SHORT-TERM IMPACT OF HARVESTING ON EURASIAN WATERMILFOIL

By

D.S. Painter & J.I. Waltho

NWRI # 85-36

Aquatic Ecology Division
National Water Research Institute
Canada Centre for Inland Waters
Burlington, Ontario, Canada L7R 4A6

MANAGEMENT PERSPECTIVE

Eurasian watermilfoil is a nuisance aquatic plant which has invaded many lakes and rivers in Canada. Mechanical harvesting is generally agreed to be the most ecologically sound control method but is criticized because multiple harvests may be required each growing season and non long-term effect on regrowth may be apparent. Environment Canada's research on mechanical harvesting of milfoil examined the short-term effects of cutting to illustrate how to make a harvesting program as efficient as possible and to determine if harvesting stressed the plant.

The short-term efficacy of harvesting was dramatically influenced by the timing of the cut in 19 harvesting scenarios examined. A June/August or June/September double cut would appear to be the most desirable scenario with very little advantage in a triple cut. Milfoil biomass on an areal basis was significantly affected in the second year, however, plant height was not affected in the second year by harvesting in the first year.

Tissue chemistry was altered by harvesting. The tissue chemistry was also altered in the spring of the second year, particularly if a September or October cut was performed; however, by the summer of the second year no differences in tissue chemistry were observed except in root total non-structural carbohydrates which were significantly reduced.

Harvesting was observed to immediately alleviate nuisance milfoil conditions but the duration of control was dependent on the timing of the cut(s). Milfoil biomass was reduced in the second year and a subsequent paper will discuss the long-term effects of several years of harvesting.

PERSPECTIVE-GESTION

Le myriophylle blanchissant (Myriophyllum spicatum) est une plante aquatique nuisible qui infeste actuellement un grand nombre de lacs et de cours d'eau au Canada. La récolte mécanique, généralement reconnue comme le moyen de contrôle écologique le plus sûr, est critiquée, parce qu'il peut être nécessaire à chaque saison de pousse de pratiquer de nombreuses récoltes et que l'effet à court terme sur la repousse peut être apparent. Les recherches d'Environnement Canada sur la récolte mécanique du myriophylle blanchissant ont porté sur les effets à court terme de la coupe pour déterminer le moyen d'établir un programme de récolte aussi efficace que possible et pour déterminer si la récolte fait subir un stress à la plante.

Parmi les dix-neuf scénarios de récolte analysés, l'efficacité à court terme a été largement influencée par l'époque de la coupe. Deux coupes, dont l'une en juin et en août ou en juin et septembre, semblent être le scénario le plus favorable, très peu d'avantages pouvant être retirés d'une troisième coupe. D'après les données obtenues dans certaines zones, la biomasse de myriophylle par unité de surface a été réduite de façon importante la deuxième année; toutefois, la récolte de la première année n'a eu aucun effet sur la hauteur de la plante au cours de la deuxième année.

La récolte a modifié la chimie tissulaire. Celle-ci était également modifiée au printemps de la deuxième année, notamment si une coup était exécutée en septembre ou en octobre; cependant, à l'été de la deuxième année, aucune différence n'a été observée dans la chimie tissulaire si ce n'est dans les hydrates de carbone totaux non structuraux de la racine, qui furent réduits de façon importante.

On a observé que la récolte ralentissait dans l'immédiat les effects nuisibles du myriophylle mais que la durée de ce contrôle dépendait de la période des coupes. La biomasse du myriophylle a été réduite au cours de la deuxième année et, dans un article ultérieur, il sera question des effets à long terme de plusieurs années de récolte.

ABSTRACT

The short-term efficacy of harvesting of Eurasian watermilfoil in Buckhorn Lake, Ontario was dramatically influenced by the timing of the cut. Nineteen harvesting scenarios were examined for their effects on milfoil regrowth and tissue chemistry as well as the amount of open water created. A June/August or June/September double cut would appear to be the most desirable scenario with very little advantage in a triple cut. Milfoil biomass was significantly affected in the second year by a cut in October of the preceding year.

Shoot and root phosphorus, nitrogen, carbon and carbohydrates were altered by harvesting. The tissue chemistry was altered in the spring of the second year, particularly if a September or October cut was performed; however, by the summer of the second year no differences in tissue chemistry were observed except in root total non-structural carbohydrates which were significantly reduced.

RÉSUMÉ

L'efficacité à court terme de la récolte du myriophylle blanchissant dans le lac Buckhorn en Ontario dépendait dans une grand mesure de la période de la coupe. On a analysé dix-neuf scénarios de récolte pour évaluer leurs effets sur la repousse et la chimie tissulaire du myriophylle, ainsi que la surface d'eau ainsi libérée. Deux coupes, en juin et août ou juin et septembre, semblent être le scénario le plus favorable, très peu d'avantages étant obtenus avec une troisième coupe. La biomasse de myriophylle a été réduite de façon importante au cours de la deuxième année par une coupe exécutée en octobre de l'année précédente.

Le phosphore, l'azote, le carbone et les hydrates de carbone des pousses et des racines ont été modifiés par la récolte. La chimie tissulaire a aussi été modifiée au printemps de la deuxième année, surtout lorsqu'une coupe avait été exécutée en septembre ou en octobre; cependant, à l'été de la deuxième année, aucune différence de chimie tissulaire n'a pu être observée, à l'exception d'une réduction marquée des hydrates de carbone totaux non structuraux de la racine.

INTRODUCTION

Mechanical harvesting is generally agreed to be the most ecologically sound control method for nuisance aquatic plants. Harvesting is, however, criticized since multiple harvests may be required each growing season and no long-term effect on regrowth may be apparent. The ecological consequences of mechanical harvesting have been studied by Wile et al. (1977), Carpenter and Gasith (1978), Cottam and Nichols (1970), Neel et al. (1973), Nichols and Cottam (1972), Breck and Kitchell (1979), and Bartell and Breck (1979). The dynamics of *Myriophyllum spicatum* biomass after harvesting have been summarized by Kimbel and Carpenter (1979). They conclude that *M. spicatum* is controlled most effectively by harvests that remove as much shoot material as possible several times during the growing season and their results suggest, but do not conclusively demonstrate, that harvests in late September-early October should most effectively reduce biomass the following year. Kimbel and Carpenter (1979) reviewed several research harvesting projects and observed that harvesting had an impact on the second year's regrowth in 12 of 13 reported projects. This paper examines the short-term effect of many harvesting scenarios on milfoil regrowth.

METHODS

The experiment was designed to determine the most effective harvesting schedule from 19 possible schedules. Twenty-four 2 x 10 meter plots were established in 1.60 to 1.75 meters of water on the west side of Nichol Island in Buckhorn Lake, Ontario, Canada on June 5-7, 1979. Single, double and triple cuts were performed as described in Table 1. The plots were cut at 0.5 meters above the sediment using scuba equipment and small sickles. Monthly sampling was performed from June 1979 to December 1979 and April 1980 to August 1980. All plant and sediment samples were obtained using SCUBA. Fresh weight and dry weight were measured at the beginning and end of the study based on one 0.25 m quadrat per plot at the beginning and triplicates per plot at the end. Plant height was determined by measuring the length of 25 random stems which achieved an allowable 95% confidence error of 5 cm. Shoot and root samples were analyzed for % water, % organic content, total non-structural carbohydrates, total nitrogen, total phosphorus and total carbon. Sediment cores were obtained and the 0 to 40 cm section was analyzed for loss on ignition, total phosphorus and total nitrogen.

Water content was determined by weight difference after samples were dried for 16 hours at 75°C. Loss on ignition (% organic content) was determined on dried plant material which was

TABLE 1. HARVESTING SCHEDULES FOR 1979

	Harvest Time(s)	Plot Title
Single Cuts	June	A
	July	E
	August	I & O
	September	M & J
	October	Q & X
		Note X was cut again in May 80
Double Cuts	June, July	N
		G
	June, September	K
	July, August	R
	July, September	B & C
	July, October	L
	August, September	T
	August, October	D
	September, October	W & V
Triple Cuts	June, July, August	F
	July, August, September	H
	August, September, October	P
	June, August, October	S
Control	No cut	U and surrounding Area

muffled at 550°C for two hours. Total non-structural carbohydrates were determined by enzymatic extraction with amyloglucosidase for conversion of starches to glucose and glucose analysis using the phenol-sulphuric acid colorimetric method (J. Burton, University of Guelph, pers. comm.). Total phosphorus, total nitrogen and total carbon were determined as per the Analytical Methods Manual (IWD, Environment Canada, 1979). The loss on ignition values were used to correct the chemical analysis, initially expressed on a dry weight basis, to an ash-free dry weight basis.

RESULTS AND DISCUSSION

Short-term effect of harvesting on milfoil growth

Plant height was chosen as the most appropriate indicator of the impact of harvesting and subsequent milfoil regrowth because the goal of harvesting is to create an unobstructed water column for recreational use. The error involved in quadrat sampling and the small size of the plots necessitated the use of a non-destructive sampling method such as plant height. The efficacy of a particular harvesting schedule was evaluated by determining the number of days the water column remained unobstructed in the top 50 cm. The 50 cm unobstructed water depth was chosen as the criteria for suggesting whether the area was useable for recreation. The days open was also subdivided into days during the tourist season (June 1 to October 15) and total days (from May 15 to November 15). Figure 1 illustrates the days open created by the 18 harvesting schedules performed in the first year. The control plot had 0 days open. Striking differences in impact are apparent for the various harvesting scenarios. The usefulness of the information to lake managers in planning harvesting timetables or determining equipment requirements is obvious. For example, a single cut should be performed early in June at the beginning of the tourist season to maximize effect per unit effort. A single cut in July has a very short impact. In fact, the properly timed June single cut was as effective or more effective than many of the double cuts except for June/August, June/September and July/September. If the 45 days of open water during the tourist season that a single June cut creates is insufficient in the eyes of the lake manager and equipment is available, then the double cuts just mentioned particularly June/August or June/September could increase the days open during the tourist season to 60-70 days and total days open to 104 in the case of June/September. The effort involved in a triple cut scenario would be wasted provided a properly timed double cut was possible. Figure 2 illustrates the actual plant heights observed in 1979, the harvesting year, and in 1980, the recovery year, for several harvesting scenarios.

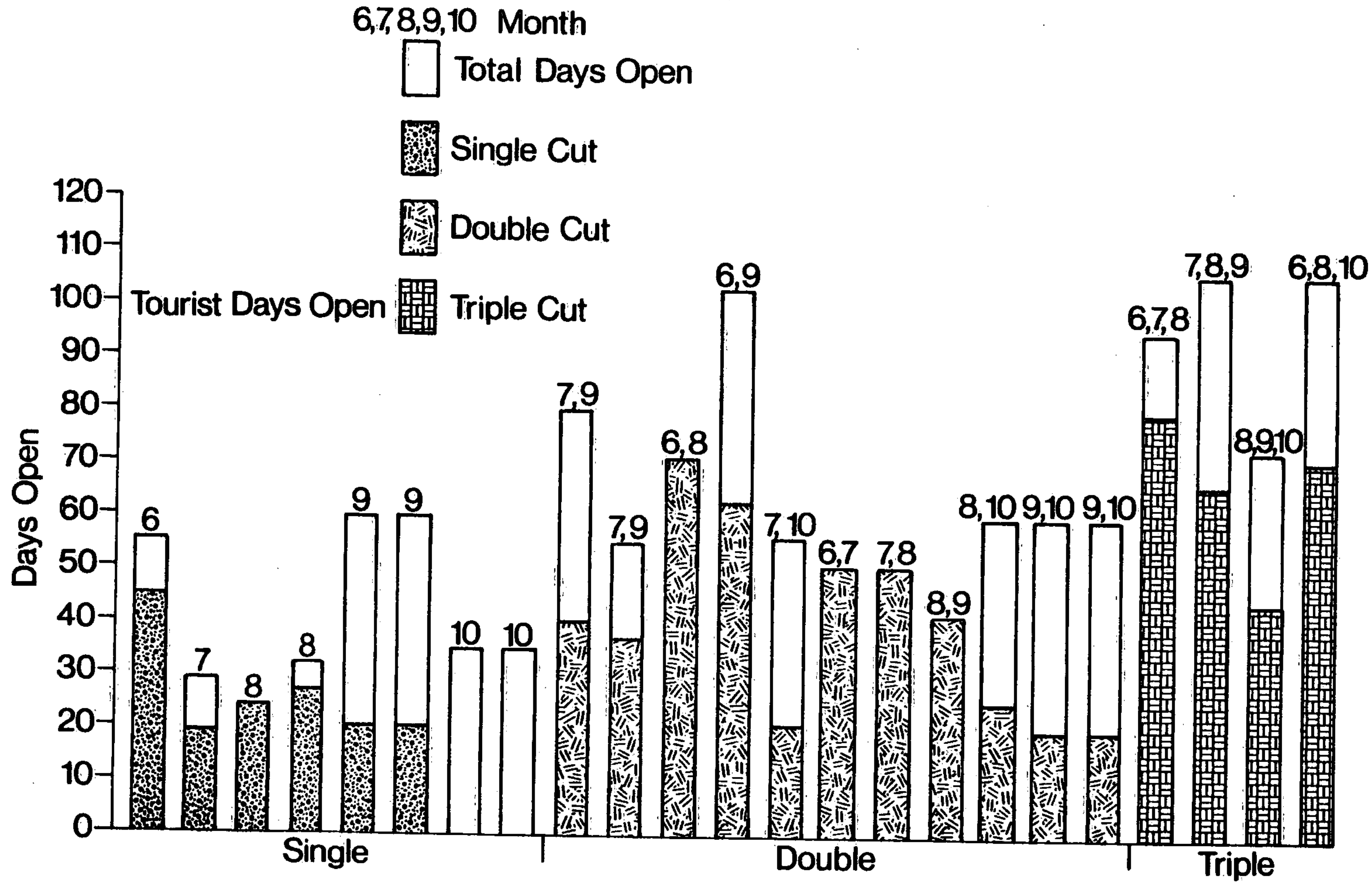


Figure 1 DAYS OPEN CREATED BY 18 HARVESTING SCHEDULES

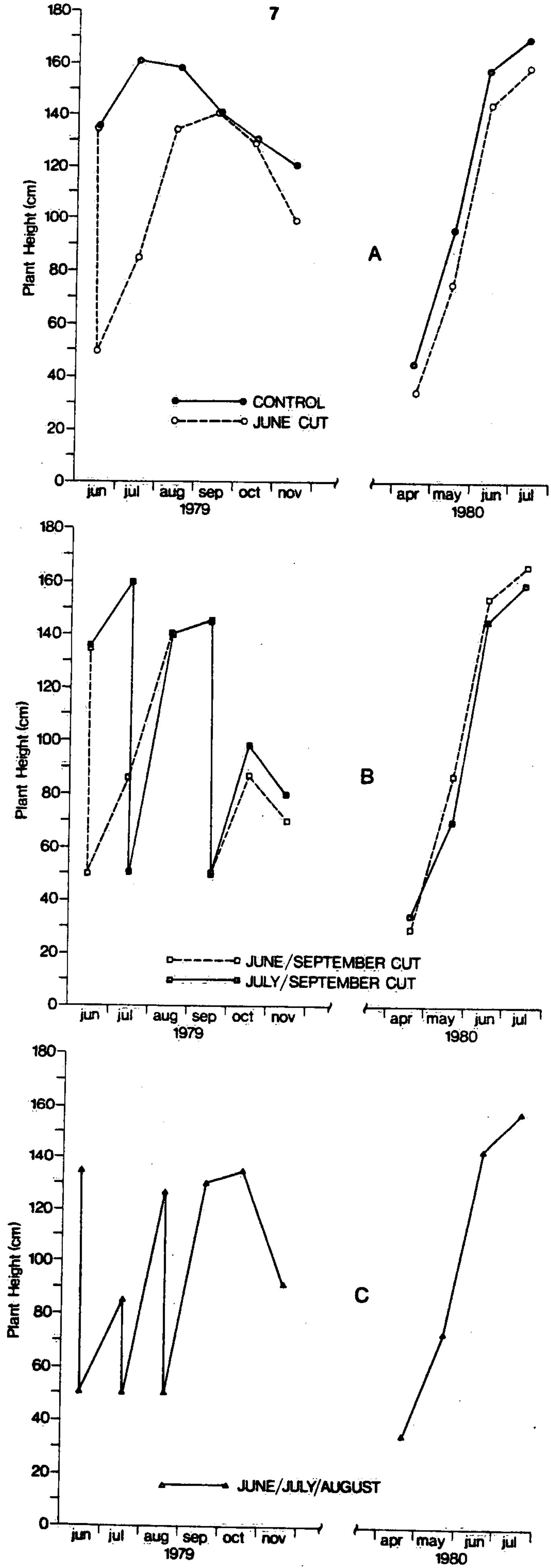


Figure 2 PLANT HEIGHT RESPONSE TO SINGLE (A), DOUBLE (B), AND TRIPLE (C) CUTS

Another approach to illustrate the impact of harvesting would be to measure the areas in figure 2 where the plant height was below the surface. If the plants were at the surface then the percent open water would be 0 and as the harvesting impact on plant height increased, the percentage open water would increase. Table 2 summarizes the % open water and days open both tourist and total for the harvesting scenarios tested. The control plot had only 10.6% open water. The best single cut (June) increased the % open water to 28.2%. The best double cut (June/September) had 40.7% open water and the triple cuts could only increase the % open water to 43.5%. The % open water and days open for replicate plots were similar.

The impact of the 1979 harvesting on regrowth during the 1980 season was also determined using the same approach. Table 2 also summarizes the % open water and days open during the 1980 season up to July 15. The control area had 31.5% open water and 19 days open. The best single cut (June 79) had 39.7% open water and 26 days open. The best double cut (July/September 79) had 40.2% open water and 26 days open. Triple cuts had no increased effect on the 1980 regrowth compared to the best double cut. A cut was performed during May 1980 on the plot that had been cut in October 1979 and resulted in 41.9% open water and 30 days open. Although the 1979 cuts did affect regrowth in 1980 the effect was minimal with an increase in % open water of only

TABLE 2. % OPEN WATER AND DAYS OPEN FOR 1979 AND 1980

Cut	1979			1980	
	% Open	Days Open		% Open	Days Open
		Tourist	Total		
Single Cuts					
A June	28.2	45	55	39.7	26
E July	20.3	19	29	37.9	24
I August	16.0	24	24	36	22
O August	18.9	27	32	36.2	22
M September	20.0	20	60	33.0	21
J September	20.0	20	60	36.0	23
Q October	17.9	0	35	34.0	21
X Oct79/May80	19.9	0	35	41.9	30
Double Cuts					
B July/Sept.	30.7	40	80	40.2	26
C July/Sept.	25.9	37	55	40.3	25
G June/Aug.	33.5	71	71	36.8	23
K June/Sept.	40.7	63	103	35.5	22
L July/Oct.	27.5	21	56	35.0	21
N June/July	32.7	51	51	34.5	22
R July/Aug.	28.7	51	51	35.0	22
T Aug./Sept.	22.8	42	42	37.8	24
W Sept./Oct.	27.3	20	60	36.0	24
V Sept./Oct.	26.7	20	60	37.5	24
D Aug./Oct.	29.0	25	60	35.3	22
Triple Cuts					
F 6/7/8	38.6	80	95	40.3	27
H 7/8/9	43.3	66	106	39.0	26
P 8/9/10	35.3	44	73	36.7	23
S 6/8/10	43.5	71	106	39.0	24
Control					
U no cut	10.6	0	0	31.5	19

10% and an increase in days open of only 10 days. The early May cut in 1980 appeared to have no advantage based on plant height.

The impact of the harvesting scenarios on the plant biomass during the second season was also determined by sampling plant biomass directly by quadrat sampling in August 1980. Figure 3 illustrates the dry weight of the milfoil per square meter in August 1980 of the 19 harvested plots and the control plot. A one way analysis of variance was performed on the plant dry weights in each plot and the plots which were found to be significantly different (95%) from the control have the standard error bars included on the figure. The only significant trend discernible is that those harvesting schedules that included a harvesting in October 1979 had significantly less biomass in August 1980. The harvesting in October 1979/May 1980 also appears to have had a significant impact on biomass when the results are interpreted on an areal dry weight basis instead of plant height.

Short-term effects of harvesting on milfoil tissue chemistry

Shoot and root tissue samples were analyzed for phosphorus, nitrogen, total carbon and total non-structural carbohydrates (TNC). The tissue chemistry was measured to determine if the harvesting effects on regrowth could be

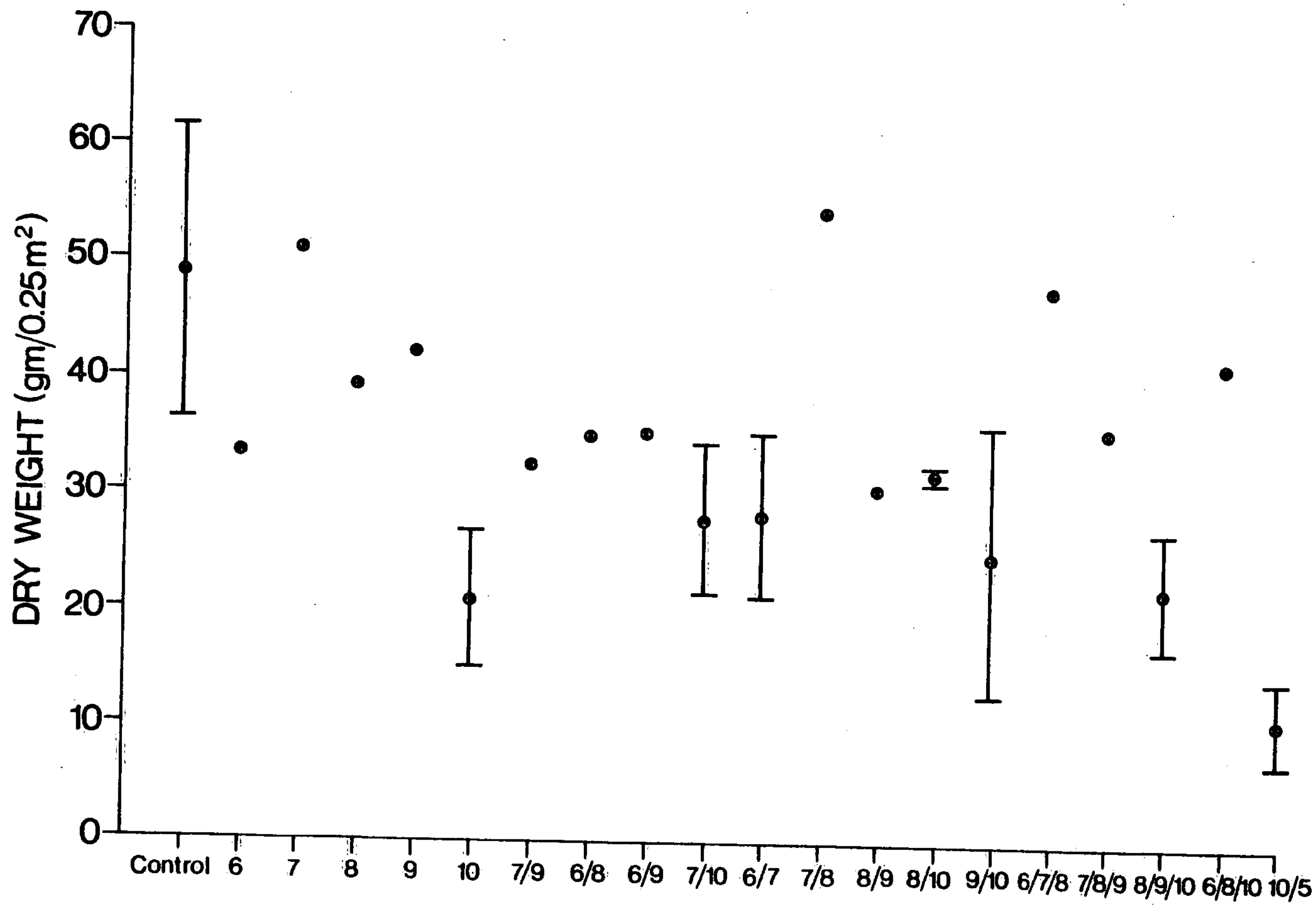
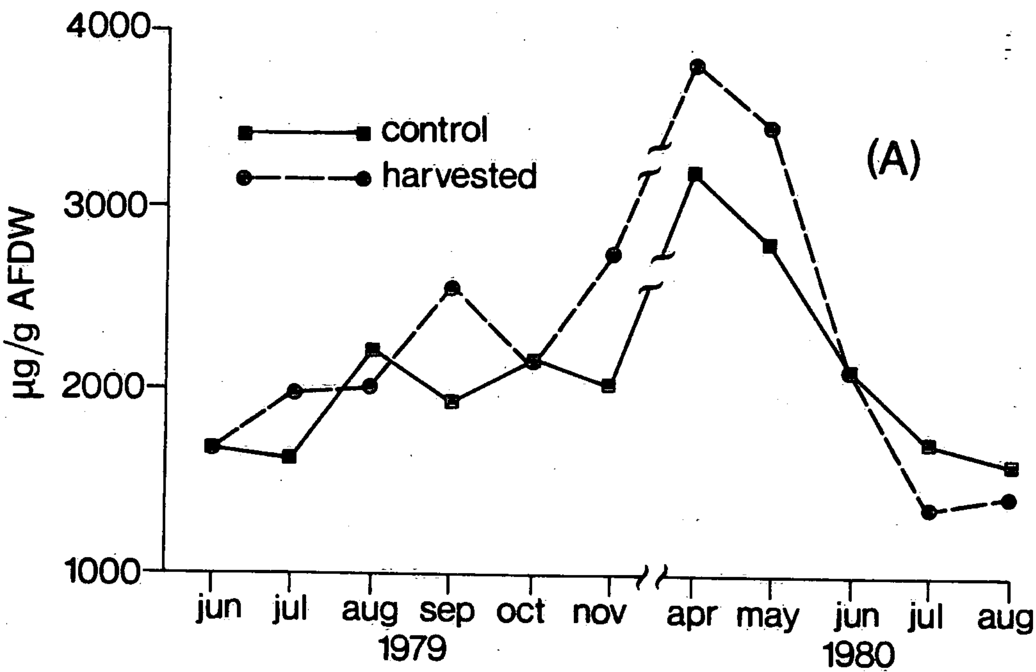


Figure 3 MEAN DRY WEIGHT IN AUGUST 1980 VERSUS CUTTING SCHEDULE (Error bars are one standard deviation, and are provided for those plots which are significantly different from control.)

explained by an analysis of the tissue chemistry and then exploiting the effects on tissue chemistry in a long-term harvesting experiment. Figures 4 through 7 illustrate the seasonal trends of tissue chemistry of the control and the June/August/October harvest. The effect of the triple harvest on shoot phosphorus can be observed in Figure 4. Tissue phosphorus increased in the month following harvesting. However, shoot phosphorus returned to values similar to control in the second month following harvest, except for the October cut, where the effect on shoot phosphorus continued through to the spring of the second year. Shoot phosphorus increased in the month following harvesting compared to the control tissue phosphorus in 24 of 36 cases or 66.7%. The average increase in tissue phosphorus was 364 ug P/g AFDW. The mean seasonal phosphorus concentration was 1934 ug P/g AFDW so the phosphorus increase due to harvesting was 19% of the seasonal mean. Figure 4 illustrates the effect of the triple cut on root phosphorus. Root phosphorus also increased in the month following harvest and returned to values similar to control in the second month. The October cut affected root phosphorus in the spring of the second year but the effect did not extend into the summer. Root phosphorus increased in the month following harvesting in 21 of 36 cases or 58%. The average increase was 187.5 ug P/g AFDW. The mean seasonal root phosphorus was 1227.5 ug P/g AFDW so the phosphorus increase due to harvesting was 15.3% of the seasonal mean.



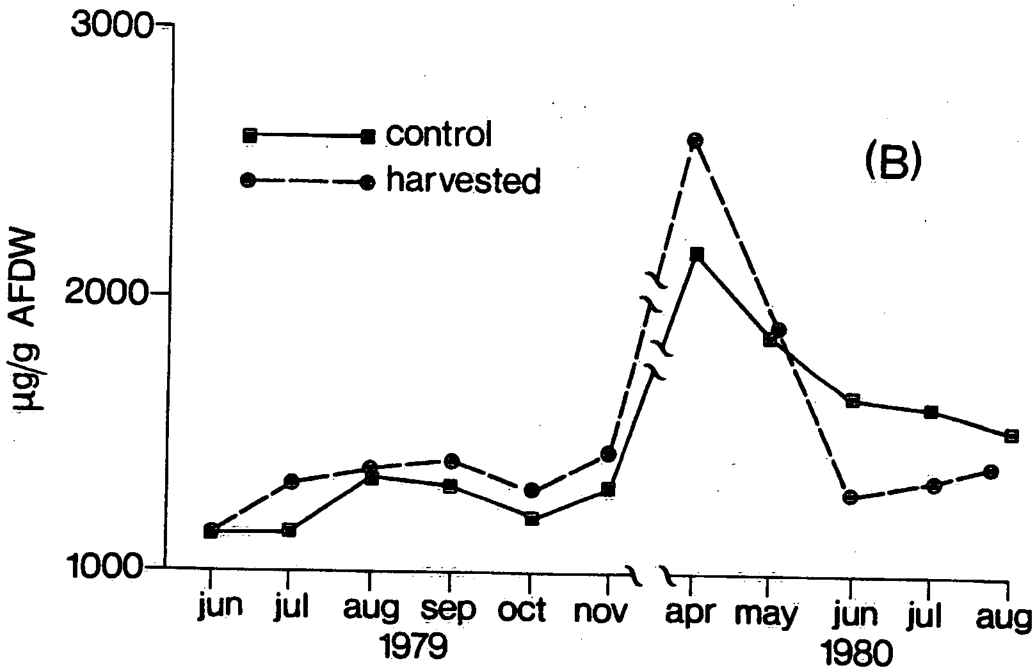


Figure 4 SHOOT PHOSPHORUS (A) AND ROOT PHOSPHORUS (B) FOR THE JUNE/AUGUST/OCTOBER CUT

Shoot nitrogen response is illustrated in Figure 5a and again the response is similar to phosphorus. The shoot nitrogen rose in the month following harvest but dropped to values similar to control in the second month. The October cut influenced the spring shoot nitrogen but the effect did not last into the summer. Shoot nitrogen increased in 19 of 28 cases or 67.9% following harvesting. The average increase was 0.324% N (AFDW) and the seasonal mean was 2.32%N; so the nitrogen increase due to harvesting was 14% of the seasonal mean. The effect of the triple cut on root nitrogen is illustrated in Figure 5b. The response of root nitrogen to cutting was similar to those previously described with increases occurring in the month following harvesting. The average increase was 0.555% N (AFDW) and the seasonal mean was 1.744% N; so the nitrogen increase due to harvesting was 32% of the seasonal mean.

Figure 6a illustrates the response of shoot carbon to the triple harvest. Shoot carbon decreased in the months following harvesting but the effect did not extend into the second season. Shoot carbon decreased in 23 of 28 cases or 82.1% following harvesting. The average decrease was 2.90% C (AFDW) and the seasonal mean was 45.37% C; so the carbon decrease due to harvesting was 6.4% of the seasonal mean. Figure 6b illustrates the response of root carbon to harvesting. The root carbon increased in the month following harvesting and returned to values similar to control root carbon in the second month. Root

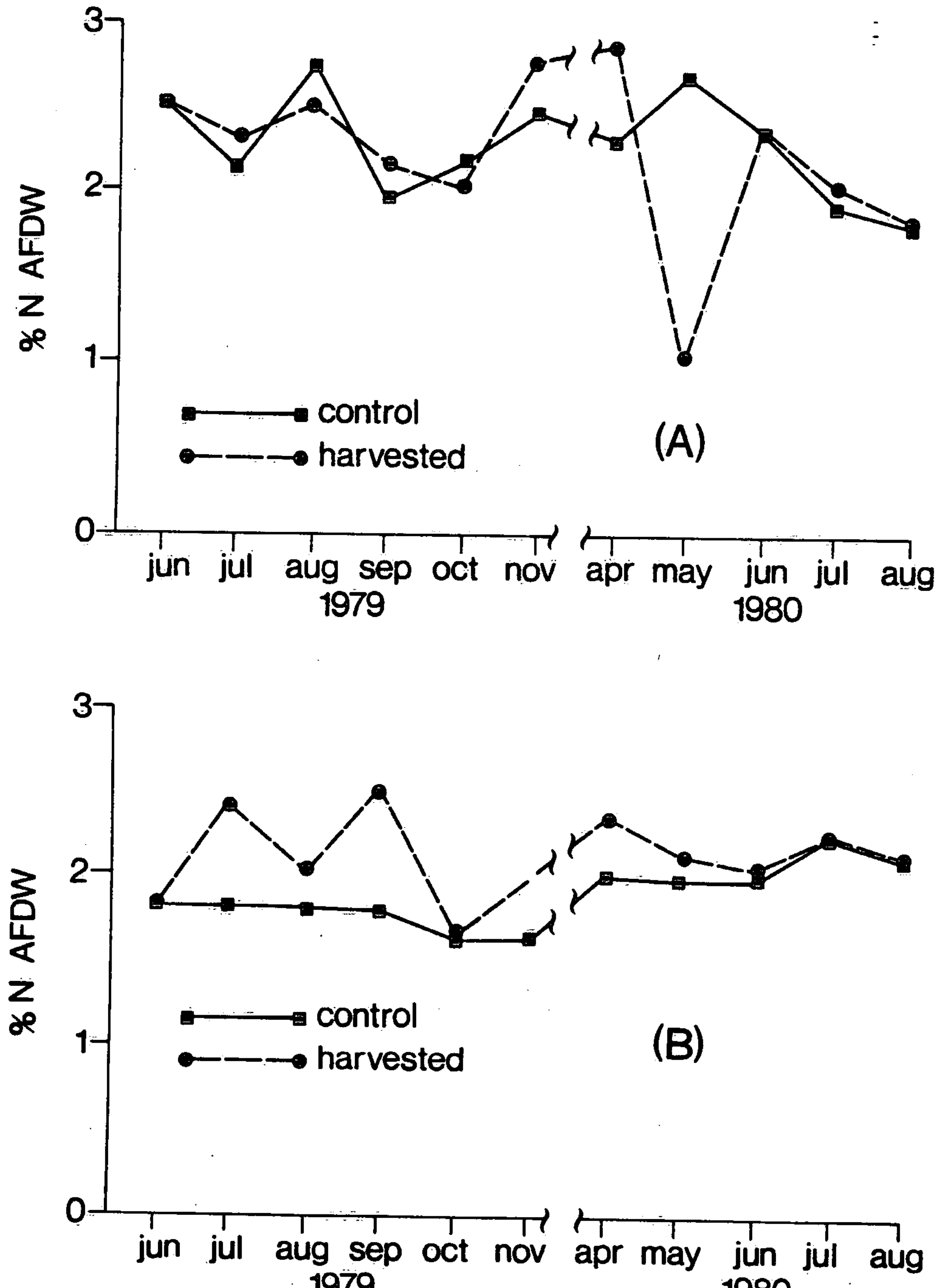


Figure 5 SHOOT NITROGEN (A) AND ROOT NITROGEN (B) FOR THE JUNE/AUGUST/OCTOBER CUT

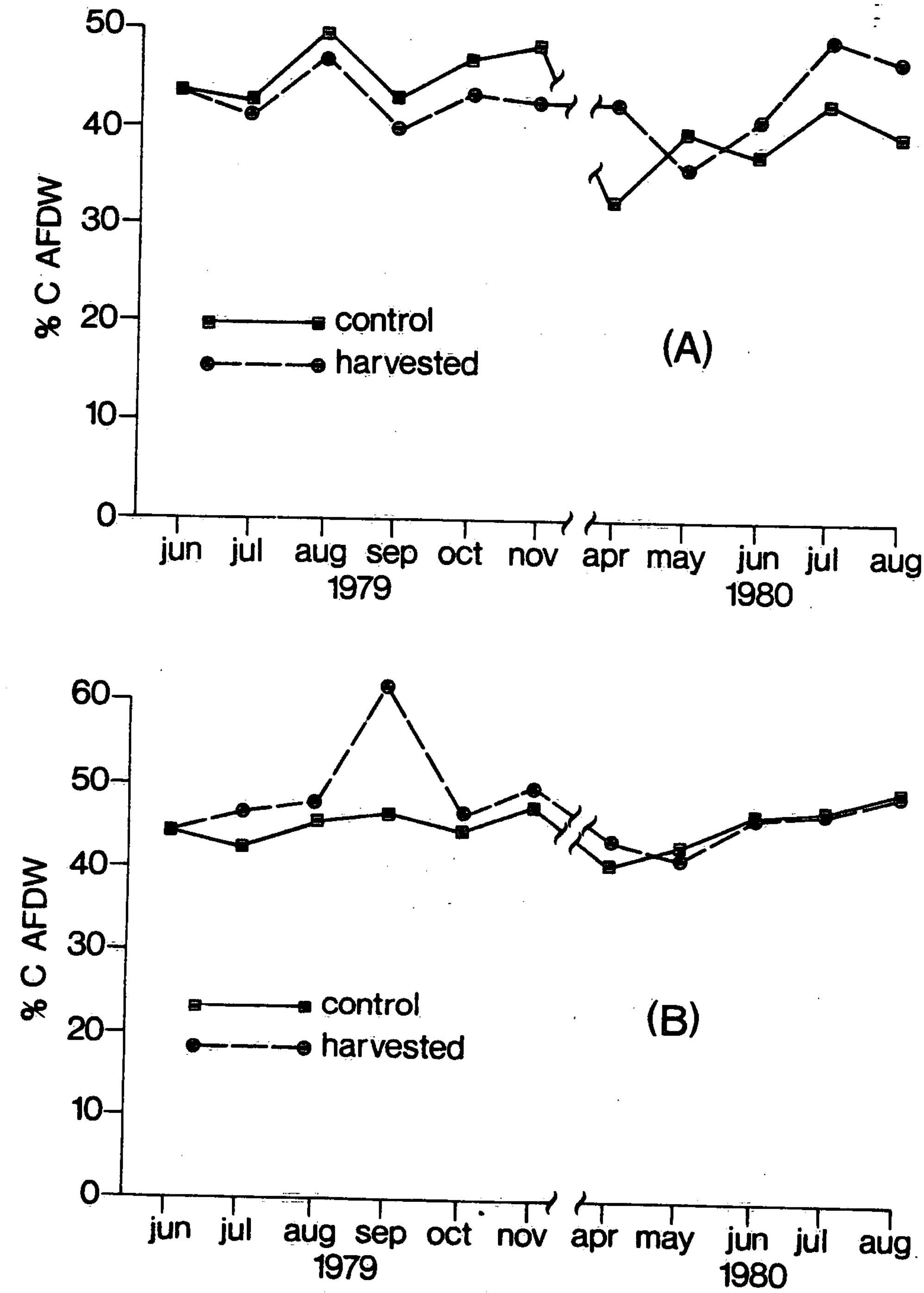


Figure 6 SHOOT CARBON (A) AND ROOT CARBON (B) FOR THE JUNE/AUGUST/OCTOBER CUT

carbon increased in 20 of 28 cases or 71.4% following harvesting. The average increase was 4.1% and the seasonal mean was 45.28%; so the root carbon increase due to harvesting was 9% of the seasonal mean.

The effect of the triple cut on shoot total non-structural carbohydrates (TNC) can be observed in Figure 7a. Shoot TNC decreased following harvesting and the effect extended throughout the first season becoming progressively more pronounced towards the end of the season. Shoot TNC in the spring of the second season was similar to control shoot TNC. However, the June shoot TNC was much reduced compared to the control. A reduction in shoot TNC in June of the second season occurred in this example but was not the norm amongst the other harvesting schedules tested. Shoot total non-structural carbohydrates decreased in 32 of 37 cases or 86.5% following harvesting. The average decrease was 11% TNC (AFDW) and the seasonal mean was 40.67% TNC; so the decrease due to harvesting was 27% of the seasonal mean. Figure 7b illustrates the response of root TNC to the triple cut. Root TNC decreased following harvest especially in the fall. Root TNC in the spring of the second season was similar to the control root TNC but the root TNC in June was lower than the control root TNC. The root TNC in June of the second season was lower than the control in 18 of 19 examples. The mean root TNC in June was 15.4% compared to the control root TNC of 28.6%, a reduction of 46.3%. Root TNC

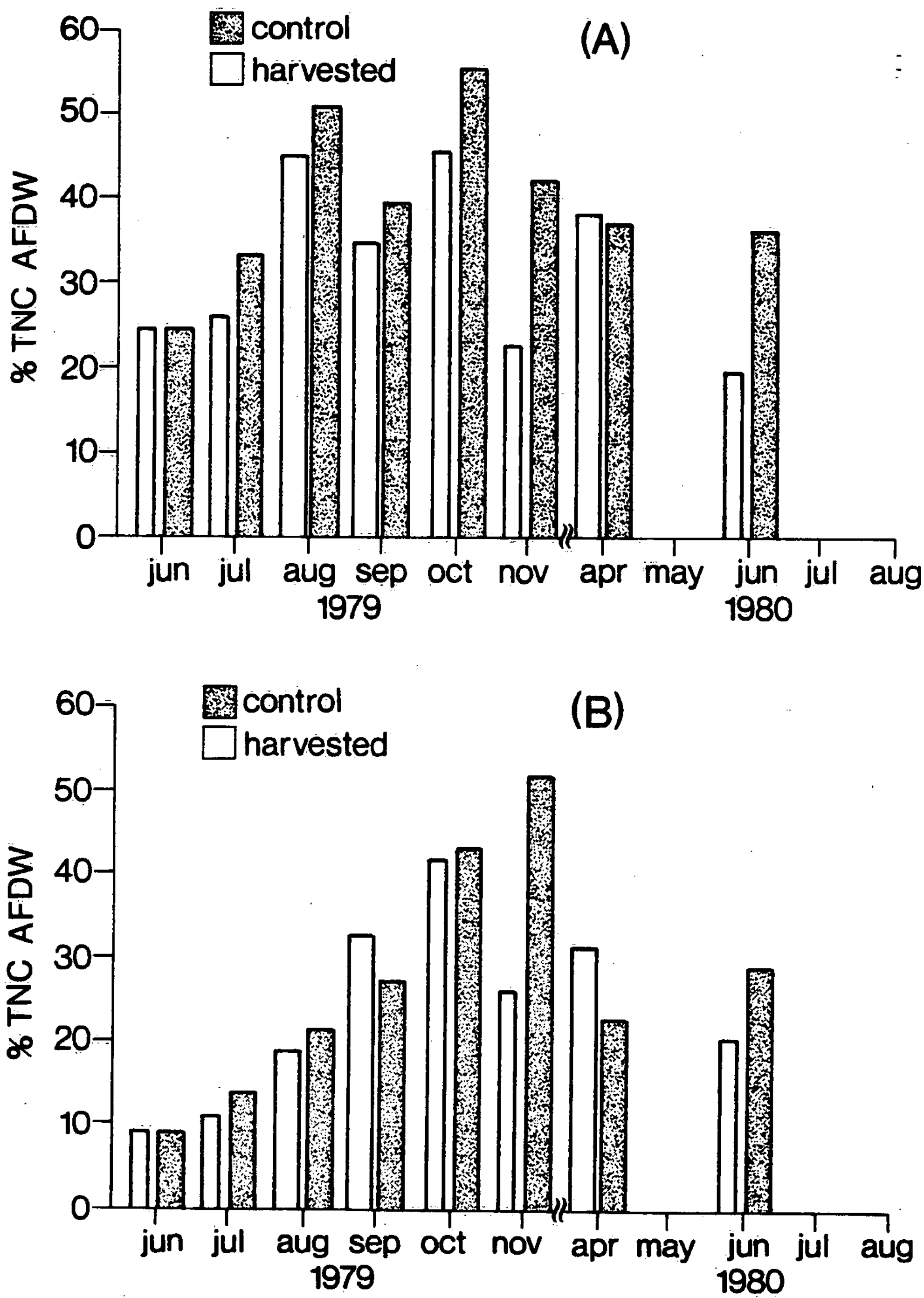


Figure 7 SEASONAL SHOOT TNC (A) AND ROOT TNC (B) FOR THE JUNE/AUGUST/OCTOBER CUT

decreased in 28 of 37 cases or 75.7% following harvesting. The average decrease was 9.9% TNC (AFDW) and the seasonal mean was 27.3% TNC; so the decrease due to harvesting was 36.3% of the seasonal mean.

The effect of harvesting on milfoil tissue chemistry was evident in 1979 and in some cases carried through to April of 1980. Effects on spring 1980 tissue chemistry were particularly evident if a cut was performed in September or October of 1979 but by the summer of 1980 no differences in tissue chemistry except root TNC were evident in any of the harvested plots.

Decreases in root total non-structural carbohydrates were also observed by Perkins and Sytsma (1981) following harvesting and are probably a result of less photosynthethic tissue available for carbohydrate production and mobilization of root reserves to support new growth. The increases in tissue phosphorus and nitrogen in both the shoots and roots are most probably due to accumulation in tissues as a result of a much reduced demand due again to a reduction in shoot material. The reduction in shoot total carbon by 6% from a seasonal mean of 46.9% C probably reflects the decrease in shoot carbohydrates by 27% from a seasonal mean of 40.7% TNC. The decrease in TNC is, however, larger than the decrease in total carbon. Therefore it appears that the structural carbon of the harvested plants probably increased on a percentage basis. Since the plant stems remaining after cutting are the stouter stems at the base of the plant the conjectured increase in structural carbon after harvesting seems reasonable. The increase in root carbon following harvesting is rather surprising considering the 36.3% drop in root total non-structural carbohydrates. As in the argument with the shoot carbon, the root structural carbon probably increased but even more dramatically than the shoots. The root masses of the harvested plants compared to the control root masses were visually observed to be much smaller after harvesting. Therefore, it would appear that a certain amount of root death occurred leaving only the stouter roots which would explain the increase in structural carbon but a decrease in root carbohydrates.

Short-term effects of harvesting on sediment chemistry

No observable changes in sediment total phosphorus or nitrogen occurred in the first or second season within the rooting depth of milfoil (0-40 cm). Total phosphorus averaged 1000 ug P/g and total nitrogen averaged 2.5% N. The total phosphorus and total nitrogen values exhibited very little change throughout the season indicating that milfoil growth demands are supplied by a sediment pool size much smaller than the total pool.

CONCLUSIONS

The timing of a harvesting program was observed to dramatically influence the short-term efficacy of the cutting when judged by the duration of open water created. Proper timing of cuts can ensure efficient use of equipment and resources. A June/August or June/September double cut would appear to be most desirable with very little advantage in a triple cut. Plant height appeared not to be affected in the second year by any harvesting schedule; however plant biomass on an areal basis was significantly affected in the second summer by a cut in October of the preceding year confirming Kimbel and Carpenter's observations (Kimbel and Carpenter, 1979).

Tissue chemistry was altered by harvesting. Total non-structural carbohydrates of both shoots and roots decreased. Shoot and root phosphorus and shoot and root nitrogen increased following harvesting. Shoot carbon decreased and root carbon increased following harvesting. The tissue chemistry was altered in the spring of the second year particularly if a September or October cut was performed; however, by the summer of the second year, no differences in tissue chemistry were observed except in root TNC which was significantly reduced.

The long-term effects of several years of a double harvest strategy will be discussed in a subsequent paper. A June/October schedule was chosen based on the observed reduction in areal biomass in the summer of the second year and an altered tissue chemistry in the spring if an October cut was performed. June was chosen for the first cut of the season because the tissue chemistry was still affected from the previous October's cut and therefore vulnerable and June was the best month for a cut during the tourist season.

REFERENCES

Bartell, S.M., and J.E. Breck. 1979. Simulated impact of macrophyte harvesting on pelagic phosphorus cycling in Lake Wingra. J.E. Breck, R.T. Prentki and O.L. Loucks (Eds.). Aquatic Plants, Lake Management, and Ecosystem Consequences of Lake Harvesting, University of Wisconsin, Inst. Environ. Studies, Madison Wis. pp 229-251.

Breck, J.E., and J.F. Kitchell. 1979. Effects of macrophyte harvesting on simulated predator-prey interactions. J.E. Breck, R.T. Prentki and O.L. Loucks (Eds.). Aquatic Plants, Lake Management, and Ecosystem Consequences of Lake Harvesting, University of Wisconsin, Inst. Environ. Studies, Madison Wis. pp 211-229.

Burton, J. pers. comm. Dept. of Animal and Food Science, University of Guelph, Guelph, Ontario.

Carpenter, S.R., and A. Gasith. 1978. Mechanical cutting of submerged macrophytes: Immediate effects on littoral water chemistry and metabolism. Water Res. 12:55-57.

Cottam, G., and S.A. Nichols. 1970. Changes in water environment resulting from aquatic plant control. Tech. Rept. OWRR B-019-WIS, University of Wisconsin-Madison. 27 pp.

IWD. 1979. Analytical Methods Manual. Environment Canada, CCIW, Burlington, Ontario.

Kimbel, J.C., and S.R. Carpenter. 1979. The dynamics of myriophyllum spicatum biomass following harvest. J.E. Breck, R.T. Prentki and O.L. Loucks (Eds.). Aquatic Plants, Lake Management, and Ecosystem Consequences of Lake Harvesting, University of Wisconsin, Inst. Envron. Studies, Madison, Wis. pp 43-51.

Neel, J.K., S.A. Peterson, and W.L. Smith. 1973. Weed harvest and lake nutrient dynamics. Ecological Research Series, EPA-660/3-73-001. US EPA Washington. 91 pp.

Nichols, S.A., and G. Cottam. 1972. Harvesting as a control for aquatic plants. Water Resources Bulletin. 8:1205-1210.

Perkins, M.A., and M.D. Sytsma. 1981. Efficacy of mechanical harvesting and its influence upon carbohydrate accumulation in Eurasian watermilfoil. Proc. 15th Aquatic Plant Control Research Planning and Operations Review, Nov. 1980. pp 464-480.

Wile, I., G. Hitchin, and G. Beggs. 1979. Impact of mechanical harvesting on Chemung Lake. J.E. Breck, R.T. Prentki and O.L. Loucks (Eds.). Aquatic Plants, Lake Management, and Ecosystem Consequences of Lake Harvesting, University of Wisconsin, Inst. Environ. Studies, Madison, Wis. pp 145-161.