. A photometric adaptation of the Somogyi method for determination of glucose. J. Biol. Chem. 153: 373-80.

Netherland, M. D. 1997. Turion ecology of hydrilla. J. Aquat. Plant Manage. 35: 1-10.

Pieterse, A. H. 1981. *Hydrilla verticillata*- a review. Abstr. Trop. Agric. 7(6): 9-34.

Schirman, R. and K. P. Buchholtz. 1966. Influence of atrazine on control and rhizome carbohydrate reserves of quackgrass. Weeds 14: 233-36.

Spencer, D. F. and L. W. J. Anderson. 1986. Photoperiod responses in monoecious and dioecious *Hydrilla verticillata*. Weed Sci. 34: 551-57.

Swank, J. C., F. E. Below, R. J. Lamber, and R. H. Hageman. 1982. Interaction of carbon and nitrogen metabolism in the productivity of maize. Plant Physiol. 70: 1185-90.

1