HARVESTING AND CARBOHYDRATE ACCUMULATION IN EURASIAN WATERMILFOIL

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ABSTRACT

The effectiveness of a multiple cut harvesting program in controlling nuisance growth of Eurasian watermilfoil (*Myriophyllum spicatum* L.) in Lake Washington was evaluated on a short term (within growing season) and long term (between growing seasons) basis. A single cut in July provided only a brief reduction in nuisance standing crop biomass. A two cut program provided an additional 36% reduction in standing crop and reduced the peak summer standing crop by half in the year of treatment. Harvesting did interrupt the accumulation of nonstructural carbohydrates in milfoil root tissues during the growing season but observed reductions were negated by overwinter accumulation. The brief reduction in standing crop that did occur in the season following the harvest could not be attributed to harvest induced reduction in carbohydrate stores.

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**INTRODUCTION**

Mechanical harvesting is commonly used in the management of nuisance growth of submersed aquatic plants. While the immediate benefit of a harvesting operation (reduction in standing crop biomass) is clear, the short term duration of that benefit within the same growing season and the long term carry-over to subsequent seasons are subjects of some question. The rate of regrowth following a harvest can be rapid and sufficient to offset initial standing crop reduction in a relatively short period of time.

Several studies have suggested the enhanced effectiveness to be derived by sustained harvesting over a number of years, or by multiple cuttings during a single growing season (7, 11). However, the number of such studies are few and the results have been somewhat variable. On the basis of observations in Lake Washington (12), it seems clear that multiple cuttings during the high use summer period would be necessary for effective control of submersed aquatic plants such as Eurasian watermilfoil (*Myriophyllum spicatum* L.).

Plants respond to seasonal changes in their environment in a relatively predictable manner, particularly with respect to carbon gain and allocation (10, 18). Nonstructural carbohydrates, stored during the previous growing season, are thought to fuel the spring "growth flush" of milfoil which allows rapid establishment of a canopy and dominance of the water column (17). Kimbel and Carpenter (7) suggested that timing of harvests to disrupt the seasonal allocation of nonstructural carbohydrates to storage tissues may result in reduced overwinter survival and inhibition of growth the following season. Such an approach to harvesting may enhance its long term effectiveness in the management of nuisance growth of aquatic plants such as milfoil.

An evaluation of the effectiveness of mechanical harvesting for control of milfoil in Lake Washington was initiated in 1980. The objectives of the study were to determine the short term (within the same growing season) and long term (between growing seasons) effect of a multiple cut harvesting program. Dry weight standing crop biomass reduction, rate of regrowth and changes in plant community composition within experimental plots were used as parameters for evaluation. In addition, the influence of the harvesting program upon nonstructural carbohydrate allocation and storage in milfoil root and shoot tissues was assessed to evaluate possible harvest induced reduction in carbohydrate stores as a basis for any long term effects on standing crop biomass.

**METHODS AND MATERIALS**

The study was conducted within Union Bay at the outlet of Lake Washington. Harvesting operations were carried out over the period 1978 to 1980 on a 0.3 hectare (0.76 acre) experimental plot dominated by milfoil. Dependent upon equipment availability and specific research objectives, timing of the harvests and the number of cuts during the growing season varied from year to year. The plot was cut once in 1978 (August), twice in 1979 (July and October) and three times in 1980 (July, August and October). The 1980 and 1981 growing seasons are the primary subjects of this report.

Sampling for standing crop biomass estimation was accomplished by SCUBA diver using a 0.25m² cylindrical sampler (12, 13). Due to difficulty in obtaining accurate, quantitative estimates of below sediment biomass, biomass values represent shoot tissues only (standing crop) and are expressed as grams dry weight/meter² (60 C). The estimated means and error bounds for each sampling date were based on five random samples taken from both harvest and control plots. In 1980, the samples were taken immediately prior to the initial cut and then at approximately one week post-cut and one month post-cut intervals. For sequential cutting on the plot, the one month post-cut condition served as both the regrowth and sequential pre-cut estimator.

Carbohydrate content of the root and shoot tissues was estimated from five whole plants manually collected from within each plot on each sampling date. Carbohydrates were sequentially extracted from freeze-dried tissues with ethanol and boiling water in order to fractionate the nonstructural carbohydrate pool into "free" and "storage" forms respectively (14). The sugar content of the ethanol and boiling water extracts was determined using the phenolsulfuric acid colorimetric technique of Dubois *et al.* (5). Carbohydrate concentrations for the two extracted fractions, expressed as mg sugar/gram dry weight, were combined to provide an estimate of Total Nonstructural Carbohydrate (TNC) for both root and shoot tissues.

The criterion variables used to test the hypothesis that harvesting interrupted TNC accumulation and storage were: within plot root to shoot; between plot shoot to shoot; and between plot root to root TNC concentrations. One-way ANOVA (p=0.05) and "least significant difference" procedures were used to test for significant differences (16).

**RESULTS**

The results of standing crop biomass sampling over the 1980 to 1981 period are summarized in Figure 1. Evident features of these data are: the significant reductions in shoot biomass as a result of harvesting in 1980; reductions in shoot biomass between July 1980 and July 1981; and lack of a "growth flush" in the spring of 1981.

The initial July, 1980 harvest resulted in a standing crop reduction of 44% relative to the control. Approximately three weeks after cutting, standing crop within the harvested plot had increased by 75% over the immediate post-cut condition but was still approximately 50% less than the unharvested control. Growth, expressed as the rate of shoot biomass accrual within the plots, was considerably different for the two. Growth rate over the three week post-cut period amounted to 1.6 and 3.6 grams dry weight/meter²/day, harvest and control plots respectively.

The second harvest (mid-August) reduced standing crop by 71% relative to the control. Regrowth, evaluated four weeks after the second cut, resulted in a standing
crop increase of approximately 2.2 times the post-cut condition but was still 55% less than the unharvested control. The rate of growth during the four week period following the second harvest was approximately the same in both plots, 1.6 and 1.3 grams dry weight/meter$^2$/day, control and harvested plots respectively.

The third harvest in late October was coincident with the period of plant senescence in Union Bay and was conducted primarily in an attempt to prevent hypothesized carbohydrate translocation to root tissues. Standing crop was greatly reduced during the winter of 1980-1981. While overwinter shoots of milfoil up to 15 cm in length were observed in both harvest and control plots, attempts to obtain biomass samples failed to produce a sufficient mass of plant material for weighing. Over-winter standing crop biomass was estimated to be less than 1 gram dry weight/m$^2$ in both plots.

Plant development during the spring and early summer of 1981 was characterized by low levels of shoot biomass and very gradual rates of increase. Samples taken during March and April consisted almost entirely of milfoil. Standing crop biomass averaged 3 grams dry weight/meter$^2$ with no significant difference between plots.

Standing crop biomass within the control plot increased to a value of 12±5.1 grams dry weight/meter$^2$ on May 13 and was significantly greater than the harvested plot biomass of 3±2.2 grams dry weight/meter$^2$ on the same date. Standing crop within the control remained significantly higher than the harvest throughout May. Milfoil accounted for approximately 90% of the standing crop in the control plot and 77% in the harvest plot.

Standing crop within both plots showed a gradual but consistent increase through July with no significant differences in estimated means on any of the June/July sampling dates. Mean values for July, 1981 were approximately 55% less than those for July, 1980.

Data on percent species composition for the 1980-1981 sampling period are summarized in Figure 2. As noted, in the spring (May) of 1981, milfoil represented 77% of the harvest plot standing crop and 90% of the control. *Potamogeton strictifolius* (Bennett) was subdominant in both plots accounting for 20% of the harvest and 7% of the control. Sampling in June indicated a further reduction in the percent composition of milfoil within both plots. In the control, milfoil averaged 81.5%, subdominant species being *Zannichellia palustris* (L.), *Potamogeton richardsonii* (Bennett) Rydb., and the macroalga *Nitella*. Within the harvest plot, milfoil accounted for only 66.5% of the standing crop with important subdominant species being *Z. palustris*, *Potamogeton berchtoldii* (Fieb.), *P. richardsonii* and *N. pia*.

Early July sampling indicated that milfoil had increased in the control plot to levels greater than 90% of the total shoot biomass while in the harvest plot it remained at levels of approximately 66%, *Z. palustris* and *P. berchtoldii* remaining subdominant. By late July, milfoil within the harvest plot had increased to a level representing approximately 84% of the total standing crop.

![Figure 1](image1.png)

*Figure 1. Variation in macrophyte standing crop biomass within harvest and control plots of Union Bay (1980-1981). Values are mean shoot biomass for all species collected in five 0.25 square meter samples from each plot on each date. Error bars represent one standard error.*

![Figure 2](image2.png)

*Figure 2. Variation in species composition (% dry weight) of macrophytes occurring in samples collected from harvested and control plots in Union Bay. Shaded areas represent the sum of vegetation exclusive of milfoil with subdominant species indicated.*

Measurement of milfoil root crown densities in the harvest and control plots were consistent with the biomass and species composition data. The number of root crowns within five, randomly selected, one square meter sampling frames were counted by diver in May, 1981. The control plot averaged 15±2 crowns/m² which was significantly greater than the 8±2 crowns/m² for the harvest plot.

The seasonal variation in the TNC concentration in harvest and control plots is shown in Figure 3. A bimodal pattern of TNC concentration was evident in both harvest and control plants, with high concentrations in summer and winter and low concentrations in fall and spring.

The control plant roots increased in TNC concentration more rapidly than the control plant shoots during the summer of 1980 and root concentrations were significantly greater on all sampling dates after August. They remained greater until spring growth began the following May.

In contrast, harvest plant root TNC concentration did not differ significantly from harvest plant shoot TNC concentration until the last week of September, approximately five weeks after the second harvest, when a large increase in root TNC concentration occurred. Harvest plant root concentrations dropped rapidly after the third harvest in late October however, and by November 3 harvest plant roots and shoots did not differ significantly in TNC concentration.

Between plots comparison indicated that harvest and control shoots TNC concentrations showed little difference in seasonal variation. However, TNC concentrations in the roots of harvest plants were significantly reduced relative to the control plant roots through most of 1980. Following the second harvest root TNC concentrations in harvested plants increased rapidly and by 10 October harvest root concentrations equaled control root concentrations. Following the third harvest, TNC stores in the harvested plant roots were again significantly reduced relative to the control plants.

The second period of TNC accumulation began immediately after fall shoot fragmentation. While plants within the harvested plot lagged behind the control plants, root and shoot tissues within both plots showed this unexpected increase. By the onset of spring growth, harvest plant root TNC concentrations were again significantly greater than harvest shoot concentration and did not differ significantly from control plant root concentrations. During and after spring growth in May 1981 harvest and control plants did not differ in either concentration or temporal utilization of TNC.

**DISCUSSION**

The seasonal nature of milfoil standing crop biomass development was evident in the Union Bay data. The rate of shoot biomass accrual in the control plot during the spring was twice that observed in September, reflecting the rapid early season growth characteristic of milfoil. The initial harvest reduced the rate of shoot biomass accrual by 55% compared with that in the control plot, while the second harvest appeared to have little influence on this rate.

Rapid regrowth following the July harvest rendered that harvest to be of limited value in controlling milfoil standing crop, even in the short term. Regrowth following the initial harvest reestablished the preharvest standing crop in three weeks. Projection of standing crop development in the harvested plot (based on observed rates of shoot biomass accrual in the control plot) indicated that, with a single harvest in July, regrowth would have resulted in a peak standing crop of approximately 111 g/m² by late September, only 19% less than in the control plot. The second harvest resulted in a 55% reduction in peak summer standing crop. Based on the biomass projections, the net effect of the second harvest was an additional 36% reduction in peak summer standing crop. Clearly, the multiple cut program did not have the cumulative effect on biomass as reported by Nichols and Cottam (11).

One of the most striking features of the study site over the 1980/81 growing seasons was the substantial reduction in macrophyte standing crop compared to previous years.
(Figure 4). Both the harvest and control plots were independently harvested in the summer of 1981 and the duration of the phenomenon through the 1981 growing season is unknown. While it is well known that milfoil biomass can vary substantially from year to year in response to fluctuation in environmental parameters (1), the basic characteristics in Lake Washington were fairly comparable over the years of study (Figure 4). The decline in 1980 and 1981 may represent a leveling off of milfoil standing crop as suggested by Carpenter for other milfoil infested lakes (4). Samples collected in 1982 (data not shown) indicate that standing crop was again at the 1981 level. No quantitative estimates of standing crop have been made since 1982. Subjectively, however, the site continues to support milfoil of nuisance proportions.

In relation to the objectives of this study, it was evident that harvesting did have a significant, albeit short term, effect upon carbohydrate utilization by milfoil in Union Bay. As a result of harvests in July and August, the pattern of midsummer increase in root tissue TNC was delayed in the harvested plots until September, one and a half months after the second harvest. Harvesting apparently inhibited translocation and storage of TNC in root tissues. This response might be attributable to the utilization of TNC for the repair of injured shoot tissues and the promotion of new shoot growth in a manner similar to the "stress response" discussed by Kozl of and Jordan (8) for the red kidney bean (Phaseolus vulgaris L.). Harvested plant roots continued to accumulate TNC until early October while control plant roots were losing TNC at this time.

The third harvest in late October was coincident with declining root tissue TNC and resulted in concentrations in the harvested roots which were significantly lower than the control roots. This however did not translate to the anticipated reduction in either TNC or plant biomass the following growing season.

Two characteristics of the TNC accumulation pattern in Union Bay milfoil seem important in limiting the effectiveness of attempting to reduce carbohydrate levels by harvesting: (1) TNC stores are rapidly replenished after the harvest; and (2) TNC concentrations increase over the winter period. Rapid restoration of carbohydrates following initial post-cut reductions have also been demonstrated in orchard grass (Dactylis glomerata L.) by Sprague and Sullivan (15) and in johnsongrass (Sorghum halepense L.) by McWhorter (9). McWhorter (9) suggested that the regrowth potential of johnsongrass was related to carbohydrate concentration and that high levels of carbohydrate and rapid restoration following cutting make either mechanical or chemical control difficult. The most effective time for the mechanical control of johnsongrass was thought to be when food reserves were lowest.

If applied to milfoil in Union Bay, the periods of lowest TNC would be early spring and late fall. We did attempt late fall harvests in Union Bay over two sequential years (1979, 1980) and it was clear that the effects on both standing crop biomass and carbohydrate reduction were largely offset by the winter activity of the plant. While there were no early spring harvests, the July 1980 harvest was coincident with the lowest observed root TNC concentration and this should have been a very effective harvest. The postharvest rate of shoot biomass accrual in the harvest plot was indeed reduced by approximately 55% relative to the unharvested control. However, this reduced rate still resulted in attaining the preharvest standing crop in three weeks.

Although Union Bay milfoil was quite resilient to attempts to reduce its TNC stores, it was not totally immune to the effects of harvesting. A reduced standing crop in the harvest plot relative to the control plot did occur in May 1981. In addition, in June of 1981, milfoil accounted for approximately 81% and 66% of the macrophyte standing crop in the control and harvested plots respectively. It seems apparent that harvesting did result in some selective reduction in milfoil.

Explanation of the small, short-lived reduction in milfoil standing crop that did occur in the season following the harvests must remain speculative in light of the failure of harvesting to maintain reduced TNC stores through the winter. While the data on root crown density are limited in that they are a single observation and no prewinter estimates were made, they do suggest that harvesting may have had some negative effect on the overwinter survival of milfoil root tissues. Curtailment of root growth and root dieback following grazing or defoliation has been reported in a number of terrestrial species (3, 6) and a few emergent aquatics (2). Kimbel and Carpenter (7) reported that 11 months after harvest, milfoil shoot biomass was significantly reduced while the shoot:root biomass ratio remained unchanged, also suggesting a reduction in root biomass with harvesting.

While the results of this study did not demonstrate a long term carry over as a result of intensive harvesting, they did indicate that harvesting had an influence upon patterns of carbohydrate utilization. Vegetative reproduction and early season canopy formation are two charac-

Figure 4. Variation in mean monthly standing crop biomass of macrophytes occurring in the study control plot over the period July 1978 to July 1981. The solid line represents variation in total incident light per month as measured at the University of Washington (Dept. Atms. Sci.). The dotted line represents mean monthly surface water temperatures in Lake Washington (Data courtesy of W. T. Edmondson, University of Washington). Standing crop data for 1978 and 1979 are from Perkins (12).

teristics of milfoil which are thought to contribute to its ability to invade and dominate aquatic plant communities. The observed patterns of nonstructural carbohydrate accumulation and utilization would indicate TNC to be an important factor in both these processes. It seems reasonable to conclude that treatment, mechanical or otherwise, directed toward controlling these processes by attempting to alter patterns of carbohydrate metabolism may have a more profound influence upon population development than would be realized as immediate within or between seasons reductions in standing crop. Fall harvesting to prevent seed development and reduce potential autofragment production coupled with midwinter treatment to remove or adversely effect overwinter biomass may prevent carbohydrate replenishment and may be an effective approach toward more long term control.

One point that is clear is that milfoil rapidly compensates for the effects of a harvest and that midsummer harvesting, unless very intensive (e.g. multiple cuts), should not be expected to provide more than immediate nuisance growth removal.

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LITERATURE CITED


