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Seasonal Biomass and Carbohydrate Allocation Patterns in Southern Minnesota Curlyleaf Pondweed Populations

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ABSTRACT

Four southern Minnesota populations of curlyleaf pondweed (*Potamogeton crispus* L.) were sampled monthly from January 2001 to November 2002 to determine seasonal phenological, biomass, and carbohydrate allocation patterns. Low periods of carbohydrate storage in the seasonal phenological cycle indicate potentially vulnerable periods in the plant's life cycle and may be the ideal time to initiate management and control efforts. Samples were separated into shoots, roots, inflorescence, and turions and then dried. Biomass (g m^{-2}) and percent total nonstructural carbohydrates (TNC) were determined for each plant component. Total biomass peaked in May and June, and ranged from 122 to 190 g m^{-2}. Turion formation and flowering were observed to coincide with peak biomass. Peak turion TNC concentrations ranged from 44 to 66%. The low point of carbohydrate storage in all four lakes occurred between January and April 2002, indicating that early spring may be the best time to initiate management.

Key words: Potamogeton crispus, phenology, total nonstructural carbohydrates, turion.

INTRODUCTION

Curlyleaf pondweed is the most widely-dispersed nuisance-forming nonnative submersed aquatic plant in the state of Minnesota. Native to Europe and Asia, curlyleaf pondweed is now thoroughly naturalized in North America. Curlyleaf pondweed reproduces primarily vegetatively with turions and forms thick monospecific beds. The dense growth out-competes native aquatic vegetation, degrades lake water quality, and causes problems to navigation and recreation (Bolduan et al. 1994).

Significant time and resources are dedicated every year to the management of curlyleaf pondweed in the Midwest. Despite this, management efforts are often applied without taking into account the plant's biology and ecology, leading to inefficient or ineffective control.

A tool that has been used to better manage Eurasian watermilfoil (Madsen 1997) and hydrilla (Madsen and Owens 1998) has been an understanding of the seasonal cycle of carbohydrate storage. Low points of carbohydrate storage indicate periods during which the plant is least likely to recover following management and control treatments. Exploiting these low points can lead to improved control of the target species (Madsen 1993a).

The goals of this study were to 1) identify seasonal biomass and carbohydrate allocation patterns in southern Minnesota curlyleaf pondweed populations and 2) use the carbohydrate allocation patterns to identify periods of low carbohydrate storage in order to indicate the best time to initiate control efforts on curlyleaf pondweed populations.

MATERIALS AND METHODS

Four Southern Minnesota lakes were monitored in this study: West Jefferson Lake (Latitude 44.25833°N, Longitude 93.77306°W) in Le Sueur County and Leiberg Lake (Latitude 44.15507°N, Longitude 94.31216°W), Lura Lake (Latitude 43.86667°N, Longitude 94.03333°W), and Lake George (Latitude 44.23333°N, Longitude 93.86944°W) in Blue Earth County. The lakes are dominated by curlyleaf pondweed and have Carlson's Trophic State Index ratings ranging from eutrophic to hypereutrophic (MPCA 2003). Sampling sites were located in areas of dense curlyleaf pondweed growth at water depths of 1.6 meters.

Systematic sampling was conducted monthly throughout the year at all sites and biweekly during periods of peak growth in May and June. Sampling began in February 2001 and continued through November 2002. Thirty samples were taken in transects using a 0.018 m^2 PVC corer at the time of each sampling (Madsen 1993b). Samples were washed in a screen-bottomed bucket (0.25 cm^2 mesh) in the lake, bagged, and placed in a cooler for transport to the lab.

Phenological characteristics were noted at the time of every sampling including flowering, turion formation, summer growth, winter growth, turion sprouting, and plant senescence. Water temperature profiles were taken at 0.5 m increments at the time of each open-water sampling and were reported as an average of 0.5, 1.0, and 1.5 m measurements. No water temperature data were collected during periods of ice cover.

Samples were washed and curlyleaf pondweed biomass sorted into shoots, turions, new turions, inflorescence, and underground biomass of roots and rhizomes. Turions, new

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turions, and sprouting turions were counted for each sample and converted to turion density (turions m^{-2}). New turions were identified by their attached leaves or by their bright green color. After the plants senesced, turions were no longer differentiated and all turions were combined. Soft turions were not included in order to avoid those that were decomposing and non-viable turions. Other species, when present, were also collected and noted. Biomass samples were dried in a Sheldon Manufacturing 1390FM forced air oven (Sheldon Manufacturing Inc., Cornelius, OR) at 55 C to a constant weight for a minimum of 48 hours. Samples were weighed on a calibrated Mettler PM300 (Mettler Toledo, Greifensee, Switzerland) balance (±0.01 g). Samples with biomass below detections limits were recorded as half the detection limit of the scale (0.005 g). The dry weight of each plant constituent was converted to g m^{-2}. The biomass was then averaged for the 30 samples and the standard error was calculated (Madsen 1997).

Plant samples were analyzed for total nonstructural carbohydrates (TNC) using a modification of the method by Swank and others (1982). The dried biomass from the 30 field samples were composited into groups of six (biomass samples 1 through 6 were composited into tissue sample 1, 7 through 12 were composited into tissue sample 2, and so on) to obtain five separate samples for each plant constituent. Compositing was performed to ensure that adequate tissue masses were available for the analytical techniques, and reduce the number of tissue analyses required. The samples were then ground on a Cyclone Sample Mill (UDY Corp., Ft. Collins, CO) with 1-mm screen. Dried ground plant material (50 mg) was weighed on a calibrated Mettler AB104-5 (Mettler Toledo, Greifensee, Switzerland) balance (±0.1 mg). Samples were extracted with a benzoic acid solution and analyzed for TNC (Nelson 1944, Madsen 1997). Samples were analyzed on a Hach DR 4000 Spectrophotometer (Hach Co., Loveland, CO) at 540 nm. Percent TNC dry weight and standard error were calculated for each plant component. Spike, known, duplicate, and blank samples were run for each sample batch. Total TNC storage (g m^{-2}) was also calculated for turions, shoots, and roots to determine the total carbohydrate storage per meter for the curlyleaf populations at that time. Carbohydrate allocation patterns and TNC low points were then determined.

RESULTS AND DISCUSSION

Biomass Allocation. The seasonal biomass allocation patterns of the curlyleaf pondweed populations in this study were similar to patterns observed in other northern hemisphere lake populations (Cypert 1967, Sastroutomo et al. 1979, Kunii 1982, Tobiessen and Snow 1984, Catling and Dobson 1985). Total dry weight biomass peaked in late spring between mid May and mid June, ranging from 122 to 190 g m^{-2} (Figure 1). Kunii (1982) found a comparable maximum biomass of 171 g m^{-2} occurring in May. Other lake studies have found maximum biomass ranging from less than 50 g m^{-2} (Rogers and Breen 1980) to 530 g m^{-2} (Quade et al. 1994). Peak biomass occurred at or near the time of peak turion production and plant senescence and summer dormancy soon followed. Turion sprouting and plant growth occurred in mid September 2001 and mid October 2002, followed by little or no growth during ice-covered conditions. Growth resumed in early spring and progressed rapidly through May and June. Low points of total biomass of 17 to 34 g m^{-2} occurred around November consisting primarily of turions.

Biomass allocation for all plant components followed distinct seasonal patterns. Shoot biomass peaked in early June 2001 and between mid May and early June 2002 ranging from 60 to 140 g m^{-2} (Figure 1). Senescence shortly followed peak shoot biomass. Root and Rhizome biomass made up only a small percentage of the total biomass. Maximum root and rhizome biomass ranged from 4 to 11 g m^{-2}, peaking between January and May. Roots were found to degenerate several weeks prior to senescence, causing the plants to separate from the bottom and form large floating mats on the surface of the lakes.

Peak turion biomass and total turion density occurred in June, prior to plant senescence. Peak turion biomass, new and old turions combined, occurred in June and ranged from 43 to 120 g m^{-2} (Figure 1) consisting of from 1,152 to 3,030 turions m^{-2} (Figure 2). Studies have found maximum

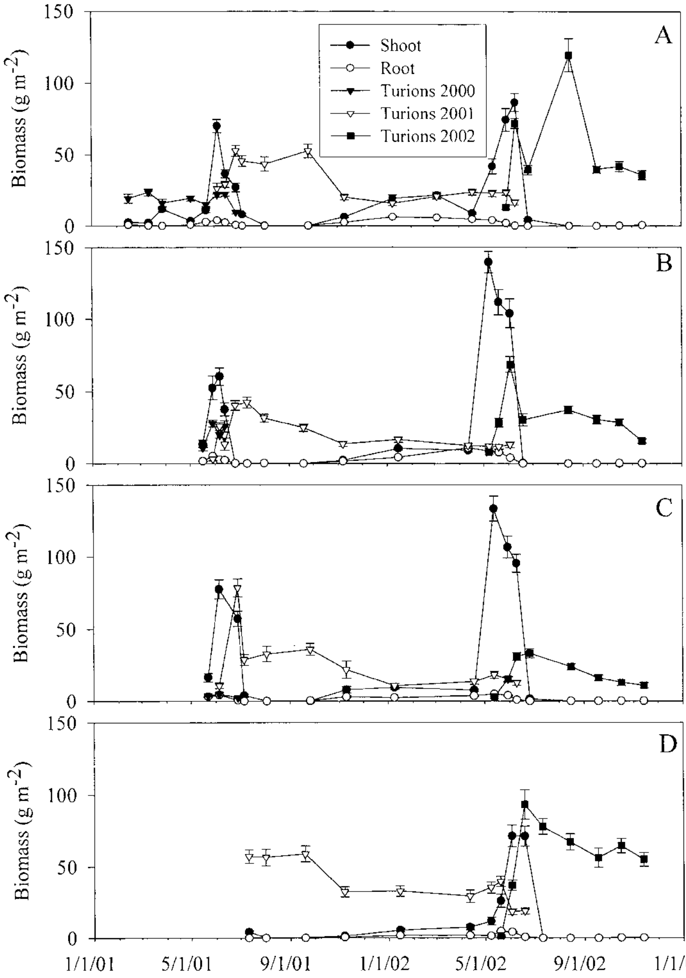

Figure 1. Curlyleaf pondweed plant component dry weight biomass (g m^{-2}) for shoots, roots, and turions from 2001 to 2003. A) Leiberg Lake, B) West Jefferson Lake, C) Lura Lake, and D) Lake George. Bars represent ± 1 standard error of the mean.

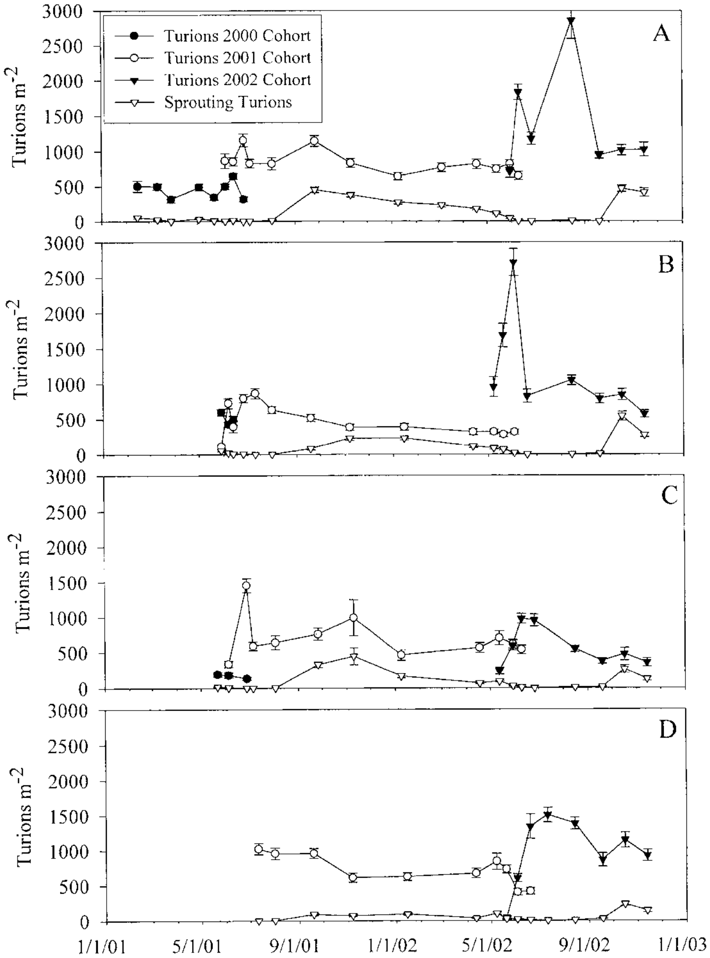

Figure 2. Curlyleaf pondweed turion density (number of turions m-2) from 2001 to 2003. A) Leiberg Lake, B) West Jefferson Lake, C) Lura Lake, D) Lake George. Bars represent ± 1 standard error of the mean.

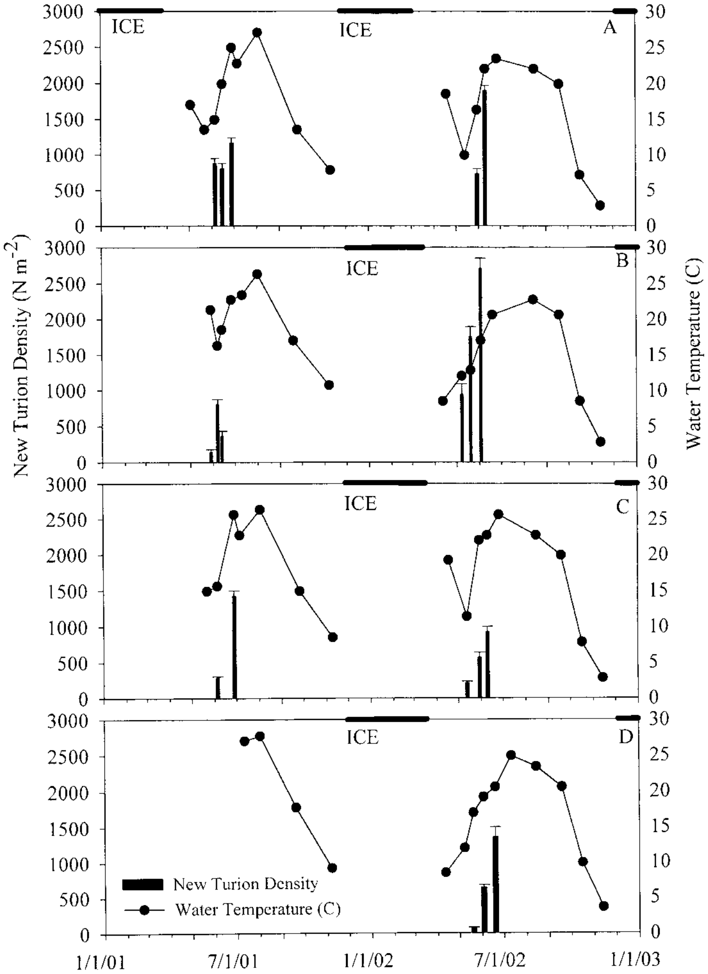

Figure 3. Production of new turions m-2 compared to mean water temperature (C) from 2001 to 2003. Line graph represents mean water temperature (C) with periods of ice cover indicated. Histogram represents the mean number of new turions m-2. A) Lieberg Lake, B) West Jefferson Lake, C) Lura Lake, D) Lake George. Error bars represent ± 1 standard error of the mean.

turion densities in lake populations ranging from 1,500 turions m^{-2} (Rogers and Breen 1980) to 2,088 turions m^{-2} (Sastroutomo et al. 1979).

An atypical peak in turion biomass and density (120 g m^{-2}; 2,863 turions m^{-2}) was observed in the August 16, 2002 sampling. Observations from the prior sampling on June 26, 2002 indicated a large floating mat of curlyleaf pondweed adjacent to the sampling sight. The weed mat may have sunk to the bottom and deposited a large number of turions in the area. The sampling transect of August 16, 2002 may have partially overlapped this area, resulting in the unusually high biomass and density of turions observed.

Turion production was first observed to occur between early May and early June at temperatures between 11 and 16 C (Figure 3), similar to the findings of Kunii (1982). Turion production peaked in June on all lakes in 2001 and 2002, ranging from 726 to 2,713 new turions m^{-2}. At peak turion production, new turions accounted for between 22% and 58% of the total biomass. Kunii (1982) reported new turion densities between 200 and 1,800 turions m^{-2}, with new turions accounting for up to 42% of the total biomass.

A significant increase in the number of sprouting turions was observed in mid September 2001 and mid October 2002 at water temperatures between 8 and 18 C (Figure 4), similar to the findings of Kunii (1982) and Sastroutomo et al. (1979). Sprouting turions accounted for 15% to 81% of the total number of turions during peak sprouting. This is most likely an underestimate, due to the ease of separation of the new growth from the turions during sample collection and washing. Similar studies have found sprouting turions accounting for 55% (Sastroutomo et al. 1979) and 60% (Rogers and Breen 1980) of total turions in field samples.

Flowering coincided with or slightly followed the initiation of turion production both years, similar to the observations of Rogers and Breen (1980) and Kunii (1982). A maximum of 363 inflorescences m^{-2} were found, consisting of up to three inflorescence per plant. Inflorescence accounted for only a small amount of biomass with a maximum recorded inflorescence biomass of 3.1 g m^{-2}. At the same time, 93.3 g m^{-2} of new turions were collected, indicating that sexual reproduction accounted for only 3% of the total reproductive biomass. Perennial submerged macrophytes often allocate very few resources to sexual propagation, relying primarily on asexual means for reproduction (Madsen 1991).

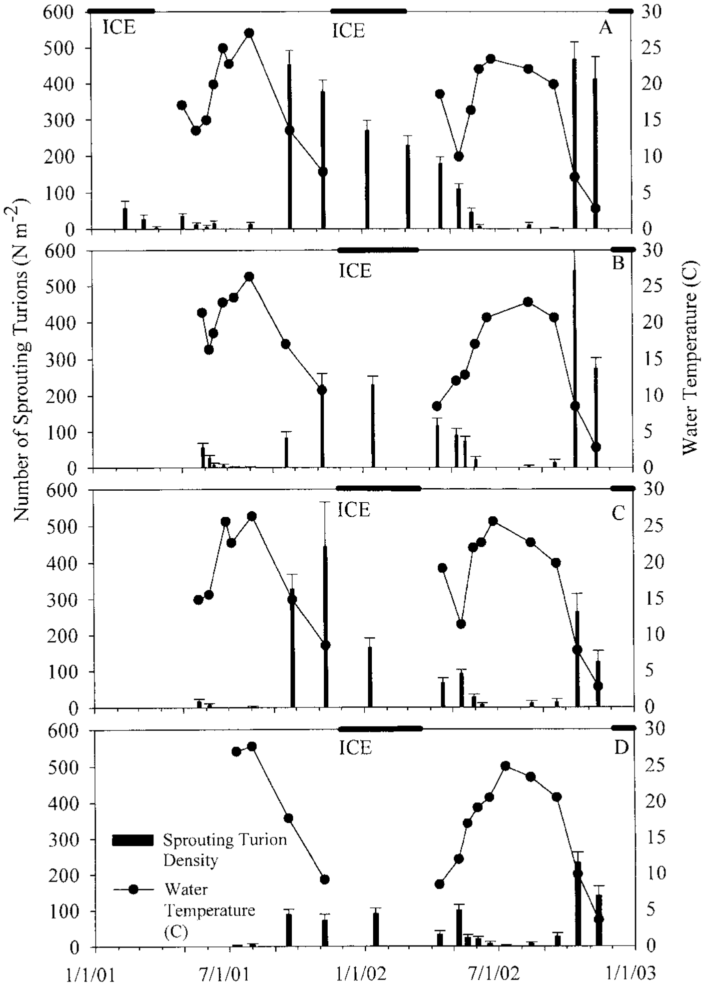

Figure 4. Sprouting turions m^{-2} compared to mean water temperature (C) from 2001 to 2003. Line graph represents mean water temperature (C) with periods of ice cover indicated. Histogram represents the mean number of sprouting turions m^{-2}. A) Lieberg Lake, B) West Jefferson Lake, C) Lura Lake, D) Lake George. Error bars represent ± 1 standard error of the mean.

Carbohydrate Allocation. Turions were found to contain the highest concentrations of TNC throughout the plant's life cycle. The production of specialized structures such as turions allows for increased carbohydrate storage efficiency, permitting a greater concentration of stored carbohydrates (Madsen 1991). Peak turion TNC concentrations ranged from 44 to 66% (Figure 5). Madsen and Owens (1998) found hydrilla turions containing as high as 70% TNC. Kunii (1989) found starch concentrations in small curlyleaf turions ranging from 30 to 40%.

Carbohydrate concentrations in turions generally peaked around September. The timing of this peak may be due to the loss of older, less viable turions through decomposition. As the summer progressed and water temperatures increased, the decomposition of turions was observed with increasing frequency. As a result, the TNC levels may have been 'concentrated' in the turion bank because of the removal of older, less viable turions. Sastroutomo (1981) observed that turions from the previous growing season had a low ability to germinate, and many decomposed in the sediment.

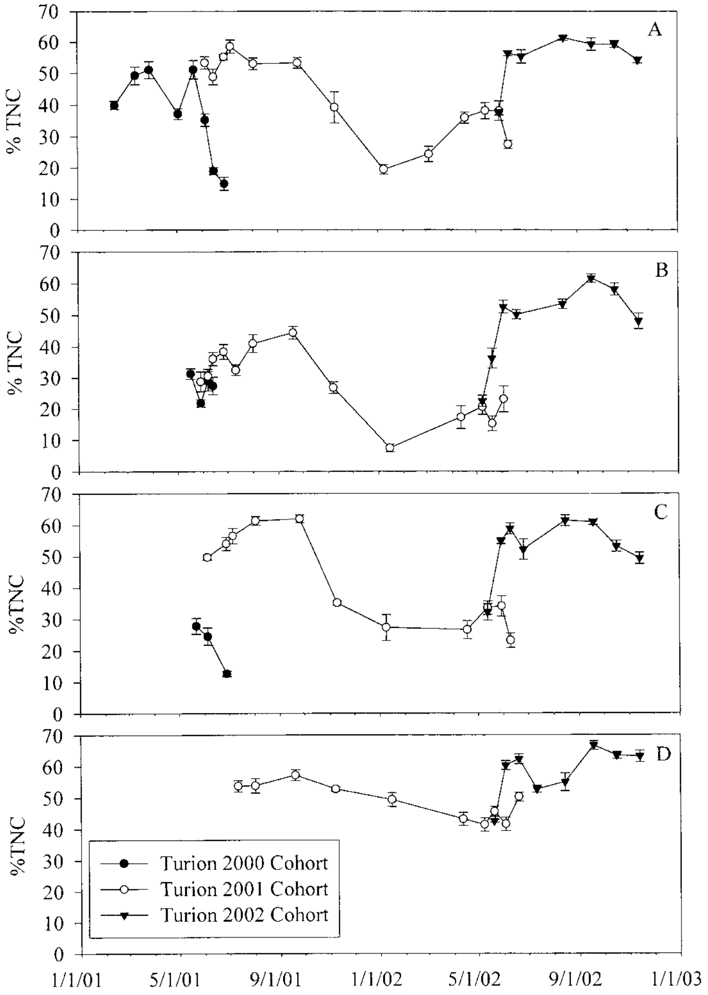

Figure 5. Turion total nonstructural carbohydrates (TNC) as a percent of dry weight from 2001 to 2003. A) Leiberg Lake, B) West Jefferson Lake, C) Lura Lake, D) Lake George. Bars represent ± 1 standard error of the mean.

Carbohydrate concentrations in turions dropped between 8 and 42% from September to November in 2001, corresponding with peak turion sprouting. The drop in turion TNC over the same period in 2002 was not as large, ranging between 5 and 22%. The lower drop in TNC in 2002 may be due to a rapid drop in water temperature in the fall, reducing the period where the plants were exposed to favorable growth conditions of water temperatures between 10 and 19 C. As a result, more energy reserves may have been retained by the turions in November 2002.

Shoot and root TNC levels were typically below 10% but, prior to turion formation, TNC levels were as high as 28% (Figure 6). In preparation for reproduction, aquatic macrophytes typically reallocate energy reserves for flowering and turion production (Madsen 1991), increasing energy reserves prior to senescence (Titus and Adams 1979). Shoot and root TNC concentrations also peaked during turion sprouting in the fall of 2002, indicating a reallocation of energy reserves from the turion to shoot and root growth.

During periods of peak growth the TNC levels in shoots and roots were significantly higher in Lake George than in the other three lakes (Figure 6). The plants in Lake George

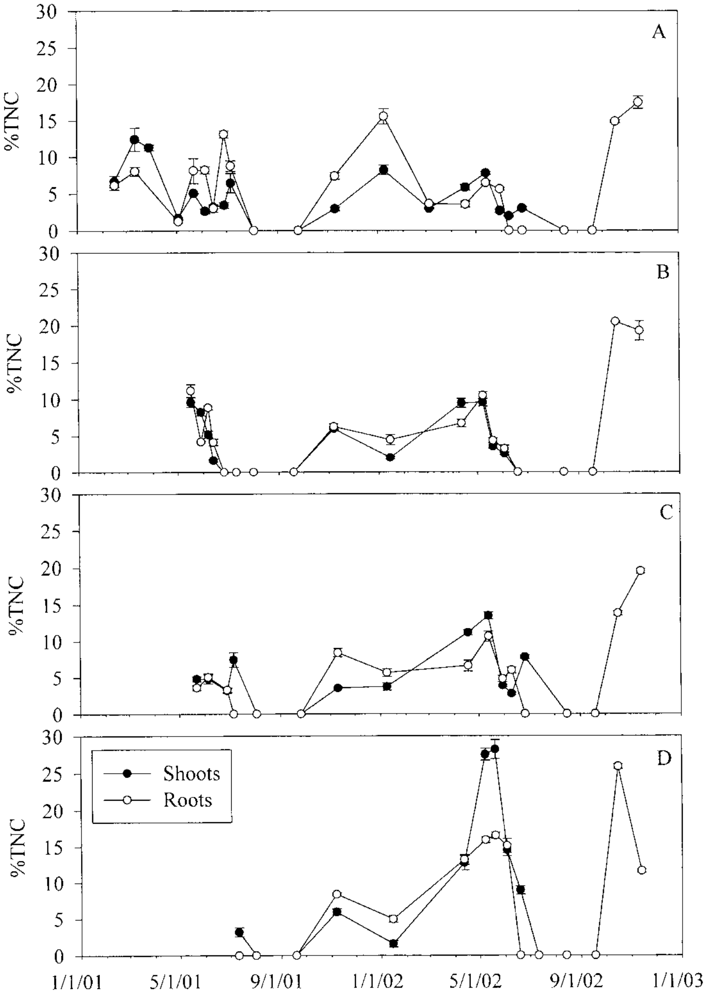

Figure 6. Shoot and root total nonstructural carbohydrates (TNC) as a percent of dry weight from 2001 to 2003. A) Leiberg Lake, B) West Jefferson Lake, C) Lura Lake, D) Lake George. Bars represent ± 1 standard error of the mean.

were noticeably more thick and robust than the plants in the other lakes and the turions tended to be larger in size. The density of the curlyleaf pondweed beds was also lower and other species were present to a greater degree in Lake George than in the other three lakes. A single species can have highly plastic responses to its environment, with plant structures varying in size and shape for a given species under different environmental conditions (Sculthorpe 1967). The lower density of curlyleaf pondweed growth in Lake George may allow for greater light penetration, possibly accounting for the more robust growth form observed. This growth form may allow for the accumulation of carbohydrates in greater concentrations than were observed in the other lakes.

Peak total energy storage in the turion bank (g TNC m^{-2}) occurred during turion formation in June 2001 and 2002, ranging from 15 to 67 g TNC m^{-2} (Figure 7). Total TNC storage in the turion bank decreased in the fall in all four lakes. The timing of this drop corresponded to the period of peak turion sprouting and may indicate a reallocation of energy away from the turion for the purpose of growth. Low points of TNC storage in the turion bank occurred between January and April 2002, ranging from 1 to 13 g TNC m^{-2}. All lakes exhibited low levels of total TNC storage over this period. Total TNC storage levels in turions were declining in November 2002, suggesting that the same pattern of low carbohydrate storage was repeated in the winter of 2002 to 2003.

The total energy reserves in shoots and roots (g TNC m^{-2}) was found to increase prior to active turion development in 2001 and 2002, indicating a reallocation of energy reserves from the shoots for turion production (Figure 7). Peak shoot/root TNC storage occurred from mid May to early June and ranged from 2 to 14 g TNC m^{-2}.

The peak total TNC in shoots and roots in 2001 was lower than the peak in 2002. The lower 2001 peak may have been due to the very cold winter of 2000 to 2001, with ice over 60 cm thick. The winter of 2001 to 2002 was mild in comparison, with a shorter period of ice coverage and ice only up to 28 cm thick. Best and Visser (1987) observed a similar biomass reduction in coontail (*Ceratophyllum demersum* L.) following a severe winter.

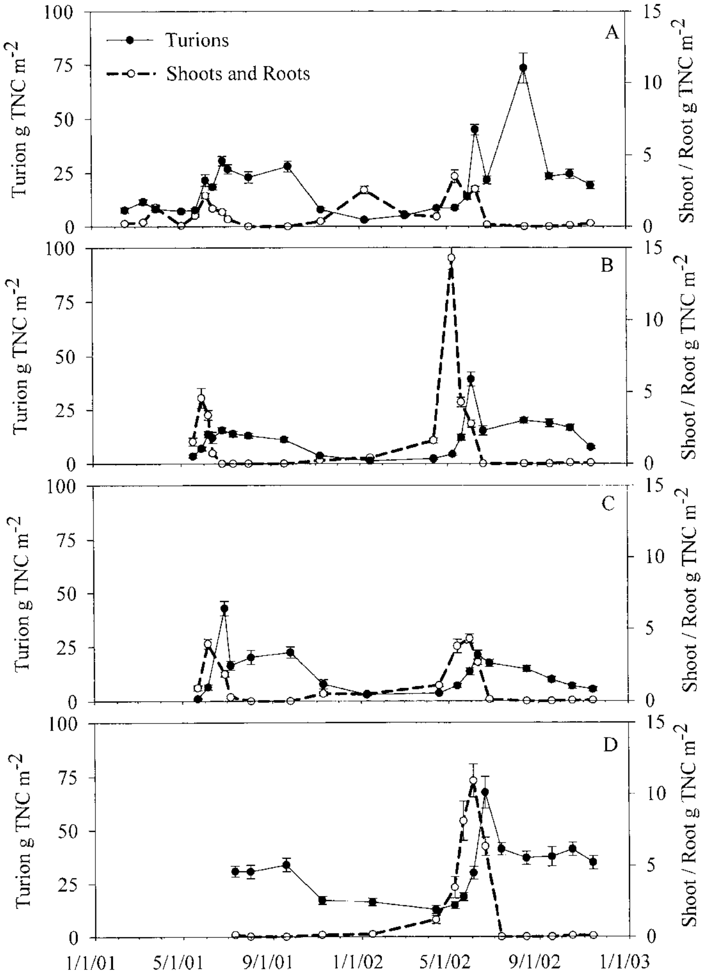

Figure 7. Turion total nonstructural carbohydrate (TNC) storage (g TNC m^{-2}) compared to total shoot/root TNC storage (g TNC m^{-2}) from 2001 to 2003. A) Leiberg Lake, B) West Jefferson Lake, C) Lura Lake, D) Lake George. Bars represent ± 1 standard error of the mean. Vertical dotted lines represent seasonal low points of carbohydrate storage.

Carbohydrate Low Points. A carbohydrate low point is defined as a seasonal minimum of stored carbohydrates. Carbohydrate low points occur when carbohydrate utilization from storage exceeds carbohydrate production (Madsen 1997). At this point the plant is the least capable of recovering from stress or disturbance, indicating the point where the success of management efforts will be maximized.

In the case of curlyleaf pondweed, the primary structure for energy storage is the turion. The turion bank was found to be the most depleted between January and April 2001 (Figure 7). Treatment at this time may have a maximum impact on the curlyleaf pondweed population and lead to improved management.

Management Recommendations. Management of curlyleaf pondweed is often conducted in May and June, when the plant is forming thick beds on the lake's surface. The problem with treatment at this time is that the turions are already being produced and, though the treatment may be very effective at reducing biomass, the turions remain to cause the same problems the following year. In order to achieve long-term curlyleaf pondweed control the production of turions must be inhibited. If successful treatment can be applied during periods of low carbohydrate storage, then the plants will be least likely to recover and the production of turions may be reduced or eliminated.

Turions were found to be the primary structure of energy storage for curlyleaf pondweed. The turion bank was found to be the most depleted in early spring, between January and April, indicating a potential weak period in the plant's life cycle. This low period of carbohydrate storage suggests that early spring treatment for curlyleaf pondweed may have a maximum impact on the population. Studies conducted on cold-water curlyleaf pondweed herbicide treatments in the spring have resulted in effective biomass reduction and the inhibition of turion production (Netherland et al. 2000, Poovey et al. 2002), indicating that early spring may be an ideal time for treatment. In addition, early spring treatment would minimize the impact on native plant species, many of which are dormant in the early spring.

Exploiting periods of low carbohydrate storage may lead to improved curlyleaf pondweed management, both through the reduction of biomass and the inhibition of turion production. Inhibiting turion production for several years would result in the eventual exhaustion of the turion bank, leading to effective long-term curlyleaf pondweed control.

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LITERATURE CITED

Best, E. P. H. and H. W. C. Visser. 1987. Seasonal growth of the submerged macrophyte *Ceratophyllum demersum* L. in mesotrophic Lake Vechten in relation to insolation, temperature, and reserve carbohydrates. Hydrobiologia 148:231-243.

Bolduan, B. R., G. C. Van Eeckhout, H. W. Quade and J. E. Gannon. 1994. *Potamogeton crispus*- the other invader. Lake Reserv. Manage. 10:113-125.

Catling, P. M. and I. Dobson. 1985. The biology of Canadian weeds. 69. *Potamogeton crispus* L. Can. J. Plant Sci. 65:655-668.

Cypert, E. 1967. The curly-leaved pondweed problem at Reelfoot Lake. J. Tenn. Acad. Sci. 42:10-11.

Kunii, H. 1982. Life cycle and growth of *Potamogeton crispus* L. in a shallow pond, Ojaga-ike. Bot. Mag. Tokyo. 95:109-124.

Kunii, H. 1989. Continuous growth and clump maintenance of *Potamogeton crispus* L. in Narutoh River, Japan. Aquat. Bot. 33:13-26.

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

Madsen, J. D. 1993a. Control points in the phenological cycle of Eurasian watermilfoil. Aquatic Plant Control Research Program, Vol A-93-1. US Army Engineer Waterways Experiment Station, Vicksburg, MS. 9 pp.

Madsen, J. D. 1993b. Biomass techniques for monitoring and assessing control of aquatic vegetation. Lake Reserv. Manage. 7:141-154.

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

Madsen, J. D. and C. S. Owens. 1998. Seasonal biomass allocation in dioecious hydrilla. J. Aquat. Plant Manage. 36:138-145.

Minnesota Pollution Control Agency (MPCA). 2003. Lake Water Quality Assessment Program, Lake Water Quality Database. http://www.pca.state.mn.us/water/waterquality.html.

Nelson, N. 1944. A photometric adaptation of the Somogyi method for determination of glucose. J. Biol. Chem. 153:375-80.

Netherland, M. D., J. D. Skogerboe, C. S. Owens and J. D. Madsen. 2000. Influence of water temperature on the efficacy of diquat and endothall versus curlyleaf pondweed. J. Aquat. Plant Manage. 38:25-32.

Poovey, A. G., J. G. Skogerboe and C. S. Owens. 2002. Spring treatment of diquat and endothall for curlyleaf pondweed control. J. Aquat. Plant Manage. 40:63-67.

Quade, H. W., G. C. Van Eeckhout, B. R. Boulduan, J. E. Gannon, C. J. Olson and C. B. Sathrum. 1994. Duck Lake diagnostic report. Clean-water Partnership Phase I. Minnesota Pollution Control Agency. St. Paul, MN. 115 pp.

Rogers, K. H. and C. M. Breen. 1980. Growth and reproduction of *Potamogeton crispus* in a South African lake. J. Ecol. 68:561-571.

Sastroutomo, S. S. 1981. Turion formation, dormancy, and germination of curly pondweed, *Potamogeton crispus* L. Aquat. Bot. 10:161-173.

Sastroutomo, S. S., I. Ikusima, M. Numata and S. Iizumi. 1979. The importance of turions in the propagation of pondweed (*Potamogeton crispus* L.). Ecol. Rev. 19(2):75-88.

Sculthorpe, C. D. 1967. The biology of aquatic vascular plants. Edward Arnold Pub. Ltd., London. 610 pp.

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. 70:1185-1190.

Titus, J. E. and M. S. Adams. 1979. Comparative carbohydrate storage and utilization patterns in the submersed macrophytes, *Myriophyllum spicatum* and *Vallisneria americana*. Am. Midl. Nat. 102:263-272.

Tobiessen, P. and P. D. Snow. 1984. Temperature and light effects on the growth of *Potamogeton crispus* in Collins Lake, New York State. Can. J. Bot. 62:2822-2826.