A SEASONAL INVESTIGATION OF NONSTRUCTURAL CARBOHYDRATES IN SUBMERGED MACROPHYTES OF SHOAL LAKE IN RELATION TO WATER DEPTH

BY

© CAROLE J. GUY

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ABSTRACT

Nonstructural carbohydrate content was examined in Ceratophyllum demersum L., Elodea canadensis Michx., Myriophyllum exalbescens Fern., Najas flexilis (Willd.) Rostk. & Schmidt, Potamogeton foliosus Raf., P. gramineus L., P. praelongus Wulfen, P. richardsonii (Benn.) Rydb., P. robbinsii Oakes, and P. zosteriformis Fern. at various depths and sites in Shoal Lake. Species tended to show a seasonal maximum in total soluble carbohydrate content during the growing season. Starch and proportions of individual sugars also showed seasonal variation. Sucrose was the predominant sugar in most species. C. demersum was unique in being the only macrophyte containing melibiose, raffinose, and stachyose. Roots contained significantly more soluble carbohydrate than shoots and leaves in M. exalbescens. Starch concentrations generally exceeded levels of soluble carbohydrate. All carbohydrate variables were negatively correlated with water depth in C. demersum, E. canadensis, and P. foliosus. Starch was significantly negatively correlated with time in C. demersum and marginally positively correlated with time in P. zosteriformis. Stepwise multiple regression identified time and pH as significant factors in relationship to carbohydrate content in some species. The first principal component for total soluble carbohydrate in 5 species was significantly correlated with light and depth.

INTRODUCTION

Although the existing literature on nonstructural carbohydrates in vascular plants is extensive, information is largely restricted to terrestrial organisms and little is known regarding the distribution and abundance of carbohydrates in submerged aquatic macrophytes. Much of the research in this area has taken place within the past decade and has produced useful yet sometimes inconsistent findings.

Carbohydrate reserves play a crucial role in plants, enabling the conservation of energy and survival during adverse conditions. Several studies have demonstrated significant seasonal patterns in carbohydrate content of submerged macrophytes (Pip & Stewart 1976, Best 1977, Shah & Abbas 1978, Titus & Adams 1979, Janauer 1982a, Best & Visser 1987). Other workers (Boyd 1970, Best 1976, Muztar et al. 1979) assumed that soluble carbohydrate levels do not fluctuate in a given species during the course of the year, while some evidence suggests that carbohydrate content may fluctuate in a species but not show distinct seasonal dependency (Best 1977).

Seasonal changes in the proportions of total soluble carbohydrate, soluble sugars and starch may provide information about patterns of carbohydrate utilization and storage in macrophytes. The proportion of sugars in several species varies seasonally (e.g. Pip & Stewart 1976, Janauer 1981a, Best & Dassen 1987), and the changing proportions of reducing and non-reducing sugars have been viewed as an indication

of carbohydrate transport and metabolism in some aquatics (Janauer 1981a, 1981b; Best & Dassen 1987, Best & Visser 1987). The distribution of soluble carbohydrate and starch in different plant organs has also been examined (Titus & Adams 1979, Janauer 1981b, 1982b; Janauer & Englmaier 1986, Best & Dassen 1987) and shows that not only roots and rhizomes serve as storage areas.

Studies indicate that soluble carbohydrate is the predominant reserve substance in many submerged species (Best 1977, Janauer 1981a, 1981b, 1982a, 1982b; Best & Dassen 1987), with at least one species lacking starch entirely (Janauer & Englmaier 1986). Starch has been found as the major reserve carbohydrate in a fewer number of species (Best & Dassen 1987, Best & Visser 1987).

Carbohydrate content has been used to measure the competitive advantage of roots in an aquatic macrophyte (Best 1977) and carbohydrate storage has been hypothesized as giving competitive advantage to a species with a short growing season (Titus & Adams 1979). Interspecific differences in total carbohydrate of macrophytes have been reported (e.g. Shah & Abbas 1978, Janauer 1982b).

A strong relationship between water depth and the chlorophyll:soluble carbohydrate ratio has been found for some submerged species (Pip & Sutherland-Guy 1987), suggesting that photosynthesis was less efficient at lower light intensities and changes in spectral quality associated with greater depth. Emersion has been shown to have a marked

effect on carbohydrate levels of one submerged species, with emergent plants having much higher carbohydrate content than submerged plants (Janauer 1986). Light conditions and CO_2 availability were suggested to be the primary factors influencing carbohydrate levels in this macrophyte.

Soluble carbohydrate may be an important parameter for indicating trophic status of lake water. Janauer (1979, 1981b) found a positive relationship between sucrose content of macrophytes and inorganic phosphorous and nitrate concentrations in water bodies. Starch content was also reported to vary with nutrient status of lake water (Janauer 1981b). The importance of soluble carbohydrate as a trophic indicator has been implied in reports of variations in carbohydrate content of plants growing at the same water depth in different locations (Muztar et al. 1979, Titus & Adams 1979, Pip & Sutherland-Guy 1987).

The objective of the present study was to examine in greater detail the seasonal fluctuation pattern of starch, total soluble carbohydrate and proportions of individual sugars in Ceratophyllum demersum L., Elodea canadensis Michx., Myriophyllum exalbescens Fern., Najas flexilis (Willd.) Rostk. & Schmidt, Potamogeton foliosus Raf., P. gramineus L., P. praelongus Wulfen, P. richardsonii (Benn.) Rydb., P. robbinsii Oakes, and P. zosteriformis Fern. Superimposed on the seasonal pattern was an investigation of horizontal and vertical differences.

SITE AND SPECIES DESCRIPTION

All plant material was collected from Shoal Lake, situated on the Manitoba - Ontario boundary (49°36' - 40' N, 95°04' - 12' W) in a basin of Early Precambrian bedrock. The mean water level elevation is 323 m above sea level. Sampling stations, with the exception of the 12-14 m site, were located on Indian Bay, which has a surface area of 21.7 km^2, excluding islands. The bottom of the bay is irregular, with a maximum depth of 10 m, and a mean depth of less than 3.5 m. The bottom sediments of Indian Bay qualify as gyttya, containing 5 to 39 % organic matter by dry weight.

Water chemistry showed variation throughout the study area at different locations depths and times. During 1984-85, the following parameter ranges were recorded within Indian Bay: pH 6.9-9.1, total dissolved solids 40-123 mg/1, total alkalinity 44-92 mg/1 $CaCO_3$, molybdenum reactive phosphorus 0.01-1.66 mg/1, nitrate-N 0.04-1 mg/1, nitrite-N 0-7 ug/1, ammonia-N 0=0.25 mg/1, chloride 0 mg/1, sulphate 0.4-4 mg/1 .

Thermal stratification was generally minimal or absent in the study area because of the large surface area and exposure of the lake. Localized thermoclines were present only at some stations and were of limited duration. Maximum temperature recorded at 12-14 m was 17-19°C in 1985, with maximum surface temperatures ranging from 21-23°C.

Midday surface incident values of photosynthetically active radiation (PAR) ranged from 0.1 to 2.4 mE s^{-1} m^{-2},

depending on amount of cloud cover (Appendix B). Light attenuation varied at any given time at different stations, with the best water clarity at the 12-14 m site. Light intensities at this location at 13-14 m were estimated at 0.5 to 1.0 % of surface incident PAR (Appendix C).

Some macrophytes showed defined vertical zonation, but 6 species could still grow in persistent communities as deep as 14 m (Appendix E). The minimum light intensities available at the respective maximum depths for the different species in Appendix E are early May values, at the sites with the greatest light attenuation where each species was recorded. Generally only Potamogeton praelongus attained the surface during the season, even in shallower water. Aside from this species which achieved shoot lengths of 4 m by mid-June, the tallest of the remaining submerged species was P. zosteriformis, with maximum shoot lengths of 2 m.

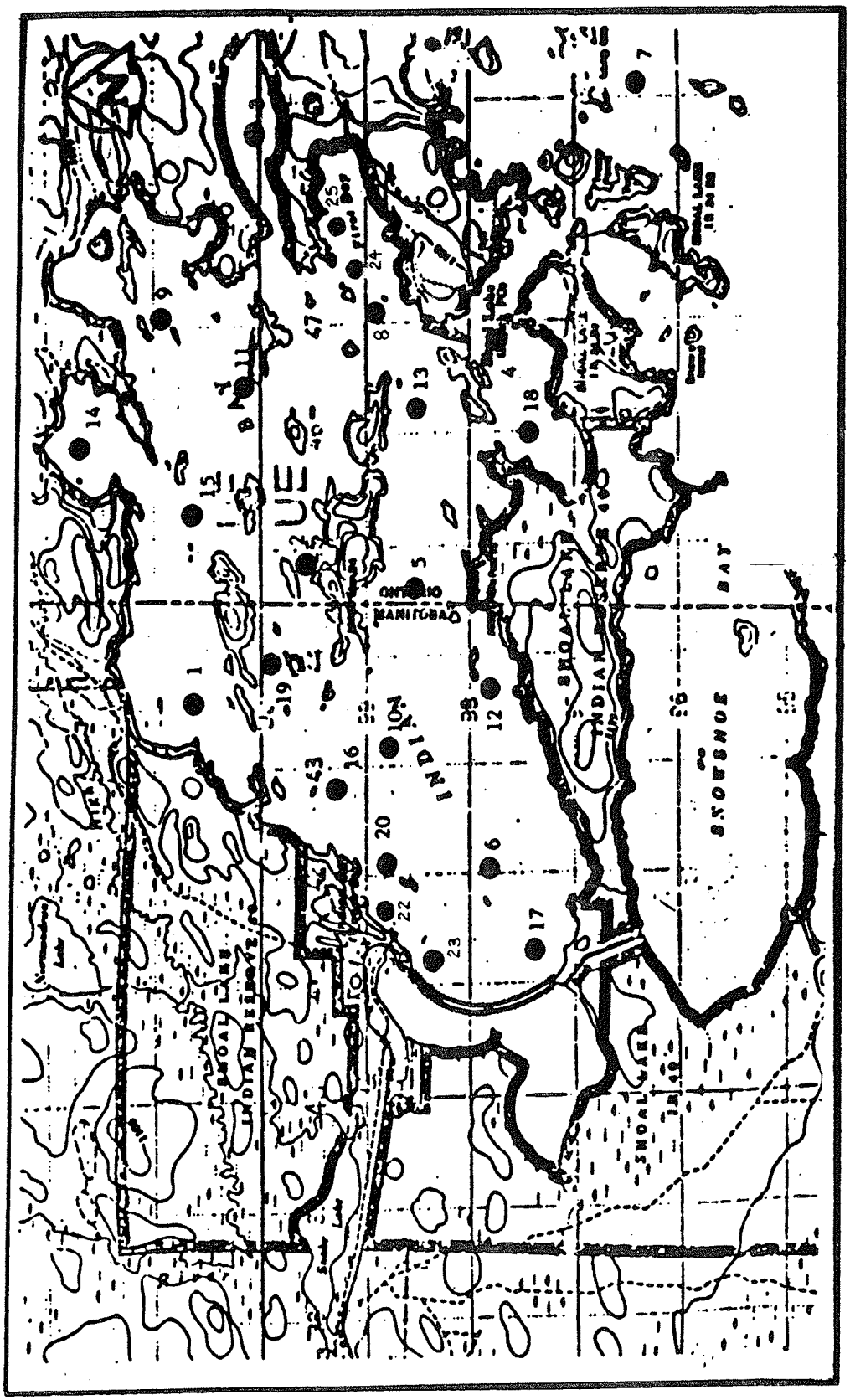
Substantial macrophyte growth had already taken place even before the ice broke up in the spring. By mid-July, above-ground macrophyte biomass for Indian Bay had a mean value of 190 g/m^2 in 1985. During mid-May to mid-July the macrophyte biomass appeared to double every 4 weeks. During this time temperature in the study area increased from an average of 13 C in mid-May to 16 C in mid-June, to 20 C in mid-July. The biomass of individual macrophytes in mid-July of 1985 is shown in Appendix F.

MATERIALS AND METHODS

The material used in this study was collected at 7 to 24 stations in Shoal Lake (Fig. 1) 9 times during the 1985 growing season as part of an ongoing study conducted by Dr. E. Pip of the limnology of the lake. Plants were obtained by SCUBA and dredging with a rake at depths ranging from 1 to 14 metres. The plants were washed at the collection site to remove as much periphyton as possible and packed in plastic bags on ice in darkness. Plant tissue was frozen within 7 hours of collection and subsequently freeze-dried. Green stems and leaves for each species were combined to give a composite sample from a number of different plants for each time and location. Shoots were all less than 1 m in length. Roots, rhizomes, or seeds, present in some species, were also examined when available.

Plant samples were cut with scissors into small segments and sub-samples of 0.1 to 0.5 g were homogenized in a mortar with 25 ml of 80% ethanol. A replicate extraction was made for samples of sufficient size. The homogenate was centrifuged at 300 x g at 0 C for 5 minutes. The volume of the supernatant was made up to 30 ml with 80% ethanol. A 25 ml sample of the crude extract was air-dried at room temperature and stored at 5 C until used later for chromatographic separation and quantification of individual sugars. The remaining 5 ml of extract was analyzed for total soluble carbohydrate using the anthrone method of Roe (1955). Absorbance for 3 aliquots was measured at 620 nm in a Beckman Du-7 or a

Fig. 1. Location of sampling stations in Shoal Lake during 1985.


ONTARIO
MANITOBA
INDIAN RESERVE
BROAD LAKE
SNOWSHOE BAY
SNOWSHOE LAKE

Pye-Unicam spectrophotometer. A calibration curve was constructed for each spectrophotometer for glucose concentrations ranging from 0 to 200 ug / ml. Linear regression equations for these standard curves were calculated ($r<0.99$, $p<0.001$, $n=10$):

Beckman: glucose(ug/ml) = $(A_{620} - 0.000468)/0.00499$
Pye-Unicam: glucose(ug/ml) = $(A_{620} + 0.00599)/0.00498$

All soluble carbohydrate values were expressed as equivalent glucose units.

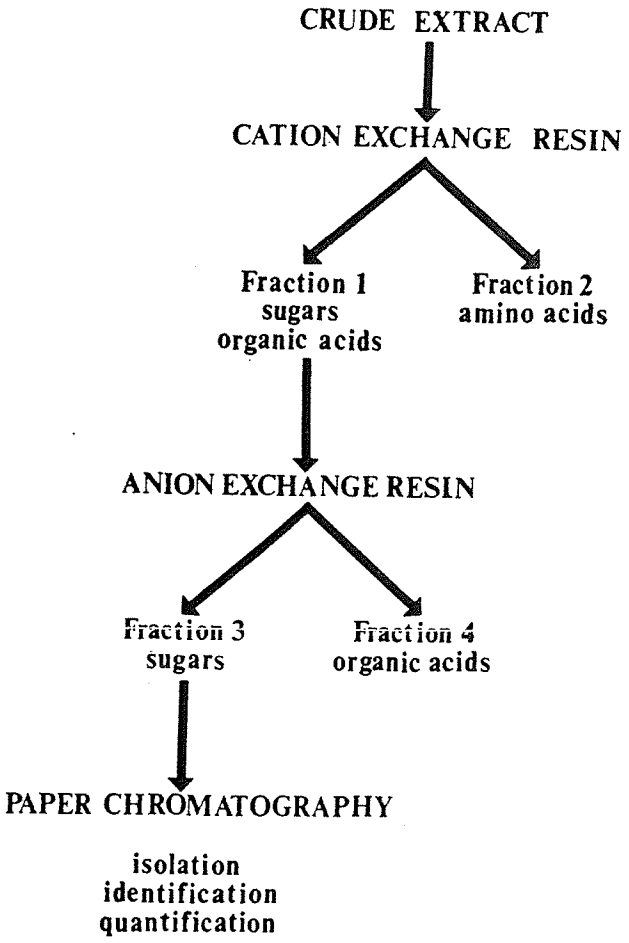
The crude plant extract was purified by using 2 successive sets of ion exchange columns, in a method modified from that of Wang(1960). Dowex 50W, a cation exchange resin, and Dowex -1, an anion exchange resin, were used, each with a mesh size of 200 - 400. Each resin was mixed with distilled water and transferred several times between 2 beakers to remove heavier particles. The mixture was allowed to settle and the supernatant decanted to remove smaller particles. The process of settling and decanting was repeated several times. Impurities were removed by boiling the resins in 2N HCl for 5 minutes and discarding the supernatant. Dowex 50W was then washed with distilled water until the pH of the eluent stabilized. Dowex -1 was placed in a 4.5 x 50 cm glass column and washed with 1N sodium formate until chloride ions could no longer be precipitated in the eluent by adding a solution of $AgNO_3$. A volume of 110 ml of 0.1N formic acid was passed through the column and the resin was washed with distilled water

until the pH of the eluent stabilized. The resins were poured into 1 x 15 cm glass columns plugged with glass wool. Eleven columns were run for each of the respective resins.

The dried crude extract from the original volume of 25 ml was dissolved in 2 ml of 80% ethanol and applied to the Dowex 50W columns. The solution was eluted with 100 ml of distilled water to remove soluble sugars and organic acids, giving Fraction 1 (Fig. 2). The resin from the set of 11 columns was placed in a beaker and washed with 1 l of 4M NH_4OH to remove amino acids (Fraction 2). The resin was recycled by washing with distilled water until pH was stable. Fraction 1 was air-dried at room temperature and dissolved in 2.0 ml of 80% ehtanol. Each sample was applied to a Dowex -1 column and eluted with 100 ml of distilled water to give Fraction 3 containing soluble sugars. The eluent was air-dried at room temperature. The Dowex -1 from the columns was placed in a 4.5 x 50 cm column and washed with 800 ml of 4N formic acid and 200 ml of 6N HCl to remove organic acids (Fraction 4). The Dowex -1 resin was recycled by successive washes of sodium formate, formic acid, and distilled water as before. Part of the 2 resins was removed and discarded after use, and volume was replenished with resin prepared as described above. The resins were completely replaced after every 3 runs.

Sugars present in Fraction 3 were isolated by using descending paper chromatography as described by Pip and Stewart (1976). Four sheets were run simultaneously in a

Fig. 2 . Procedure for purification of crude plant extract.


CRUDE EXTRACT
CATION EXCHANGE RESIN
Fraction 1
sugars
organic acids
Fraction 2
amino acids
ANION EXCHANGE RESIN
Fraction 3
sugars
Fraction 4
organic acids
PAPER CHROMATOGRAPHY
isolation
identification
quantification

52:13:35 mixture of butanol, acetic acid, and water (Putman, 1957) for 42 hr. Six replicates were run for each sample.

Sugars were visualized by developing alternate lanes on each chromatogram in aniline diphenylamine phosphate in acetone and oven-heating at approximately 100 C, as described by Bacon and Dickinson (1957) and Smith (1960). Regions of undeveloped strips corresponding to spots on the developed lanes were eluted separately in 5.0 ml of 10% isopropanol, air-dried, and redissolved in 1.0 ml of 10% isopropanol. The quantity of different sugars was determined using the anthrone method (Roe, 1955).

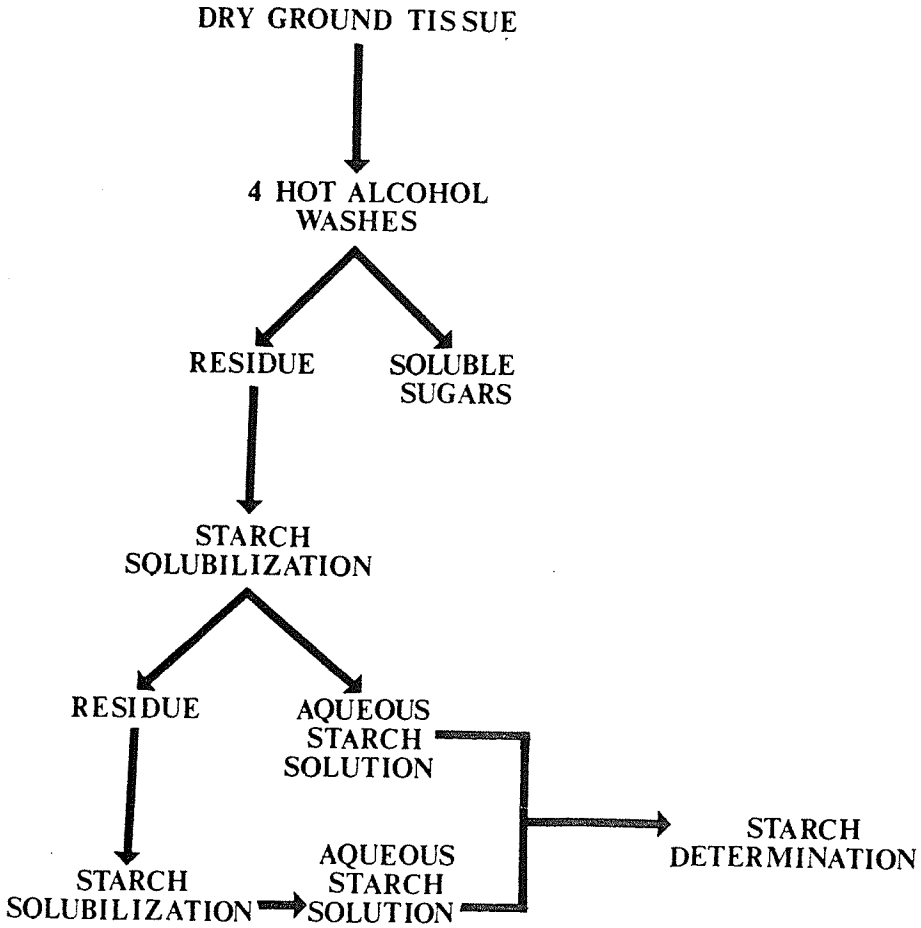
Developed spots were identified by comparing to color reactions and R values, relative to fructose, of arabinose, fructose, galactose, glucose, lactose, maltose, melibiose, myo-inositol, raffinose, stachyose, sucrose, trehalose and xylose standards. Four sugars found in Ceratophyllum demersum samples were further analyzed with NMR spectroscopy. These were compared to standards of lactose, melibiose, raffinose, myo-inositol, melezitose and stachyose. Sample sugars were prepared by pooling eluted spots from several chromatograms. Each of the 4 pooled samples was filtered and evaporated to obtain a total dry weight of 2 - 3 mg. The dry sugars were dissolved in 0.5 ml of 80% ethanol and filtered by passing through a pasteur pipette containing a glass wool plug. The solutions were freeze-dried and redissolved in 0.5 ml of D_2O and placed in NMR tubes. Standard sugars were prepared by dissolving 3 mg of each

sugar in 0.5 ml of D_2O. Proton and ^{13}C NMR spectra were prepared at 300 and 75.47 Mhz respectively, using the spectrograph at the University of Manitoba Chemistry Department.

Starch content was determined by a modification of a method from McCready et al. (1950), as summarized in Fig. 3. Plant tissue was ground to flour using a mortar and pestle. A sample ranging from 0.07 to 0.20 g was mixed with a few drops of 80% ethanol and 5.0 ml of distilled water in a centrifuge tube. Twenty ml of hot (60-65 C) ethanol was added and the solution was centrifuged at 9770 x g for 7 minutes at room temperature. The supernatant was decanted and the residue was given 3 additional washes with 20 ml volumes of hot 80% ethanol. A fifth wash was performed on selected samples in order to measure any soluble carbohydrate remaining in the residue. The soluble carbohydrate removed in each wash was quantified by the anthrone test. Correction factors were calculated for each species to account for soluble carbohydrate remaining in the residue after the 4 alcohol washes; thus preventing overestimation of starch.

After the final centrifugation, 1.0 ml of water was added to the residue and the mixture was transferred to a 15 ml glass centrifuge tube. Starch in the residue was solubilized by adding 1.3 ml of 52% perchloric acid and stirring for 20 minutes. Five ml of water was used to rinse the original centrifuge tube and was added to the perchloric

Fig. 3. Procedure for determination of starch content of macrophyte tissue.


DRY GROUND TISSUE
4 HOT ALCOHOL WASHES
RESIDUE
SOLUBLE SUGARS
STARCH SOLUBILIZATION
RESIDUE
AQUEOUS STARCH SOLUTION
STARCH SOLUBILIZATION
AQUEOUS STARCH SOLUTION
STARCH DETERMINATION

acid mixture. This volume was centrifuged at medium speed for 5 minutes in a clinical centrifuge. The aqueous starch solution was decanted into a graduated cylinder and starch remaining in the residue was solubilized as before with perchloric acid and water. The two supernatants were combined and brought to a total volume of 20 ml with distilled water.

The starch solution was then filtered and diluted with distilled water to contain 20 to 80 micrograms of starch per ml. This was accomplished by diluting 1.0 ml of solution to 20 to 40 ml. One ml of the dilute solution was cooled in a test tube in a 25 C water bath and 2.0 ml of anthrone reagent were added. Samples were mixed well, while maintained at 25 C, and were heated for 7.5 minutes at 100 C. The tubes were immediately placed in a 25 C water bath and the absorbance was read at 630 nm on a Beckman Du-7 spectrophotometer. The blank was a mixture of water, perchloric acid and anthrone reagent. A standard curve was constructed for 0 to 80 micrograms of glucose per ml. The corresponding regression equation was calculated ($r<0.99$, $p<0.001$, $n=10$):

$$\text{glucose(ug/ml)} = (A_{630} + 0.0297)/0.0168$$

Glucose found was multiplied by 0.90 to convert to starch (McCready et al. 1950).

The single extraction method for soluble carbohydrate and the extraction with successive hot alcohol washes were compared using representative samples for each species from

various locations and times of collection. The method involving the series of hot alcohol washes gave consistently higher values than the cold alcohol method with one wash. Appropriate correction factors were calculated for each species to account for underestimation of soluble carbohydrate in the single extraction method.

Standard sugar solutions were prepared to approximate the sugar content and composition of the crude sample extracts. Volumes representing a 10 to 40 mg range in total carbohydrate were passed through the 2 sets of ion exchange columns in the method previously described. Sugars were isolated as before by descending paper chromatography and were quantified by the anthrone method. Correction factors based on percent recovery were calculated for each of the sugars and were applied to data obtained for all of the unknowns.

Statistical tests were carried out in this study using the SAS statistical package at the University of Manitoba.

RESULTS

A. Total soluble carbohydrate

Comparison of the 2 extraction methods for soluble carbohydrate showed that the cold alcohol extraction removed 47.3 to 68.2 % of the soluble carbohydrate extracted in the series of 4 hot alcohol washes (Table 1).

Total soluble carbohydrate content of shoots and leaves, in terms of mg equivalent glucose per g, was quite variable for most species during the 1985 growing season (Table 2). Mean seasonal values ranged from 38.1 for Najas flexilis to 87.6 for Potamogeton richardsonii.

Total soluble carbohydrate content of macrophytes at various depths and stations during the 1985 season is shown in Figs. 4 to 13. Linear regression analysis for each sampling time gave the following significant negative correlations of soluble carbohydrate and depth: Ceratophyllum demersum on June 27 (R^2=0.68, $p<0.001$, n=12), Elodea canadensis on July 10-11 (R^2=0.67, $p<0.01$, n=12), P. foliosus on May 2 (R^2=0.30, $p<0.02$, n=18) and July 10-11 (R^2=0.56, $p<0.001$, n=51), Myriophyllum exalbescens on August 29 (R^2=0.16, $p<0.05$, n=27), and P. zosteriformis on May 16 (R^2=0.78, $p<0.001$, n=12). Negative relationships with depth that lacked significance due to limited depth representation were observed for P. zosteriformis on June 27 and August 29.

Positive correlations between soluble carbohydrate and depth were found for C. demersum on May 2 (R^2=0.35, $p<0.001$, n=30) and May 16 (R^2=0.22, $p<0.005$, n=36), and M. exalbescens

on May 16 (R^2=0.23, $p<0.05$, n=18). Positive correlations were also observed for E. canadensis on May 2 and for P. foliosus on August 8, although these were not significant. Sample size for N. flexilis, P. gramineus, P. praelongus, P. richardsonii, and P. robbinsii was small and vertical relationships could not be examined.

Mean carbohydrate content for each species and sampling date were analyzed for differences in SNK and Tukey's tests (Table 3). Carbohydrate levels in different plant organs were also compared (Table 4). Levels of soluble carbohydrate showed little seasonal fluctuation during 1985 in C. demersum. The mean value for the July sampling time was significantly higher than that of the other sampling dates. E. canadensis also showed a seasonal peak in carbohydrate content, with the mean level for August 8 significantly exceeding levels on all other sampling dates. The July 10-11 mean was significantly higher than the May, June 13, and August 29 sampling times. The soluble carbohydrate content of stems and leaves was not significantly different from the level in roots, for the one sample on May 30 where roots were available.

Soluble carbohydrate content for M. exalbescens was significantly higher on April 27, May 2, and May 16 than on June 27, July 10-11, and August 29. The carbohydrate content of roots was significantly higher than that of leaves and stems, in the 5 samples where roots were represented. Differences between the 2 categories of plant organs ranged from 10 to 40 mg/g.

Table 1. Proportion of soluble carbohydrate extracted in cold alcohol method, relative to the quantity removed by successive hot alcohol washes.

Species	Percent Recovery (±SE)
Myriophyllum exalbescens	68.2(2.1)
Potamogeton gramineus	67.0(3.2)
P. robbinsii	56.1(3.6)
Najas flexilis	55.5(3.0)
Ceratophyllum demersum	53.0(2.1)
Elodea canadensis	51.8(5.0)
Potamogeton praelongus	50.2(2.4)
P. foliosus	50.1(2.4)
P.richardsonii	47.3(4.0)
P. zosteriformis	45.6(2.9)

Table 2. Overall seasonal soluble carbohydrate content (mg equiv glucose g^{-1}) of macrophytes during the 1985 season. N represents the number of samples, many of which were examined in replicate.

Species	Carbohydrate Range	Mean	N	Depth Range (m)	Mean Depth (m)
Potamogeton richardsonii	71.9 - 97.7	87.6	5	1.5 - 2	1.8
P. foliosus	20.9 - 137	71.7	32	1 - 6.5	5.0
P. praelongus	44.0 - 100	71.3	3	---	2.0
P. zosteriformis	23.4 - 110	63.6	22	2 - 14	4.6
P. gramineus	34.5 - 84.8	59.7	4	2 - 3	2.7
Myriophyllum exalbescens	20.4 - 86.6	53.0	25	1 - 13	2.7
Ceratophyllum demersum	31.1 - 75.5	45.5	38	1 - 6.5	3.9
Potamogeton robbinsii	29.6 - 55.8	43.8	6	1 - 5	2.6
Elodea canadensis	20.2 - 91.8	41.0	14	1 - 14	4.4
Najas flexilis	32.8 - 44.5	38.1	3	1 - 1.75	1.4

P. foliosus also showed statistically significant relationships in soluble carbohydrate content, with a seasonal maximum observed on May 30 and June 13. There was no consistent relationship between carbohydrate levels in roots and levels in stems and leaves, and means were not significantly different for the 2 samples with roots.

The soluble carbohydrate content of P. zosteriformis showed an overall seasonal increase from May to July and a decrease during the remainder of the season. The mean glucose levels on June 27 and July 10-11 were significantly higher than the mean levels for May and August dates. Roots and rhizomes contained significantly less soluble carbohydrate than leaves and stems for the single sample where roots were available.

The remaining macrophyte species were represented on a fewer number of sampling dates and trends for the full growing season could not be examined. P. richardsonii gave no apparent pattern in soluble carbohydrate content over 3 dates, and levels in seeds and shoots/leaves were not significantly different. Carbohydrate levels in P. praelongus were significantly higher on June 13 than on June 27. Content in seeds was not significantly different from amounts in shoots and leaves in the species. P. gramineus and P. robbinsii yielded significant seasonal peaks in soluble carbohydrate content on June 13 and July 10-11, respectively. Levels in N. flexilis were significantly higher on August 29 than on 2 earlier dates.

Seasonal soluble carbohydrate levels were examined at selected depths for C. demersum, M. exalbescens, P. foliosus, and P. zosteriformis (Figs. 14 to 17). Carbohydrate content in C. demersum remained relatively constant throughout the season at 2 and 3.5 m, fluctuating between 40 and 50 mg/g. Levels at 5 m varied more than at the shallower depths, with a maximum in July. Soluble carbohydrate levels of M. exalbescens over a depth range of 1 to 3.5 m tended to decrease from early to mid-season. Soluble reserves increased from mid-July to early August at 1.5 and 2 m, while samples from 2 and 3.5 m showed a decrease in carbohydrate at the end of the season. Levels tended to be higher at 2 m than at 1, 1.5, and 3 m. Soluble carbohydrate content of P. foliosus increased during the early part of the growing season (May 2 to June 13) for a depth range of 4 to 6 m. Samples from 4, 5, and 6 m showed a decrease in total soluble sugars from June 13 to July 10-11. Levels tended to be higher at 4 m than at 5 and 6 m. Carbohydrate in P. zosteriformis for 2, 3.5, and 12 to 14 m reached maximum values in mid-season (June 27 or July 10-11) and declined sharply in August for 2 and 3.5 m samples. Values at 12 to 14 m were lower than or similar to those at the shallower depths. Carbohydrate levels at 2 m exceeded levels at 3.5 m in July and August.

Macrophytes growing at the same depth in different locations showed variation in soluble carbohydrate content during the 1985 growing season (Table 5). Species represented at stations 22 and 23 tended to have a higher soluble

carbohydrate content at station 22, with differences being significant for M. exalbescens and P. praelongus on June 27. An exception to this trend was observed in M. exalbescens on August 29, when plants at station 22 had significantly more soluble reserves. Differences observed between sites showed some inconsistencies between species. Soluble carbohydrate levels were significantly higher at site 1 than at site 22 in C. demersum on May 2, while the reverse significant relationship was observed in M. exalbescens. On June 13,C. demersum contained significantly more soluble carbohydrate at station 2 than at station 9. P. foliosus, in contrast, had significantly higher levels at the latter site.

Interspecific differences in mean soluble carbohydrate content were observed for the various sampling dates although trends were inconsistent (Table 6). Comparisons were made using SNK and Tukey's tests (Appendix G). The number of species represented on the dates ranged from 2 on April 27 to 10 on June 27.

E. canadensis contained less soluble carbohydrate than all other species represented on May 2, May 16, May 30, June 13, and August 29, and had the greatest number of significant differences with other species on May 2 and August 29. On August 8 however, E. canadensis had significantly more soluble sugars than 7 other species. On the same date, P. robbinsii had less carbohydrate than all other species, with 7 significant comparisons. P. foliosus had significantly more soluble carbohydrate than M. exalbescens on April 27. This

species also exceeded all other species in soluble sugar content on May 2, May 30, and June 13, with some significant comparisons. P. richardsonii and P. zosteriformis had a higher carbohydrate level than other species on June 27 and July 10-11. On the latter date, these 2 species were significantly different from all other species except from P. gramineus and from each other. P. richardsonii had the greatest number of significant differences with other species on June 27. M. exalbescens and P. foliosus had significantly more soluble carbohydrate than the 4 other species present on May 16.

Fig. 4. Total soluble carbohydrate content in stems and leaves of Ceratophyllum demersum on various sampling dates during the 1985 growing season. Vertical bars represent standard error and numbers beside circles indicate sampling sites. Depth (in meters) for each collection time is shown on the horizontal axis. Statistically significant relationships between depth and total soluble carbohydrate content are shown for May 2, May 16, and June 27.

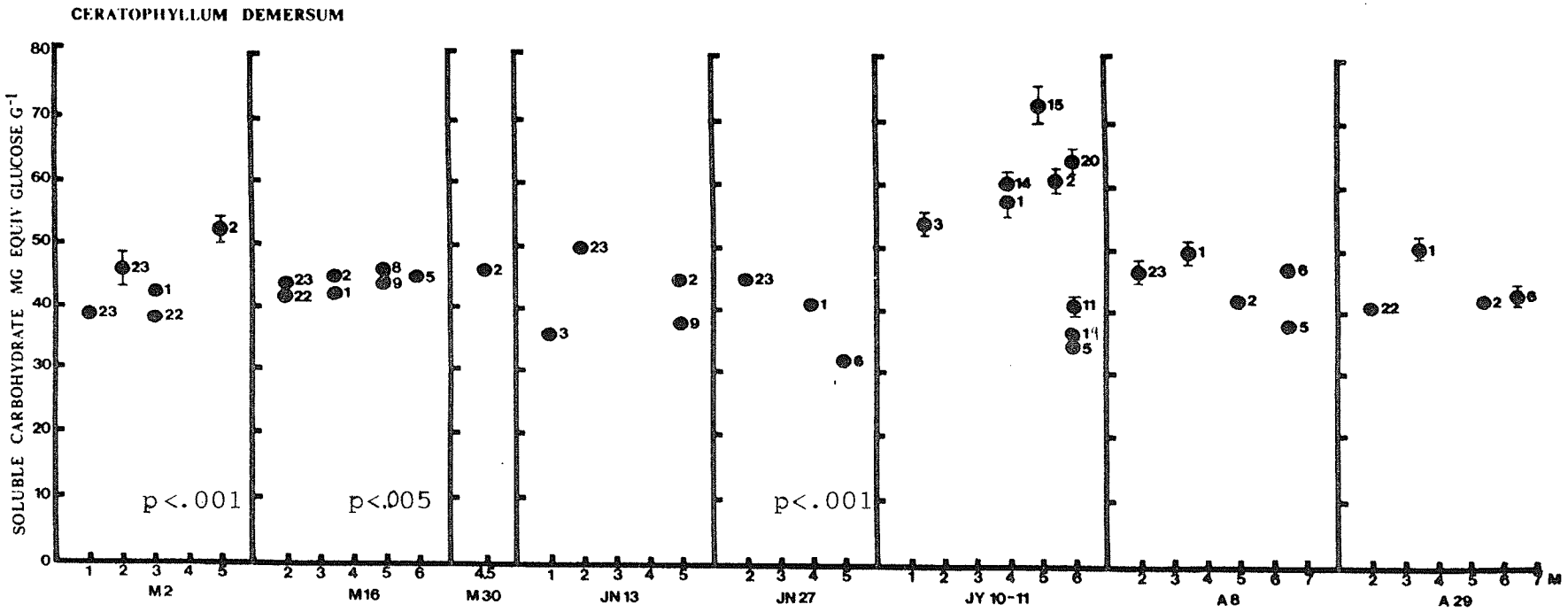

CERATOPHYLLUM DEMERSUM
SOLUBLE CARBOHYDRATE MG EQUIV GLUCOSE G-1
p<.001
p<.005
p<.001
M2
M16
M30
JN13
JN27
JY 10-11
A8
A 29

Fig. 5. Total soluble carbohydrate content in stems and leaves (closed circles) and roots (open circles) of Elodea canadensis on various sampling dates during the 1985 growing season. Vertical bars represent standard error and numbers beside circles indicate sampling sites. Depth (in meters) for each collection time is shown on the horizontal axis. A statistically significant relationship between depth and total soluble carbohydrate content is shown for July 10-11.

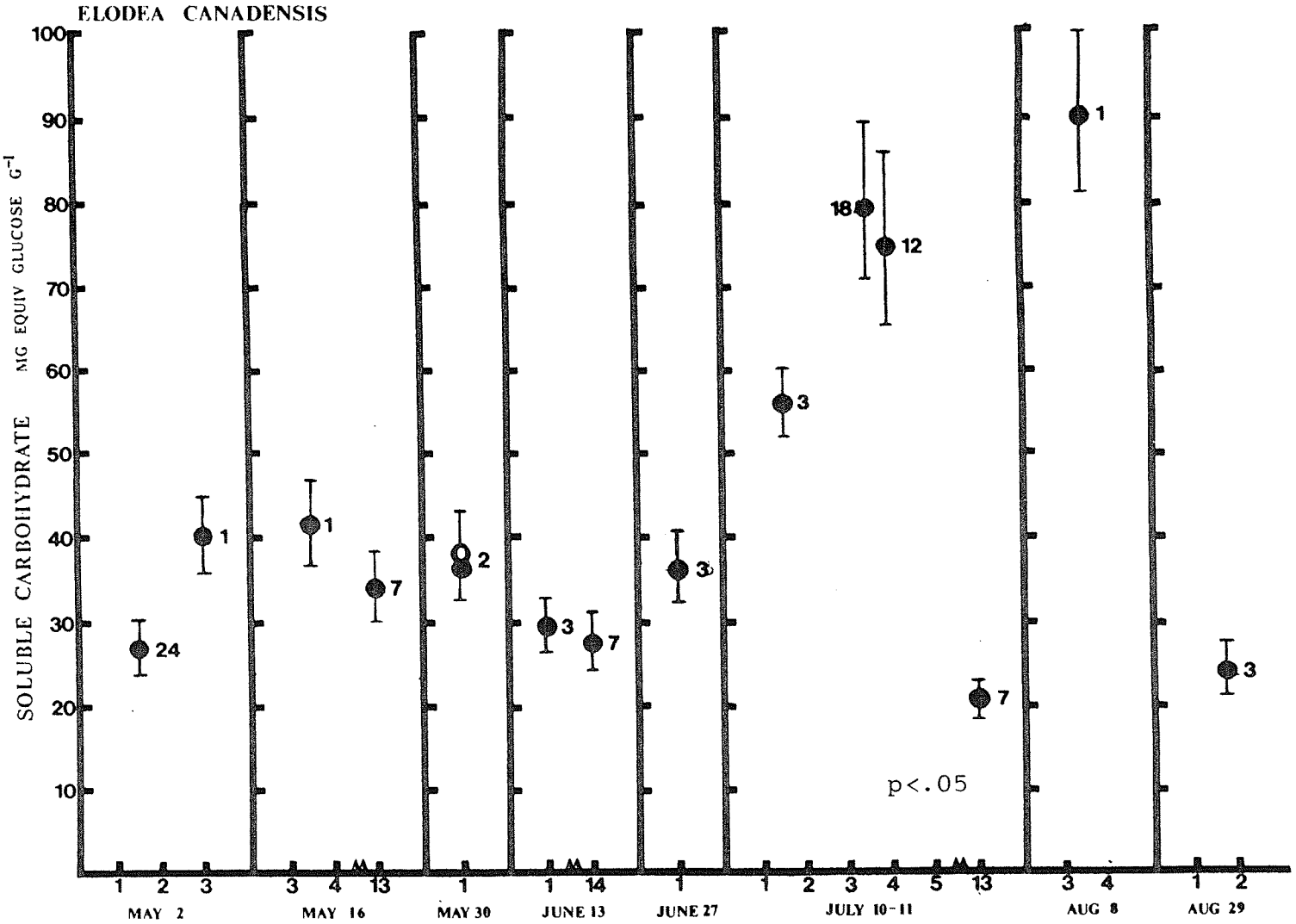

ELODEA CANADENSIS
SOLUBLE CARBOHYDRATE MG EQUIV GLUCOSE G⁻¹
100
90
80
70
60
50
40
30
20
10
24
1
1
7
2
3
7
3
3
18
12
3
7
1
3
p<.05
1 2 3
3 4 13
1
1 14
1
1 2 3 4 5 13
3 4
1 2
MAY 2
MAY 16
MAY 30
JUNE 13
JUNE 27
JULY 10-11
AUG 8
AUG 29

Fig. 6. Total soluble carbohydrate content in stems and leaves (closed circles) and roots (open circles) of Myriophyllum exalbescens on various sampling dates during the 1985 growing season. Vertical bars represent standard error and numbers beside circles indicate sampling sites. Depth (in meters) for each collection time is shown on the horizontal axis. Statistically significant relationships between depth and total soluble carbohydrate are indicated for May 16 and August 29.

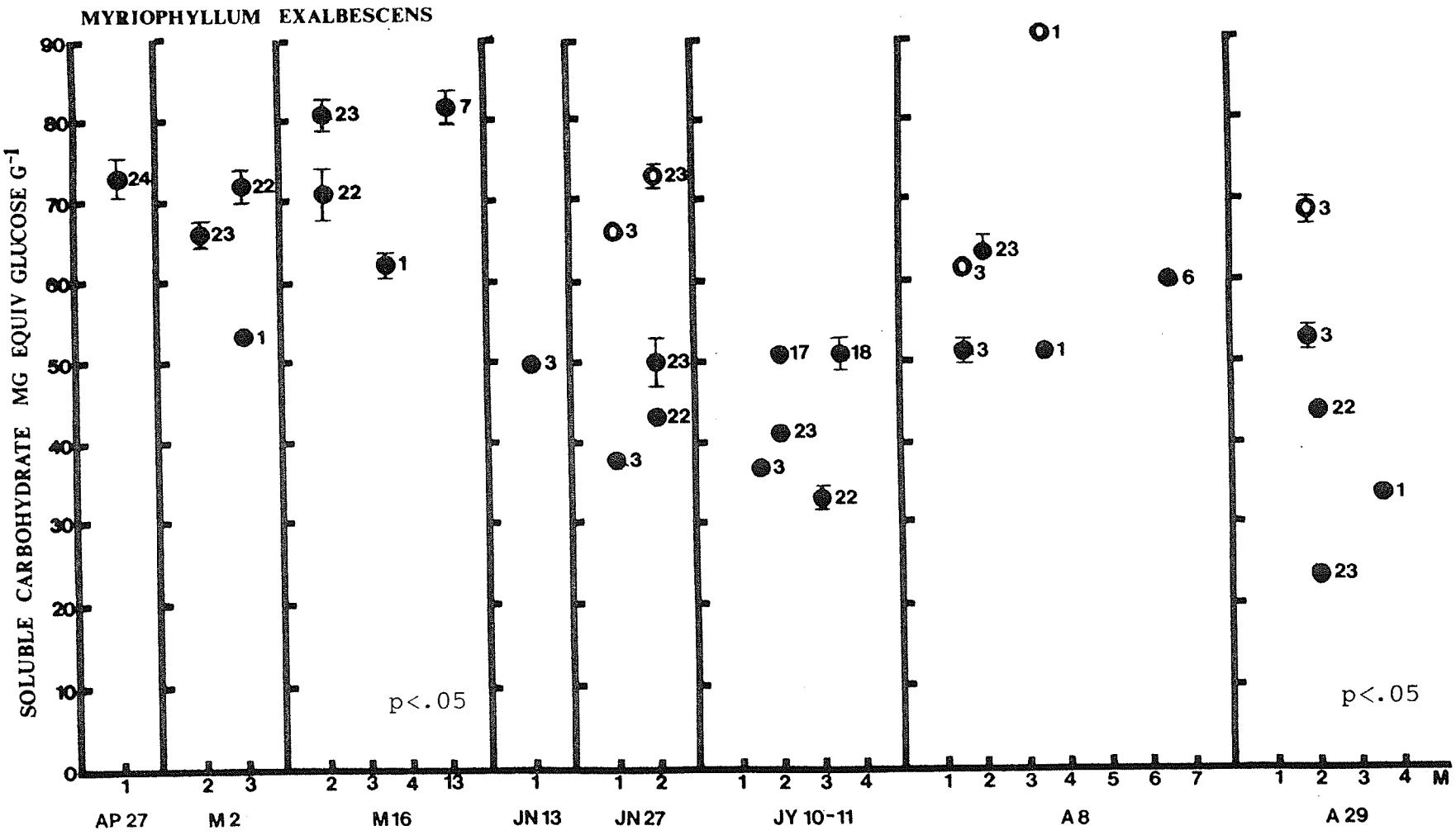

MYRIOPHYLLUM EXALBESCENS
SOLUBLE CARBOHYDRATE MG EQUIV GLUCOSE G-1
p<.05
p<.05
AP 27
M 2
M16
JN 13
JN 27
JY 10-11
A 8
A 29
M

Fig. 7. Total soluble carbohydrate content in stems and leaves of Najas flexilis at collection site 3 during the 1985 growing season. Vertical bars represent standard error. Sampling depth (in meters) is shown on the horizontal axis.

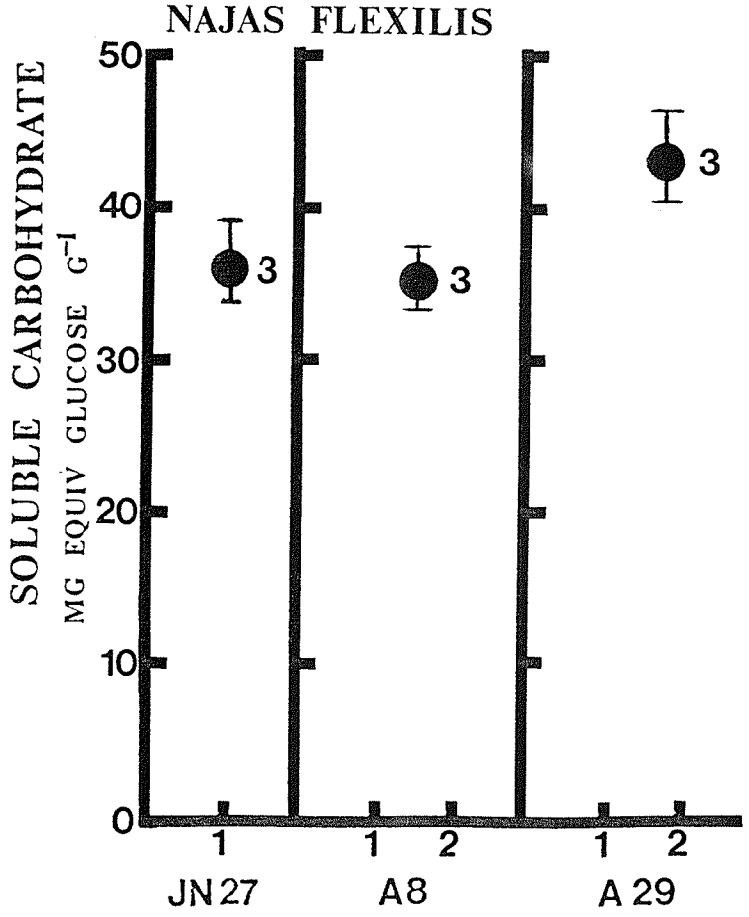

NAJAS FLEXILIS
SOLUBLE CARBOHYDRATE
MG EQUIV GLUCOSE G^{-1}
50
40
30
20
10
0
3
3
3
1
1
2
1
2
JN 27
A 8
A 29

Fig. 8. Total soluble carbohydrate content in stems and leaves (closed circles) and roots (open circles) of Potamogeton foliosus on various sampling dates during the 1985 growing season. Vertical bars represent standard error and numbers beside circles indicate sampling sites. Depth (in meters) for each collection time is shown on the horizontal axis. Statistically significant relationships between depth and total soluble carbohydrate content are shown for May 2 and July 10-11.

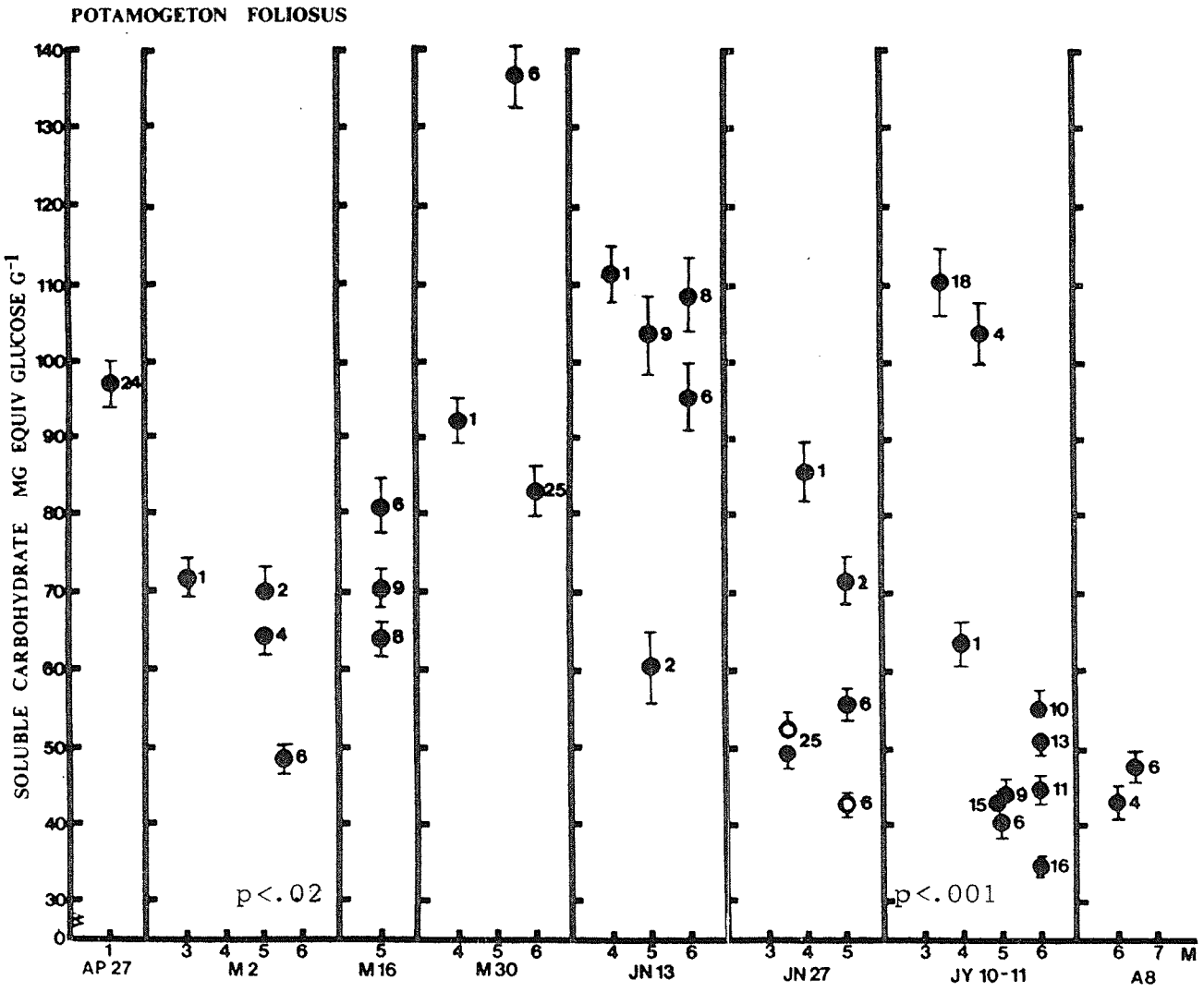

POTAMOGETON FOLIOSUS
SOLUBLE CARBOHYDRATE MG EQUIV GLUCOSE G-1
140
130
120
110
100
90
80
70
60
50
40
30
0
p<.02
p<.001
AP 27
M 2
M 16
M 30
JN 13
JN 27
JY 10-11
A8
M

Fig. 9. Total soluble carbohydrate content in stems and leaves of Potamogeton gramineus at collection site 22 during the 1985 growing season. Vertical bars represent standard error. Sampling depth (in meters) is shown on the horizontal axis.

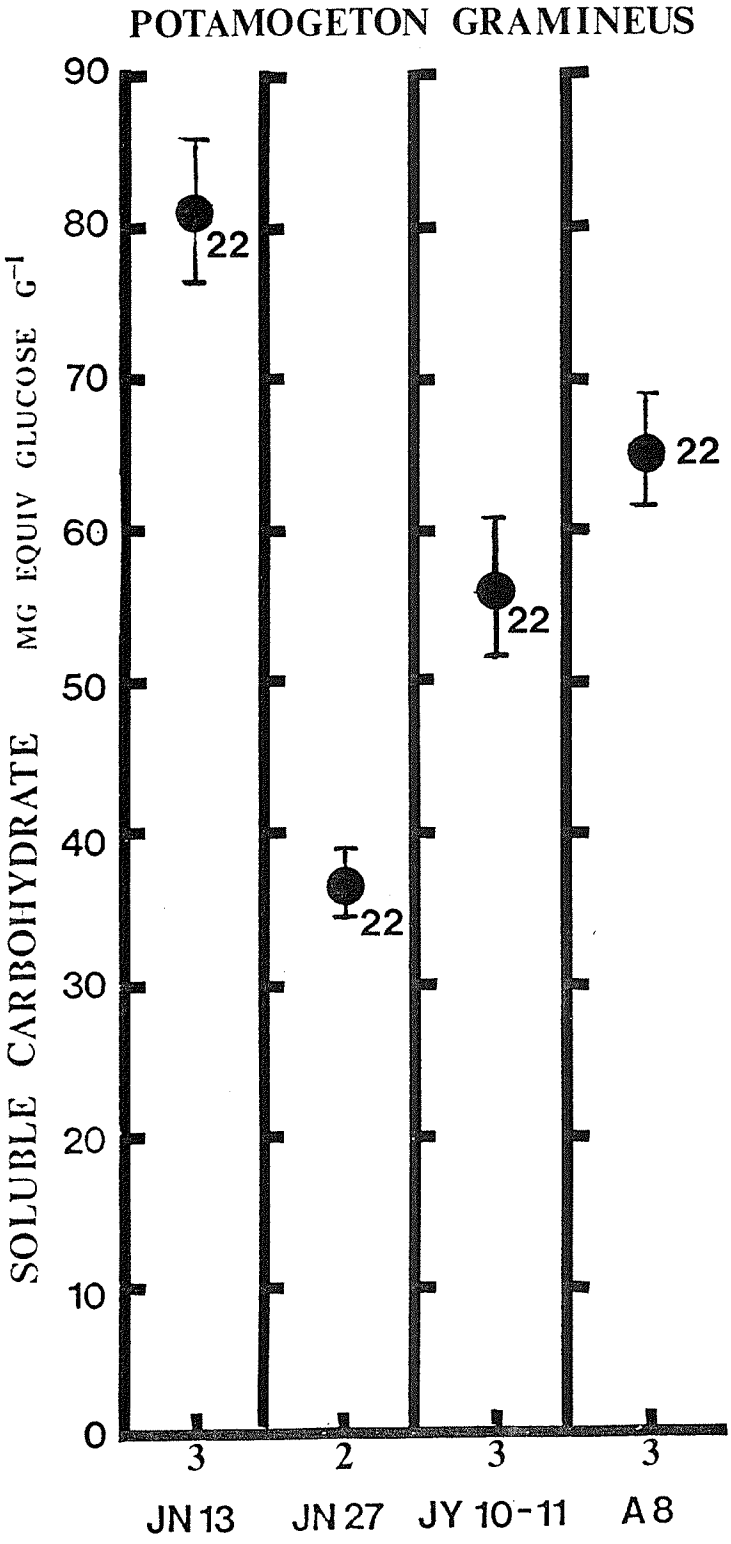

POTAMOGETON GRAMINEUS
SOLUBLE CARBOHYDRATE MG EQUIV GLUCOSE G^{-1}
90
80
70
60
50
40
30
20
10
0
22
22
22
22
3
2
3
3
JN 13
JN 27
JY 10-11
A 8

Fig. 10. Total soluble carbohydrate content in stems and leaves (closed circles) and seeds (open circle) of Potamogeton praelongus at collection sites 22 and 23 during June of the 1985 growing season. Vertical bars represent standard error. Sampling depth (in meters) is shown on the horizontal axis.

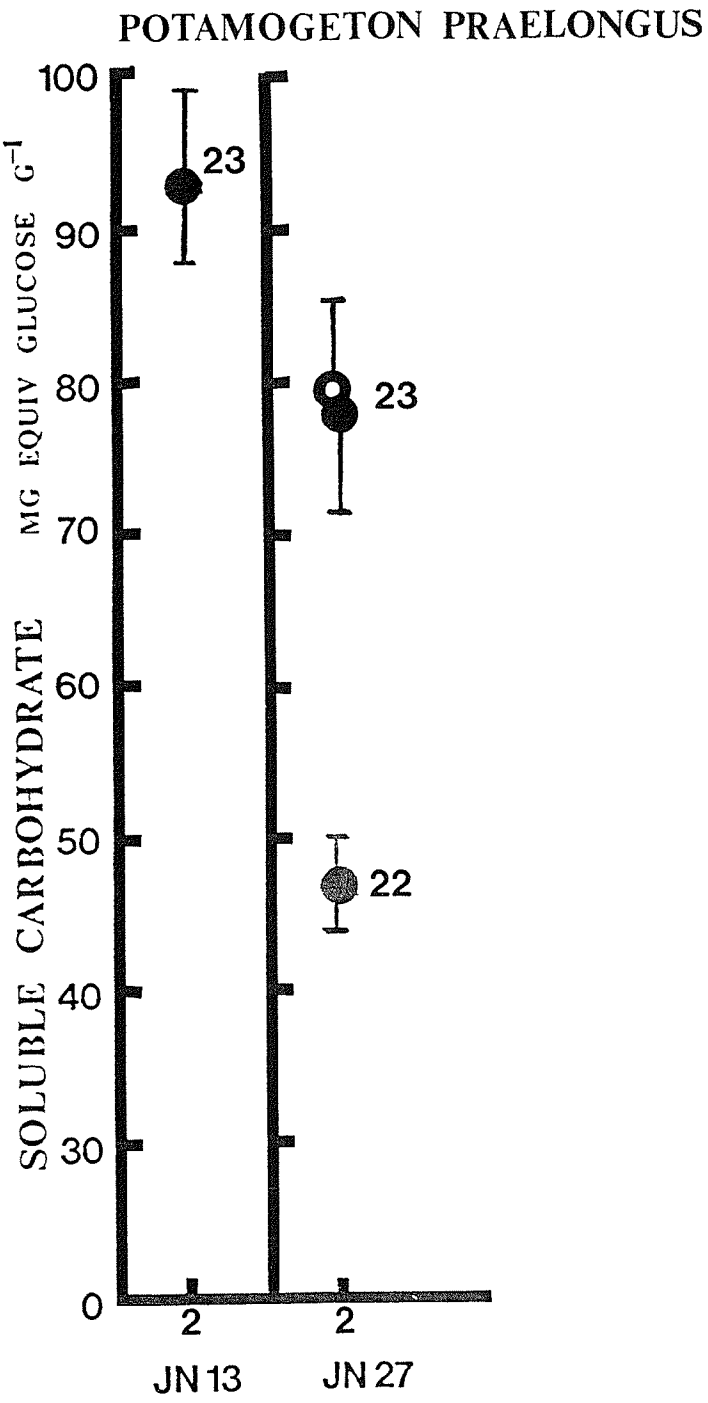

POTAMOGETON PRAELONGUS
SOLUBLE CARBOHYDRATE MG EQUIV GLUCOSE G⁻¹
100
90
80
70
60
50
40
30
0
23
23
22
2
2
JN 13
JN 27

Fig. 11. Total soluble carbohydrate content in stems and leaves (closed circles) and seeds (open circle) of Potamogeton richardsonii on various sampling dates during the 1985 growing season. Vertical bars represent standard error and numbers beside circles indicate sampling sites. Depth (in meters) for each collection time is shown on the horizontal axis.

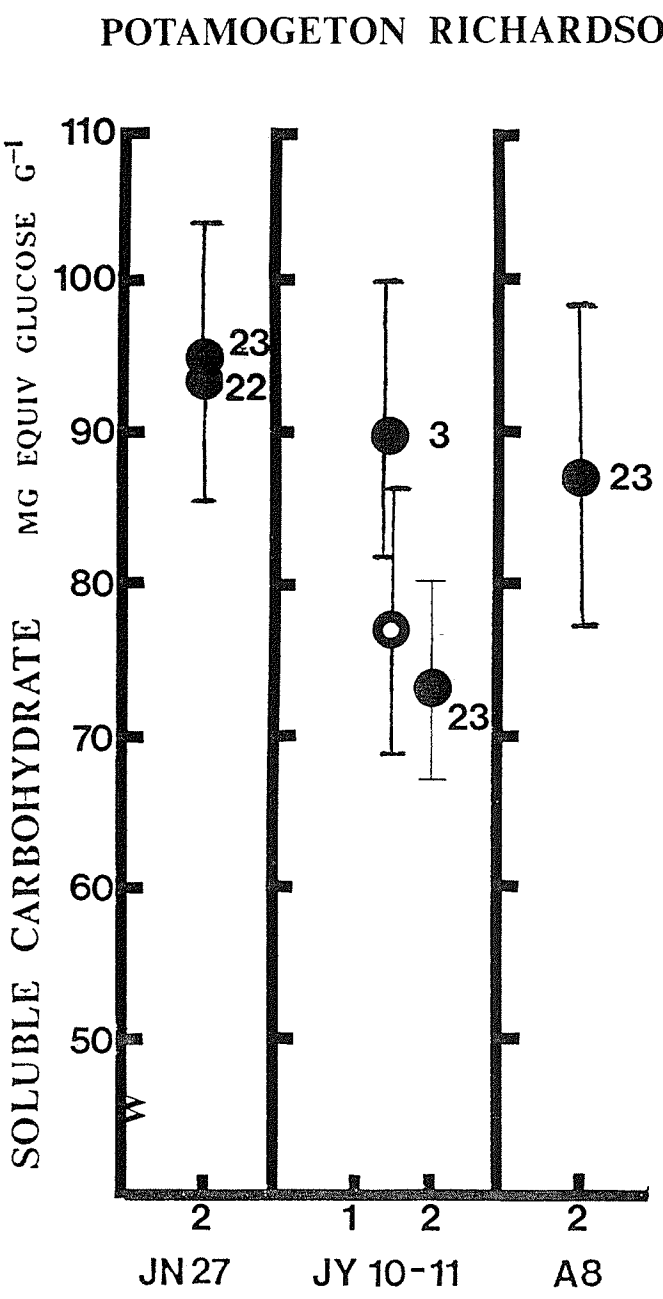

POTAMOGETON RICHARDSONII
SOLUBLE CARBOHYDRATE MG EQUIV GLUCOSE G⁻¹
110
100
90
80
70
60
50
W
23
22
3
23
23
2
1
2
2
JN 27
JY 10-11
A8

Fig. 12. Total soluble carbohydrate content of stems and leaves of Potamogeton robbinsii on various sampling dates during the 1985 growing season. Vertical bars represent standard error and numbers beside circles indicate sampling sites. Depth (in meters) for each collection time is shown on the horizontal axis.

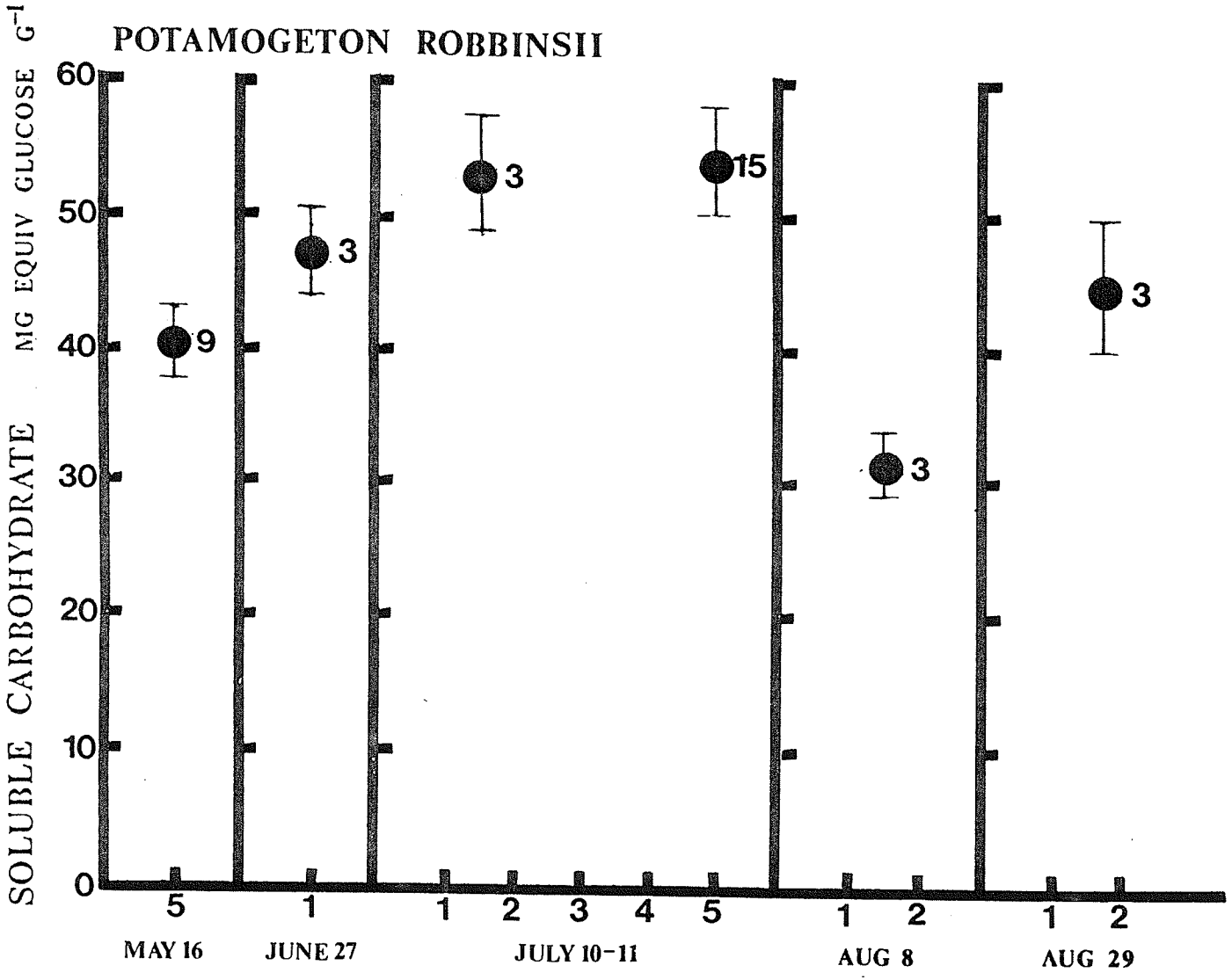

POTAMOGETON ROBBINSII
SOLUBLE CARBOHYDRATE MG EQUIV GLUCOSE G⁻¹
60
50
40
30
20
10
0
9
3
3
15
3
3
5
1
1 2 3 4 5
1 2
1 2
MAY 16
JUNE 27
JULY 10-11
AUG 8
AUG 29

Fig. 13. Total soluble carbohydrate content of stems and leaves (closed circles) and roots (open circle) of Potamogeton zosteriformis on various sampling dates during the 1985 growing season. Vertical bars represent standard error and numbers beside circles indicate sampling sites. Depth (in meters) for each collection time is shown on the horizontal axis. A statistically significant relationship between depth and total soluble carbohydrate content is shown for May 16.

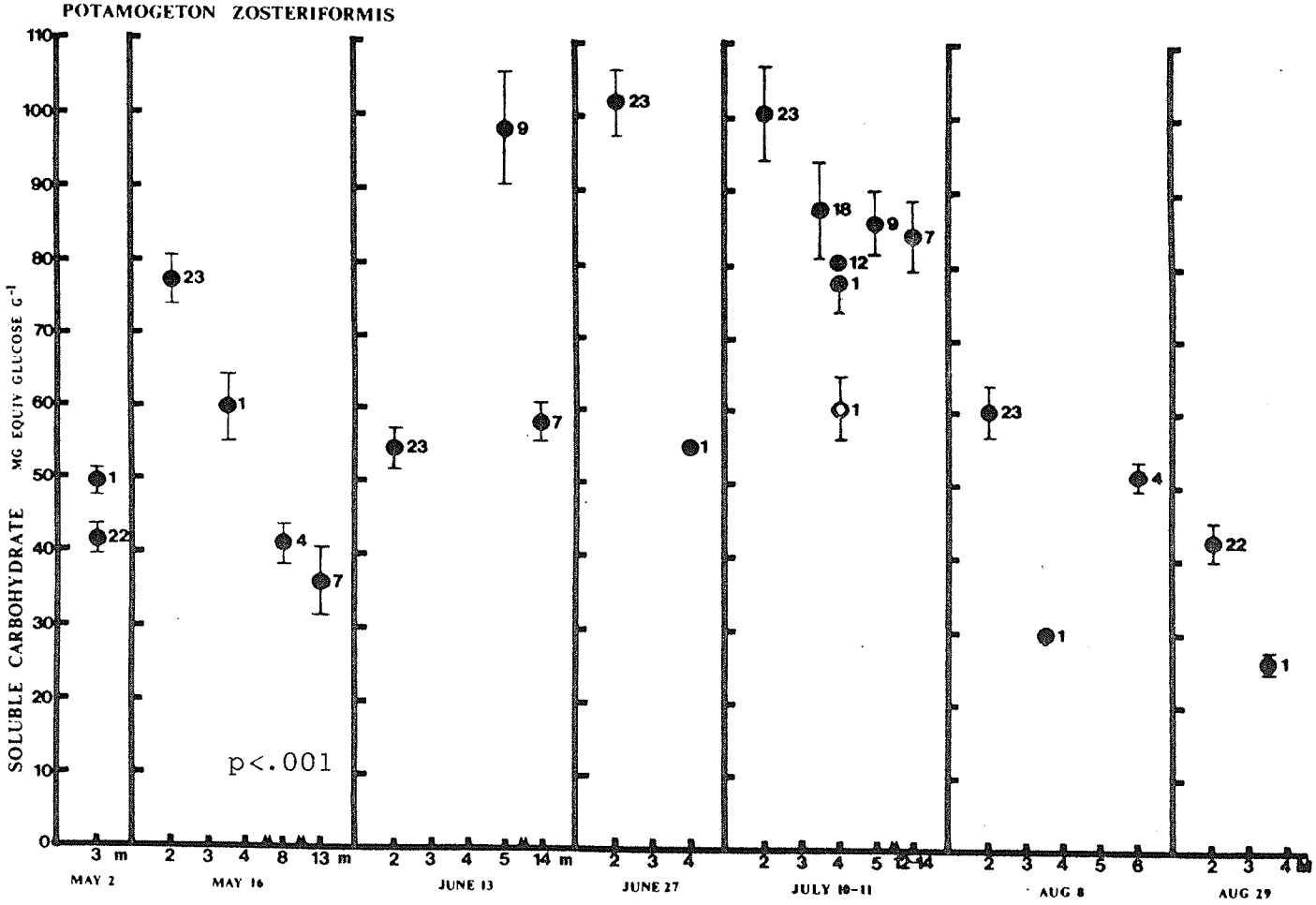

POTAMOGETON ZOSTERIFORMIS
SOLUBLE CARBOHYDRATE MG EQUIV GLUCOSE G⁻¹
p<.001
MAY 2
MAY 16
JUNE 13
JUNE 27
JULY 10-11
AUG 8
AUG 29

Table 3. Significant seasonal differences in soluble carbohydrate content of macrophytes in 1985. 1=Ap 27 2=My 2 3=My 16 4=My 30 5=Jn 13 6=Jn 27 7=Jy 10-11 8=Aug 8 9=Aug 29

Ceratophyllum demersum

ALPHA=0.05 DF=172 MSE=44.49

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
2	30	43.43	7	7
3	36	43.78	7	7
4	6	46.30	7	n.s.
5	18	42.12	7	7
6	12	39.64	7	7
7	33	54.49	2-6 8 9	2 3 5 6 8 9
8	21	44.84	7	7
9	24	44.12	7	7

Elodea canadensis

ALPHA=0.05 DF=49 MSE=142.4

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
2	9	31.30	7 8	7 8
3	9	36.35	7 8	7 8
4	9	36.73	7 8	7 8
5	6	28.38	7 8	7 8
6	3	36.04	7 8	8
7	12	57.46	2-6 8 9	2-5 8 9
8	3	90.97	2-7 9	2-7 9
9	6	24.26	7 8	7 8

Myriophyllum exalbescens

ALPHA=0.05 DF=136 MSE=127.0

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
1	6	73.41	5-7 9	6 7 9
2	18	63.99	5-7 9	6 7 9
3	18	74.90	5-9	5-9
5	3	50.18	1-3 8	3
6	18	43.24	1-3 8	1 2 3 8
7	24	42.10	1-3 8	1 2 3 8
8	18	57.05	3 5-7 9	3 6 7 9
9	24	38.55	1-3 8	1 2 3 8

Table 3 (Cont.)

Najas flexilis

ALPHA=0.05 DF=6 MSE=2.593

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
6	3	35.80	9	9
8	3	35.16	9	9
9	3	43.22	6 8	6 8

Potamogeton foliosus

ALPHA=0.05 DF=157 MSE=421.2

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
1	3	96.70	2 3 6-8	2 3 6-8
2	18	64.46	1 4 5	4 5
3	15	73.02	1 4 5 8	4 8
4	12	98.38	2 3 6-8	2 3 6-8
5	24	93.13	2 3 6-8	2 3 6-8
6	24	65.33	1 4 5	4 5
7	51	59.21	1 4 5	1 4 5
8	12	45.18	1-7	1 3-5

Potamogeton gramineus

ALPHA=0.05 DF=17 MSE=5.485

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
5	6	80.36	6-8	6-8
6	6	36.31	5 7 8	5 7 8
7	3	55.70	5 6 8	5 6 8
8	6	64.58	5-7	5-7

Potamogeton praelongus

ALPHA=0.05 DF=19 MSE=208.3

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
5	6	92.82	6	6
6	12	62.39	5	5

Table 3 (Cont.)

Potamogeton richardsonii

ALPHA=0.05 DF=24 MSE=49.12

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
6	6	93.93	n.s.	n.s.
7	9	83.99	n.s.	n.s.
8	6	86.56	n.s.	n.s.

Potamogeton robbinsii

ALPHA=0.05 DF=25 MSE=6.763

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
3	6	40.18	6-8	6-8
6	3	47.10	3 7 8	3 7 8
7	9	53.25	3 6 8 9	3 6 8 9
8	6	31.10	3 6 7 9	3 6 7 9
9	6	44.48	7 8	7 8

Potamogeton zosteriformis

ALPHA=0.05 DF=86 MSE=202.1

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
2	12	40.97	5-7	5-7
3	12	53.40	5-7 9	6 7
5	9	69.91	2 3 8 9	2 8 9
6	6	78.11	2 3 8 9	2 3 8 9
7	30	84.44	2 3 8 9	2 3 8 9
8	15	50.35	5-7 9	5-7
9	6	33.96	3 5-8	5-7

Table 4. Total soluble carbohydrate content for plant organs of 6 macrophyte species during the 1985 season. Means with the same letter were not significantly different, as determined in SNK and Tukey's tests at alpha=0.05.

ELODEA CANADENSIS				
DATE	N	TISSUE	MEAN	
May 30	3	Roots	37.85	A
	6	Shoots/leaves	36.16	A
MYRIOPHYLLUM EXALBESCENS				
DATE	N	TISSUE	MEAN	
June 27	6	Roots	69.75	A
	15	Shoots/leaves	45.22	B
August 8	6	Roots	76.25	A
	9	Shoots/leaves	51.47	B
August 29	3	Roots	68.70	A
	6	Shoots/leaves	53.03	B
POTAMOGETON FOLIOSUS				
DATE	N	TISSUE	MEAN	
June 27	6	Roots	47.62	A
	12	Shoots/leaves	52.26	A
POTAMOGETON PRAELONGUS				
DATE	N	TISSUE	MEAN	
June 27	3	Seeds	78.79	A
	6	Shoots/leaves	78.02	A
POTAMOGETON RICHARDSONII				
DATE	N	TISSUE	MEAN	
July 10-11	6	Seeds	76.57	A
	6	Shoots/leaves	89.42	A
POTAMOGETON ZOSTERIFORMIS				
DATE	N	TISSUE	MEAN	
July 10-11	3	Roots	60.21	A
	6	Shoots/leaves	77.43	B

Fig. 14. Total soluble carbohydrate content in stems and leaves of Ceratophyllum demersum at selected depths during the 1985 growing season. Sampling dates are indicated on the horizontal axis. Vertical bars represent standard error.

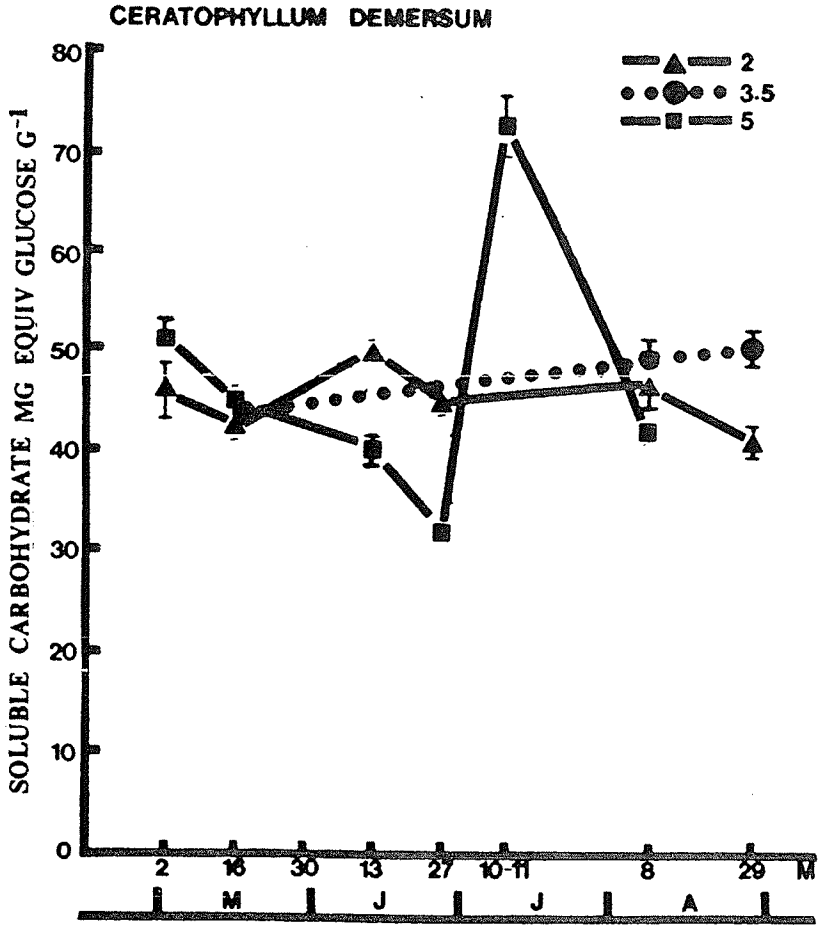

CERATOPHYLLUM DEMERSUM
SOLUBLE CARBOHYDRATE MG EQUIV GLUCOSE G-1
80
70
60
50
40
30
20
10
0
2
3.5
5
2
16
30
13
27
10-11
8
29
M
M
J
J
A

Fig. 15. Total soluble carbohydrate content in stems and leaves of Myriophyllum exalbescens at selected depths during the 1985 growing season. Sampling dates are indicated on the horizontal axis. Vertical bars represent standard error.

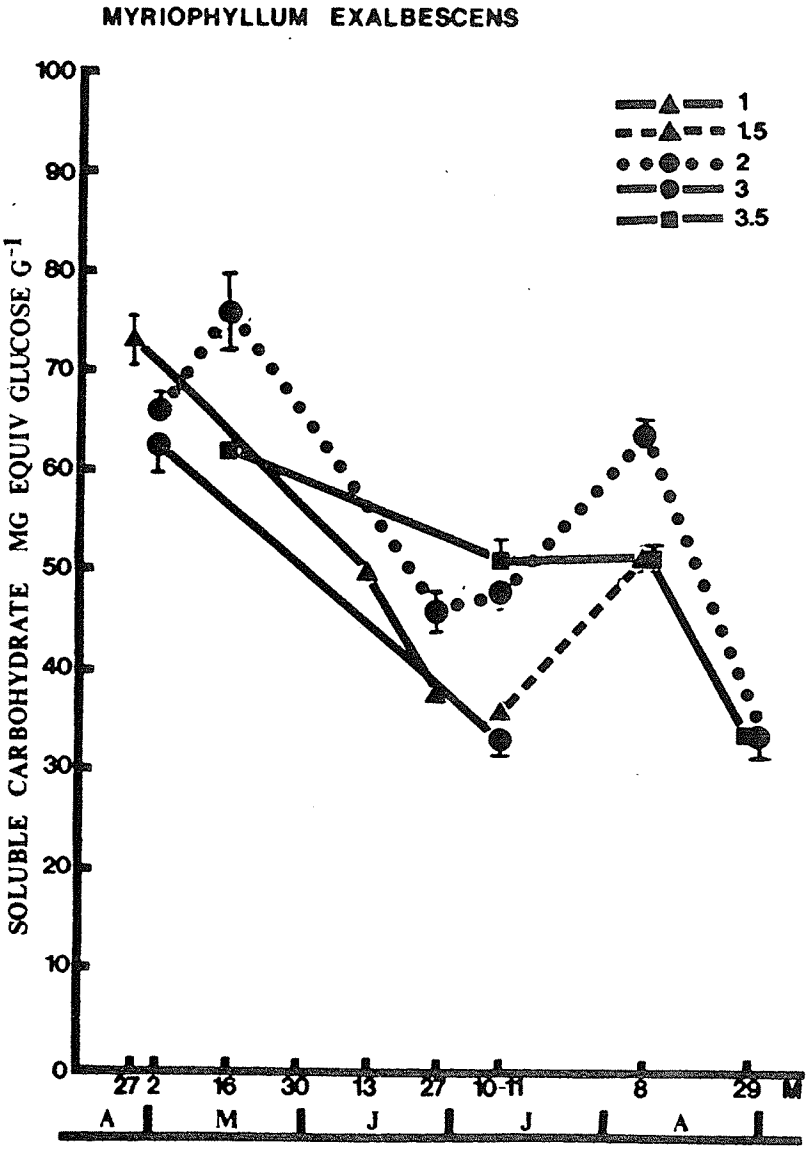

MYRIOPHYLLUM EXALBESCENS
SOLUBLE CARBOHYDRATE MG EQUIV GLUCOSE G-1
100
90
80
70
60
50
40
30
20
10
0
1
1.5
2
3
3.5
27 2
16
30
13
27
10-11
8
29
M
A
M
J
J
A

Fig. 16. Total soluble carbohydrate content in stems and leaves of Potamogeton foliosus at selected depths during the 1985 growing season. Sampling dates are indicated on the horizontal axis. Vertical bars represent standard error.

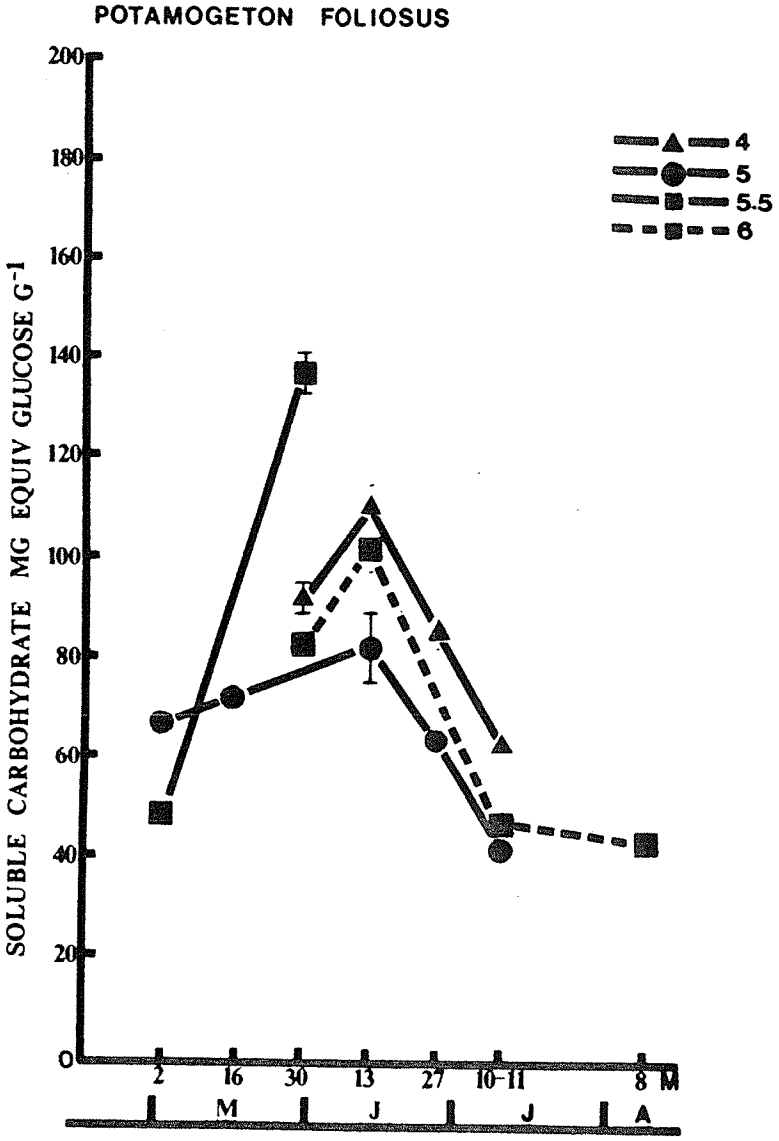

POTAMOGETON FOLIOSUS
SOLUBLE CARBOHYDRATE MG EQUIV GLUCOSE G-1
200
180
160
140
120
100
80
60
40
20
0
4
5
5.5
6
2
16
30
13
27
10-11
8 M
M
J
J
A

Fig. 17. Total soluble carbohydrate content in stems and leaves of Potamogeton zosteriformis at selected depths during the 1985 growing season. Sampling dates are indicated on the horizontal axis. Vertical bars represent standard error.

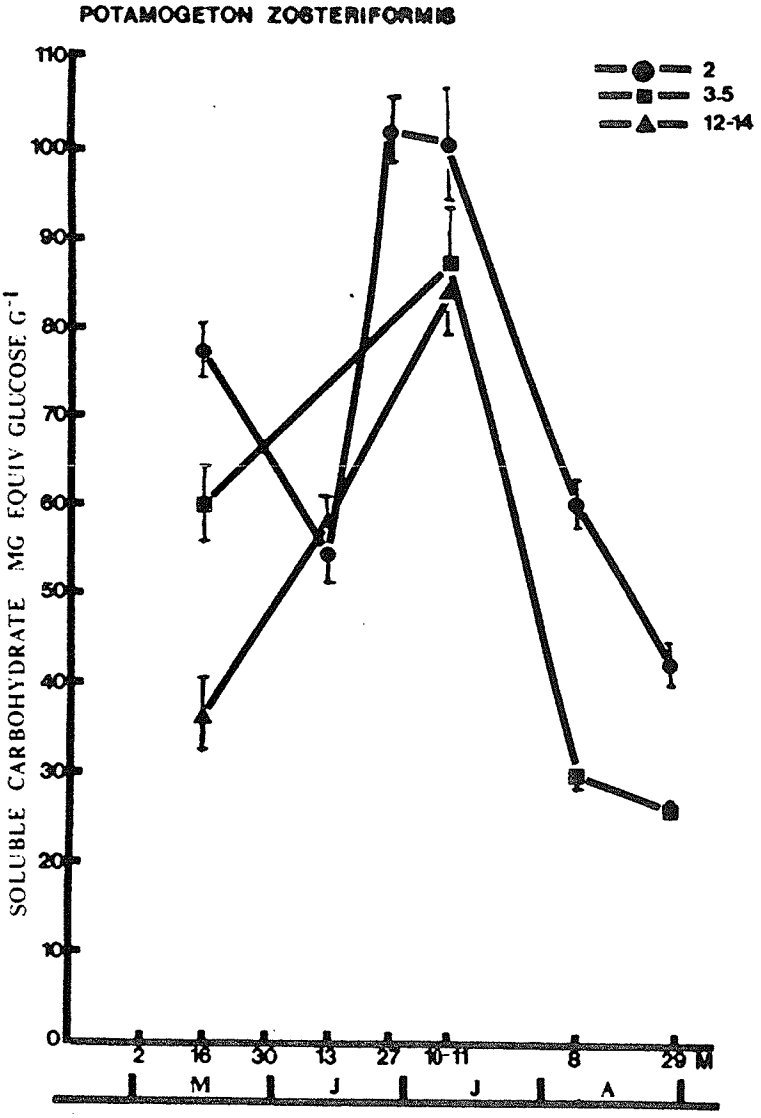

POTAMOGETON ZOSTERIFORMIS
2
3.5
12-14
SOLUBLE CARBOHYDRATE MG EQUIV GLUCOSE G-1
110
100
90
80
70
60
50
40
30
20
10
0
2
16
30
13
27
10-11
8
29 M
M
J
J
A

Table 5. Significant inter-site differences in soluble carbohydrate content of macrophytes (mg g^{-1}) during the 1985 season. Means with the same letter were not significantly different, as determined in SNK and Tukey's tests at alpha=0.05.

DATE	CERATOPHYLLUM DEMERSUM DEPTH(M)	SITE	N	MEAN	
May 2	3	1	6	42.4	A
		22	6	38.2	B
May 16	2	23	6	43.5	A
		22	6	41.6	A
	3.5	2	6	45.1	A
		1	6	42.2	A
	5	8	3	45.6	A
		9	3	44.6	A
Jn 13	5	2	3	44.7	A
		9	6	37.7	B
Jy 10-11	4	14	3	60.4	A
		1	3	57.4	A
	6	20	6	63.9	A
		11	3	40.8	B
		19	3	36.2	B
		5	3	35.2	B
Aug 8	6.5	6	3	47.1	A
		5	3	37.8	B

DATE	MYRIOPHYLLUM EXALBESCENS DEPTH(M)	SITE	N	MEAN	
May 2	3	22	6	72.3	A
		1	6	53.4	B
May 16	3	23	3	81.4	A
		22	6	71.2	A
Jn 27	2	23	6	50.2	A
		22	6	41.7	B
Jy 10-11	2	17	6	51.2	A
		23	3	42.2	B
Aug 29	2	22	6	44.0	A
		23	6	23.4	B

Table 5.(cont.)

DATE	DEPTH(M)	SITE	N	MEAN	
POTAMOGETON FOLIOSUS					
May 2	5	2	6	69.4	A
		4	6	64.0	A
May 16	5	6	6	80.4	A
		9	6	70.2	B
		8	3	63.9	B
Jn 13	5	9	3	103	A
		2	6	60.2	B
	6	8	3	108	A
		6	6	95.4	A
Jn 27	5	2	6	71.4	A
		6	6	55.2	B
Jy 10-11	5	9	3	43.8	A
		15	6	42.7	A
		6	6	40.2	A
	6	10	6	55.0	A
		13	3	51.1	A
		11	6	44.4	B
		16	6	34.4	C
POTAMOGETON PRAELONGUS					
Jn 27	2	23	6	78.0	A
		22	6	46.8	B
POTAMOGETON RICHARDSONII					
Jn 27	2	23	3	94.6	A
		22	3	93.3	A
POTAMOGETON ZOSTERIFORMIS					
May 2	3	22	6	41.2	A
		1	6	40.7	A
Jy 10-11	4	12	6	80.3	A
		1	6	77.4	A

Table 6. Significant interspecific differences in soluble carbohydrate content of stems and leaves for each sampling date during the 1985 growing season. Significant differences, as determined in SNK and Tukey's tests, are indicated by X's.

MAY 2	*P. foliosus*	*M. exalbescens*	*C. demersum*	*P. zosteriformis*	*E. canadensis*	$\bar{X}$
P. foliosus						64.46
M. exalbescens						63.99
C. demersum						43.43
P. zosteriformis	X	X				40.97
E. canadensis	X	X	X	X		31.30

MAY 16	*M. exalbescens*	*P. foliosus*	*P. zosteriformis*	*C. demersum*	*P. robbinsii*	*E. canadensis*	$\bar{X}$
M. exalbescens							74.90
P. foliosus							73.02
P. zosteriformis	X	X					53.40
C. demersum	X	X	X				43.78
P. robbinsii	X	X	X				40.18
E. canadensis	X	X	X				36.35

Table 6 (Cont.)

MAY 30	*P.foliosus*	*C.demersum*	*E.canadensis*	$\bar{X}$
P.foliosus				98.38
C.demersum	X			46.30
E.canadensis	X			36.73

JUNE 13	*P.foliosus*	*P.praelongus*	*P.gramineus*	*P.zosteriformis*	*M.exalbescens*	*C.demersum*	*E.canadensis*	$\bar{X}$
P.foliosus								93.13
P.praelongus								92.82
P.gramineus								80.36
P.zosteriformis	X							69.91
M.exalbescens	X	X						50.12
C.demersum	X	X	X	X				42.12
E.canadensis	X	X	X	X				28.38

Table 6 (Cont.)

JUNE 27	P.richardsonii	P.zosteriformis	P.foliosus	P.praelongus	P.robbinsii	M.exalbescens	C.demersum	P.gramineus	E.canadensis	N.flexilis	$\bar{X}$
P.richardsonii											93.93
P.zosteriformis											78.11
P.foliosus	X										65.33
P.praelongus	X										62.39
P.robbinsii	X										47.10
M.exalbescens	X	X									43.24
C.demersum	X	X	X	X							39.64
P.gramineus	X	X	X	X							36.31
E.canadensis	X	X	X								36.04
N.flexilis	X	X	X								35.80

JULY 10-11	P.zosteriformis	P.richardsonii	P.foliosus	E.canadensis	P.gramineus	C.demersum	P.robbinsii	M.exalbescens	$\bar{X}$
P.zosteriformis									84.44
P.richardsonii									83.99
P.foliosus	X	X							59.21
E.canadensis	X	X							57.46
P.gramineus									55.70
C.demersum	X	X							54.49
P.robbinsii	X	X							53.25
M.exalbescens	X	X							42.10

Table 6 (Cont.)

AUGUST 8	E.canadensis	P.richardsonii	P.gramineus	M.exalbescens	P.zosteriformis	P.foliosus	C.demersum	N.flexilis	P.robbinsii	$\bar{X}$
E.canadensis										90.97
P.richardsonii										86.56
P.gramineus	X	X								64.58
M.exalbescens	X	X								57.05
P.zosteriformis	X	X	X	X						50.35
P.foliosus	X	X	X	X						45.18
C.demersum	X	X	X	X						44.84
N.flexilis	X		X	X						35.16
P.robbinsii	X	X	X	X	X	X	X			31.10

AUGUST 29	P.robbinsii	C.demersum	N.flexilis	M.exalbescens	P.zosteriformis	E.canadensis	$\bar{X}$
P.robbinsii							44.48
C.demersum							44.12
N.flexilis							43.22
M.exalbescens							38.55
P.zosteriformis							33.96
E.canadensis	X	X		X			24.26

B. Starch

Using selected samples of all species, it was found that the series of 4 alcohol washes was efficient in removing soluble carbohydrate prior to starch determination. Based on a total of 5 washes, the cumulative proportion of soluble carbohydrate removed in the first 4 washes was large, varying from 99.2 % in P. richardsonii to 100 % in N. flexilis (Table 7). Correction factors, subtracted from determined starch values, had a mean value of 0.33 mg/g for the 10 macrophyte species.

Starch content during the 1985 growing season showed variation in all species (Table 8). Mean seasonal values ranged from 36.6 mg/g for P. gramineus to 144 mg/g for P. richardsonii. There was no apparent relationship between vertical distribution and mean starch content.

Starch content of macrophytes at various depths and stations during the 1985 season in shown in Figs. 18 to 27. Linear regression analysis for the sampling dates revealed the following negative correlations between starch content and depth: C. demersum on June 13 (R^2=0.49, $p<0.02$, n=12) and August 29 (R^2=0.83, $p<0.001$, n=12), P. foliosus on May 2 (R^2=0.81, $p<0.001$, n=12), May 30 (R^2=0.72, $p<0.005$, n=9), June 27 (R^2=0.56, $p<0.01$, n=12), and July 10-11 (R^2=0.28, $p<0.005$, n=27), and P. zosteriformis on August 8 (R^2=0.48, $p<0.05$, n=9). Negative relationships with depth were also suggested for M. exalbescens on May 2 and for P. zosteriformis on June 27 and August 29. These relationships were not

significant due to insufficient depth representation. Positive correlations of starch content with depth were observed for M. exalbescens on August 8 (R^2=0.79, $p<0.005$, n=9) and August 29 (R^2=0.87, $p<0.001$, n=12). Positive relationships with depth were also suggested for P. zosteriformis on July 10-11, M. exalbescens on July 10-11, and P. foliosus on August 8. Again limited depth representation prevented these from being significant. Vertical differences were not examined in E. canadensis, N. flexilis, P. gramineus, P. praelongus, P. richardsonii, and P. robbinsii due to small sample size.

Mean starch content for each species and sampling date was analyzed for differences in SNK and Tukey's tests (Table 9). Only shoots and leaves were available for analysis. The starch content of C. demersum tended to decrease seasonally. Levels on May 2 and May 16 were significantly higher than June, July, and August 8 values. There were few significant seasonal differences in mean starch levels for M. exalbescens in 1985, with the mean on June 27 significantly exceeding the June 13 level. P. foliosus showed a tendency to accumulate starch after a seasonal minimum in mid-May. The mean starch content for June 27, July 10-11, and August 8 was significantly higher than the May 16 level. An overall seasonal increase in starch content was observed in P. zosteriformis. The mean value for August 29 was significantly higher than in June and July. The August 8 level was significantly higher than in June.

The small number of sampling dates made it difficult to fully examine seasonal trends in the remaining species, although some significant differences were observed. The starch content of N. flexilis was significantly higher on August 8 than on June 27. In P. gramineus the mean starch level for June 13 and July 10-11 was significantly greater than on August 8. The starch content of P. praelongus was significantly higher on June 13 than on June 27. Levels in P. richardsonii on June 27 significantly exceeded the mean for the July sampling date.

Starch content in C. demersum, M. exalbescens, P. foliosus, and P. zosteriformis was examined at selected depths (Figs. 28 to 31). Starch levels in C. demersum tended to decline sharply from early to mid-season at 2, 3.5, and 5 m. Samples from 2 m showed a steady accumulation from June 13 to the end of August. Starch content at 3.5 m also increased, from August 8 to August 29. Starch in M. exalbescens showed inconsistent seasonal patterns over a depth range of 1 to 3.5 m, and levels tended to increase with depth. In P. foliosus, starch showed an overall seasonal increase at 4 and 6 m, and a similar accumulation with time was suggested in P. zosteriformis at depths of 2 and 3.5 m.

Variation in starch content was observed for macrophytes growing at the same depth in different locations during the 1985 growing season (Table 10). There was a greater number of significant differences in starch than in soluble carbohydrate, although the sample number for starch analysis

was smaller. Starch content in M. exalbescens was significantly greater at station 22 than at station 23 on May 16, June 27, and August 29. In C. demersum, the starch level was significantly higher at site 23 than at site 22 on May 16. Plants at station 9 contained significantly more starch than at station 2 for C. demersum and P. foliosus on June 13. Starch content in P. foliosus was significantly higher at site 8 than at site 6 on May 16, while the reverse significant relationship occurred for this species on June 13.

Interspecific differences in mean starch content were observed for some of the sampling dates during 1985 (Table 11). Comparisons were made using SNK and Tukey's tests (Appendix). No significant differences were found for the 4 species represented on May 2 and the 5 species represented on May 16. The starch content of P. praelongus was significantly greater than all other species in June 13. P. robbinsii and P. richardsonii showed the greatest number of significant differences with other species on June 27, with the lowest and highest starch content, respectively. Relatively high starch content was observed in P. foliosus and relatively low levels in C. demersum on July 10-11, and these species had the greatest number of significant differences on this date. On August 8, P. foliosus and P. zosteriformis contained more starch than all other species, with some significant comparisons. P. zosteriformis also contained significantly more starch than other species on August 29. P. gramineus had lower levels of starch than all other species

on June 13, July 10-11, and August 8 and gave some significant comparisons with other species.

Table 7. Proportion of soluble carbohydrate removed after 4 of a total of 5 alcohol washes and corresponding correction factors for starch content.

Species	N	Percent Soluble Carbohydrate	Correction Factor (mg/g)
Najas flexilis	6	100	0.00
Potamogeton zosteriformis	9	99.9	0.07
Elodea canadensis	9	99.6	0.20
Potamogeton foliosus	9	99.6	0.23
P. praelongus	6	99.6	0.40
Ceratophyllum demersum	9	99.5	0.23
Myriophyllum exalbescens	9	99.5	0.23
Potamogeton gramineus	9	99.5	0.30
P. robbinsii	9	99.3	1.00
P. richardsonii	6	99.2	0.60

Table 8 . Overall seasonal starch content (mg g^{-1}) of macrophytes during the 1985 season. N represents the number of samples studied.

Species	Starch Range	Mean	N	Depth Range (m)	Mean Depth (m)
Ceratophyllum demersum	16.4 - 165	56.3	31	1 - 6.5	4.0
Elodea canadensis	37.8 - 170	104	9	1 - 13	3.1
Myriophyllum exalbescens	21.0 - 194	92.8	21	1 - 13	2.7
Najas flexilis	94.5 - 126	109	2	1 - 1.5	1.2
Potamogeton foliosus	36.7 - 228	118	30	3 - 6.5	5.0
P. gramineus	30.9 - 40.3	36.6	3	2 - 3	2.7
P. praelongus	90.1 - 147	118	2	---	2.0
P. richardsonii	101 - 188	144	2	1.5 - 2	1.8
P. robbinsii	25.3 - 132	82.2	6	1 - 5	2.6
P. zosteriformis	23.9 - 174	110	12	2 - 14	4.1

Fig. 18. Starch content in stems and leaves of Ceratophyllum demersum on various sampling dates during the 1985 growing season. Vertical bars represent standard error and numbers beside circles indicate sampling sites. Depth (in meters) for each collection time is shown on the horizontal axis. Statistically significant relationships between depth and starch content are shown for June 13 and August 29.

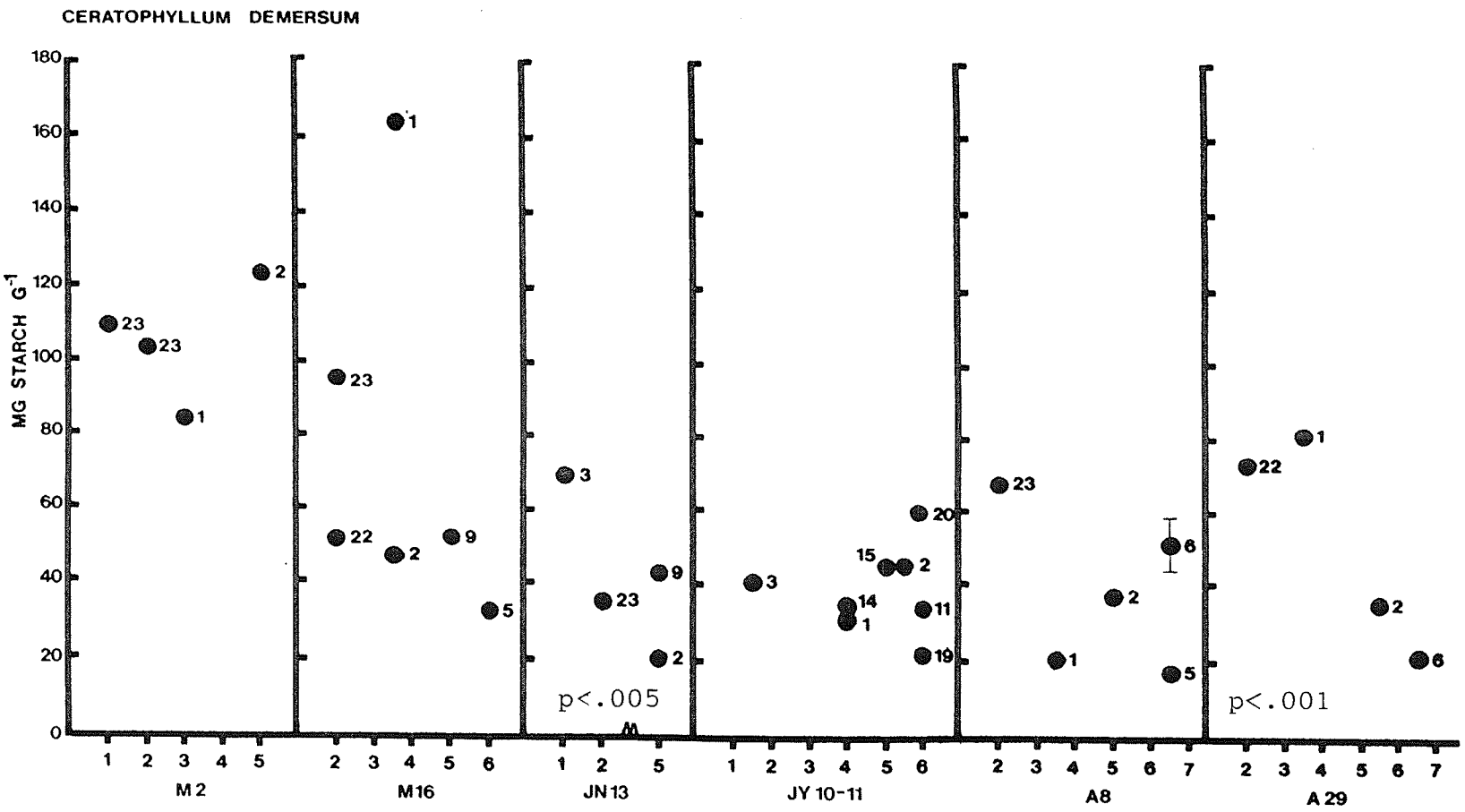

CERATOPHYLLUM DEMERSUM
MG STARCH G-1
180
160
140
120
100
80
60
40
20
0
M2
M16
JN13
JY 10-11
A8
A29
p<.005
p<.001

Fig. 19. Starch content in stems and leaves of Elodea canadensis on various sampling dates during the 1985 growing season. Numbers beside circles indicate sampling sites. Depth (in meters) for each collection time is shown on the horizontal axis.

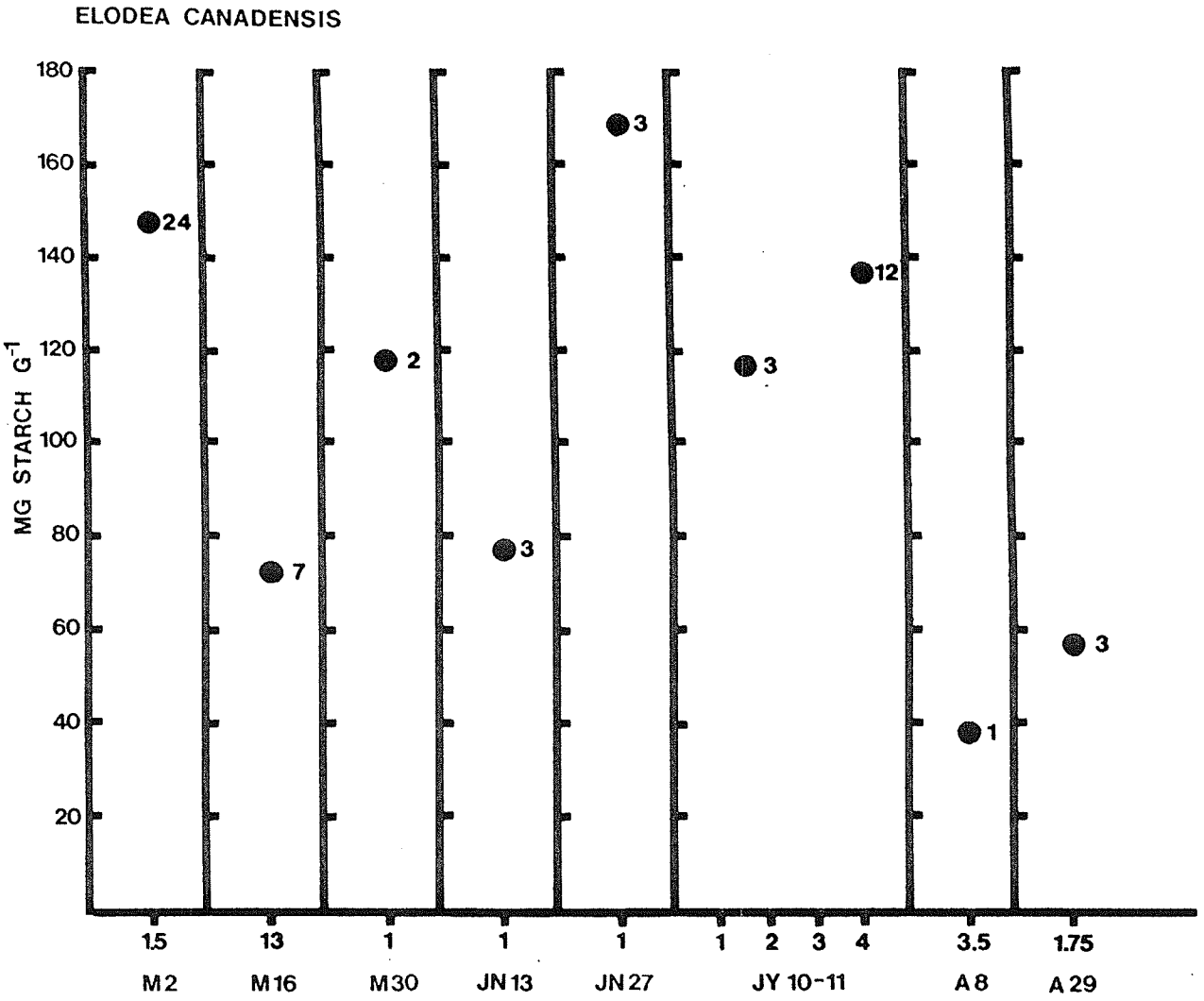

ELODEA CANADENSIS
MG STARCH G-1
180
160
140
120
100
80
60
40
20
24
7
2
3
3
3
12
1
3
1.5
M2
13
M16
1
M30
1
JN13
1
JN27
1
2
3
4
JY 10-11
3.5
A8
1.75
A29

Fig. 20. Starch content in stems and leaves of Myriophyllum exalbescens on various sampling dates during the 1985 growing season. Vertical bars represent standard error and numbers beside circles indicate sampling sites. Depth (in meters) for each collection time is shown on the horizontal axis. Statistically significant relationships between depth and starch content are shown for August 8 and August 29.

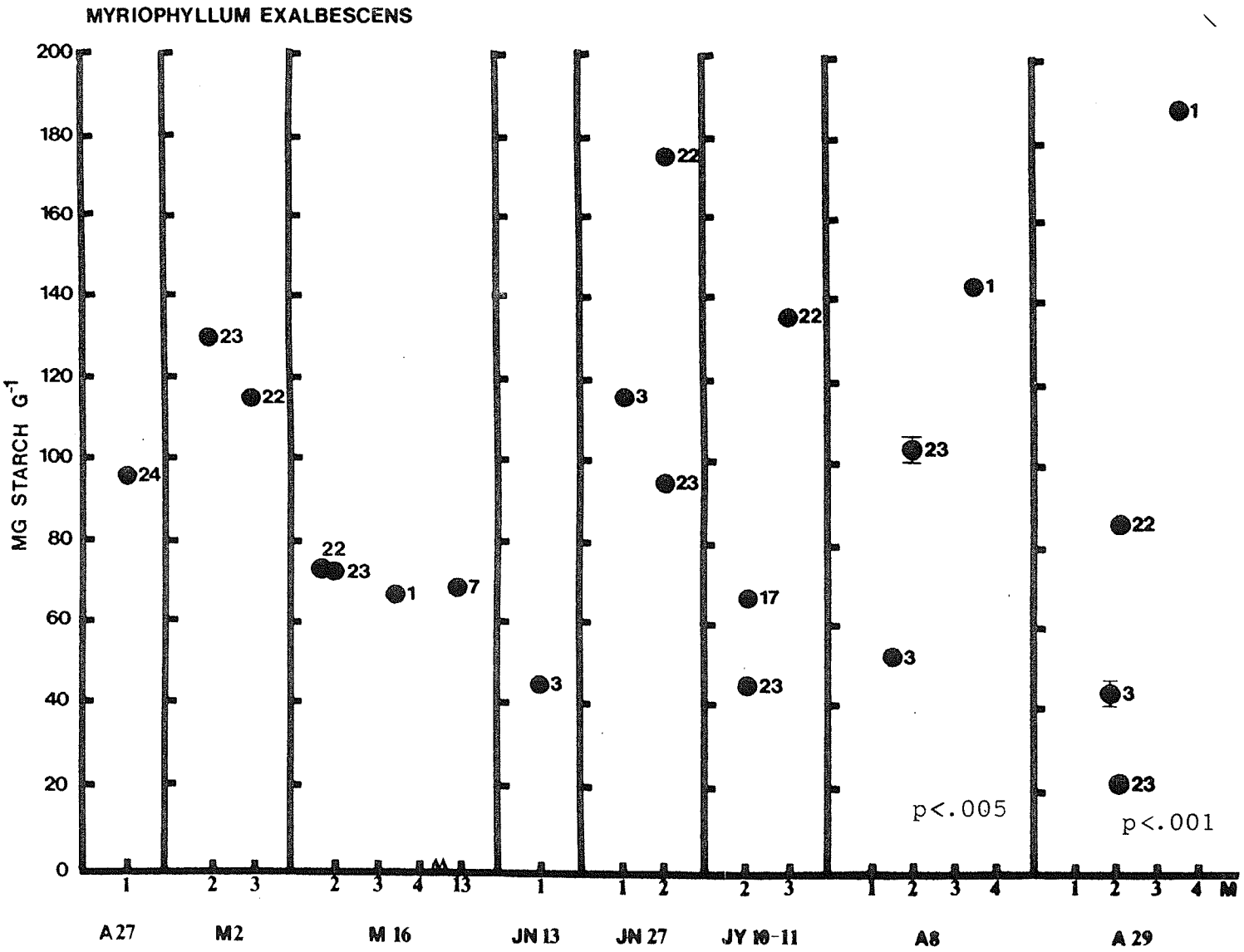

MYRIOPHYLLUM EXALBESCENS
MG STARCH G-1
200
180
160
140
120
100
80
60
40
20
0
24
23
22
22
23
1
7
3
22
23
3
22
17
23
1
22
23
1
22
3
3
23
p<.005
p<.001
1 2 3 2 3 4 13 1 1 2 2 3 1 2 3 4 1 2 3 4 M
A 27
M2
M 16
JN 13
JN 27
JY 10-11
A8
A 29

Fig. 21. Starch content in stems and leaves of Najas flexilis at sampling site 3 during the 1985 growing season. Depth (in meters) for the 2 collection dates is shown on the horizontal axis.

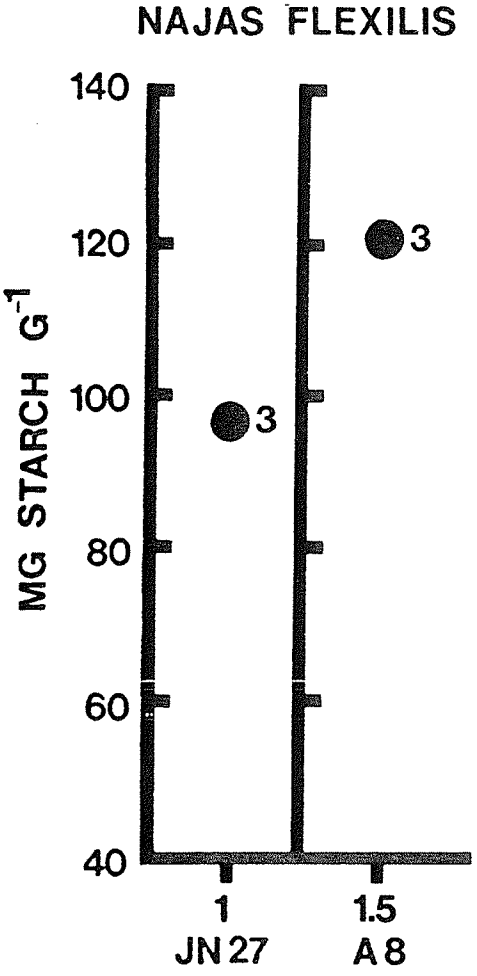

NAJAS FLEXILIS
140
120
100
80
60
40
MG STARCH G^{-1}
3
3
1
JN 27
1.5
A 8

Fig. 22. Starch content in stems and leaves of Potamogeton foliosus on various sampling dates during the 1985 growing season. Vertical bars represent standard error and numbers beside circles indicate sampling sites. Depth (in meters) for each collection time is shown on the horizontal axis. Statistically significant relationships between depth and starch content are shown for May 2, May 30, June 27, and July 10-11.

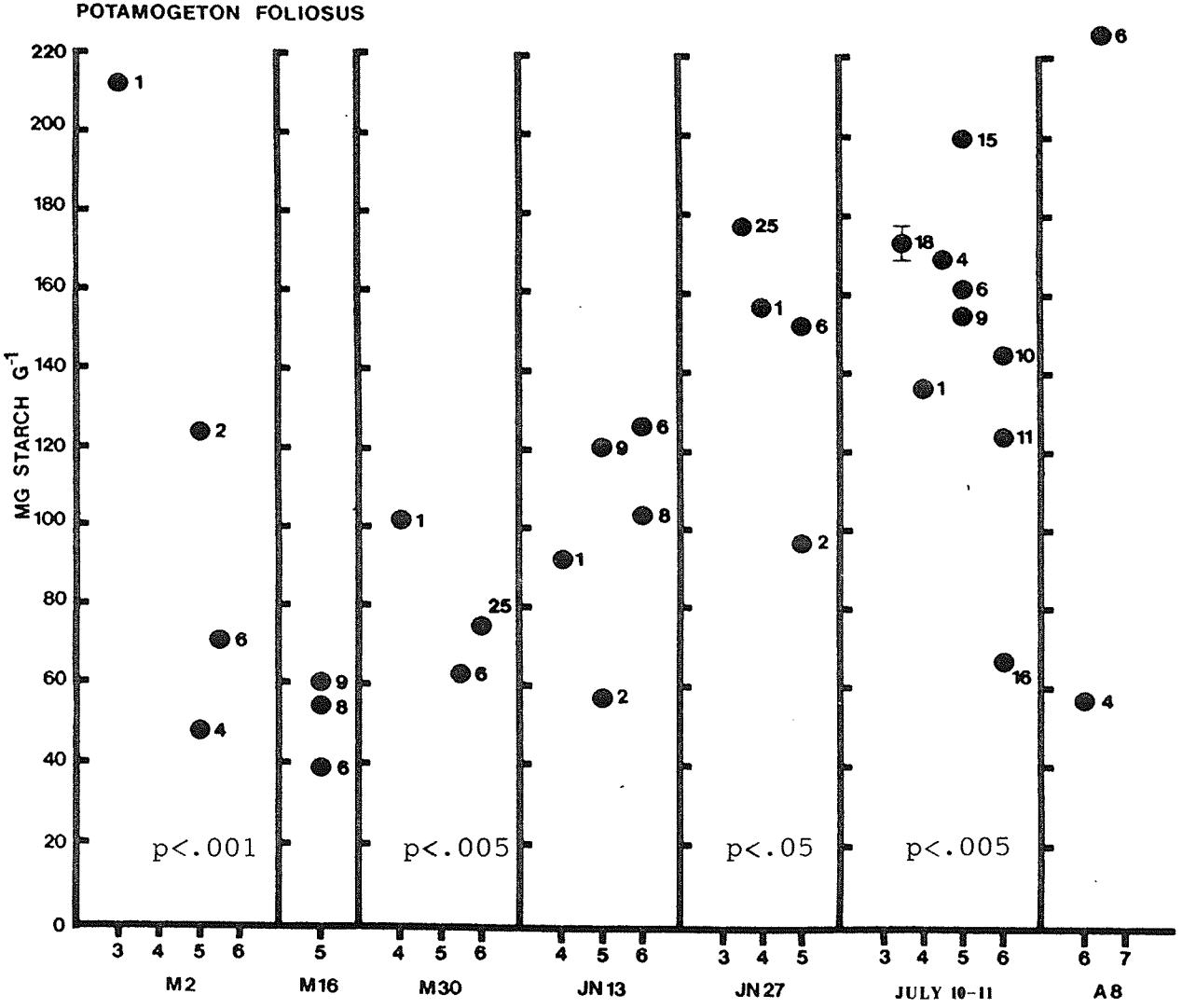

POTAMOGETON FOLIOSUS
MG STARCH G-1
220
200
180
160
140
120
100
80
60
40
20
0
p<.001
p<.005
p<.05
p<.005
M2
M16
M30
JN13
JN27
JULY 10-11
A8

Fig. 23. Starch content in stems and leaves of Potamogeton gramineus at sampling site 22 on various dates during the 1985 growing season. Depth (in meters) for each collection time is indicated on the horizontal axis.

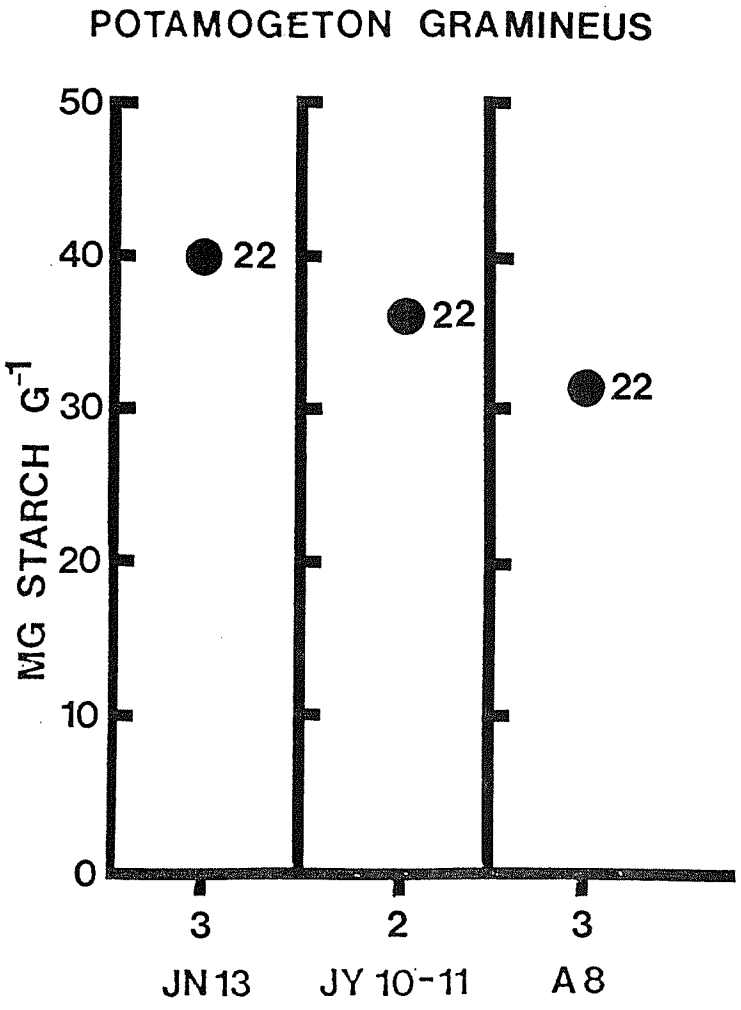

POTAMOGETON GRAMINEUS
MG STARCH G-1
50
40
30
20
10
0
22
22
22
3
2
3
JN 13
JY 10-11
A 8

Fig. 24. Starch content in stems and leaves of Potamogeton praelongus at sampling site 23 during June of the 1985 growing season. Sampling depth (in meters) is indicated on the horizontal axis.

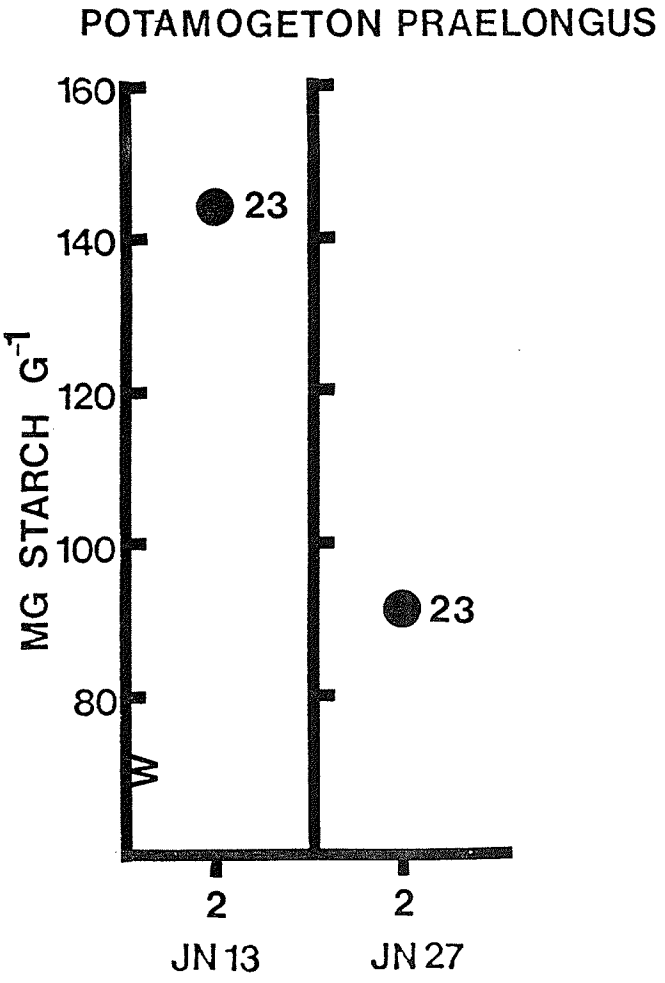

POTAMOGETON PRAELONGUS
160
140
120
100
80
MG STARCH G-1
W
23
23
2
2
JN 13
JN 27

Fig. 25. Starch content in stems and leaves of Potamogeton richardsonii at sampling sites 22 and 3 during the 1985 growing season. Collection depth (in meters) is indicated on the horizontal axis.

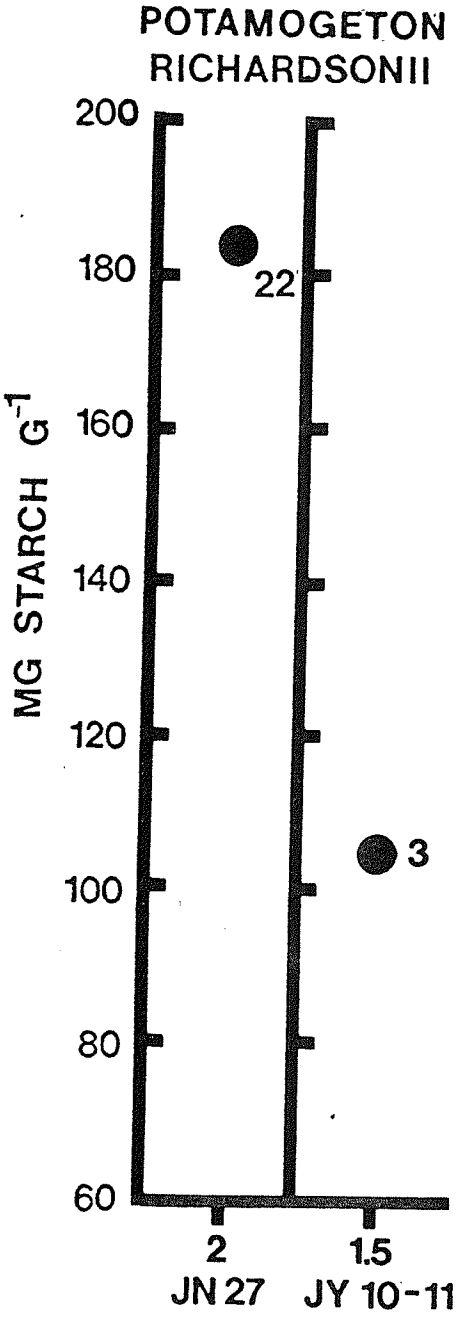

POTAMOGETON
RICHARDSONII
MG STARCH G^{-1}
200
180
160
140
120
100
80
60
22
3
2
JN 27
1.5
JY 10-11

Fig. 26. Starch content of stems and leaves of Potamogeton robbinsii at sampling sites 3 and 9 on various dates during the 1985 growing season. Collection depth (in meters) is indicated on the horizontal axis.

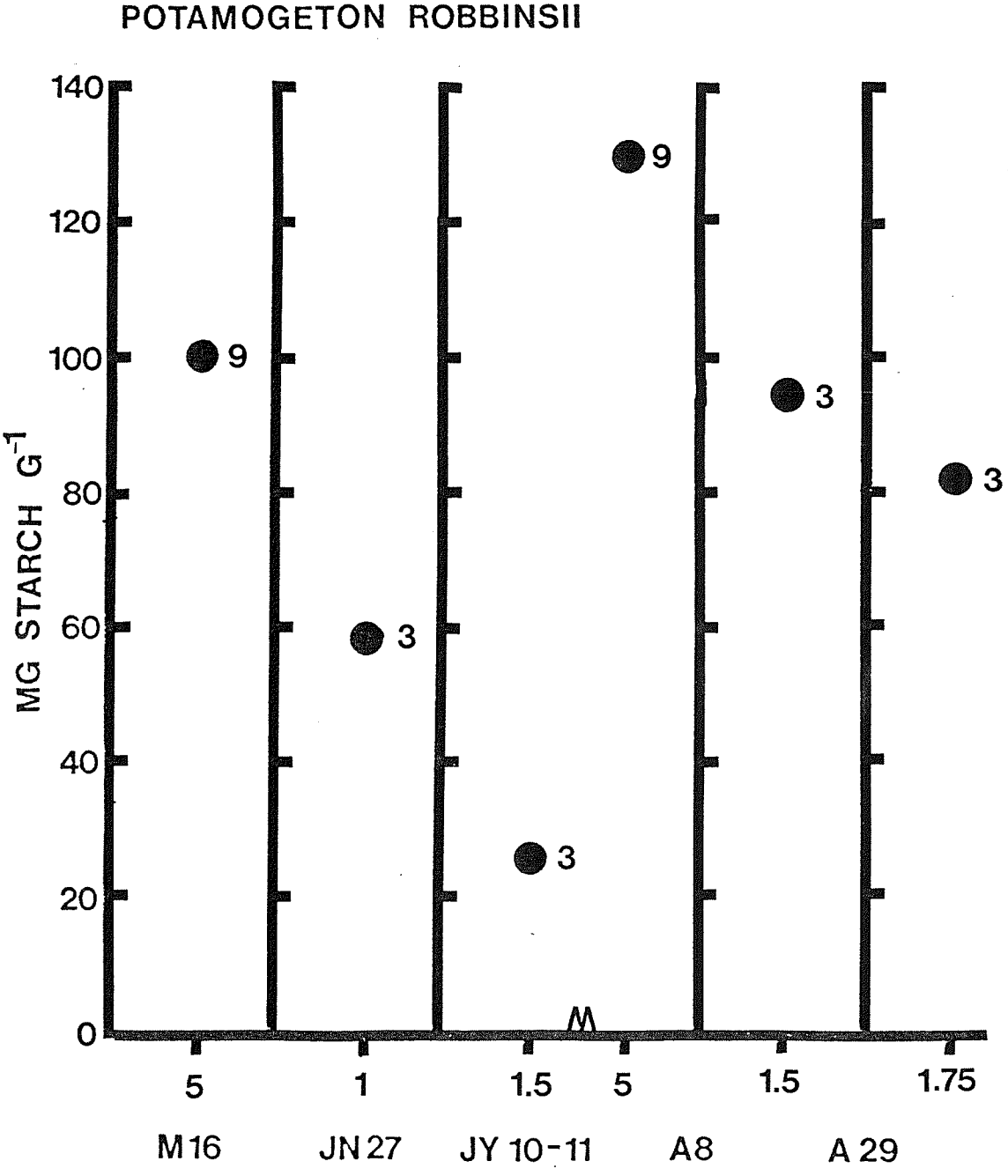

POTAMOGETON ROBBINSII
MG STARCH G-1
140
120
100
80
60
40
20
0
9
3
3
9
3
3
M
5
1
1.5
5
1.5
1.75
M16
JN27
JY 10-11
A8
A 29

Fig. 27. Starch content in stems and leaves of Potamogeton zosteriformis on various sampling dates during the 1985 growing season. Vertical bar represents standard error and numbers beside circles indicate sampling sites. Depth (in meters) for each collection time is shown on the horizontal axis. Statistically significant relationships between depth and starch content are shown for July 10-11 and August 8.

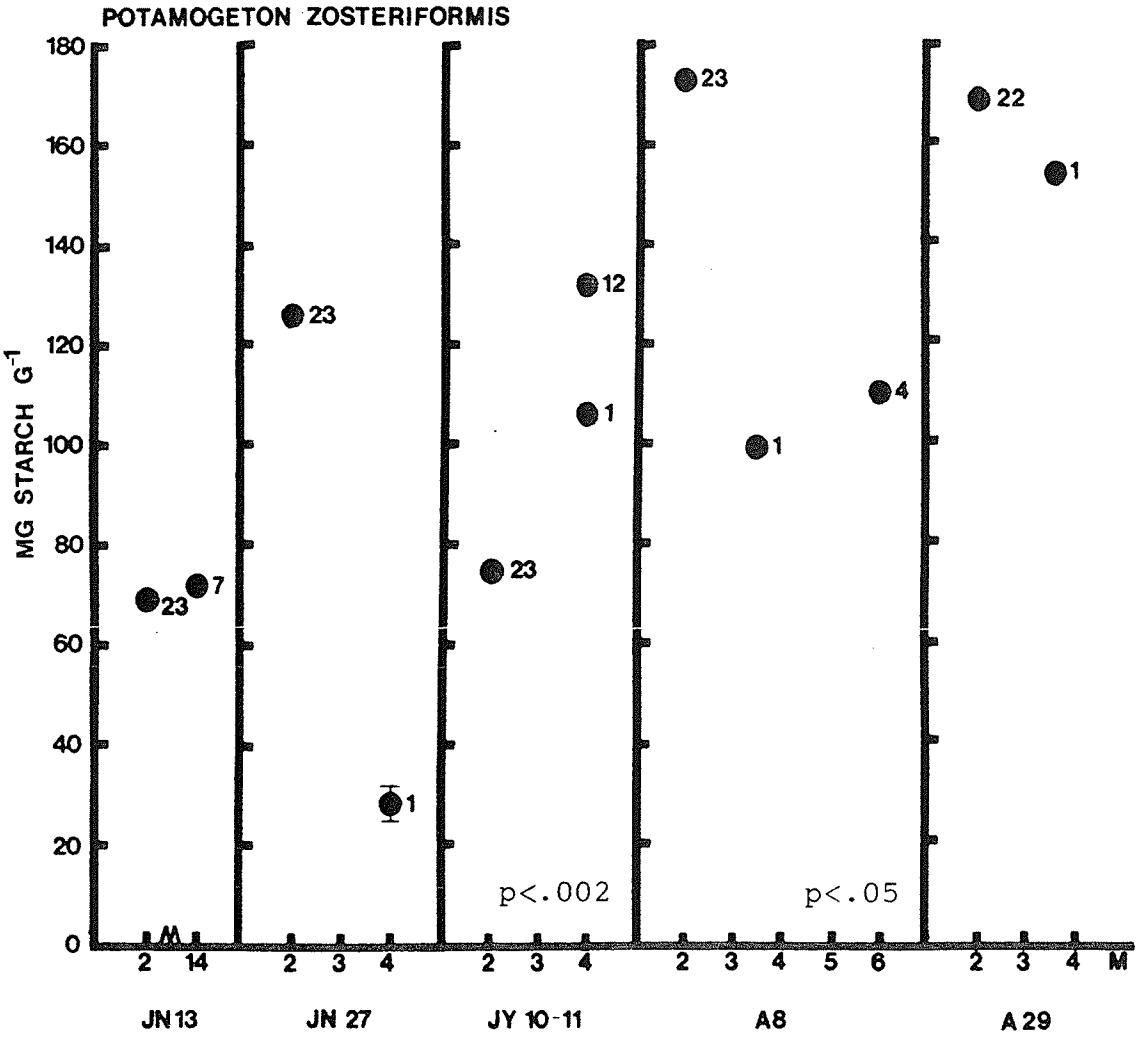

POTAMOGETON ZOSTERIFORMIS
MG STARCH G-1
180
160
140
120
100
80
60
40
20
0
23
7
23
1
23
12
1
23
1
4
22
1
p<.002
p<.05
M
2 14
2 3 4
2 3 4
2 3 4 5 6
2 3 4 M
JN 13
JN 27
JY 10-11
A8
A 29

Fig. 28. Starch content in stems and leaves of Ceratophyllum demersum at selected depths during the 1985 growing season. Sampling dates are indicated on the horizontal axis. Vertical bars represent standard error.

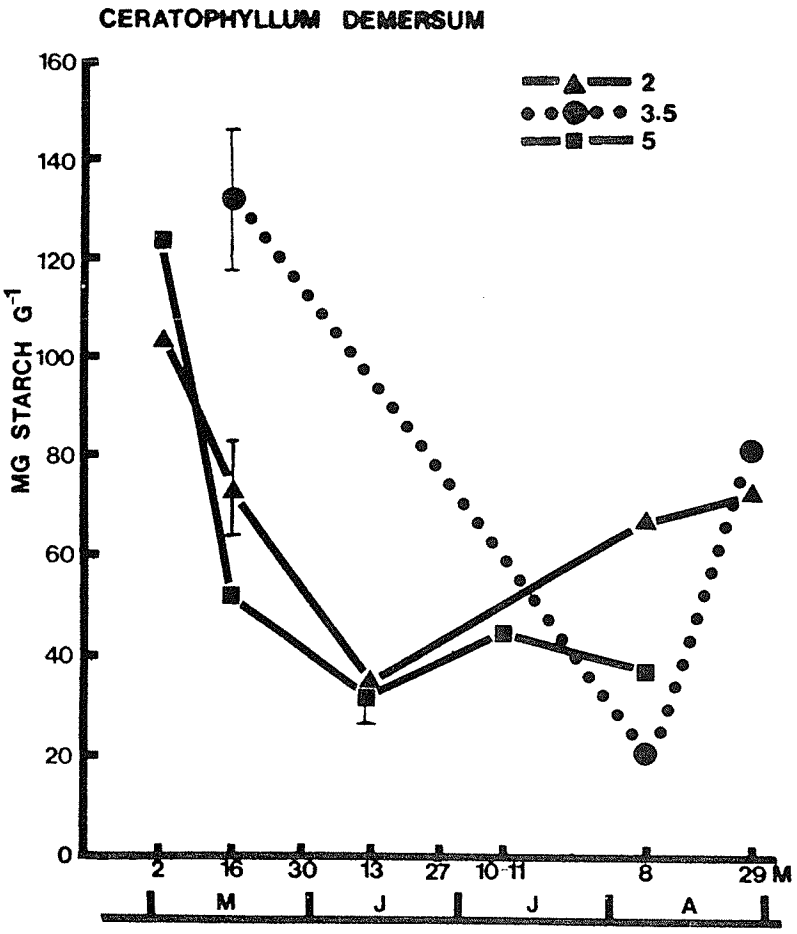

CERATOPHYLLUM DEMERSUM
MG STARCH G-1
160
140
120
100
80
60
40
20
0
2
3.5
5
2
16
30
13
27
10-11
8
29 M
M
J
J
A

Fig. 29. Starch content in stems and leaves of Myriophyllum exalbescens at selected depths during the 1985 growing season. Sampling dates are indicated on the horizontal axis. Vertical bars represent standard error.

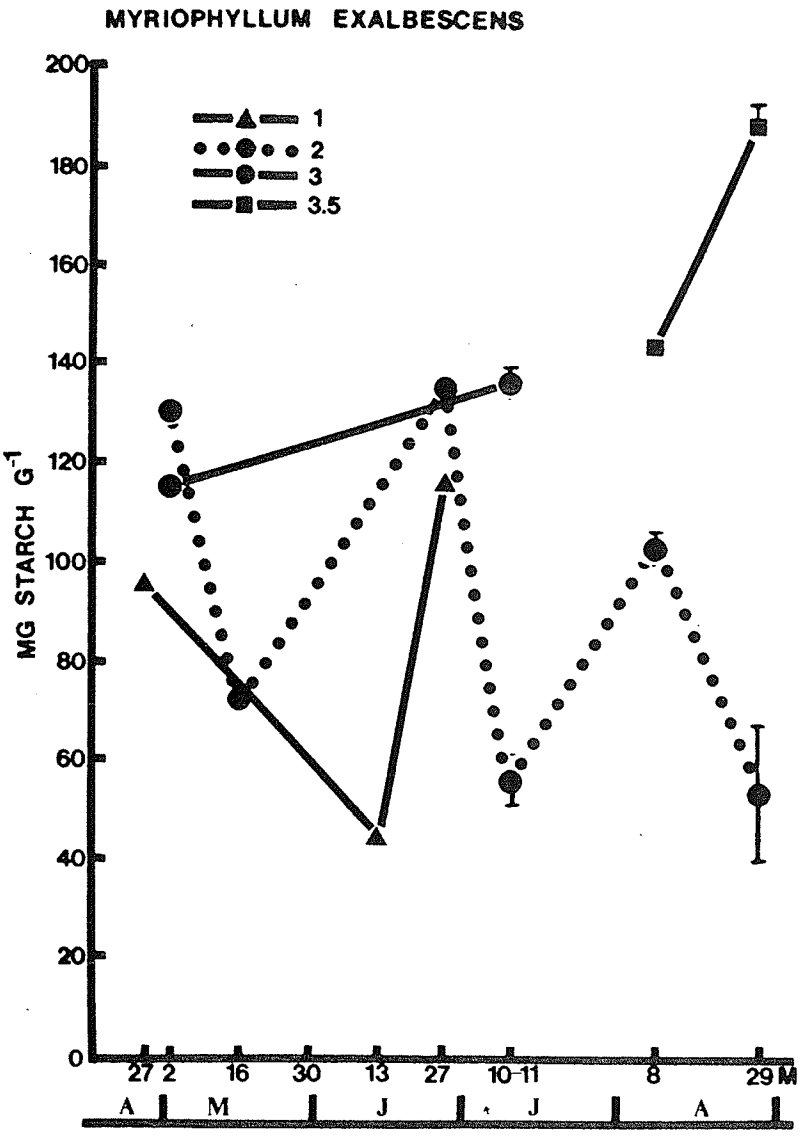

MYRIOPHYLLUM EXALBESCENS
MG STARCH G-1
200
180
160
140
120
100
80
60
40
20
0
1
2
3
3.5
27
2
16
30
13
27
10-11
8
29
M
A
M
J
J
A

Fig. 30. Starch content in stems and leaves of Potamogeton foliosus at selected depths during the 1985 growing season. Sampling dates are indicated on the horizontal axis. Vertical bars represent standard error.

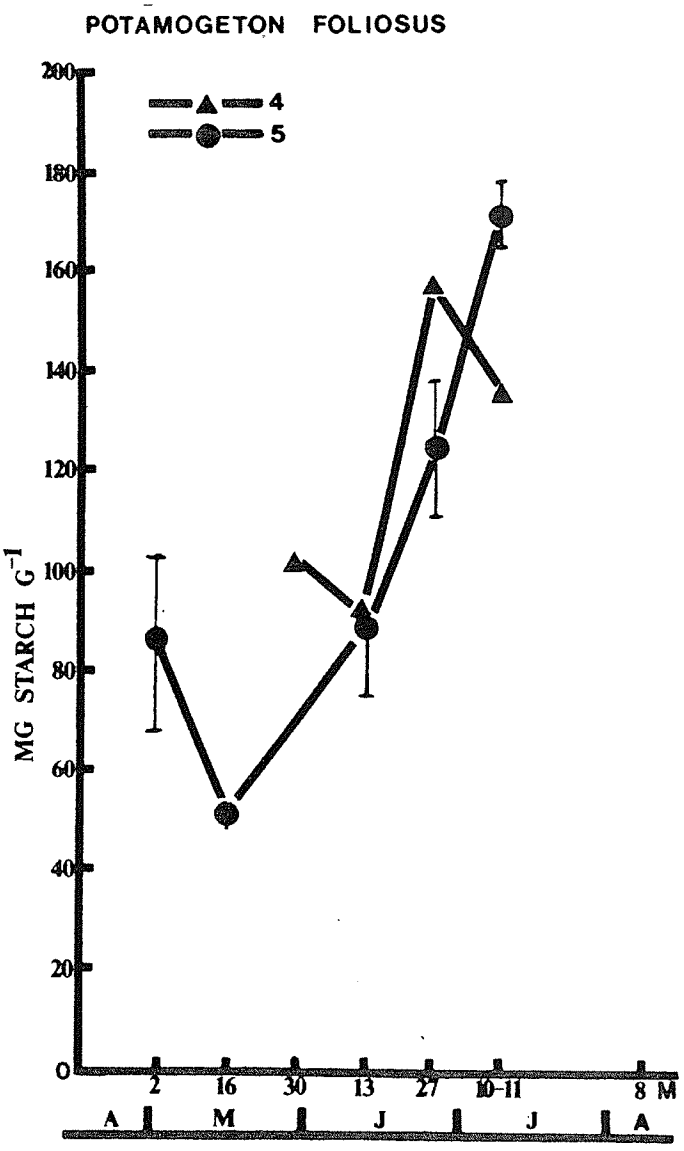

POTAMOGETON FOLIOSUS
4
5
MG STARCH G^{-1}
200
180
160
140
120
100
80
60
40
20
0
2
16
30
13
27
10-11
8 M
A
M
J
J
A

Fig. 31. Starch content in stems and leaves of Potamogeton zosteriformis at selected depths during the 1985 growing season. Sampling dates are indicated on the horizontal axis.

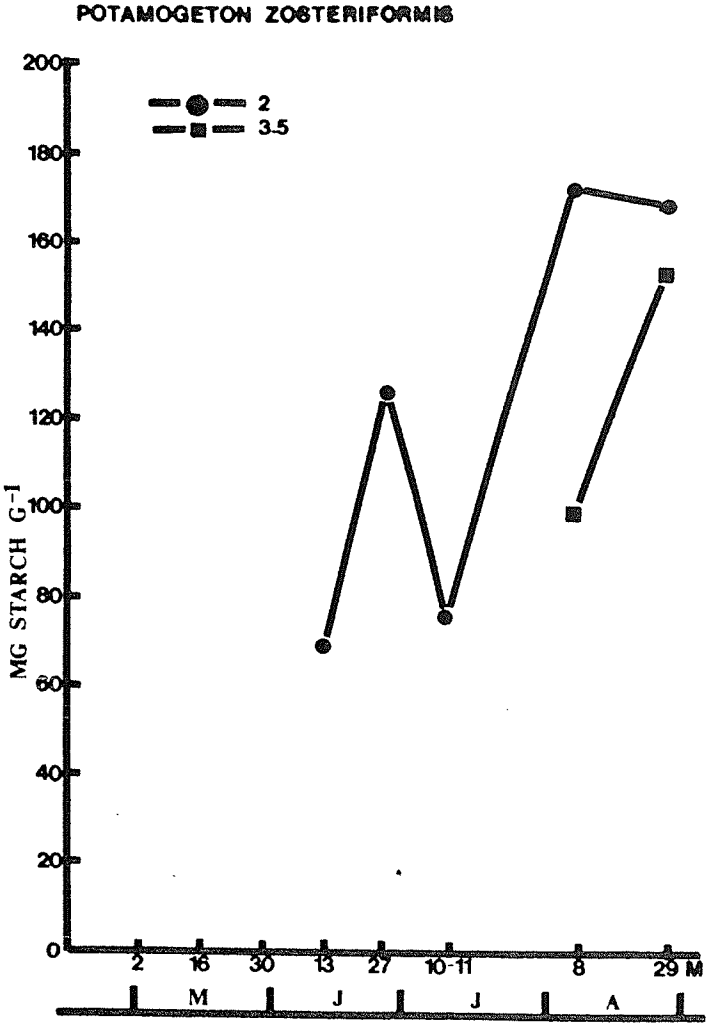

POTAMOGETON ZOSTERIFORMIS
2
3.5
MG STARCH G-1
200
180
160
140
120
100
80
60
40
20
0
2
16
30
13
27
10-11
8
29 M
M
J
J
A

Table 9. Significant seasonal differences in starch content of macrophytes in 1985.
1=Ap 27 2=My 2 3=My 16 4=My 30 5=Jn 13
6=Jn 27 7=Jy 10-11 8=Aug 8 9=Aug 29

Ceratophyllum demersum
ALPHA=0.05 DF=87 MSE=682.0

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
2	12	105.14	3 5 7-9	3 5 7-9
3	18	73.25	2 5 7-9	2 5 7 8
5	12	42.02	2 3	2 3
7	24	38.80	2 3	2 3
8	15	38.77	2 3	2 3
9	12	52.89	2 3	2

Elodea canadensis
ALPHA=0.05 DF=19 MSE=35.65

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY's
2	3	148.34	3-9	3-9
3	3	71.89	2 4 6-9	2 4 6-8
4	3	118.89	2 3 5 6 8 9	2 3 5 6 8 9
5	3	77.60	2 4 6-9	2 4 6-9
6	3	169.27	2-4 7-9	2-4 7-9
7	6	126.80	2 3 5 6 8 9	2 3 5 6 8 9
8	3	38.49	2-7 9	2-7 9
9	3	57.17	2-8	2 4-8

Myriophyllum exalbescens
ALPHA=0.05 DF=55 MSE=1587

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
1	3	95.84	n.s.	n.s.
2	6	122.65	5	n.s.
3	12	70.23	n.s.	6
5	3	44.98	2 6	6
6	9	128.76	5	3 5
7	9	82.89	n.s.	n.s.
8	9	102.95	n.s.	n.s.
9	12	84.71	n.s.	n.s.

Table 9 (Cont.)

Najas flexilis

ALPHA=0.05 DF=4 MSE=14.74

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
6	3	96.55	8	8
8	3	120.93	6	6

Potamogeton foliosus

ALPHA=0.05 DF=83 MSE=1828

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
2	12	113.95	3	3
3	9	51.33	6-8	2 6-8
4	9	79.95	6-8	6 7
5	15	100.11	3	7
6	12	145.73	3 4	3 4
7	27	147.23	3 4	3-5
8	6	142.24	3 4	3

Potamogeton gramineus

ALPHA=0.05 DF=6 MSE=1.242

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
5	3	39.86	7 8	8
7	3	37.20	5 8	8
8	3	32.80	5 7	5 7

Potamogeton praelongus

ALPHA=0.05 DF=4 MSE=10.35

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
5	3	144.29	6	6
6	3	91.13	5	5

Table 9 (Cont.)

Potamogeton richardsonii

ALPHA=0.05 DF=4 MSE=15.17

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
6	3	184.01	7	7
7	3	104.81	6	6

Potamogeton robbinsii

ALPHA=0.05 DF=13 MSE=1262

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
3	3	100.31	n.s.	n.s.
6	3	58.68	n.s.	n.s.
7	6	77.95	n.s.	n.s.
8	3	95.41	n.s.	n.s.
9	3	82.75	n.s.	n.s.

Potamogeton zosteriformis

ALPHA=0.05 DF=31 MSE=6.923

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
5	6	70.28	8 9	8 9
6	6	77.17	8 9	8 9
7	9	104.81	9	9
8	9	127.36	5 6 9	5 6
9	6	161.44	5-8	5-7

Table 10. Significant inter-site differences in starch content of macrophytes (mg/g) during the 1985 season. Means with the same letter were not significantly different, as determined in SNK and Tukey's tests at alpha=0.05.

CERATOPHYLLUM DEMERSUM					
DATE	DEPTH(M)	SITE	N	MEAN	
May 16	2	23	3	95.5	A
		22	3	51.6	B
	3.5	1	3	164	A
		2	3	43.6	B
Jn 13	5	9	3	43.0	A
		2	3	20.6	B
Jy 10-11	4	14	3	33.5	A
		1	3	30.9	A
	6	20	3	59.9	A
		11	3	33.9	B
		19	3	21.8	C
Aug 8	6.5	6	3	51.2	A
		5	3	17.2	B

MYRIOPHYLLUM EXALBESCENS					
DATE	DEPTH(M)	SITE	N	MEAN	
May 16	2	22	3	72.8	A
		23	3	72.7	B
Jn 27	2	22	3	176	A
		23	3	94.5	B
Jy 10-11	2	17	3	67.0	A
		23	3	45.4	B
Aug 29	2	22	3	85.5	A
		23	3	21.4	B

POTAMOGETON FOLIOSUS					
DATE	DEPTH(M)	SITE	N	MEAN	
May 2	5	2	3	124	A
		4	3	48.1	B
May 16	5	9	3	60.7	A
		8	3	54.4	B
		6	3	38.8	C

Table 10(cont.)

DATE	POTAMOGETON FOLIOSUS DEPTH(M)	SITE	N	MEAN	
Jn 13	5	9	3	121	A
		2	3	57.2	B
	6	6	3	126	A
		8	3	104	B
Jn 27	5	6	3	152	A
		2	3	97.0	B
Jy 10-11	5	15	3	199	A
		6	3	162	B
		9	3	155	B
	6	10	3	145	A
		11	3	124	B
		16	3	60.7	C

DATE	POTAMOGETON ZOSTERIFORMIS DEPTH(M)	SITE	N	MEAN	
Jy 10-11	4	12	3	132	A
		1	3	106	B

Table 11. Significant interspecific differences in starch content of stems and leaves for each sampling date during the 1985 growing season. Significant differences, as determined in SNK and Tukey's tests, are indicated by X's.

JUNE 13	*P.praelongus*	*P.foliosus*	*E.canadensis*	*P.zosteriformis*	*M.exlabescens*	*C.demersum*	*P.gramineus*	$\bar{X}$
P.praelongus								144.3
P.foliosus	X							100.1
E.canadensis	X							77.60
P.zosteriformis	X							70.28
M.exalbescens	X	X						44.98
C.demersum	X	X						42.02
P.gramineus	X	X						39.86

JUNE 27	*P.richardsonii*	*E.canadensis*	*P.foliosus*	*M.exalbescens*	*N.flexilis*	*P.praelongus*	*P.zosteriformis*	*P.robbinsii*	$\bar{X}$
P.richardsonii									184.0
E.canadensis									169.3
P.foliosus									145.7
M.exalbescens	X								128.8
N.flexilis	X								96.55
P.praelongus	X								91.13
P.zosteriformis	X	X	X						77.17
P.robbinsii	X	X	X	X					58.68

Table 11 (Cont.)

JULY 10-11	P.foliosus	E.canadensis	P.richardsonii	P.zosteriformis	M.exalbescens	P.robbinsii	C.demersum	P.gramineus	$\bar{X}$
P.foliosus									147.2
E.canadensis									126.8
P.richardsonii									104.8
P.zosteriformis									104.8
M.exalbescens	X								82.89
P.robbinsii	X								77.95
C.demersum	X	X	X	X					38.80
P.gramineus	X	X		X					37.20

AUGUST 8	P.foliosus	P.zosteriformis	N.flexilis	M.exalbescens	P.robbinsii	C.demersum	E.canadensis	P.gramineus	$\bar{X}$
P.foliosus									142.2
P.zosteriformis									127.4
N.flexilis									120.9
M.exalbescens									103.0
P.robbinsii									95.41
C.demersum	X	X							38.77
E.canadensis	X	X							38.49
P.gramineus	X	X							32.80

Table 11 (Cont.)

AUGUST 29	P. zosteriformis	M. exalbescens	P. robbinsii	E. canadensis	C. demersum	$\bar{X}$
P. zosteriformis						161.4
M. exalbescens	X					84.71
P. robbinsii	X					82.75
E. canadensis	X					57.17
C. demersum	X					52.89

C. Total nonstructural carbohydrate

The starch:soluble carbohydrate ratio showed differences among the 10 macrophytes during the course of the growing season (Table 12), with mean values ranging from 0.67 in P. gramineus to 2.69 in N. flexilis. Only P. gramineus had a ratio of less than 1, while 6 species had ratios approaching or exceeding 2.

Variation in the composition of total nonstructural carbohydrates was observed during the season (Figs. 32 to 41). Seven of the species examined gave no significant comparisons in SNK and Tukey's tests (Table 13). The small number of samples was sometimes responsible for the lack of significance and in some cases only 2 or 3 sampling dates were represented. The proportion of carbohydrate in the form of starch had an overall range of 30 to 85 %, with levels generally exceeding 40 %.

The proportion of starch in C. demersum was significantly higher on May 2 (70 %) than on July 10-11 and August 8. There was a tendency for the proportion of starch in P. foliosus to increase as the season progressed. Levels on June 27, July 10-11, and August 8 were significantly higher than the level on May 16. This seasonal trend was also observed in P. zosteriformis, where the proportion of starch increased consistently between June 27 and August 29. Levels in late August (83 %) were significantly higher than on June 27 and July 10-11. The proportion of starch was also significantly greater on August 8 than on June 27.

Starch in E. canadensis remained relatively abundant (66 %) throughout the season, with the exception of the August 8 sampling date. The proportion of starch gave a seasonal minimum in M. exalbescens and P. robbinsii, on May 16 - June 13 and July 10-11, respectively.

Few significant interspecific differences in starch: soluble carbohydrate ratios were observed during the 1985 season (Table 14). This was at least in some cases related to the small number of samples in which starch could be analyzed. On May 2, S:C ratios for E. canadensis significantly exceeded ratios for C. demersum, M. exalbescens, and P. foliosus; and on May 30 ratios were significantly larger than in P. foliosus. E. canadensis also had a larger S:C ratio than all other species represented on June 13 and June 27, although comparisons were not consistently significant in SNK and Tukey's tests.

Table 12. Overall seasonal starch:soluble carbohydrate ratios (mg mg^{-1}) for macrophytes during the 1985 season.

Species	Starch:Carbo. Ratio	Mean	N
Ceratophyllum demersum	0.42 - 3.89	1.31	30
Elodea canadensis	0.42 - 5.49	2.61	10
Myriophyllum exalbescens	0.82 - 5.61	1.96	20
Najas flexilis	---	2.69	1
Potamogeton foliosus	0.46 - 4.85	2.05	29
P. gramineus	0.49 - 1.02	0.67	3
P. praelongus	1.17 - 1.55	1.36	2
P. richardsonii	1.18 - 1.97	1.58	2
P. robbinsii	0.48 - 3.06	1.82	5
P. zosteriformis	0.52 - 5.95	2.19	12

Table 13. Significant seasonal differences in proportion of starch in carbohydrate content of macrophytes during the 1985 season. 1=Apr 27 2=May 2 3=May 16 4=May 30 5=Jn 13 6=Jn 27 7=Jy 10-11 8=Aug 8 9=Aug 29 Alpha=0.05

CERATOPHYLLUM DEMERSUM

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
2	4	.7001	5 7 8 9	7 8
3	6	.5808	n.s.	n.s.
5	4	.4819	2	n.s.
7	8	.4069	2	2
8	5	.4378	2	2
9	4	.5121	2	n.s.

ELODEA CANADENSIS

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
2	1	.8464	n.s.	n.s.
3	1	.6794	n.s.	n.s.
4	1	.7640	n.s.	n.s.
5	1	.7246	n.s.	n.s.
6	1	.8245	n.s.	n.s.
7	2	.6628	n.s.	n.s.
8	1	.2973	n.s.	n.s.
9	1	.7021	n.s.	n.s.

MYRIOPHYLLUM EXALBESCENS

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
1	1	.5663	n.s.	n.s.
2	2	.6385	n.s.	n.s.
3	4	.4878	n.s.	n.s.
5	1	.4730	n.s.	n.s.
6	3	.7129	n.s.	n.s.
7	3	.6291	n.s.	n.s.
8	3	.6031	n.s.	n.s.
9	4	.6031	n.s.	n.s.

Table 13 (Cont.)

NAJAS FLEXILIS

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
6	1	.7295	n.s.	n.s.
8	1	.7748	n.s.	n.s.

POTAMOGETON FOLIOSUS

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
2	4	.6033	n.s.	n.s.
3	3	.4165	6 7 8	6 7 8
4	3	.4391	6 7 8	6 7
5	5	.5079	n.s.	7
6	4	.6876	3 4	3 4
7	9	.7164	3 4	3 4 5
8	2	.6994	3 4	3

POTAMOGETON GRAMINEUS

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
5	1	.3315	n.s.	n.s.
6	1	.5061	n.s.	n.s.
8	1	.3368	n.s.	n.s.

POTAMOGETON PRAELONGUS

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
5	1	.6085	n.s.	n.s.
6	1	.5380	n.s.	n.s.

POTAMOGETON RICHARDSONII

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
6	1	.6636	n.s.	n.s.
7	1	.5581	n.s.	n.s.

Table 13(Cont.)

POTAMOGETON ROBBINSII				
DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
3	1	.7140	n.s.	n.s.
6	1	.5547	n.s.	n.s.
7	1	.3271	n.s.	n.s.
8	1	.7542	n.s.	n.s.
9	1	.6504	n.s.	n.s.

POTAMOGETON ZOSTERIFORMIS				
DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
5	2	.5562	9	n.s.
6	2	.4470	8 9	8 9
7	3	.5502	9	9
8	3	.7317	6	6
9	2	.8285	5 6 7	6 7

Table 14. Significant interspecific differences in starch:soluble carbohydrate ratios of macrophytes during the 1985 season. 1=C.demersum 2=E.canadensis 3=M.exalbescens 4=N.flexilis 5=P.foliosus 6=P.gramineus 7=P.praelongus 8=P.richardsonii 9=P.robbinsii 10=P.zosteriformis

MAY 2
ALPHA=0.05 DF=7 MSE=0.453

SPECIES	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
2	1	5.49	1 3 5	1 3 5
1	4	2.40	2	2
3	2	1.78	2	2
5	4	1.74	2	2

MAY 16
ALPHA=0.05 DF=10 MSE=0.670

SPECIES	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
9	1	2.46	n.s.	n.s.
2	1	2.11	n.s.	n.s.
1	6	1.90	n.s.	n.s.
3	4	0.97	n.s.	n.s.
5	3	0.73	n.s.	n.s.

MAY 30
ALPHA=0.05 DF=2 MSE=0.111

SPECIES	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
2	1	3.28	5	5
5	3	0.83	2	2

Table 14 (Cont.)

JUNE 13
ALPHA=0.05 DF=8 MSE=0.176

SPECIES	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
2	1	2.62	6	n.s.
7	1	1.55	n.s.	n.s.
10	2	1.26	n.s.	n.s.
1	4	1.06	n.s.	n.s.
5	5	1.05	n.s.	n.s.
3	1	0.90	n.s.	n.s.
6	1	0.49	2	n.s.

JUNE 27
ALPHA=0.05 DF=6 MSE=1.21

SPECIES	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
2	1	4.68	n.s.	n.s.
3	3	2.81	n.s.	n.s.
4	1	2.69	n.s.	n.s.
5	4	2.39	n.s.	n.s.
8	1	1.97	n.s.	n.s.
9	1	1.24	n.s.	n.s.
7	1	1.17	n.s.	n.s.
6	1	1.02	n.s.	n.s.
10	2	0.88	n.s.	n.s.

JULY 10-11
ALPHA=0.05 DF=21 MSE=0.879

SPECIES	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
5	9	3.10	n.s.	1
3	3	2.15	n.s.	n.s.
2	3	1.71	n.s.	n.s.
10	3	1.25	n.s.	n.s.
8	1	1.18	n.s.	n.s.
1	8	0.70	n.s.	5
9	1	0.48	n.s.	n.s.

Table 14 (Cont.)

AUGUST 8
ALPHA=0.05 DF=9 MSE=1.00

SPECIES	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
4	1	3.25	n.s.	n.s.
9	1	3.06	n.s.	n.s.
5	2	3.05	n.s.	n.s.
10	3	2.78	n.s.	n.s.
3	3	1.87	n.s.	n.s.
1	5	0.86	n.s.	n.s.
6	1	0.51	n.s.	n.s.
2	1	0.42	n.s.	n.s.

AUGUST 29
ALPHA=0.05 DF=7 MSE=2.61

SPECIES	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
10	2	4.98	n.s.	n.s.
2	1	2.35	n.s.	n.s.
3	4	2.32	n.s.	n.s.
9	1	1.85	n.s.	n.s.
1	4	1.18	n.s.	n.s.

Fig. 32. Proportion of starch (upper) and soluble carbohydrate (lower) in stems and leaves of Ceratophyllum demersum on various sampling dates during the 1985 growing season. Depth (in meters) for each collection time is indicated on the horizontal axis.

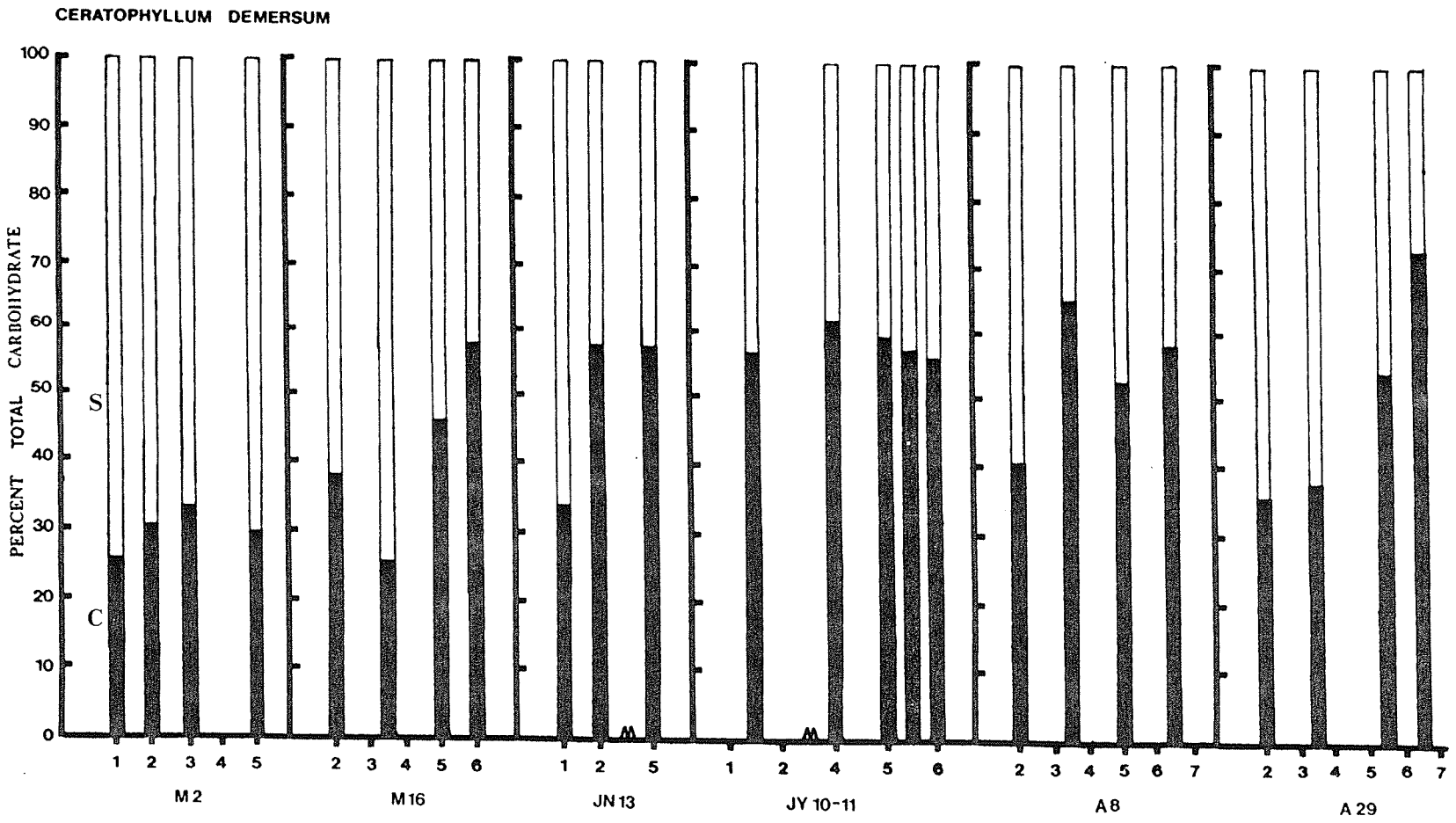

CERATOPHYLLUM DEMERSUM
PERCENT TOTAL CARBOHYDRATE
100
90
80
70
60
50
40
30
20
10
0
S
C
1 2 3 4 5
M 2
2 3 4 5 6
M16
1 2 5
JN 13
1 2 4 5 6
JY 10-11
2 3 4 5 6 7
A 8
2 3 4 5 6 7
A 29

Fig. 33. Proportion of starch (upper) and soluble carbohydrate (lower) in stems and leaves of Elodea canadensis on various sampling dates during the 1985 growing season. Depth (in meters) for each collection time is indicated on the horizontal axis.

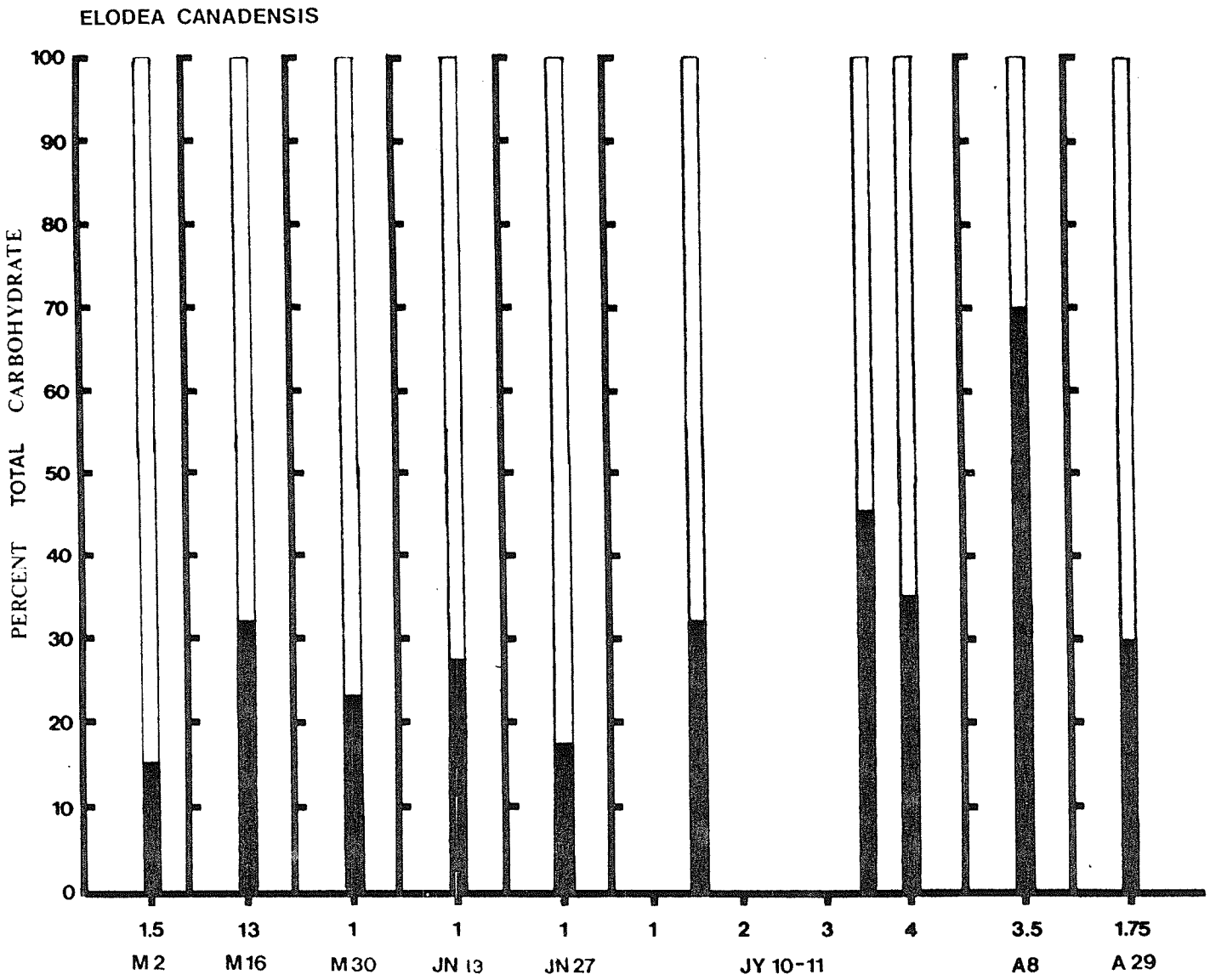

ELODEA CANADENSIS
PERCENT TOTAL CARBOHYDRATE
100
90
80
70
60
50
40
30
20
10
0
1.5
M 2
13
M16
1
M30
1
JN 13
1
JN 27
1
2
3
JY 10-11
4
3.5
A8
1.75
A 29

Fig. 34. Proportion of starch (upper) and soluble carbohydrate (lower) in stems and leaves of Myriophyllum exalbescens on various sampling dates during the 1985 growing season. Depth (in meters) for each collection time is indicated on the horizontal axis.

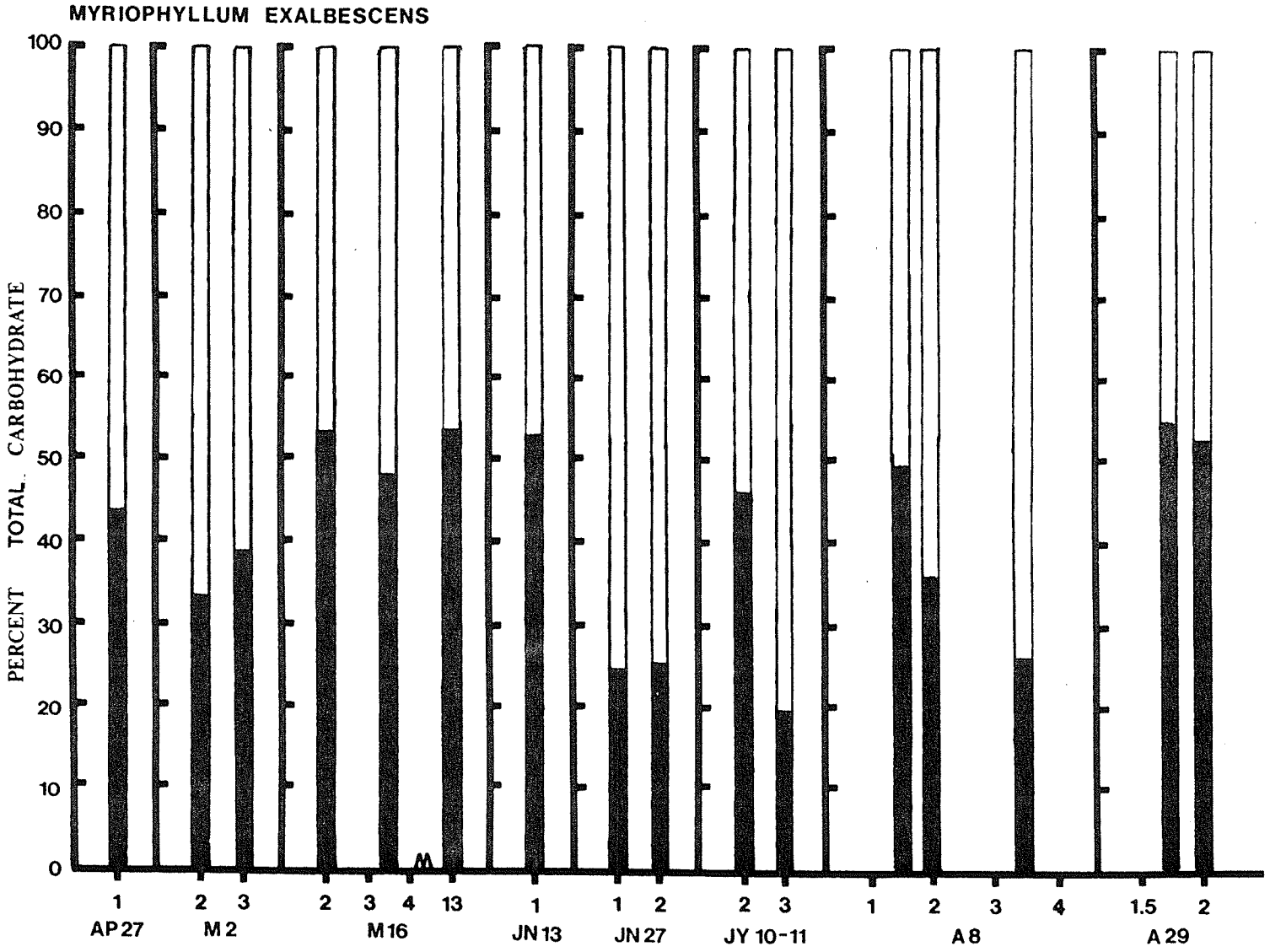

MYRIOPHYLLUM EXALBESCENS
PERCENT TOTAL CARBOHYDRATE
100
90
80
70
60
50
40
30
20
10
0
1
AP 27
2
3
M 2
2
3
4
13
M 16
1
JN 13
1
2
JN 27
2
3
JY 10-11
1
2
3
4
A 8
1.5
2
A 29

Fig. 35. Proportion of starch (upper) and soluble carbohydrate (lower) in stems and leaves of Najas flexilis on 2 sampling dates during the 1985 growing season. Depth (in meters) for each collection time is indicated on the horizontal axis.

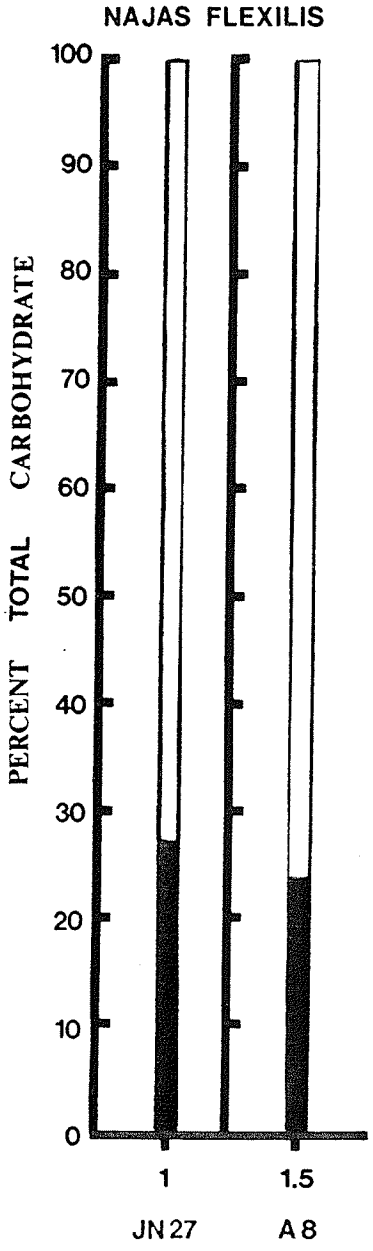

NAJAS FLEXILIS
PERCENT TOTAL CARBOHYDRATE
100
90
80
70
60
50
40
30
20
10
0
1
1.5
JN 27
A 8

Fig. 36. Proportion of starch (upper) and soluble carbohydrate (lower) in stems and leaves of Potamogeton foliosus on various sampling dates during the 1985 growing season. Depth (in meters) for each collection time is indicated on the horizontal axis.

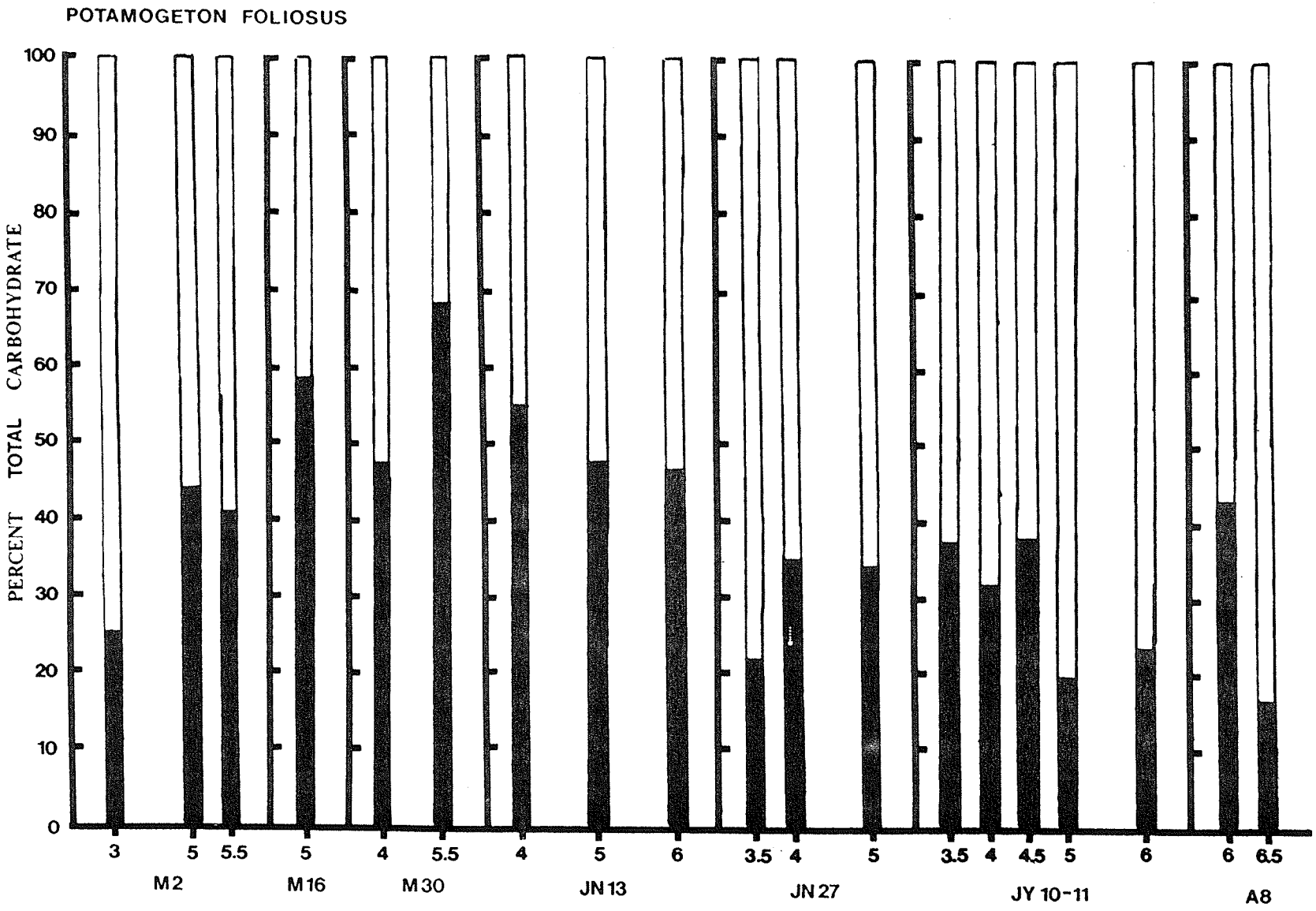

POTAMOGETON FOLIOSUS
PERCENT TOTAL CARBOHYDRATE
100
90
80
70
60
50
40
30
20
10
0
3
5
5.5
5
4
5.5
4
5
6
3.5
4
5
3.5
4
4.5
5
6
6
6.5
M2
M16
M30
JN13
JN27
JY 10-11
A8

Fig. 37. Proportions of starch (upper) and soluble carbohydrate (lower) in stems and leaves of Potamogeton gramineus on various sampling dates during the 1985 growing season. Depth (in meters) for each collection time is indicated on the horizontal axis.

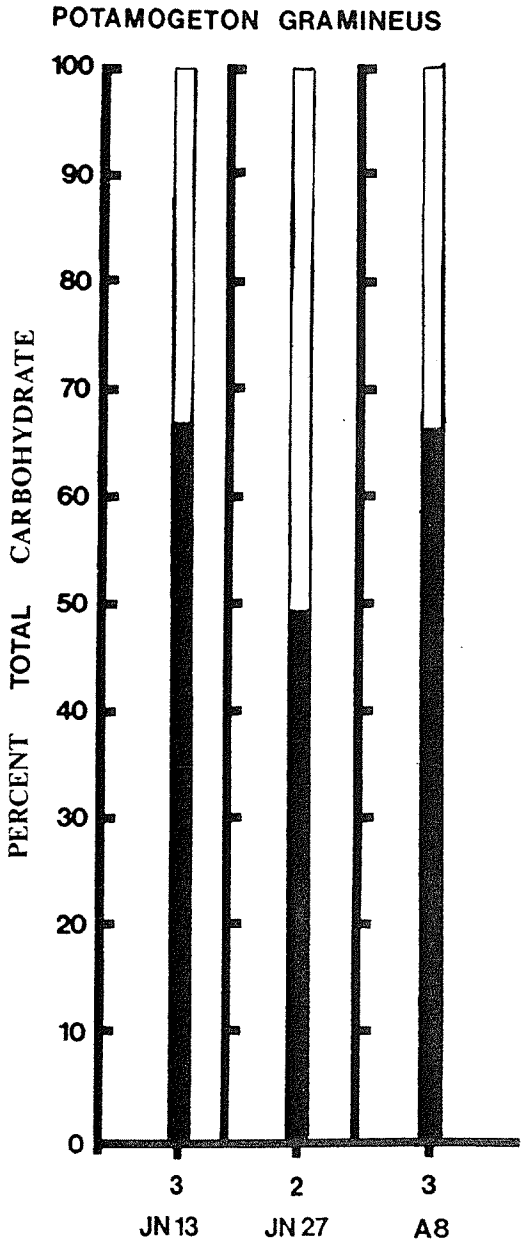

POTAMOGETON GRAMINEUS
PERCENT TOTAL CARBOHYDRATE
100
90
80
70
60
50
40
30
20
10
0
3
JN 13
2
JN 27
3
A8

Fig. 38. Proportion of starch (upper) and soluble carbohydrate (lower) in stems and leaves of Potamogeton praelongus during June of the 1985 growing season. Depth (in meters) is indicated on the horizontal axis.

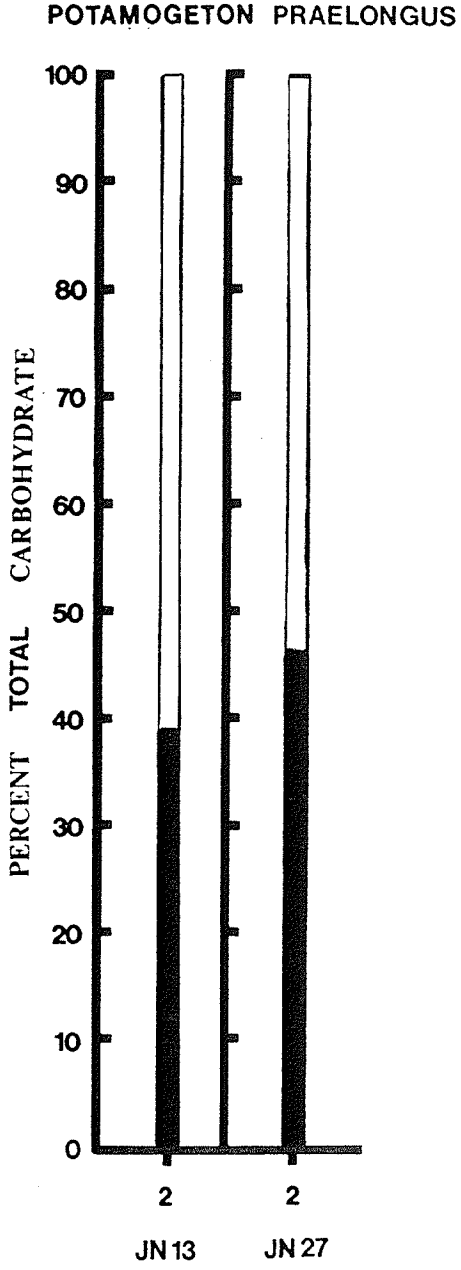

POTAMOGETON PRAELONGUS
PERCENT TOTAL CARBOHYDRATE
100
90
80
70
60
50
40
30
20
10
0
2
2
JN 13
JN 27

Fig. 39. Proportion of starch (upper) and soluble carbohydrate (lower) in stems and leaves of Potamogeton richardsonii on 2 sampling dates during the 1985 growing season. Depth (in meters) is indicated on the horizontal axis.

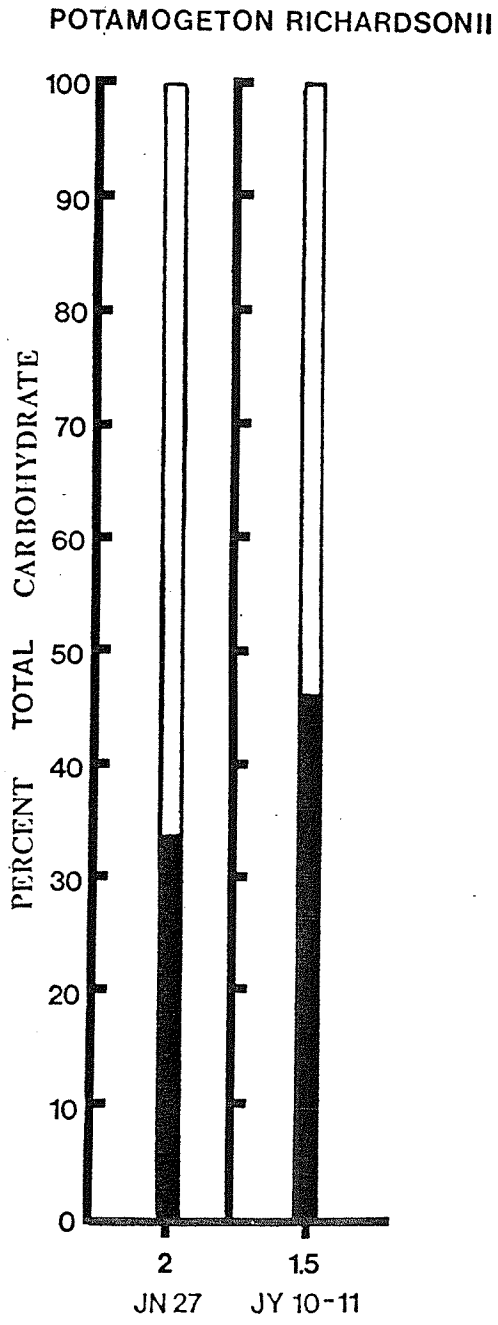

POTAMOGETON RICHARDSONII
PERCENT TOTAL CARBOHYDRATE
100
90
80
70
60
50
40
30
20
10
0
2
1.5
JN 27
JY 10-11

Fig. 40. Proportion of starch (upper) and soluble carbohydrate in stems and leaves of Potamogeton robbinsii on various sampling dates during the 1985 growing season. Depth (in meters) for each collection time is indicated on the horizontal axis.

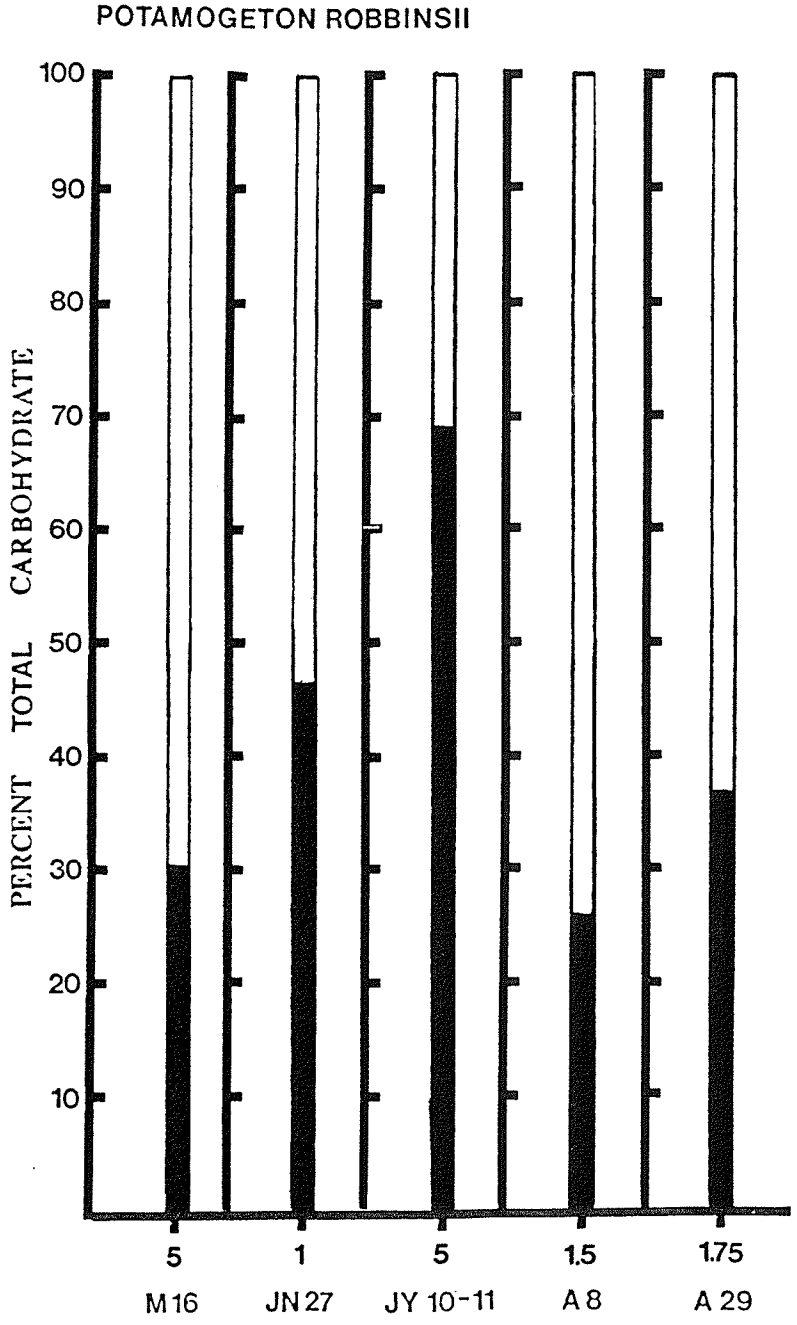
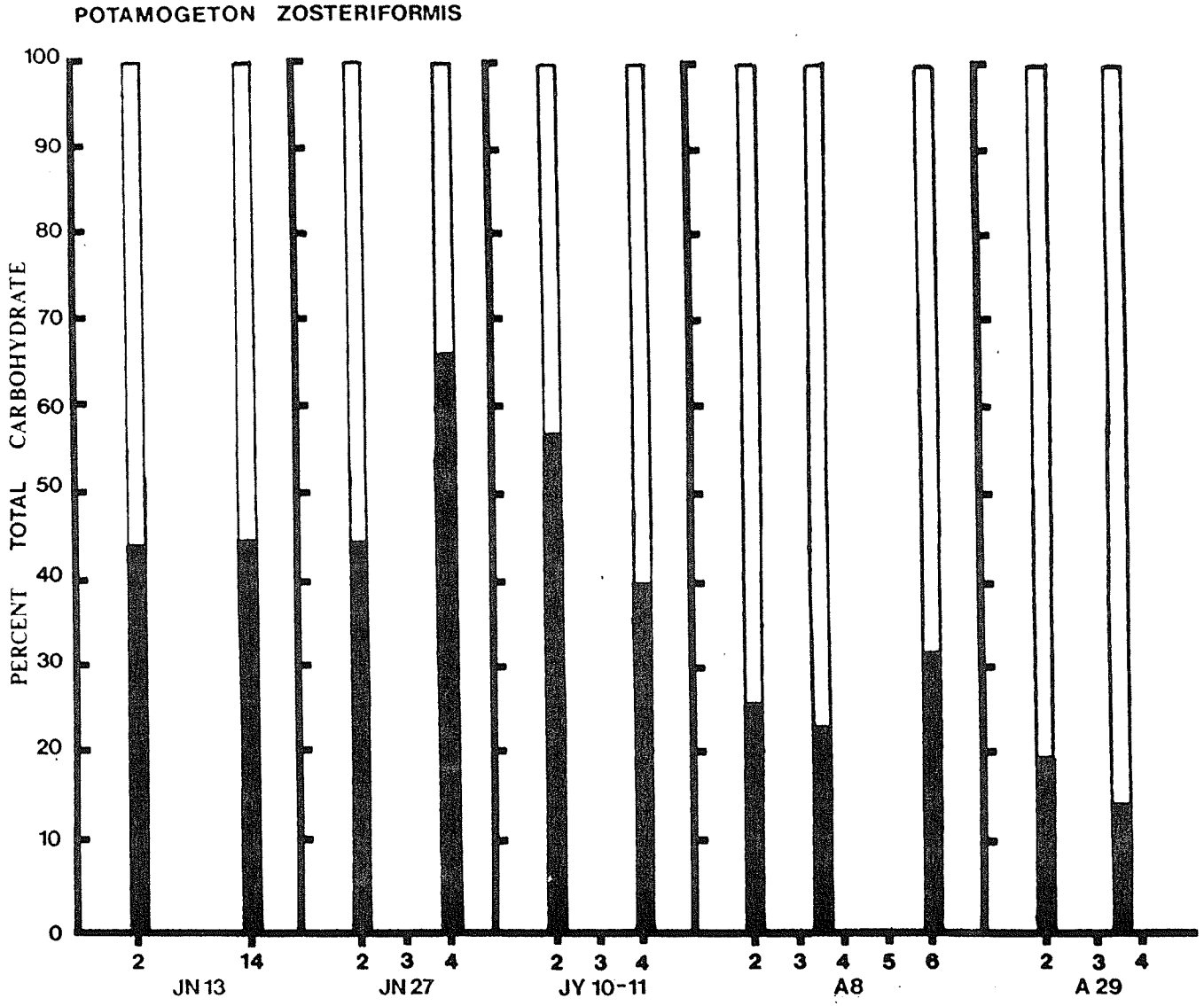

POTAMOGETON ROBBINSII
PERCENT TOTAL CARBOHYDRATE
100
90
80
70
60
50
40
30
20
10
5
M16
1
JN 27
5
JY 10-11
1.5
A 8
1.75
A 29

Fig. 41. Proportion of starch (upper) and soluble carbohdyrate (lower) in stems and leaves of Potamogeton zosteriformis on various sampling dates during the 1985 growing season. Depth (in meters) for each collection time is indicated on the horizontal axis.


POTAMOGETON ZOSTERIFORMIS
PERCENT TOTAL CARBOHYDRATE
100
90
80
70
60
50
40
30
20
10
0
2
14
2
3
4
2
3
4
2
3
4
5
6
2
3
4
JN 13
JN 27
JY 10-11
A8
A 29

D. Individual soluble sugars

The recovery efficiency of the ion-exchange and paper chromatography isolation procedure varied for the 6 reference sugars (Table 15). The proportions recovered ranged from 67.8 to 85.6 % for raffinose and stachyose, respectively. Recovery of total soluble sugars in the chromatographic isolation procedure was compared to the amount quantified in the crude extract (Table 16). The efficiency of the ion-exchange and paper chromatography ranged from 32.6 % of total soluble carbohydrate in M. exalbescens to 81.4 % in P. praelongus, with a mean for all species of 56.7 %.

Chromatographic data for reference compounds and crude sample extracts are summarized in Table 17. Good separation of individual sugars was achieved in the 10 species of macrophytes, and all were found to contain fructose, glucose, and sucrose (Fig. 42). The color reactions for sugars in crude sample extracts compared well with those of standards, with fructose being orange-brown, glucose blue-grey, and sucrose brown. Sugars from crude sample extracts tended to have slightly lower R_{fr} values than the standards.

The 4 additional sugars isolated from C. demersum (Fig. 43) were not positively identified by paper chromatography. The first (A) and third (C) spots from the origin resembled stachyose and raffinose, respectively, in terms of color reaction. The fourth spot from the origin (D) gave a blue reaction similar to that of melibiose and lactose. The 3

Table15. Recovery efficiency of reference sugars in chromatographic isolation procedure.

Sugar	Percent Recovery (±SE)
Stachyose	85.6(3.2)
Melibiose	79.0(4.6)
Sucrose	77.8(3.5)
Fructose	75.6(3.7)
Glucose	70.6(3.0)
Raffinose	67.8(2.8)

Table 16. Recovery efficiency of soluble carbohydrate in chromatographic isolation method.

Species	N	Percent Recovery (±SE)
P. praelongus	3	81.4(6.7)
P. zosteriformis	8	69.5(6.8)
P. richardsonii	3	65.9(3.6)
P. gramineus	3	64.4(8.6)
E. canadensis	11	63.4(4.1)
P. robbinsii	5	60.6(5.4)
P. foliosus	32	56.0(3.1)
N. flexilis	3	39.6(6.2)
C. demersum	21	33.6(3.0)
M. exalbescens	25	32.6(2.2)

Table 17. R values relative to fructose, and color reactions with diphenylamine for reference compounds and sugars isolated from crude sample extracts.

Sugar	N	R_{fruc} X 100	Color
Stachyose	10	23	Bn
Unknown A	10	30	Bn
Unknown B	10	35	Bl
Raffinose	10	38	Bn
Melibiose	10	44	Bl
Unknown C	10	46	Bn
Unknown D	10	53	Bl
Lactose	4	53	Bl
Maltose	4	55	Bl-Vt
Unknown E	10	67	Bn
Sucrose	10	75	Bn
Unknown F	10	86	Bl-Gy
Galactose	10	88	Bn-Gy
Glucose	10	89	Bl-Gy
Unknown G	10	100	Or-Bn
Fructose	10	100	Or-Bn
Arabinose	4	104	Or
Xylose	4	111	Or-Bn
Melezitose*			
Myo-inositol*			
Trehalose*			

* no detected reaction with diphenylamine

Colors: Bl=blue Bn=brown Gy=grey Or=orange Vt=violet

Fig.42. Typical chromatogram of crude sample extract, indicating separation of fructose (F), glucose (G), and sucrose (S).

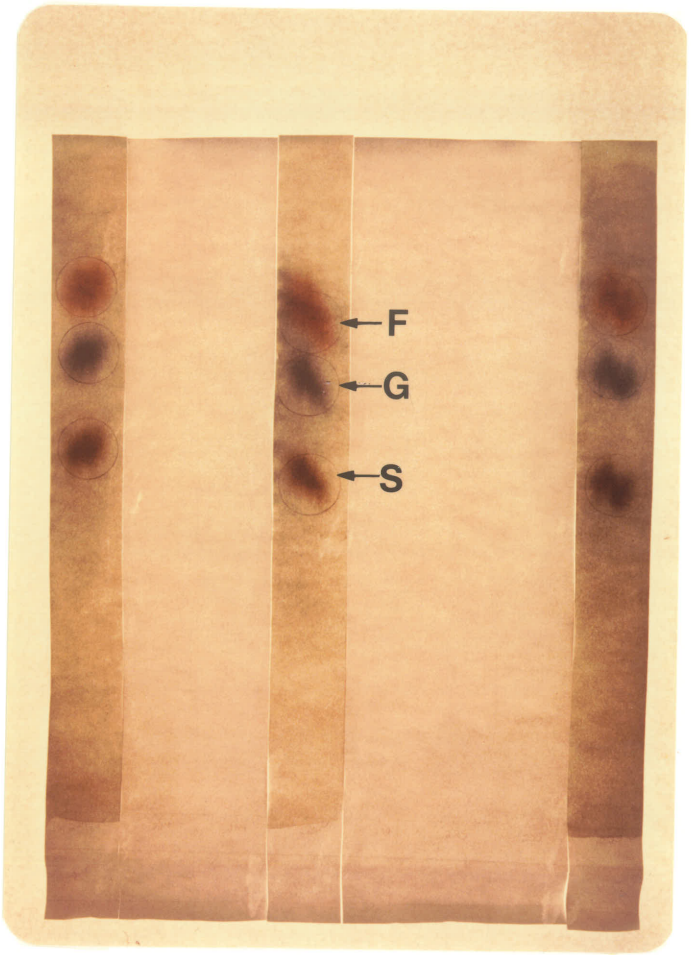
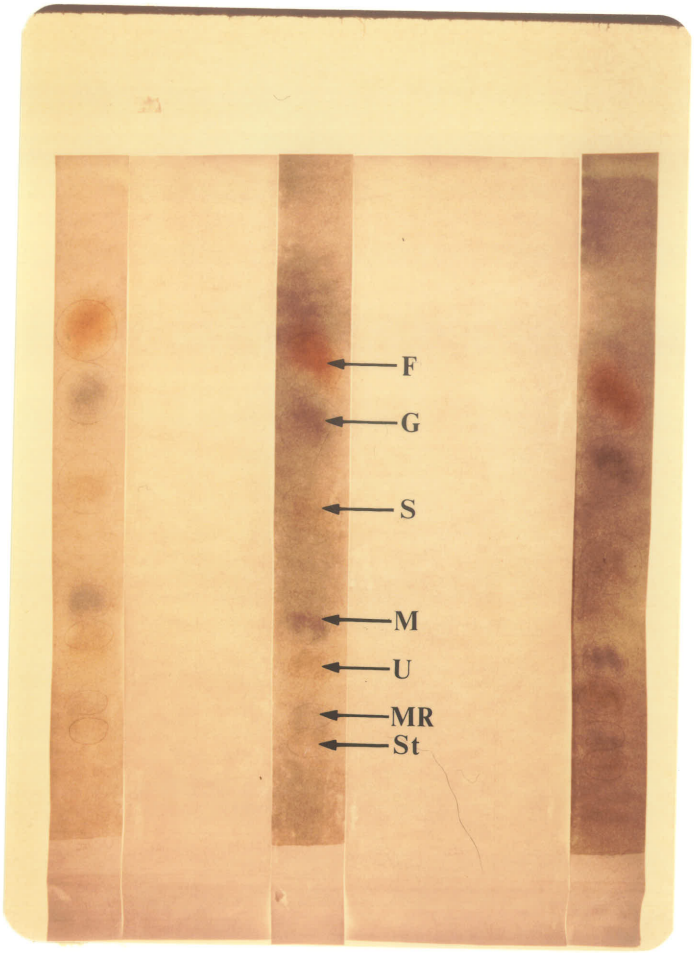

F
G
S

Fig.43. Typical chromatogram of soluble sugars in C. demersum, indicating separation of 7 components: fructose (F), glucose (G), sucrose (S), melibiose (M), unknown (hydrolysis product of stachyose) (U), melibiose/raffinose (MR), and stachyose (St).


F
G
S
M
U
MR
St

spots also resembled these standards in their separation sequence, although R_{fr} values of sugars from crude sample extracts were consistently higher than stachyose, raffinose, and melibiose. The second spot from the origin (B) gave a blue color reaction and did not compare well with any of the reference compounds.

Analysis of NMR spectra (Figs. 44 to 56) provided more detailed information regarding the identity of crude extract sugars. The major component of spot A was confirmed to be stachyose in ^{13}C and proton NMR spectra. Peaks at 5.31, 4.87, and 4.10 in the proton spectrum matched those of stachyose. Small peaks at 5.12 and 5.01 indicated the presence of a minor component. In the ^{13}C spectrum, the 2 C-1 peaks of galactose at 99.2 (terminal) and 99.5 (internal) agreed with values of similar tetrasaccharides. The minor components did not produce strong signals in ^{13}C.

Melibiose was detected as the major component in spot D, using proton spectra. Peaks at 4.55, 4.87, and 5.12 matched well with the melibiose standard.

NMR analysis provided evidence that spot B was a mixture of raffinose and melibiose. In the proton spectrum, peaks at 4.55, 4.87, and 5.12 agreed well with the standard melibiose spectrum, representing protons on C-1 of glucose, C-1 of galactose, and C-1 of glucose. Peaks at 4.08, 4.87, and 5.30 compared well with raffinose, representing protons on C-3 of fructose, C-1 of galactose, and C-1 of glucose. All carbons for both melibiose and raffinose could be

assigned in the ^{13}C spectrum. Exact identification of all peaks was difficult in the 69 to 72 ppm range, as there were 12-14 carbons with resonance in this range.

The presence of melibiose in 2 spots (B and D) with distinct R_{fr} values suggested that the presence of this sugar in spot B was due to the partial hydrolysis of raffinose.

Spot C, hypothesized to be raffinose in paper chromatography, gave ^{13}C and proton spectra resembling spectra of stachyose. Doublets at 5.31 and 4.87 and single peaks at 4.11 and 4.09 were in good agreement with the standard spectrum of stachyose. However additional doublets at 5.02 and 4.30 suggested the presence of another component. The ^{13}C spectrum clearly showed the appropriate shifts for the glucose and fructose components. The terminal galactose and internal galactose of stachyose were both accounted for in the spectrum. The R_{fr} of the third spot, however, did not compare well with that of the stachyose reference. Spot A, also identified as stachyose in NMR analysis, more closely agreed with the reference compound in terms of R_{fr}. The large R_{fr} value suggested that the constituent of spot C was not a tetrasaccharide, although the appropriate constituents of stachyose were present (fructose, glucose, and 2 galactose units). It was hypothesized that the spot consisted of a mixture of hydrolysis products of stachyose. Due to the inconclusive results regarding the identity of the 4 sugars unique to C. demersum, the sugars were combined

in subsequent statistical analyses.

The content of individual sugars in the macrophytes during 1985 is shown in Figs. 57 to 74. Regression analysis revealed the following significant negative relationships of sugars in leaves and stems with water depth: sucrose in E. canadensis on July 10-11 (R^2=0.43, $p<0.005$, n=20), fructose (R^2=0.21, $p<0.05$, n=24) and glucose (R^2=0.19, $p<0.05$, n=24) in M. exalbescens on August 29, fructose in P. foliosus on July 10-11 (R^2=0.19, $p<0.002$, n=50), and sucrose in P. foliosus on May 30 (R^2=0.34, $p<0.05$, n=12), June 27 (R^2=0.53, $p<0.001$, n=25), and July 10-11 (R^2=0.49, $p<0.001$, n=50). Positive relationships with depth were less frequent: fructose (R^2=0.45, $p<0.005$, n=17) and glucose (R^2=0.27, $p<0.05$, n=17) in M. exalbescens on May 16, and glucose in P. foliosus on June 13 (R^2=0.38, $p<0.005$, n=20). Proportions of individual sugars were also analyzed using linear regression, but this did not increase the number of significant relationships with depth.

Seasonal changes of individual sugars in the various macrophytes were examined in terms of proportions of total soluble carbohydrate. Proportions of sugars (Figs 75 to 84) showed some significant seasonal differences in SNK and Tukey's tests (Tables 18 to 29). Sucrose was the predominant sugar for the major part of the growing season in E. canadensis, P. foliosus, P. gramineus, P. praelongus, P. richardsonii, P. robbinsii, and P. zosteriformis. The proportion of sucrose reached levels as high as 72 % in P. foliosus and

E. canadensis on June 13, and 85 % in P. gramineus on August 8.

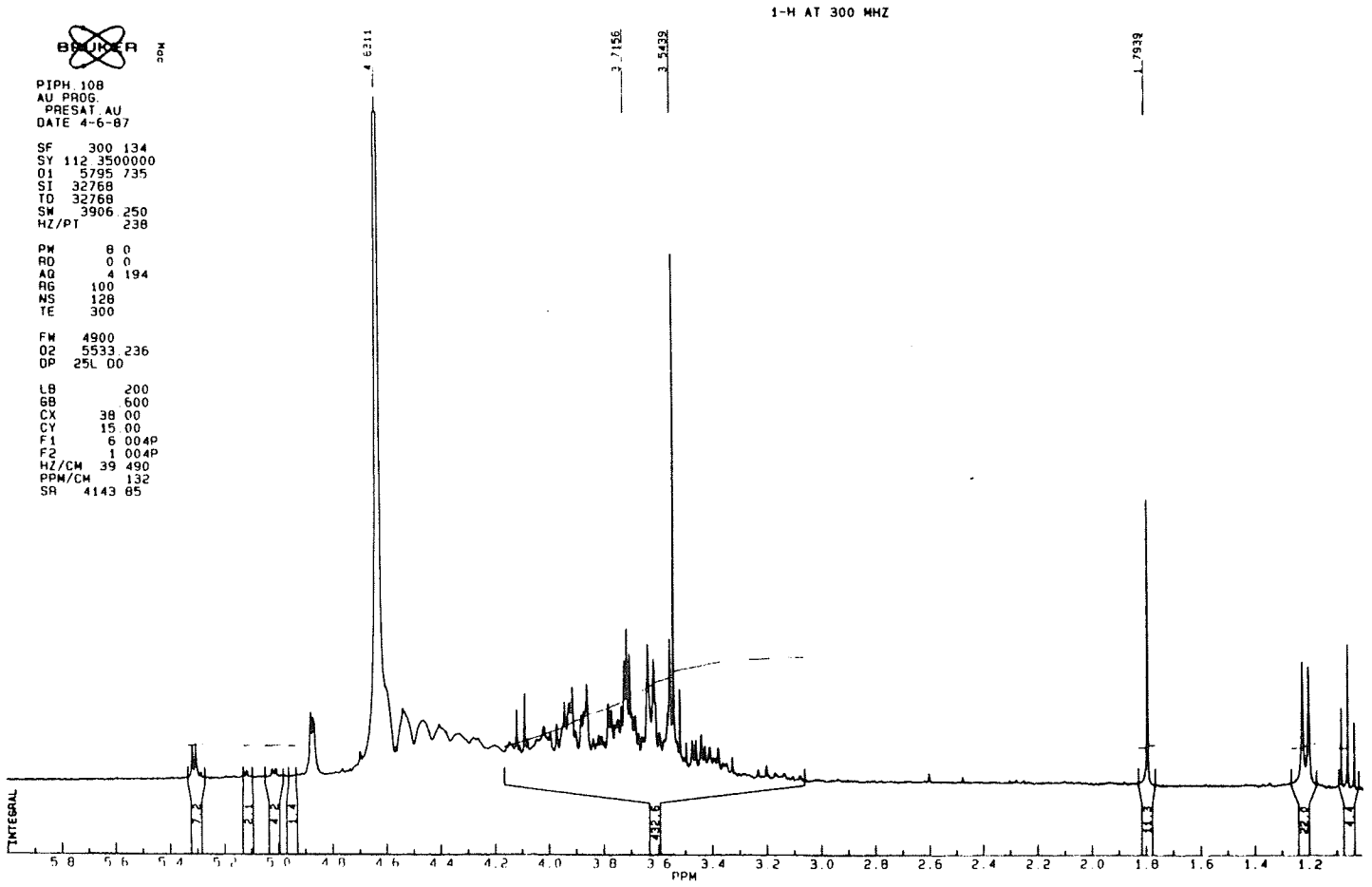
The most abundant sugar in E. canadensis on all sampling dates in 1985 was sucrose. The proportion did not change significantly with time, although levels did fluctuate and were highest on May 30 and June 13. The relative sucrose content in P. foliosus showed considerable seasonal variation and exceeded 40 % of total soluble sugars on May 16, June 13, July 10-11, and August 8. A significant seasonal maximum in the proportion of sucrose was observed on June 13. Levels of individual sugars in roots and shoots/leaves were not significantly different in the single P. foliosus sample containing roots. The predominant sugar in the roots was sucrose. The proportions of sucrose also fluctuated with time in P. robbinsii, with levels being highest on July 10-11 and August 8. A significant seasonal increase was observed in the proportion of sucrose in P. richardsonii, with levels on July 10-11 and August 8 exceeding the mean on June 27. There was also a tendency for a seasonal increase in the proportion of sucrose in P. zosteriformis, with levels on July 10-11 being significantly greater than proportional levels on May 2.

Glucose was the predominant sugar in M. exalbescens during the initial part of the 1985 season. The proportion of this sugar was found to be significantly higher on May 2 and June 27 than in July and August. The proportion of sucrose was higher than that of the other sugars in July and

August, and was significantly greater than the proportion of sucrose on May 2 and June 27. The proportion of glucose was significantly higher in shoots/leaves than in roots on June 27. No other significant comparisons in sugar content were observed for M. exalbescens samples containing roots. Glucose was the most abundant sugar in N. flexilis on 2 of the 3 sampling dates on which this species was represented.

The combined proportion of melibiose, raffinose, and stachyose in C. demersum accounted for the major proportion of soluble sugars for all sampling times in the 1985 growing season. The proportion of these sugars did not show any significant seasonal differences. Relative amounts of fructose and glucose in C. demersum frequently exceeded sucrose levels, and the 2 sugars were often present in similar quantities.

Fig.44. Proton NMR spectrum of Unknown A (stachyose).


1-H AT 300 MHZ
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PPM
PIPH 108
AU PROG.
PRESAT.AU
DATE 4-6-87
SF 300 134
SY 112 3500000
O1 5795 735
SI 32768
TD 32768
SW 3906 250
HZ/PT 238
PW 8 0
RD 0 0
AQ 4 194
RG 100
NS 128
TE 300
FW 4900
O2 5533 236
OP 25L 00
LB 200
GB 600
CX 38 00
CY 15 00
F1 6 004P
F2 1 004P
HZ/CM 39 490
PPM/CM 132
SR 4143 85
4.6311
3.7156
3.5439
1.7939
INTEGRAL
7.2
3.1
4.2
1.4
132.6
11.3
22.8
11.1
PPM

Fig.45. ^{13}C NMR spectrum for Unknown A (stachyose).

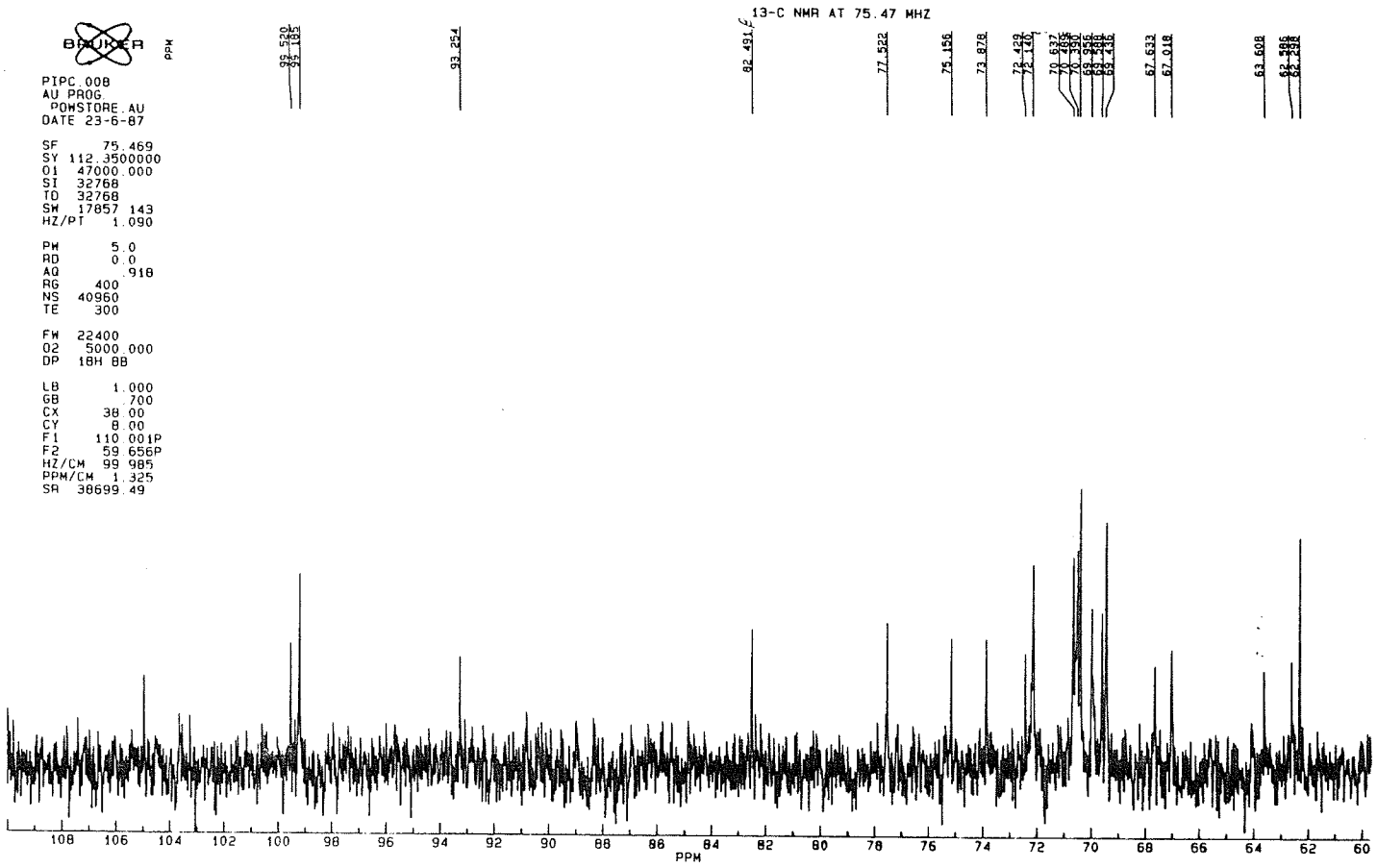
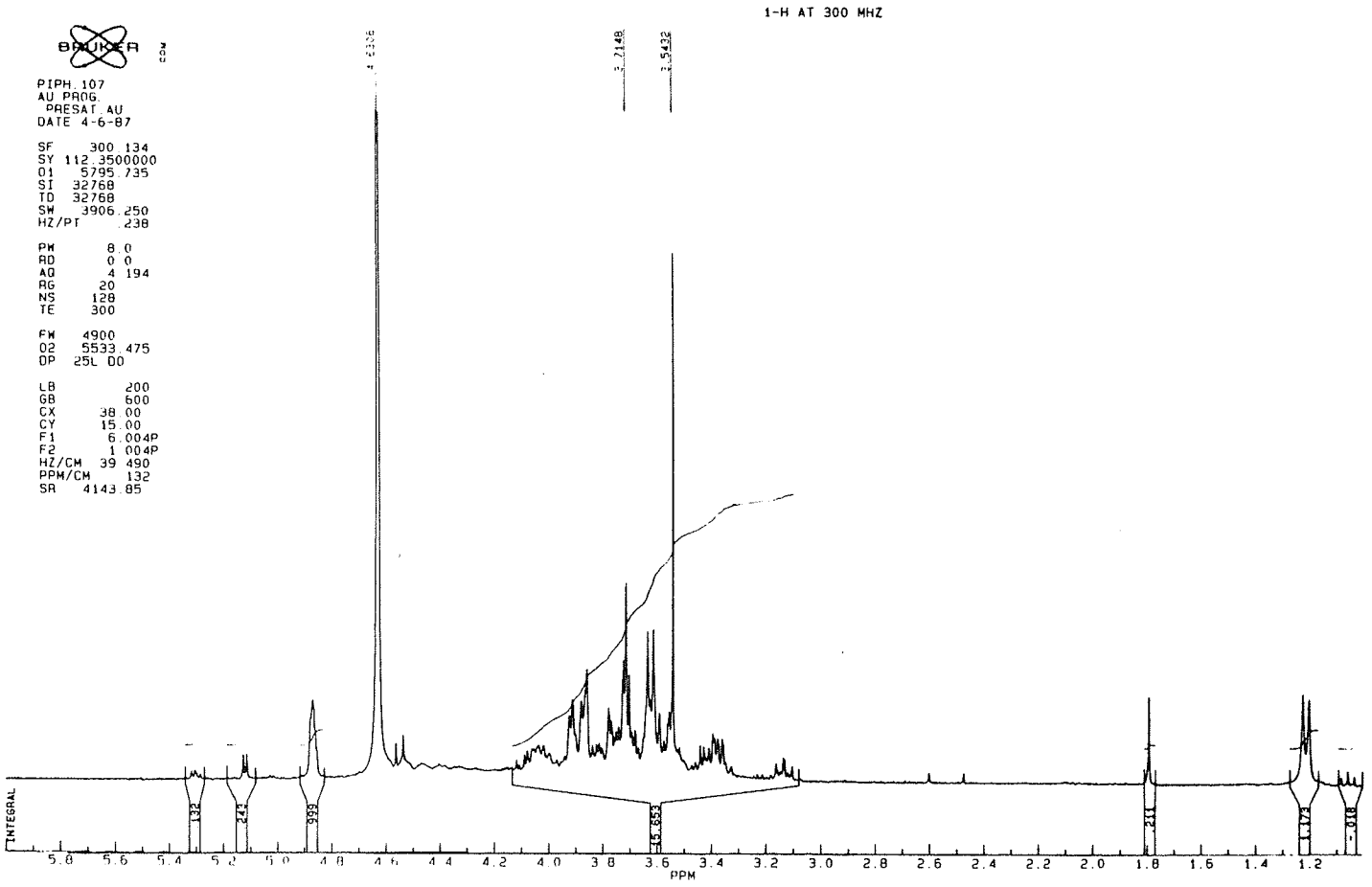

13-C NMR AT 75.47 MHZ
PPM
PIPC.008
AU PROG
POWSTORE.AU
DATE 23-6-87
SF 75.469
SY 112.3500000
O1 47000.000
SI 32768
TD 32768
SW 17857.143
HZ/PT 1.090
PW 5.0
RD 0.0
AQ .918
RG 400
NS 40960
TE 300
FW 22400
O2 5000.000
DP 18H 8B
LB 1.000
GB .700
CX 38.00
CY 8.00
F1 110.001P
F2 59.656P
HZ/CM 99.985
PPM/CM 1.325
SR 38699.49
93.520
93.254
82.491
77.522
75.156
73.878
72.429
72.140
70.637
67.633
67.018
63.608
62.386
62.298
108
106
104
102
100
98
96
94
92
90
88
86
84
82
80
78
76
74
72
70
68
66
64
62
60
PPM

Fig. 46. Proton NMR spectrum of Unknown B (raffinose/stachyose).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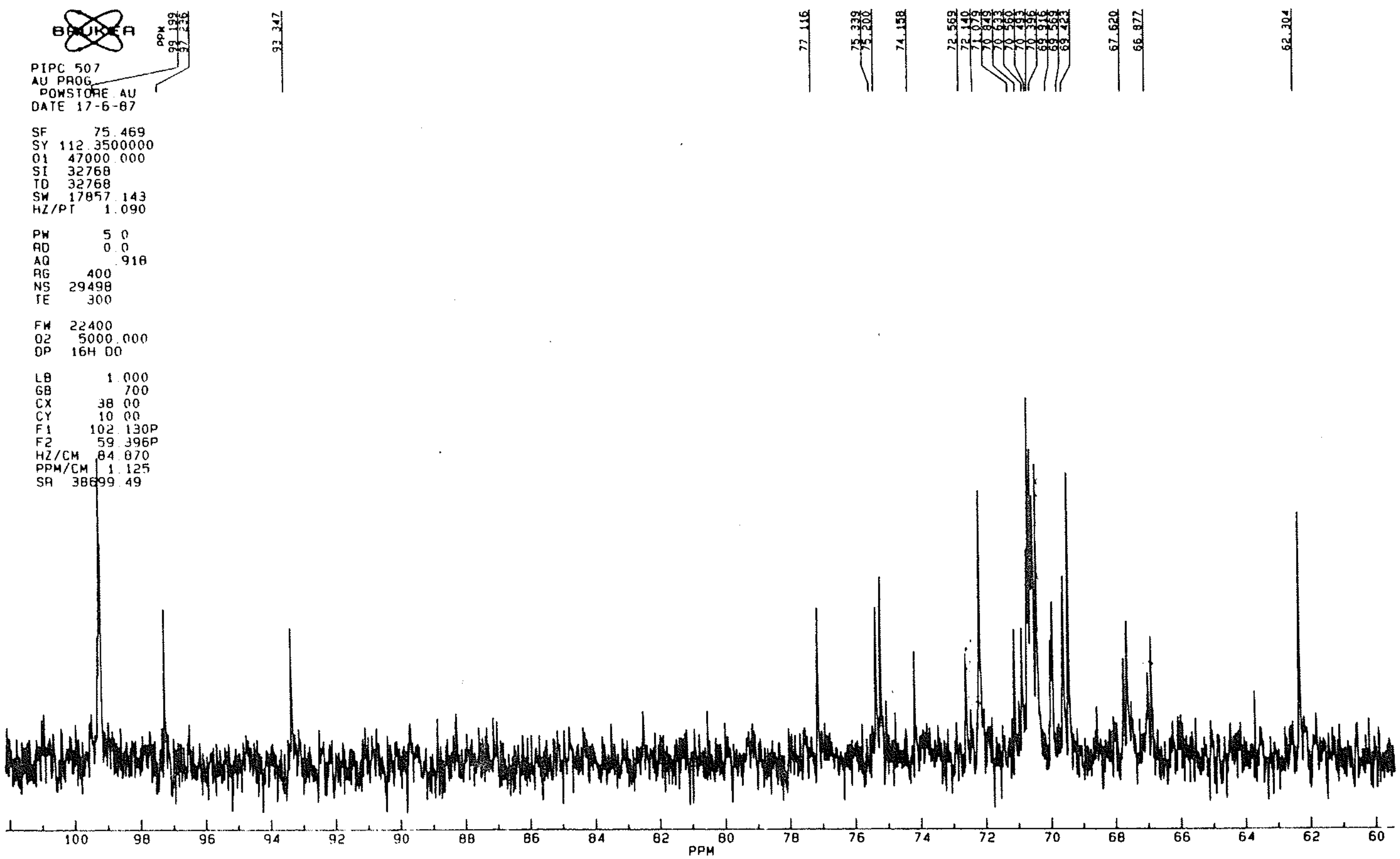
PRESAT.AU
DATE 4-6-87
SF 300.134
SY 112.3500000
01 5795.735
SI 32768
TD 32768
SW 3906.250
HZ/PT .238
PW 8.0
AD 0.0
AQ 4.194
RG 20
NS 128
TE 300
FW 4900
02 5533.475
OP 25L.00
LB 200
GB 600
CX 38.00
CY 15.00
F1 6.004P
F2 1.004P
HZ/CM 39.490
PPM/CM 132
SR 4143.85
3.7148
3.5432
INTEGRAL
1.32
2.42
9.99
15.65
2.11
3.17
1.10
PPM

Fig.47. ^{13}C NMR spectrum of Unknown B (raffinose/stachyose).


BRUKER
PPM
99.199
97.236
93.347
77.116
75.339
75.200
74.158
72.569
72.140
71.079
70.849
70.633
70.560
70.493
70.396
69.916
69.569
69.423
67.620
66.877
62.304
PIPC 507
AU PROG
POWSTORE.AU
DATE 17-6-87
SF 75.469
SY 112.3500000
O1 47000.000
SI 32768
TD 32768
SW 17857.143
HZ/PT 1.090
PW 5.0
RD 0.0
AQ .918
RG 400
NS 29498
TE 300
FW 22400
O2 5000.000
DP 16H DO
LB 1.000
GB .700
CX 38.00
CY 10.00
F1 102.130P
F2 59.396P
HZ/CM 84.870
PPM/CM 1.125
SR 38699.49
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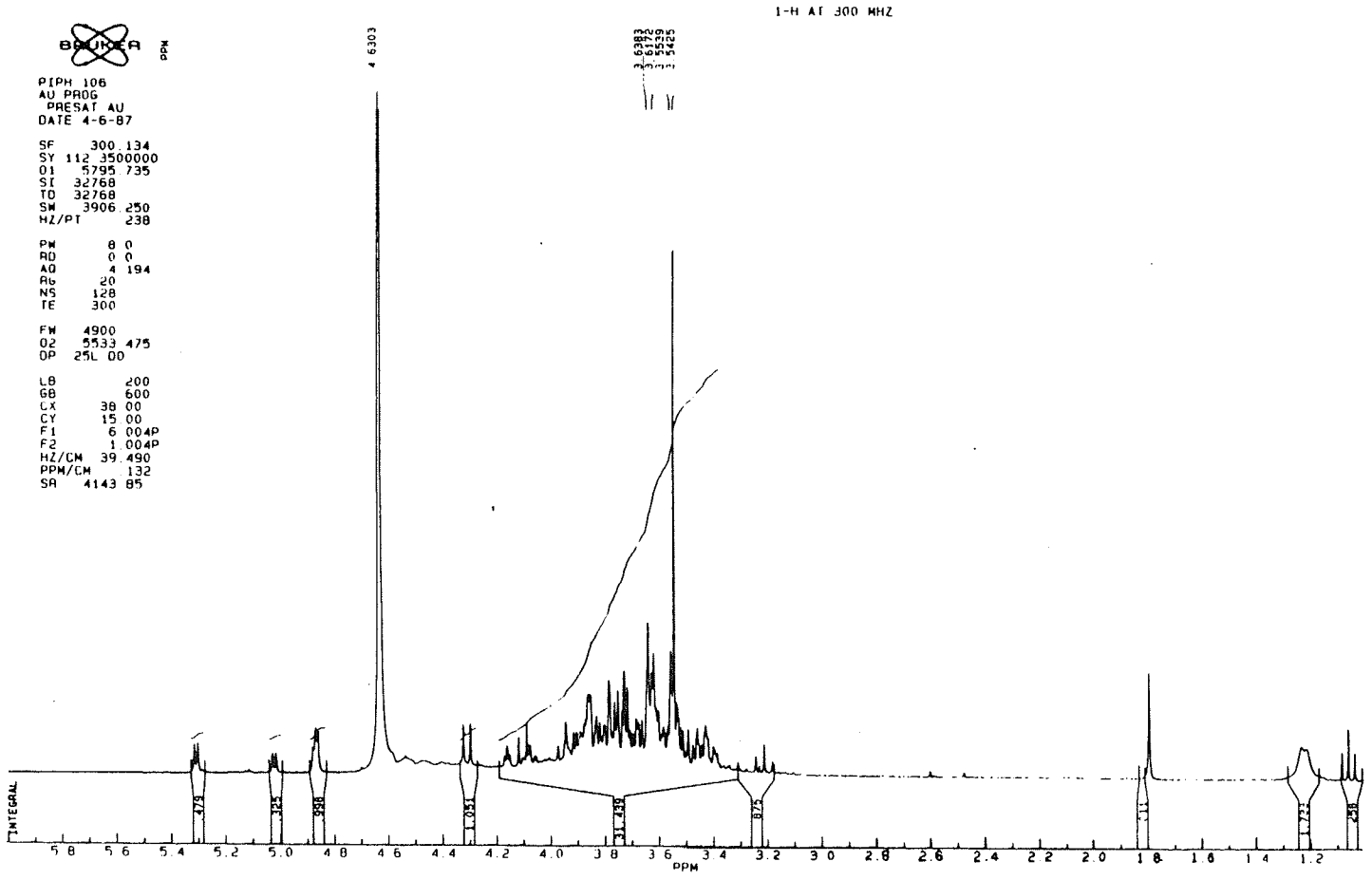
PPM

Fig.48. Proton NMR spectrum of Unknown C.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PPM
PIPH 106
AU PROG
PRESAT AU
DATE 4-6-87
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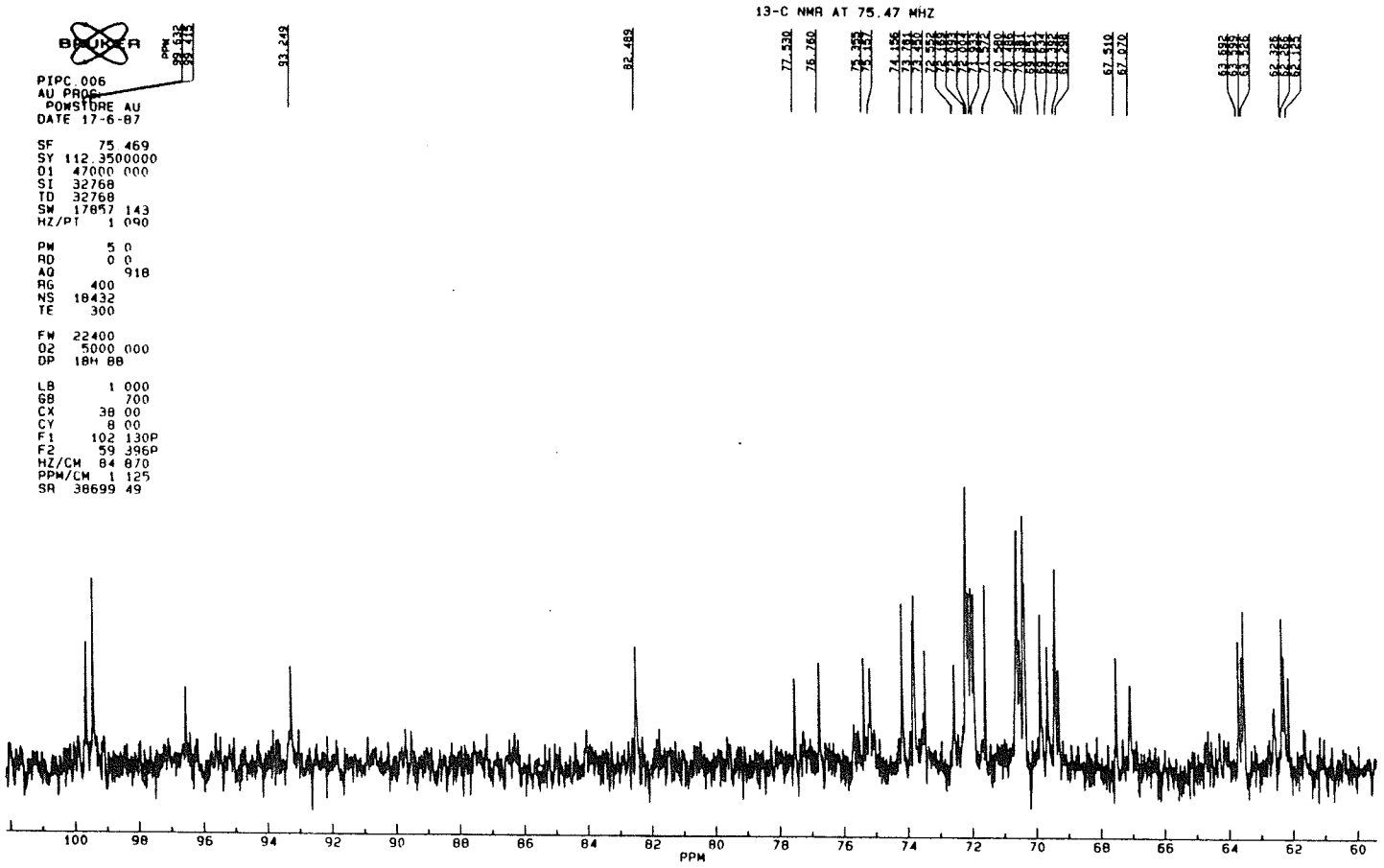
SY 112.3500000
O1 5795.735
SI 32768
TD 32768
SW 3906.250
HZ/PT 238
PW 8.0
RD 0.0
AQ 4.194
RG 20
NS 128
TE 300
FW 4900
O2 5533.475
OP 25L.00
LB .200
GB .600
CX 38.00
CY 15.00
F1 6.004P
F2 1.004P
HZ/CM 39.490
PPM/CM 1.32
SA 4143.85
4.6303
3.6383
3.6232
3.6139
3.5425
INTEGRAL
4.79
3.25
9.98
1.051
31.439
8.15
3.11
1.723
2.58
PPM

Fig.49. ^{13}C NMR spectrum of Unknown C.


13-C NMR AT 75.47 MHZ
PIPC.006
AU PROG:
POWSTORE AU
DATE 17-6-87
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SI 32768
TD 32768
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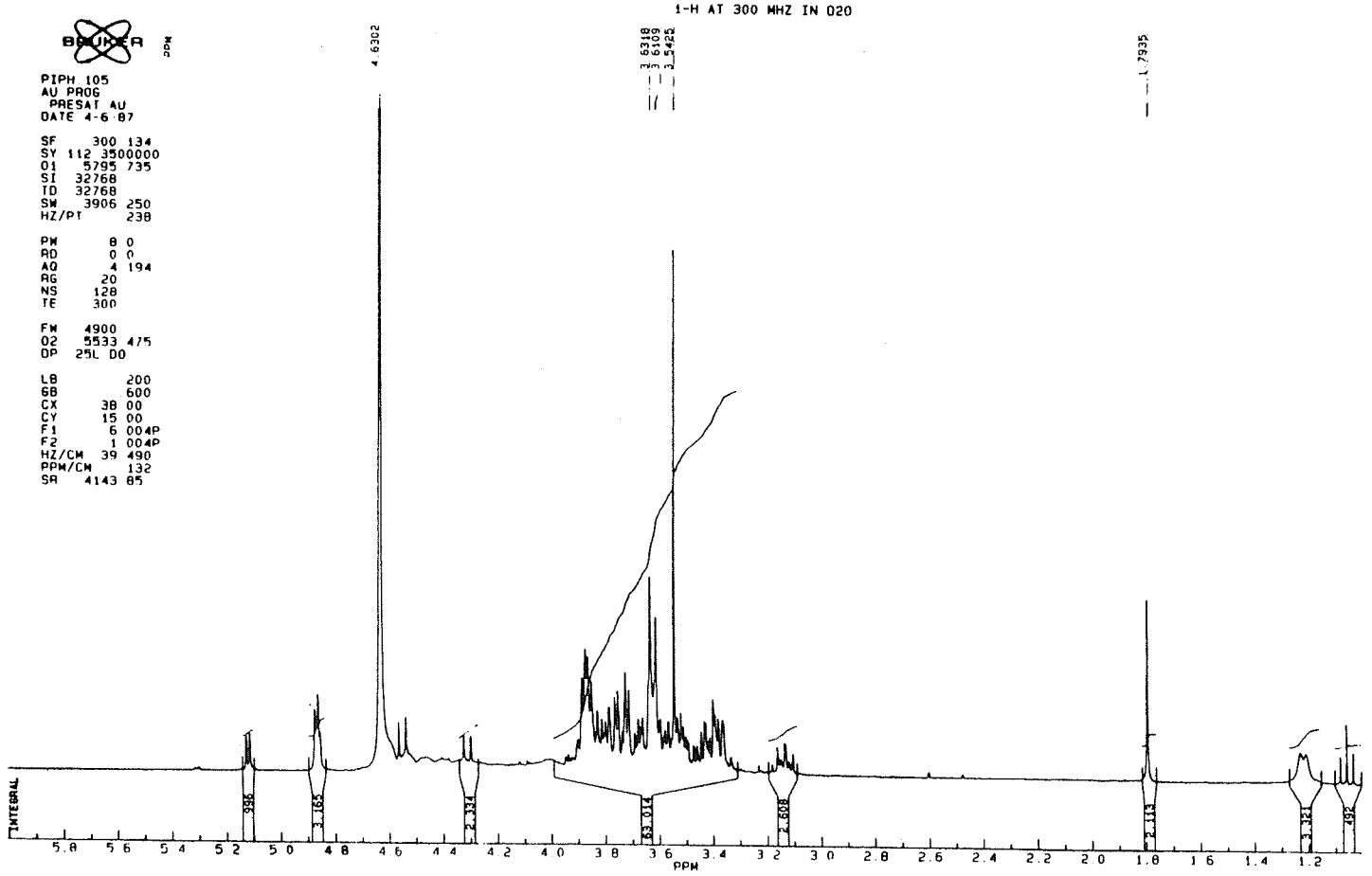
HZ/PT 1.090
PW 5.0
RD 0.0
AQ 918
RG 400
NS 18432
TE 300
FW 22400
O2 5000.000
DP 18H 8B
LB 1.000
GB 700
CX 38.00
CY 8.00
F1 102.130P
F2 59.396P
HZ/CM 84.870
PPM/CM 1.125
SR 38699.49
PPM
100
98
96
94
92
90
88
86
84
82
80
78
76
74
72
70
68
66
64
62
60

Fig. 50. Proton NMR spectrum for Unknown D (melibiose).


1-H AT 300 MHZ IN D20
BRUKER
PPM
PIPH 105
AU PROG
PRESAT AU
DATE 4-6-87
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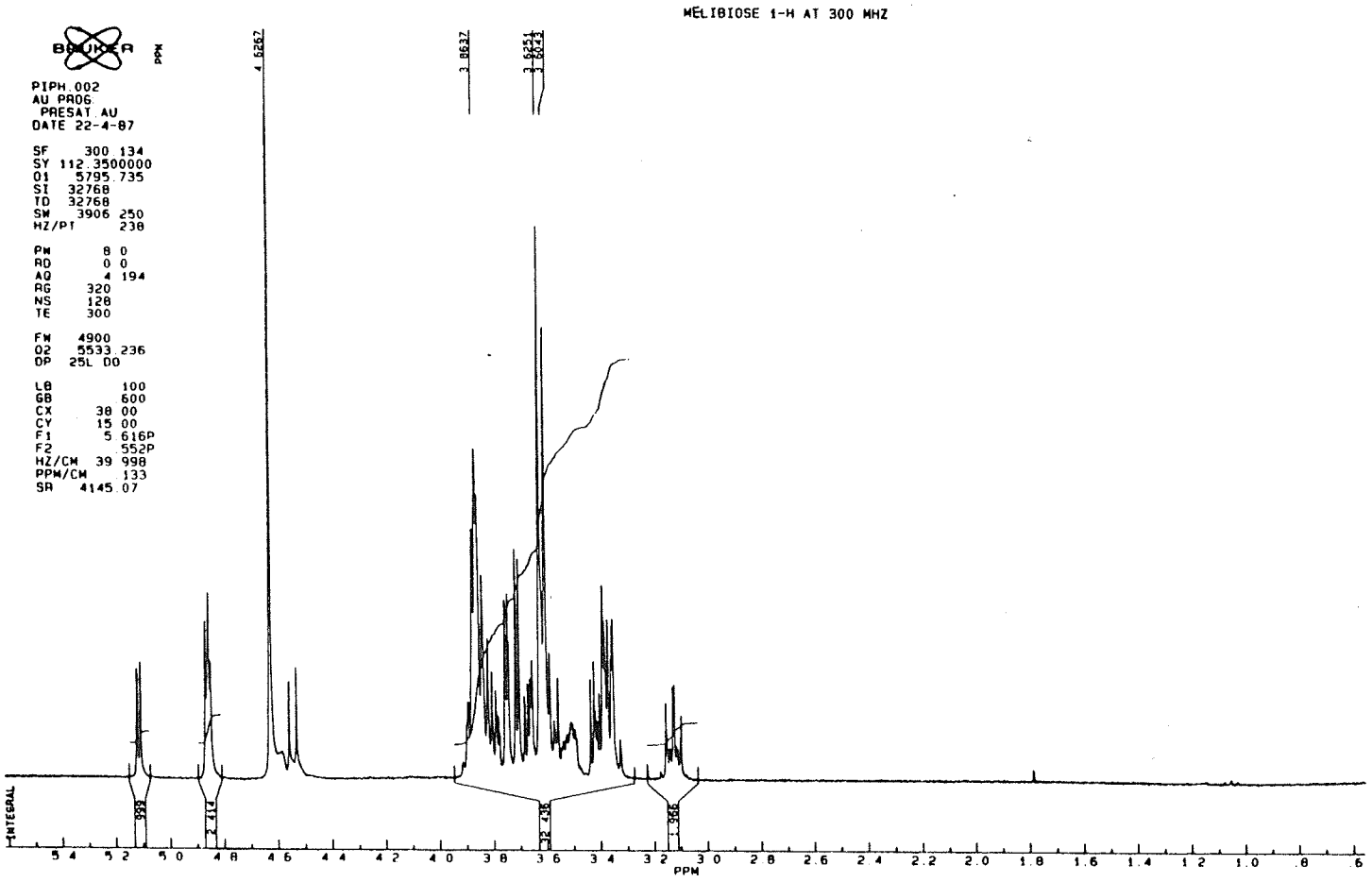
SY 112 3500000
O1 5795 735
SI 32768
TD 32768
SW 3906 250
HZ/PT 238
PW 8 0
RD 0 0
AQ 4 194
RG 20
NS 128
TE 300
FW 4900
O2 5533 475
DP 25L DO
LB 200
GB 600
CX 38 00
CY 15 00
F1 6 004P
F2 1 004P
HZ/CM 39 490
PPM/CM 132
SR 4143 85
4.6302
3.6318
3.6109
3.5422
1.7935
INTEGRAL
3.96
3.185
2.334
63.014
2.608
2.113
3.321
.492
PPM

Fig. 51. Proton NMR spectrum of melibiose.


MELIBIOSE 1-H AT 300 MHZ
BRUKER
PPM
PIPH.002
AU PROG
PRESAT.AU
DATE 22-4-87
SF 300.134
SY 112.3500000
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SI 32768
TD 32768
SW 3906.250
HZ/PT 238
PW 8 0
RD 0 0
AQ 4 194
RG 320
NS 128
TE 300
FW 4900
O2 5533.236
OP 25L.00
LB 100
GB 600
CX 38.00
CY 15.00
F1 5.616P
F2 552P
HZ/CM 39.998
PPM/CM .133
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3.8637
3.6251
3.6243
INTEGRAL
PPM

Fig. 52. Proton NMR spectrum of raffinose.

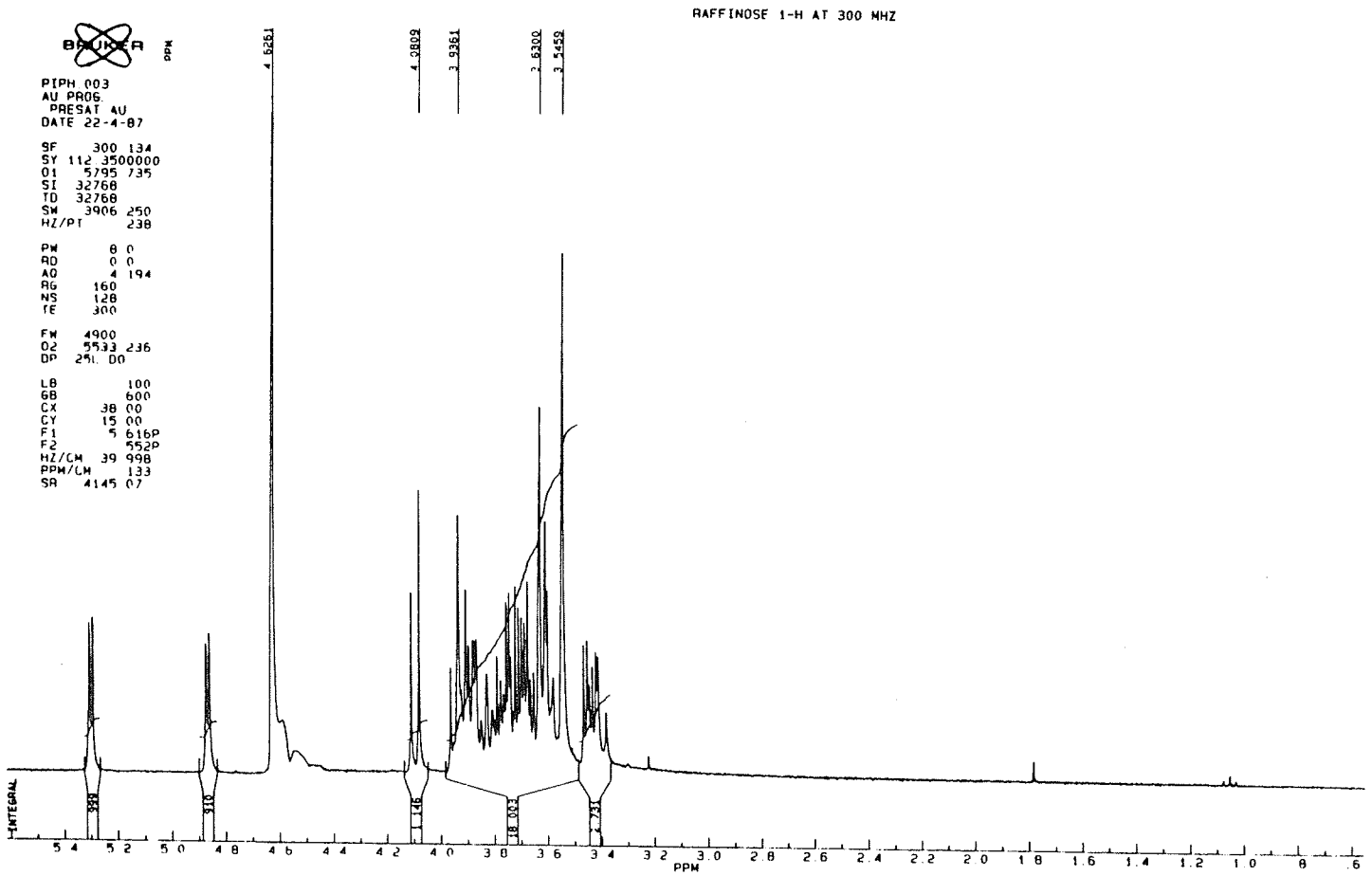
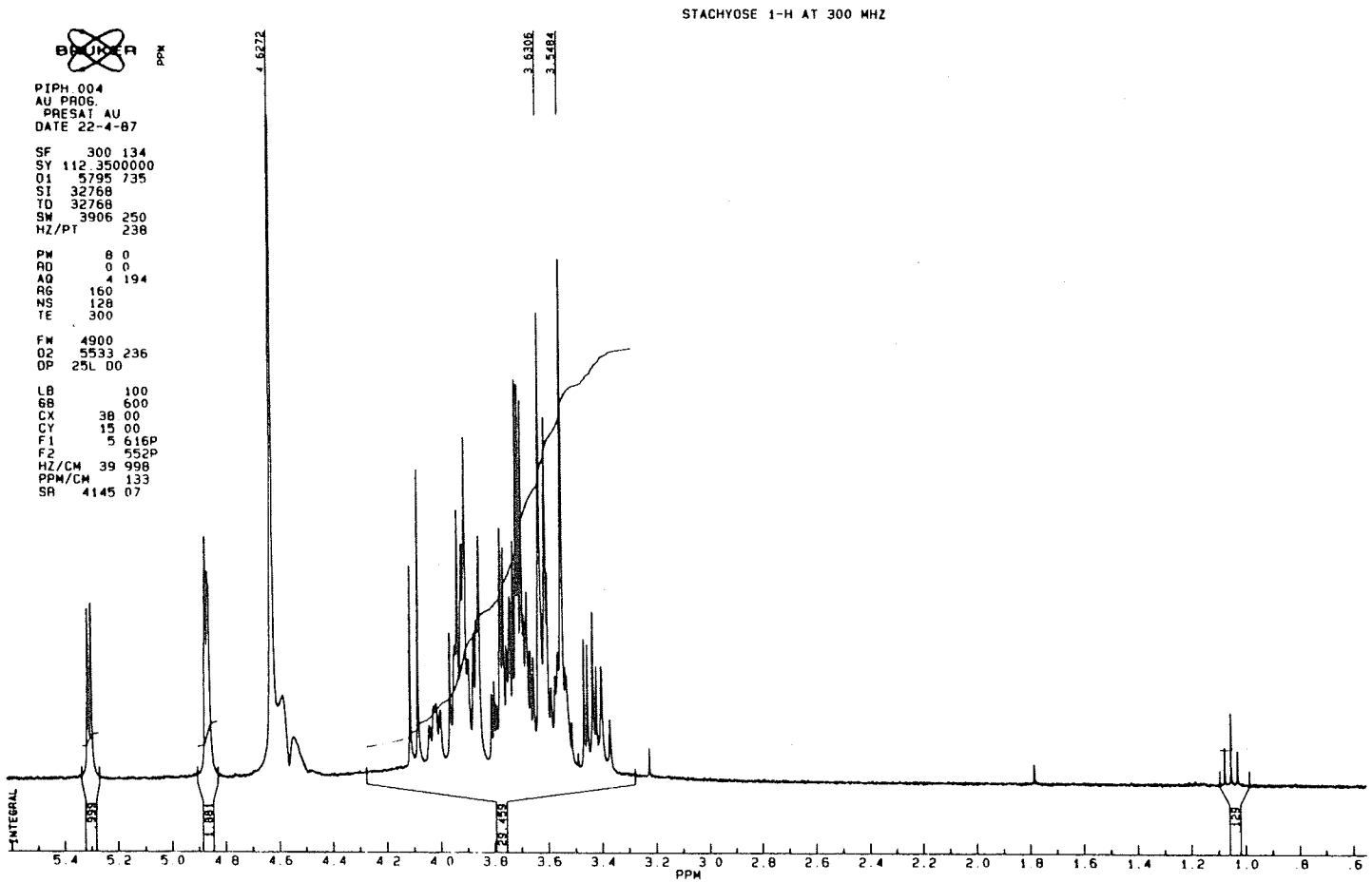

RAFFINOSE 1-H AT 300 MHZ
BRUKER
PPM
PIPH 003
AU PROG
PRESAT AU
DATE 22-4-87
SF 300 134
SY 112 3500000
01 5795 735
SI 32768
TD 32768
SW 3906 250
HZ/PT 238
PW 8 0
RD 0 0
AQ 4 194
RG 160
NS 128
TE 300
FW 4900
O2 5533 236
DP 251 00
LB 100
GB 600
CX 38 00
CY 15 00
F1 5 616P
F2 552P
HZ/CM 39 998
PPM/CM 133
SR 4145 07
4.6261
4.2809
3.9361
3.6300
3.5452
INTEGRAL
3.99
3.10
1.46
18.00
2.23
PPM

Fig. 53. Proton NMR spectrum of stachyose.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BRUKER
PPM
PIPH 004
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PRESAT AU
DATE 22-4-87
SF 300 134
SY 112 3500000
O1 5795 735
SI 32768
TD 32768
SW 3906 250
HZ/PT 238
PW 8 0
AD 0 0
AQ 4 194
RG 160
NS 128
TE 300
FW 4900
O2 5533 236
OP 25L DO
LB 100
GB 600
CX 38 00
CY 15 00
F1 5 616P
F2 552P
HZ/CM 39 998
PPM/CM 133
SR 4145 07
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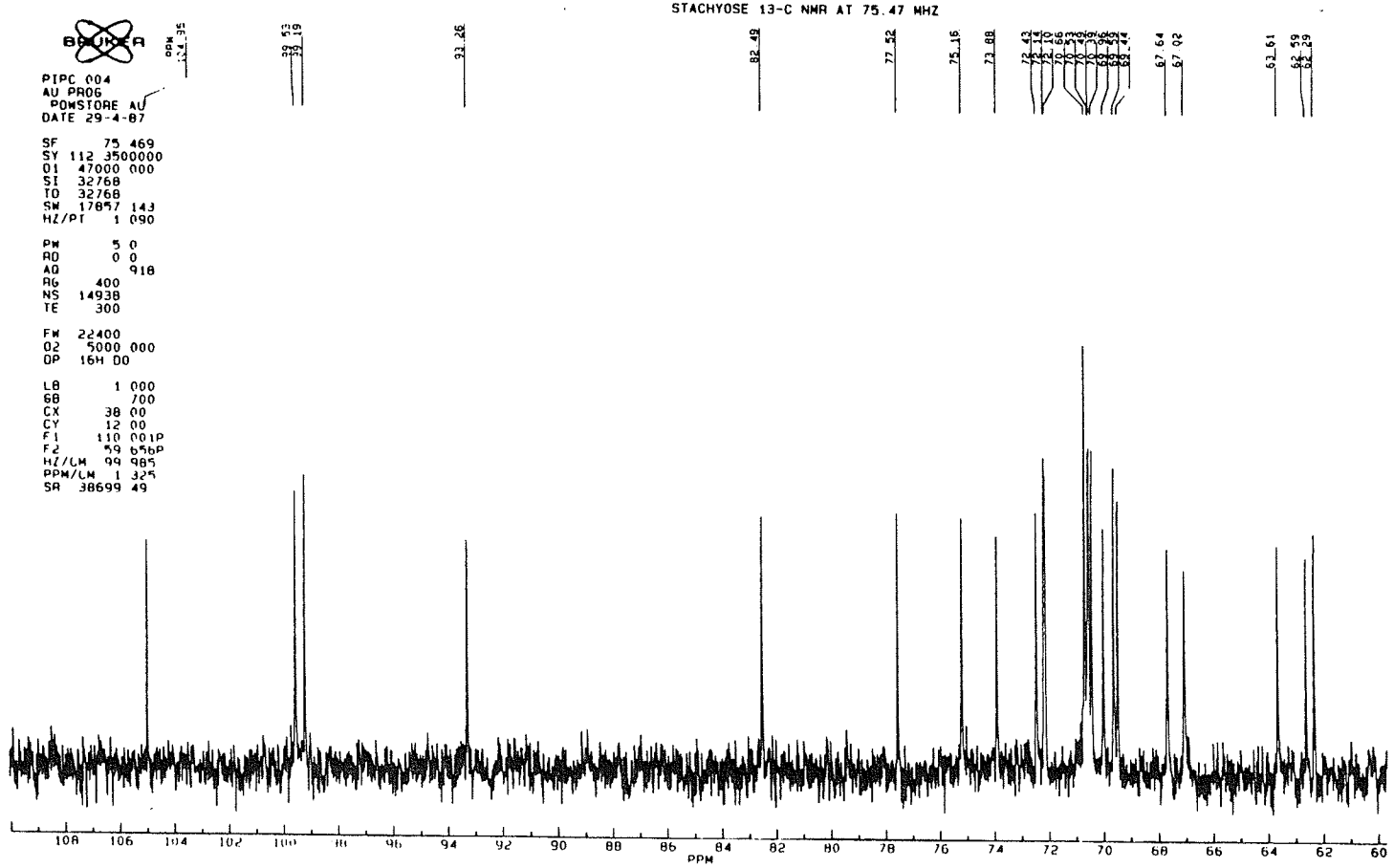
3.5484
INTEGRAL
PPM

Fig. 54. ^{13}C NMR spectrum of stachyose.


STACHYOSE 13-C NMR AT 75.47 MHZ
BRUKER
PPM
102.95
99.53
99.19
93.26
82.49
77.52
75.16
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72.43
72.14
72.10
70.66
70.53
70.32
70.16
69.96
69.80
69.44
67.64
67.02
61.61
62.59
62.29
PIPC 004
AU PROG
POWSTORE AU
DATE 29-4-87
SF 75.469
SY 112.3500000
D1 47000.000
SI 32768
TD 32768
SW 17857.143
HZ/PT 1.090
PW 5.0
RD 0.0
AQ 918
RG 400
NS 14938
TE 300
FW 22400
O2 5000.000
OP 16H DO
LB 1.000
GB .700
CX 38.00
CY 12.00
F1 110.001P
F2 59.656P
HZ/CM 99.985
PPM/CM 1.325
SR 38699.49
108 106 104 102 100 98 96 94 92 90 88 86 84 82 80 78 76 74 72 70 68 66 64 62 60
PPM

Fig. 55. Proton NMR spectrum of lactose.

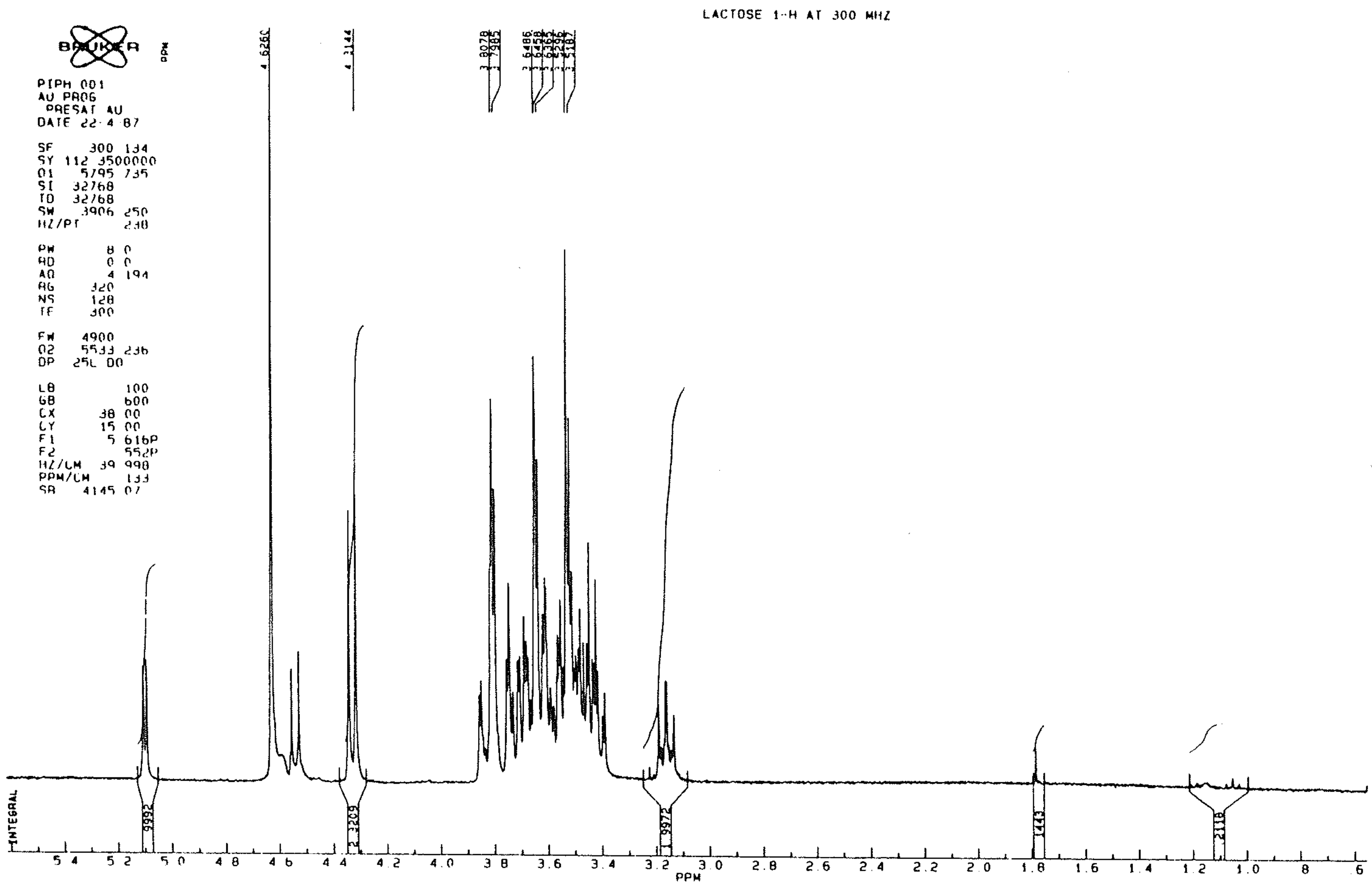

LACTOSE 1-H AT 300 MHZ
BRUKER
PIPH 001
AU PROG
PRESAT AU
DATE 22-4-87
SF 300 134
SY 112 3500000
O1 5795 735
SI 32768
TD 32768
SW 3906 250
HZ/PT 238
PW 8 0
RD 0 0
AQ 4 194
RG 320
NS 128
TE 300
FW 4900
O2 5533 236
DP 25L 00
LB 100
GB 600
CX 38 00
CY 15 00
F1 5 616P
F2 552P
HZ/CM 39 998
PPM/CM 133
SR 4145 07
PPM
4 6260
4 3144
3 8078
3 7985
3 6486
INTEGRAL
9992
2 3209
9972
1443
2118
5 4
5 2
5 0
4 8
4 6
4 4
4 2
4 0
3 8
3 6
3 4
3 2
3 0
2 8
2 6
2 4
2 2
2 0
1 8
1 6
1 4
1 2
1 0
8
6
PPM

Fig. 56. Proton NMR spectrum of myo-inositol.

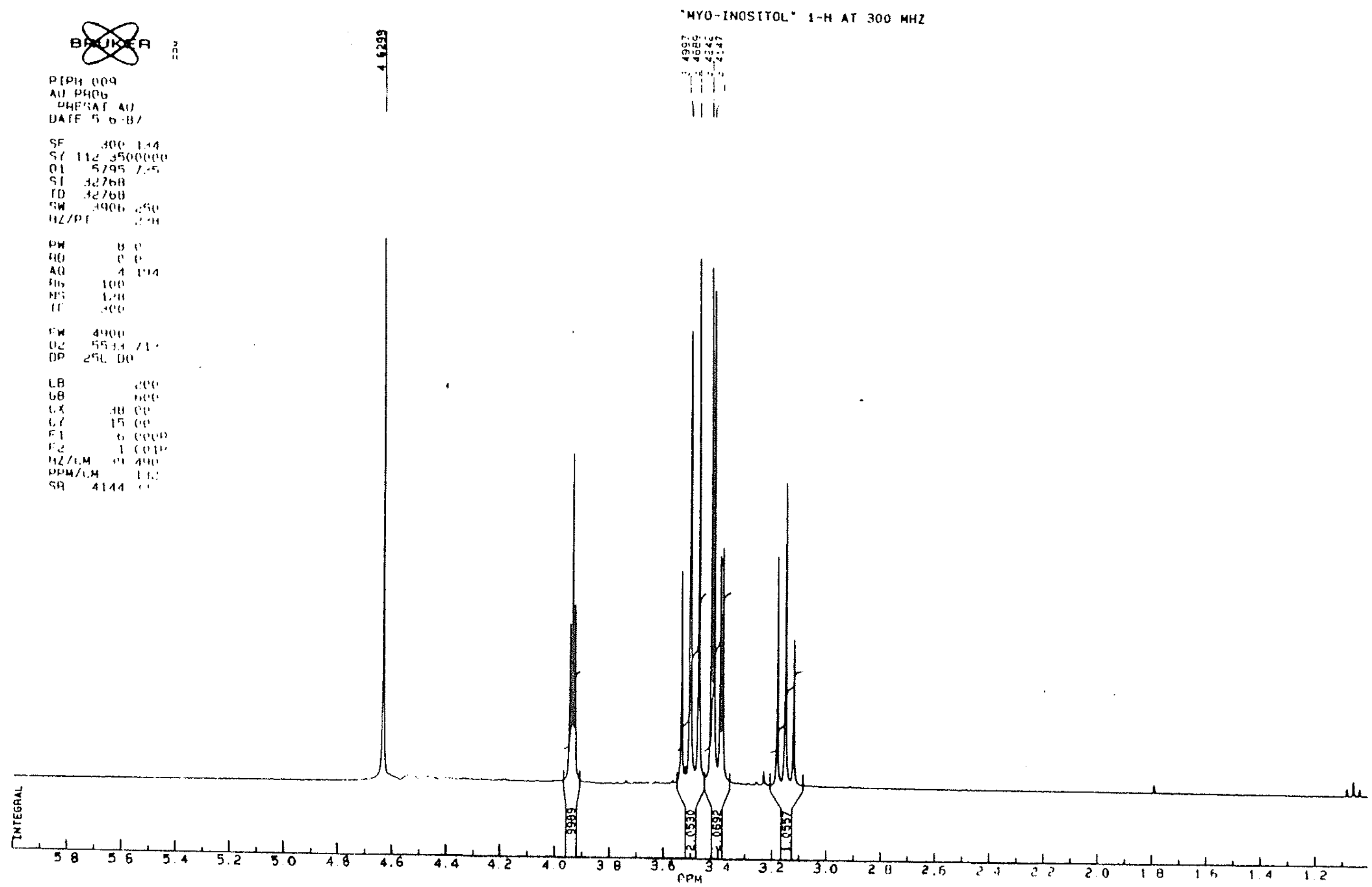

"MYO-INOSITOL" 1-H AT 300 MHZ
BRUKER
DATE 5-6-87
4.6299
INTEGRAL
.9989
2.0530
2.0592
1.0557
PPM
5.8
5.6
5.4
5.2
5.0
4.8
4.6
4.4
4.2
4.0
3.8
3.6
3.4
3.2
3.0
2.8
2.6
2.4
2.2
2.0
1.8
1.6
1.4
1.2

Fig. 57. Fructose content in stems and leaves of Ceratophyllum demersum on various sampling dates during the 1985 growing season. Vertical bars represent standard error and numbers beside circles indicate sampling sites. Depth (in meters) for each collection time is shown on the horizontal axis.

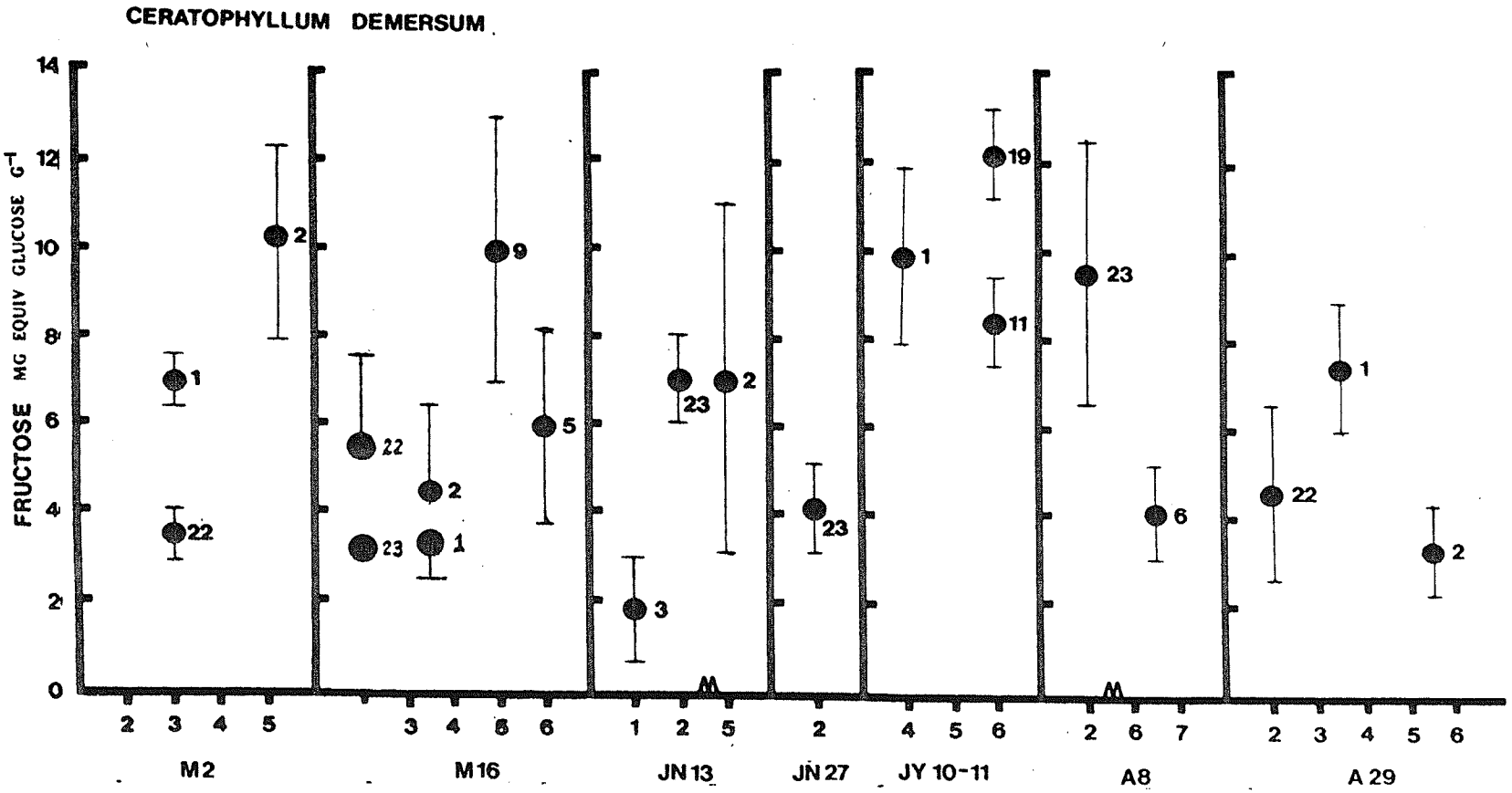

CERATOPHYLLUM DEMERSUM
FRUCTOSE MG EQUIV GLUCOSE G⁻¹
0
2
4
6
8
10
12
14
M2
M16
JN 13
JN 27
JY 10-11
A8
A 29

Fig. 58. Glucose content in stems and leaves of Ceratophyllum demersum on various sampling dates during the 1985 growing season. Vertical bars represent standard error and numbers beside circles indicate sampling sites. Depth (in meters) for each collection time is shown on the horizontal axis.

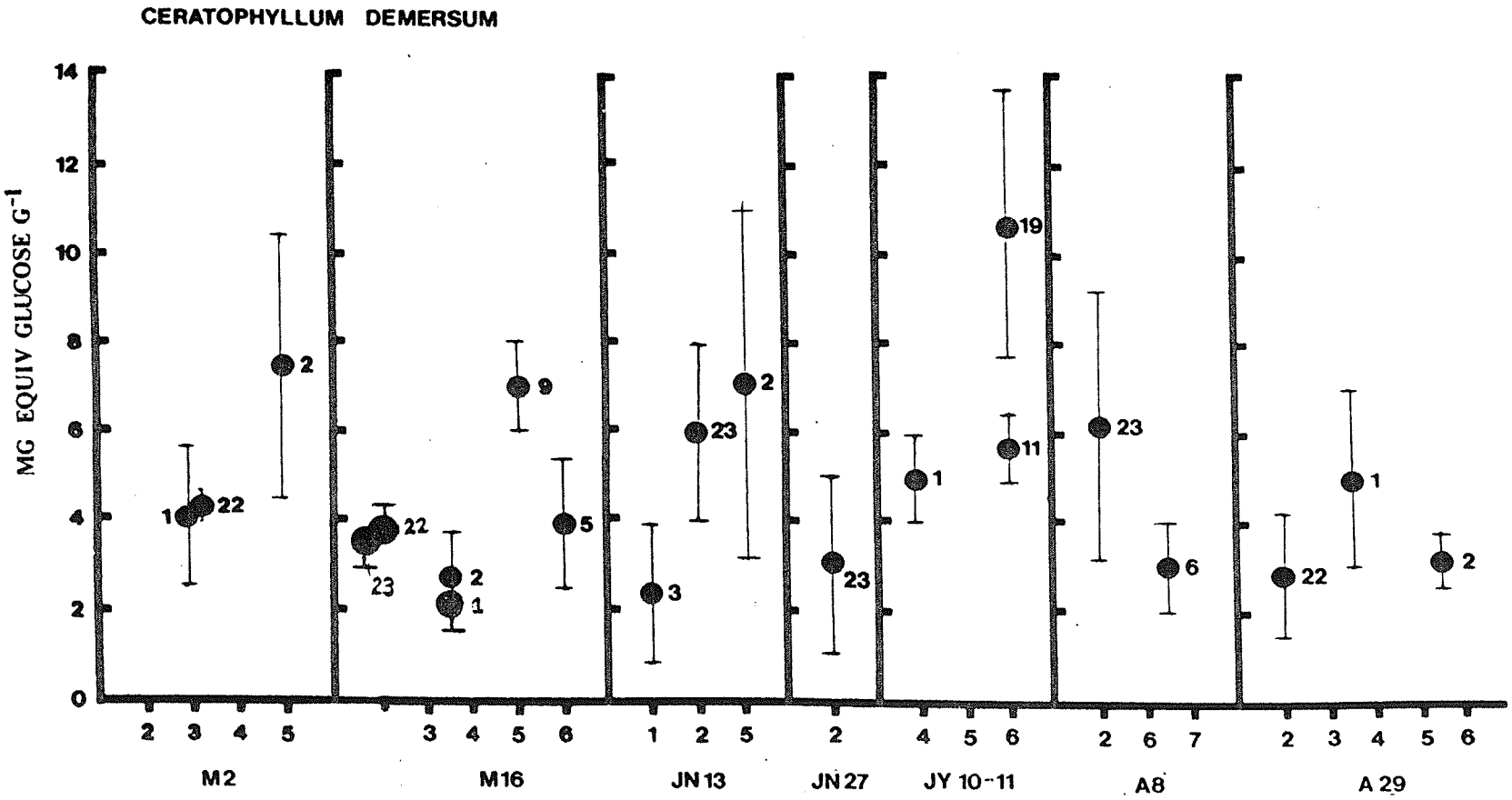

CERATOPHYLLUM DEMERSUM
MG EQUIV GLUCOSE G-1
14
12
10
8
6
4
2
0
1
22
2
22
23
2
1
9
5
3
23
2
19
11
1
23
6
22
1
2
2 3 4 5
3 4 5 6
1 2 5
2
4 5 6
2 6 7
2 3 4 5 6
M2
M16
JN 13
JN 27
JY 10-11
A8
A 29

Fig. 59. Sucrose content in stems and leaves of Ceratophyllum demersum on various sampling dates during the 1985 growing season. Vertical bars represent standard error and numbers beside circles indicate sampling sites. Depth (in meters) for each collection time is shown on the horizontal axis.

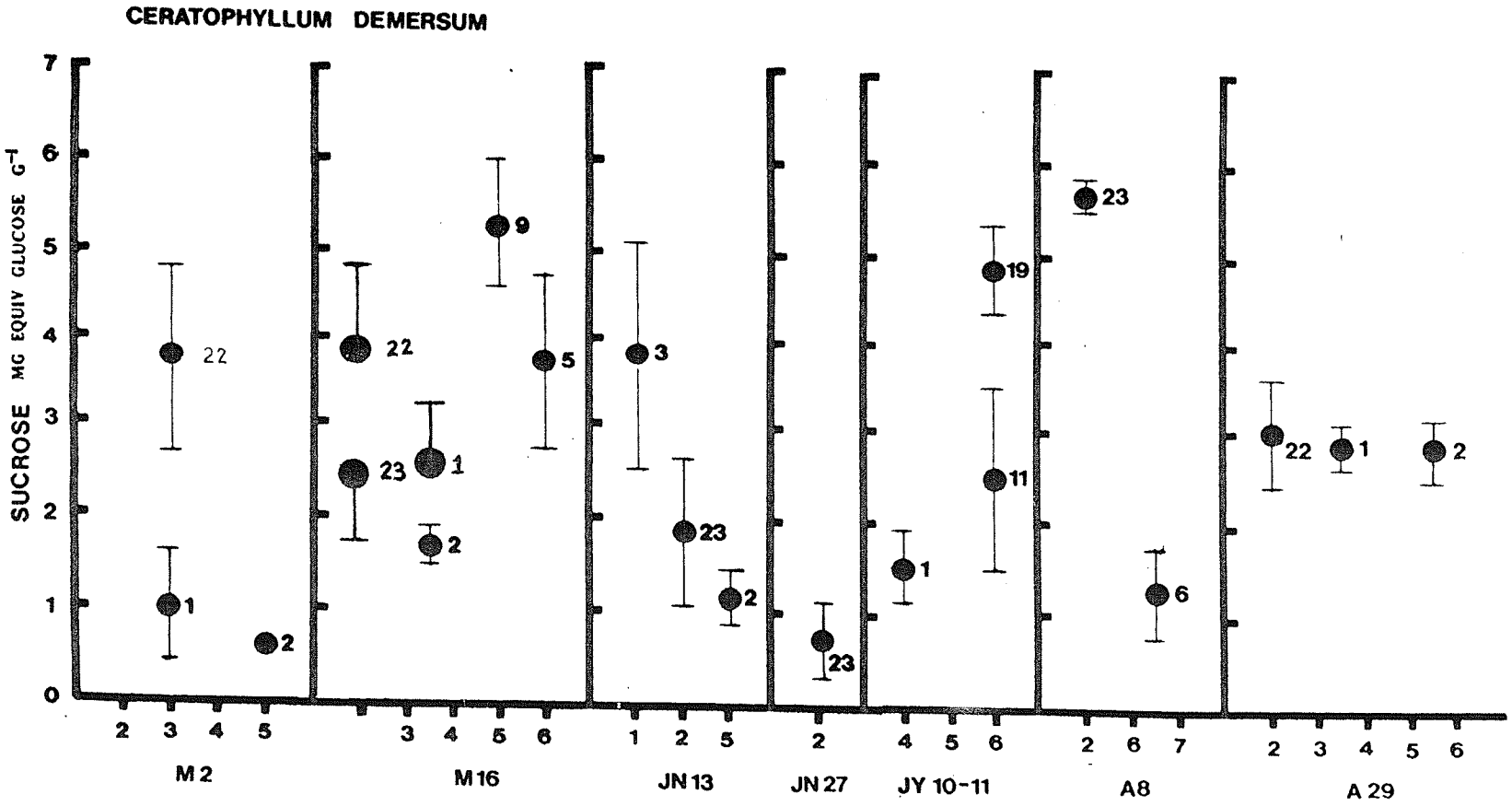

CERATOPHYLLUM DEMERSUM
SUCROSE MG EQUIV GLUCOSE G⁻¹
0
1
2
3
4
5
6
7
22
1
2
22
23
1
2
9
5
3
23
2
23
1
11
19
23
6
22
1
2
2 3 4 5
M 2
3 4 5 6
M 16
1 2 5
JN 13
2
JN 27
4 5 6
JY 10-11
2 6 7
A8
2 3 4 5 6
A 29

Fig. 60. Fructose content in stems and leaves of Elodea canadensis on various sampling dates during the 1985 growing season. Vertical bars represent standard error and numbers beside circles indicate sampling sites. Depth (in meters) for each collection time is shown on the horizontal axis.

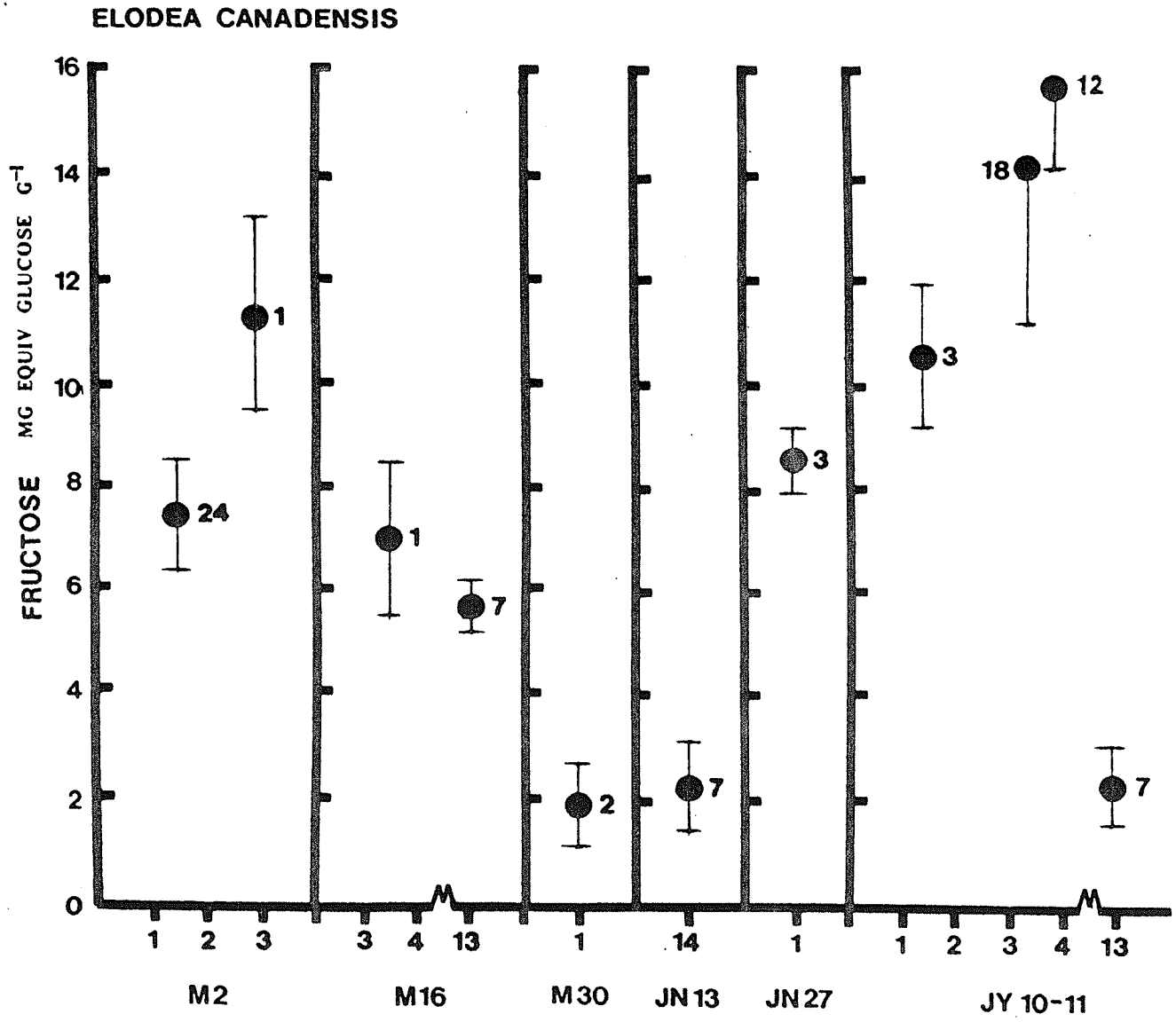

ELODEA CANADENSIS
FRUCTOSE MG EQUIV GLUCOSE G⁻¹
16
14
12
10
8
6
4
2
0
24
1
1
7
2
7
3
18
12
7
1 2 3
3 4 13
1
14
1
1 2 3 4 13
M2
M16
M30
JN 13
JN 27
JY 10-11

Fig. 61. Glucose content in stems and leaves on Elodea canadensis on various sampling dates during the 1985 growing season. Vertical bars represent standard error and numbers beside circles indicate sampling sites. Depth (in meters) for each collection time is shown on the horizontal axis.

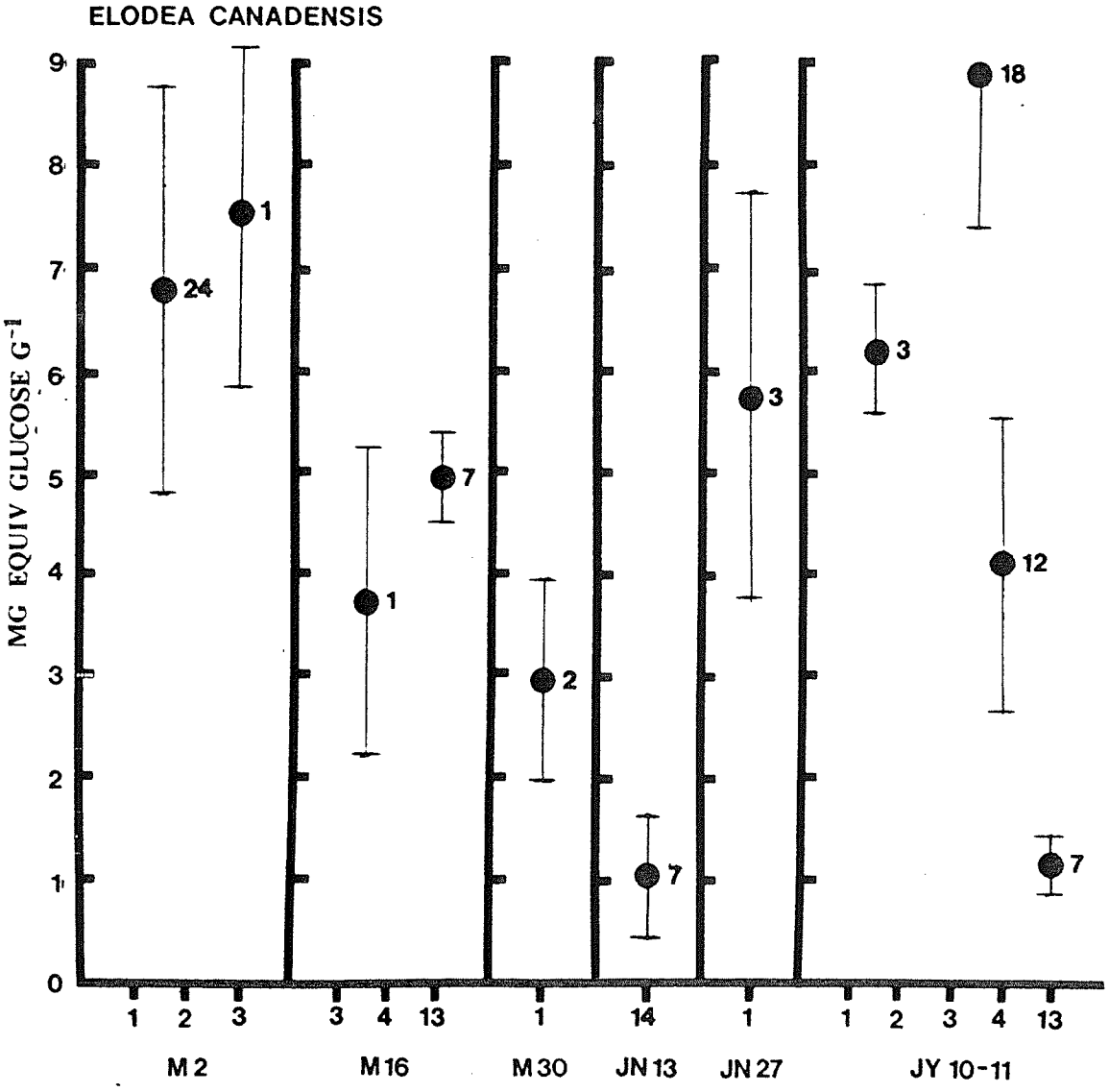

ELODEA CANADENSIS
MG EQUIV GLUCOSE G⁻¹
0
1
2
3
4
5
6
7
8
9
24
1
1
7
2
7
3
3
18
12
7
1 2 3
3 4 13
1
14
1
1 2 3 4 13
M 2
M 16
M 30
JN 13
JN 27
JY 10-11

Fig. 62. Sucrose content in stems and leaves of Elodea canadensis on various sampling dates during the 1985 growing season. Vertical bars represent standard error and numbers beside circles indicate sampling sites. Depth (in meters) for each collection time is shown on the horizontal axis. A statistically significant relationship between depth and sucrose content is shown for July 10-11.

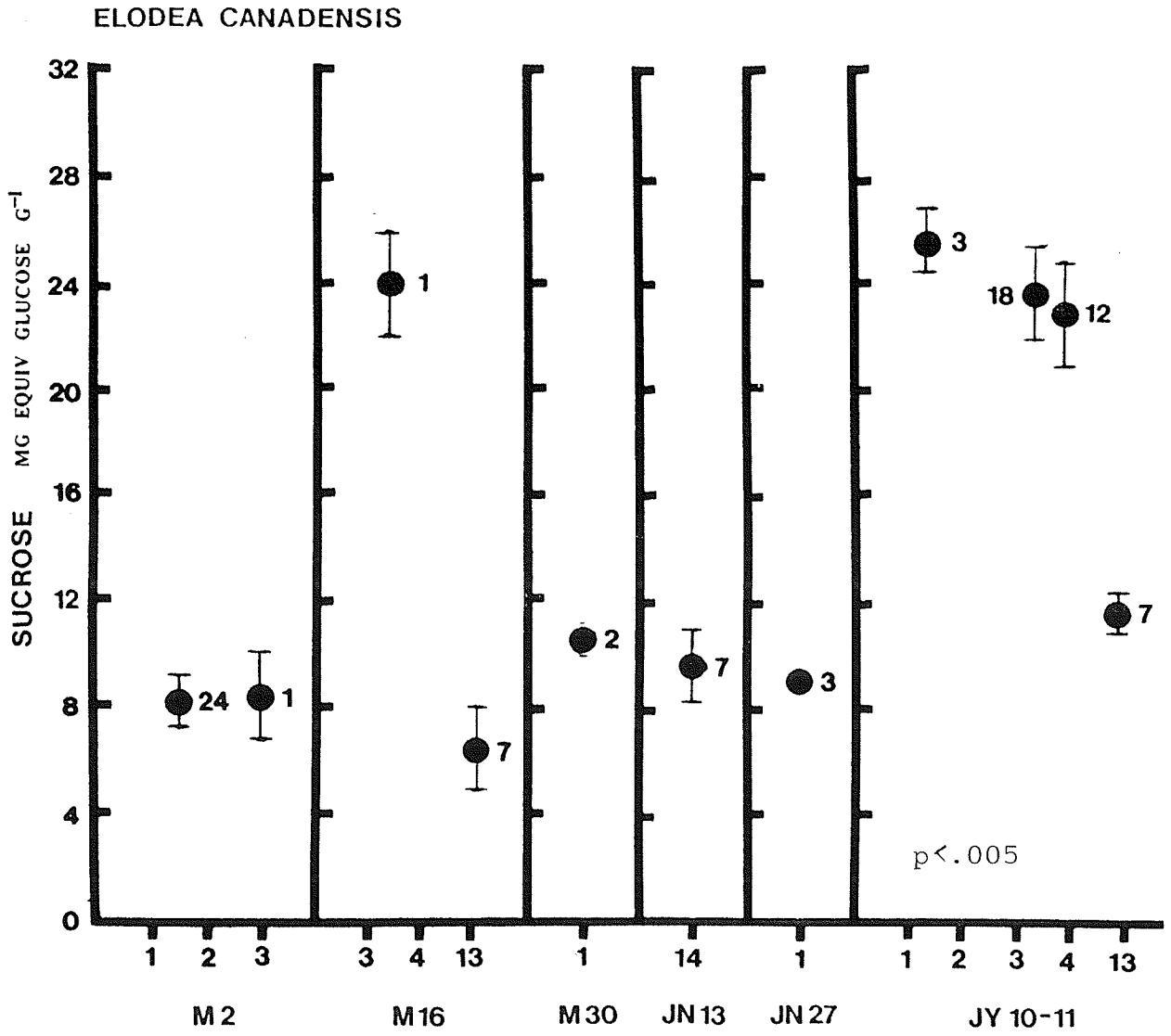

ELODEA CANADENSIS
SUCROSE MG EQUIV GLUCOSE G⁻¹
32
28
24
20
16
12
8
4
0
24
1
1
7
2
7
3
3
18
12
7
p<.005
1 2 3
3 4 13
1
14
1
1 2 3 4 13
M 2
M16
M30
JN 13
JN 27
JY 10-11

Fig. 63. Fructose content in stems and leaves (closed circles) and roots (open circles) of Myriophyllum exalbescens on various sampling dates during the 1985 growing season. Vertical bars represent standard error and numbers beside circles indicate sampling sites. Depth (in meters) for each collection time is shown on the horizontal axis. Statistically significant relationships between depth and fructose content are shown for May 16 and August 29.

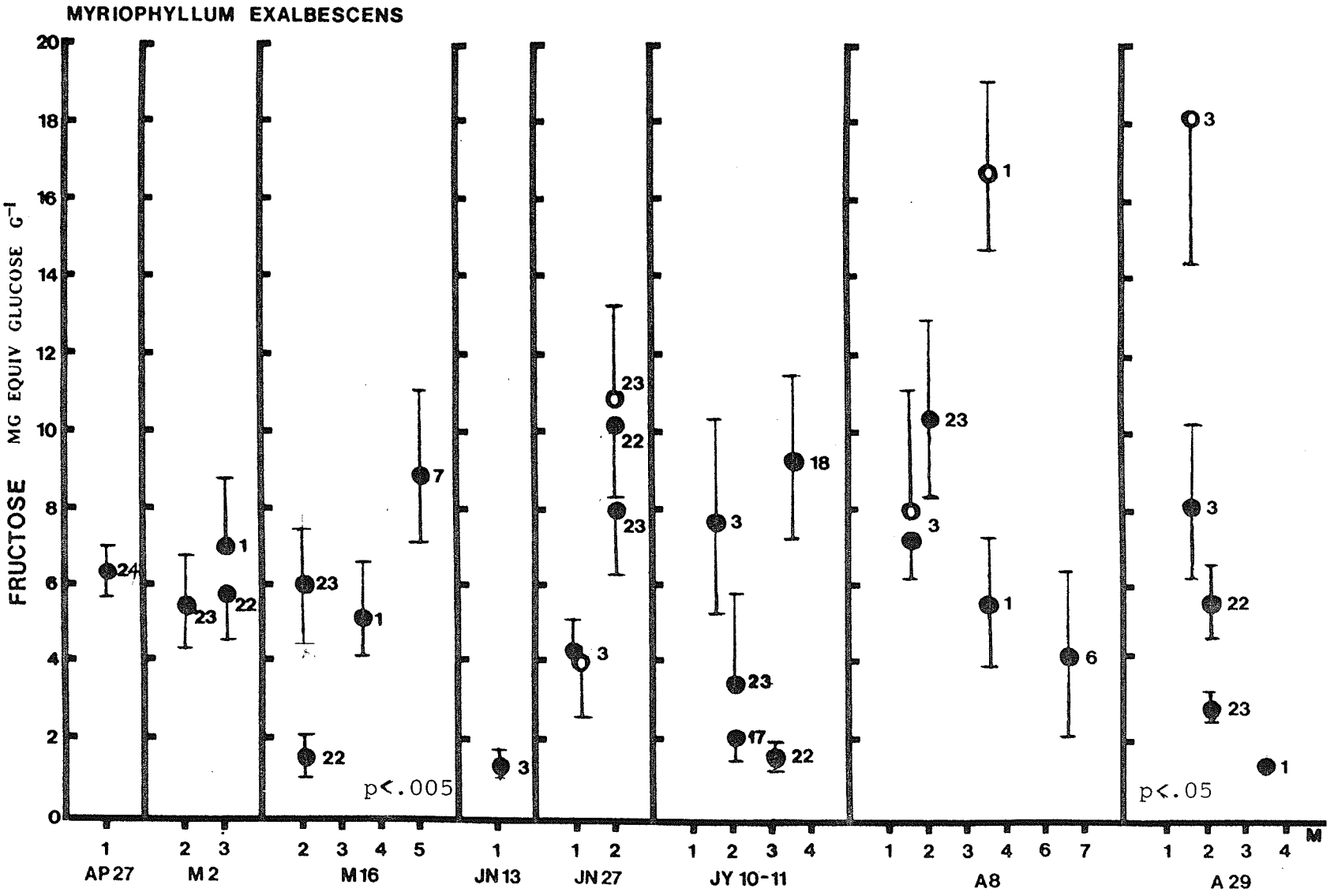

MYRIOPHYLLUM EXALBESCENS
FRUCTOSE MG EQUIV GLUCOSE G⁻¹
20
18
16
14
12
10
8
6
4
2
0
24
23
1
22
23
22
1
7
22
p<.005
3
3
23
22
23
3
23
17
22
18
3
1
1
6
3
23
1
p<.05
3
22
23
1
1 AP 27
2 3 M 2
2 3 4 5 M16
1 JN 13
1 2 JN 27
1 2 3 4 JY 10-11
1 2 3 4 6 7 A8
1 2 3 4 A 29
M

Fig. 64. Glucose content in stems and leaves (closed circles) and roots (open circles) of Myriophyllum exalbescens on various sampling dates during the 1985 growing season. Vertical bars represent standard error and numbers beside circles indicate sampling sites. Depth (in meters) for each collection time is shown on the horizontal axis. Statistically significant relationships between depth and glucose content are shown for May 16 and August 29.

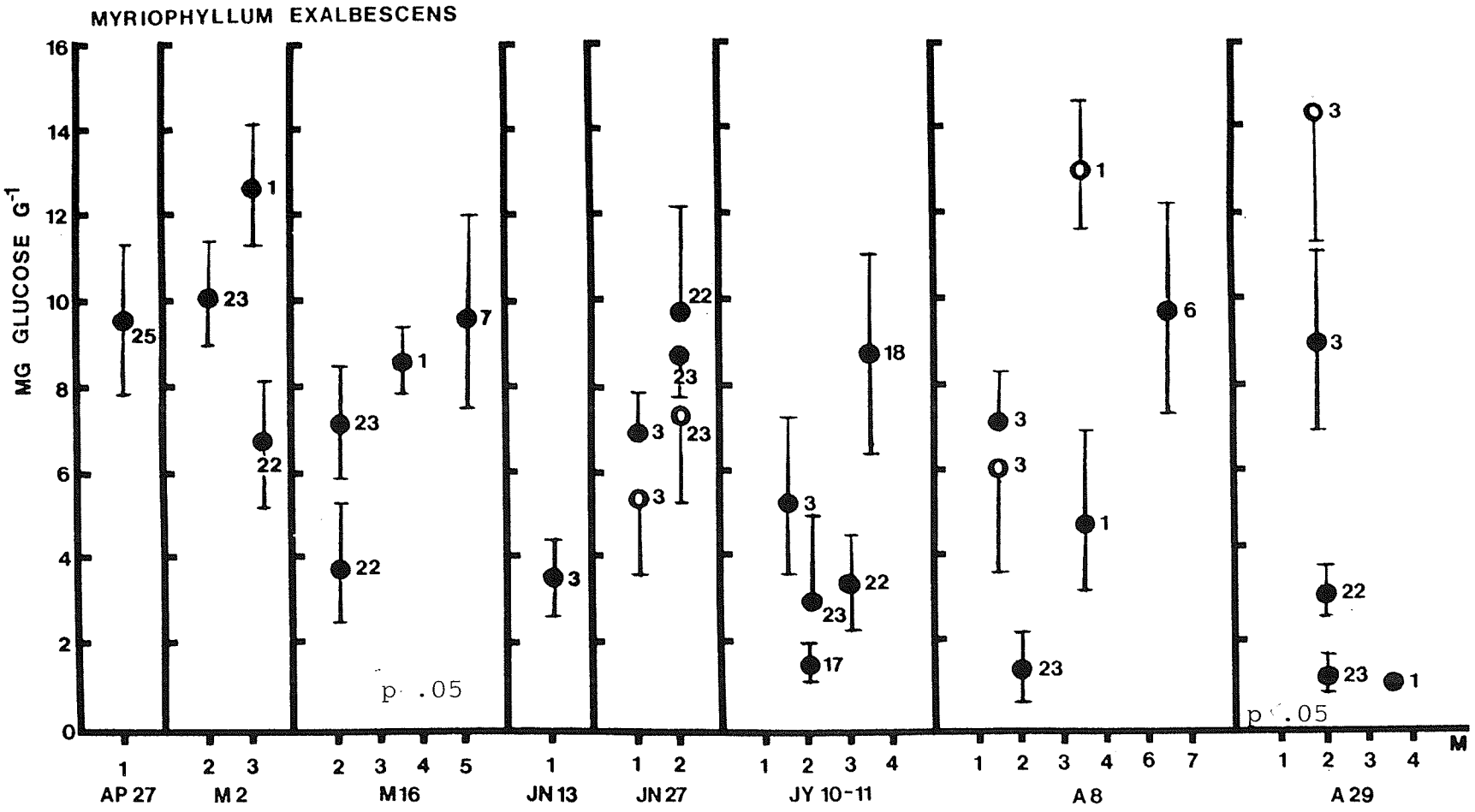

MYRIOPHYLLUM EXALBESCENS
MG GLUCOSE G-1
0
2
4
6
8
10
12
14
16
25
23
1
22
23
22
1
7
3
3
22
23
3
23
3
18
22
17
3
3
23
1
1
6
3
3
22
23
1
p .05
p .05
1
AP 27
2 3
M 2
2 3 4 5
M16
1
JN 13
1 2
JN 27
1 2 3 4
JY 10-11
1 2 3 4 6 7
A 8
1 2 3 4
A 29
M

Fig. 65. Sucrose content in stems and leaves (closed circles) and roots (open circles) of Myriophyllum exalbescens on various sampling dates during the 1985 growing season. Vertical bars represent standard error and numbers beside circles indicate sampling sites. Depth (in meters) for each collection time is shown on the horizontal axis.

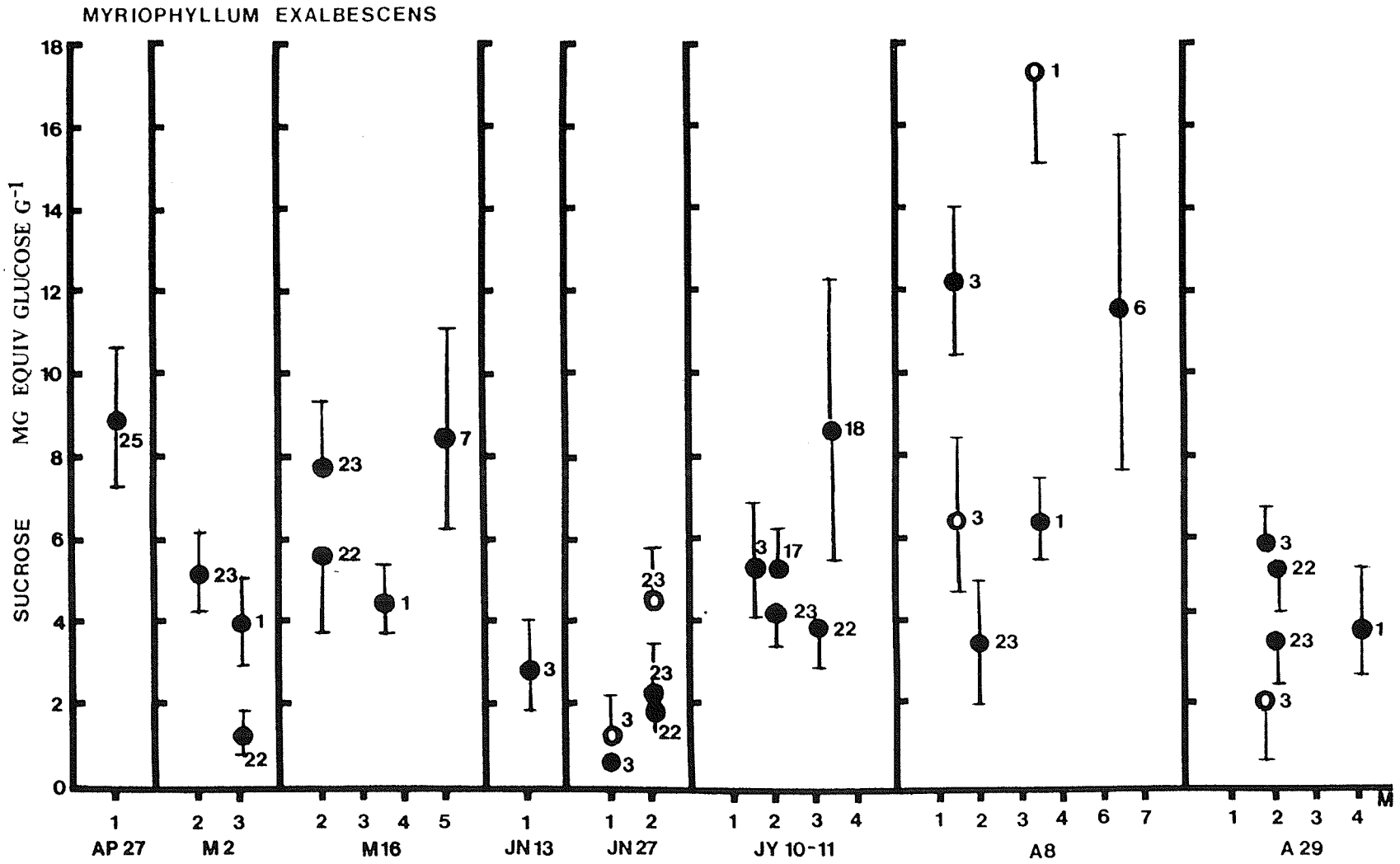

MYRIOPHYLLUM EXALBESCENS
SUCROSE MG EQUIV GLUCOSE G-1
0
2
4
6
8
10
12
14
16
18
25
23
22
1
7
3
18
17
6
AP 27
M 2
M16
JN 13
JN 27
JY 10-11
A8
A 29
M

Fig. 66. Fructose, glucose, and sucrose content in stems and leaves on Najas flexilis at sampling site 3 during the 1985 growing season. Vertical bars represent standard error. Depth (in meters) for each collection time is shown on the horizontal axis.

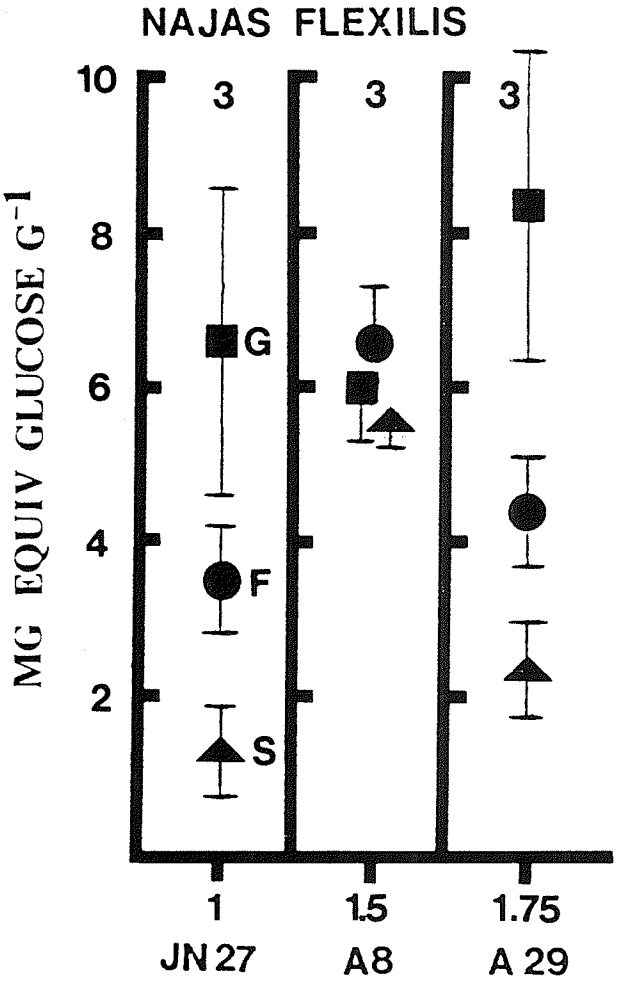

NAJAS FLEXILIS
MG EQUIV GLUCOSE G^{-1}
10
8
6
4
2
3
3
3
G
F
S
1
1.5
1.75
JN 27
A 8
A 29

Fig. 67. Fructose content in stems and leaves (closed circles) and roots (open circles) of Potamogeton foliosus on various sampling times during the 1985 growing season. Vertical bars represent standard error and numbers beside circles indicate sampling sites. Depth (in meters) for each collection time is shown on the horizontal axis. A statistically significant relationship between depth and fructose content is shown for July 10-11.

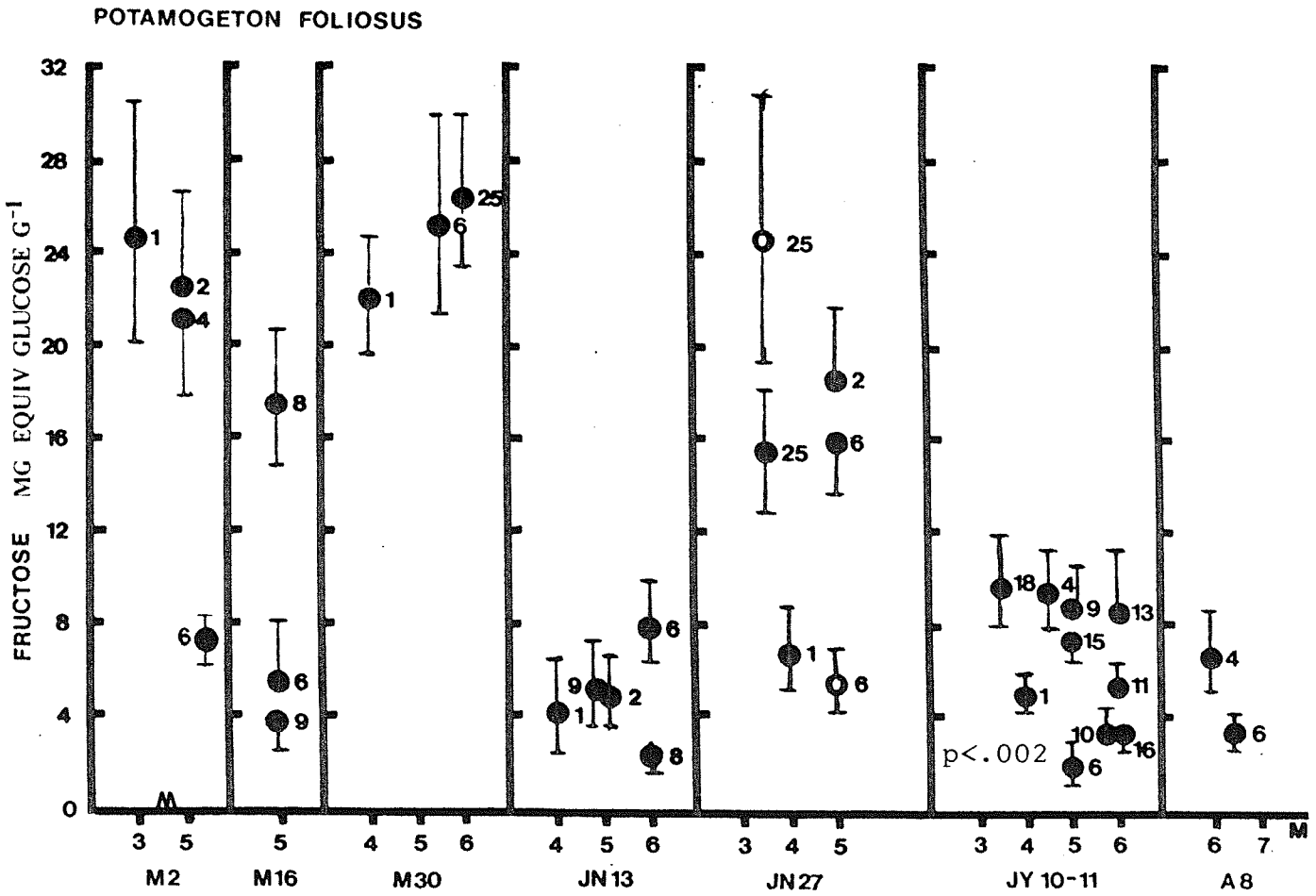

POTAMOGETON FOLIOSUS
FRUCTOSE MG EQUIV GLUCOSE G-1
32
28
24
20
16
12
8
4
0
p<.002
M2
M16
M30
JN13
JN27
JY 10-11
A8
M

Fig. 68. Glucose content in stems and leaves (closed circles) and roots (open circles) of Potamogeton foliosus on various sampling dates during the 1985 growing season. Vertical bars represent standard error and numbers beside circles indicate sampling sites. Depth (in meters) for each collection time is shown on the horizontal axis. A statistically significant relationship between depth and glucose content is shown for June 13.

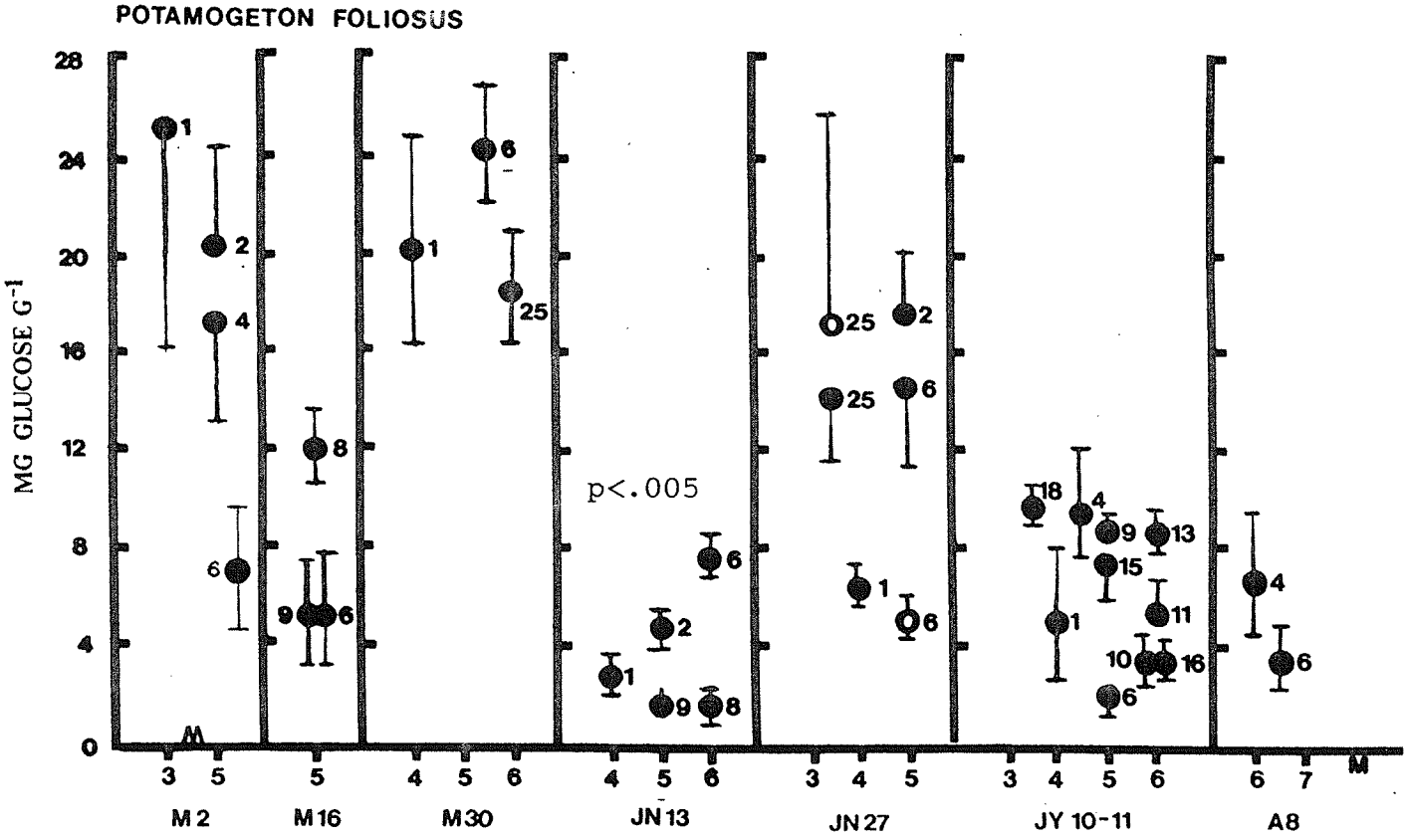

POTAMOGETON FOLIOSUS
MG GLUCOSE G-1
28
24
20
16
12
8
4
0
p<.005
M2
M16
M30
JN13
JN27
JY 10-11
A8
M

Fig 69. Sucrose content in stems and leaves (closed circles) and roots (open circles) of Potamogeton foliosus on various sampling dates during the 1985 growing season. Vertical bars represent standard error and numbers beside circles indicate sampling sites. Depth (in meters) for each collection time is shown on the horizontal axis. Statistically significant relationships between depth and sucrose content are shown for May 30, June 27, and July 10-11.

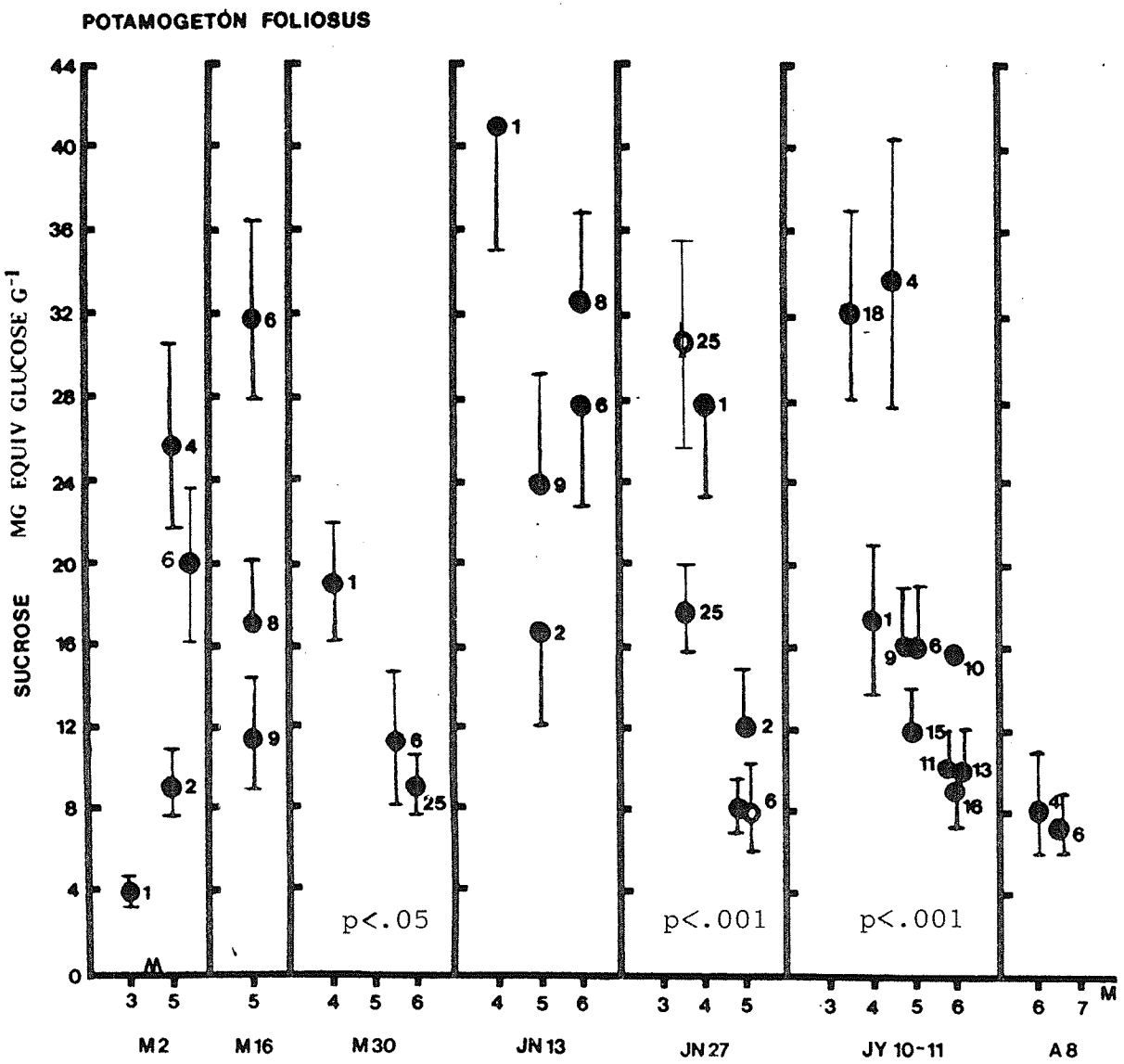

POTAMOGETÓN FOLIOSUS
SUCROSE MG EQUIV GLUCOSE G-1
44
40
36
32
28
24
20
16
12
8
4
0
p<.05
p<.001
p<.001
3 5
5
4 5 6
4 5 6
3 4 5
3 4 5 6
6 7 M
M2
M16
M30
JN13
JN27
JY 10-11
A8

Fig. 70. Fructose, glucose, and sucrose content in stems and leaves of Potamogeton gramineus at station 22 on various sampling dates during the 1985 growing season. Vertical bars represent standard error. Depth (in meters) for each collection time is indicated on the horizontal axis.

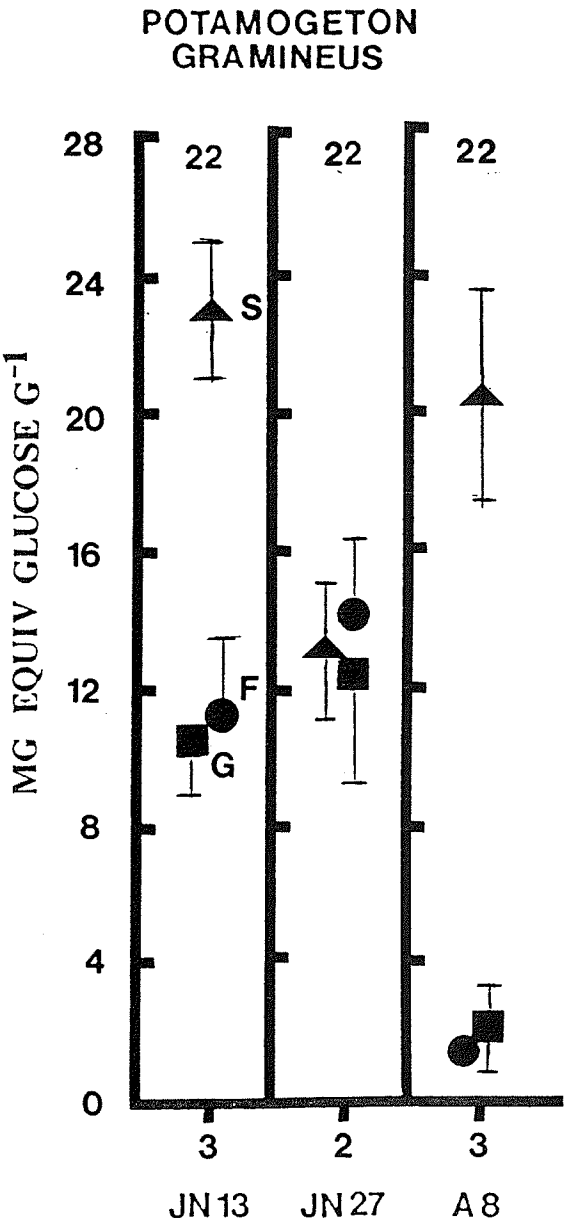

POTAMOGETON
GRAMINEUS
MG EQUIV GLUCOSE G^{-1}
28
24
20
16
12
8
4
0
22
22
22
S
F
G
3
2
3
JN 13
JN 27
A 8

Fig. 71. Fructose, glucose, and sucrose content in stems and leaves of Potamogeton praelongus at a depth of 2 m during June of the 1985 growing season. Vertical bars represent standard error and numbers beside circles indicate sampling site.

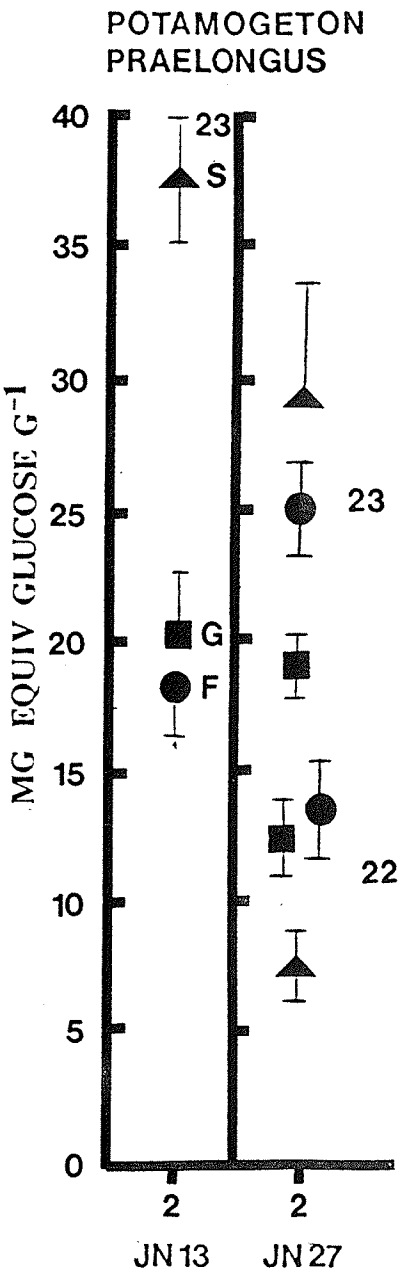

POTAMOGETON
PRAELONGUS
MG EQUIV GLUCOSE G^{-1}
40
35
30
25
20
15
10
5
0
23
S
G
F
23
22
2
2
JN 13
JN 27

Fig. 72. Fructose, glucose, and sucrose content in stems and leaves of Potamogeton richardsonii on various sampling dates during the 1985 growing season. Vertical bars represent standard error. Collection sites, as indicated, were 3, 22, and 23. Depth (in meters) for each sampling time is shown on the horizontal axis.

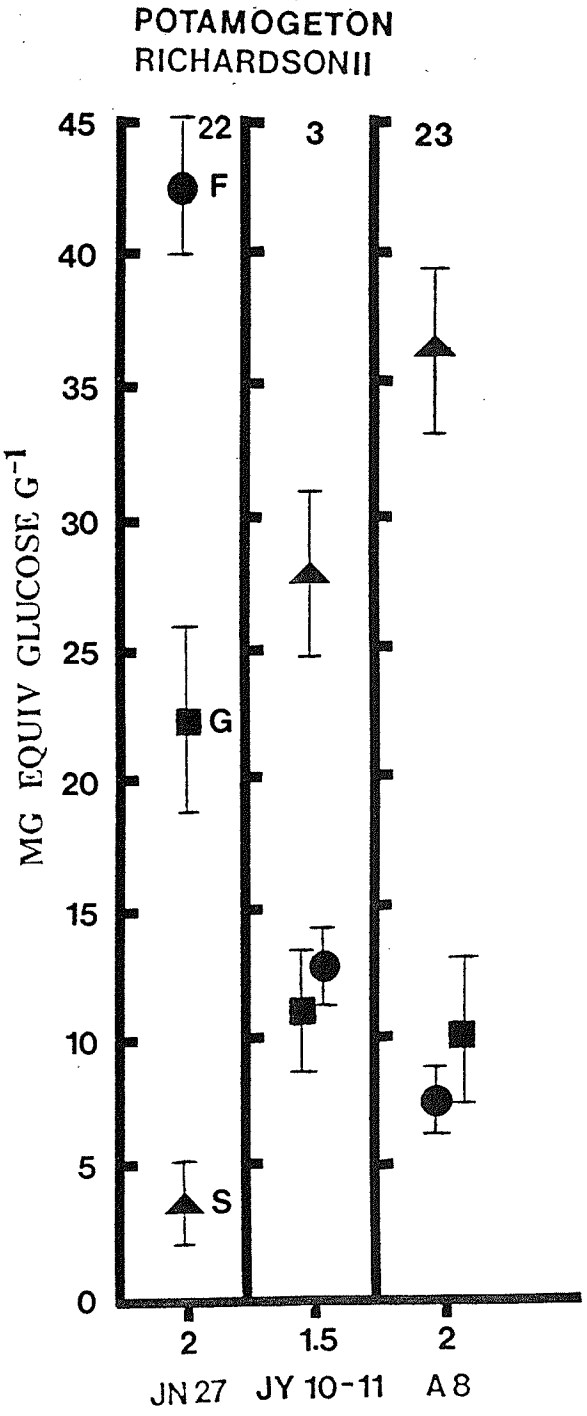

POTAMOGETON
RICHARDSONII
MG EQUIV GLUCOSE G^{-1}
45
40
35
30
25
20
15
10
5
0
22
3
23
F
G
S
2
1.5
2
JN 27
JY 10-11
A 8

Fig. 73. Fructose, glucose, and sucrose content in stems and leaves of Potamogeton robbinsii on various sampling dates during the 1985 growing season. Vertical bars represent standard error and collection sites, as indicated, were 3, 5, and 9. Depth (in meters) for each sampling date is shown on the horizontal axis.

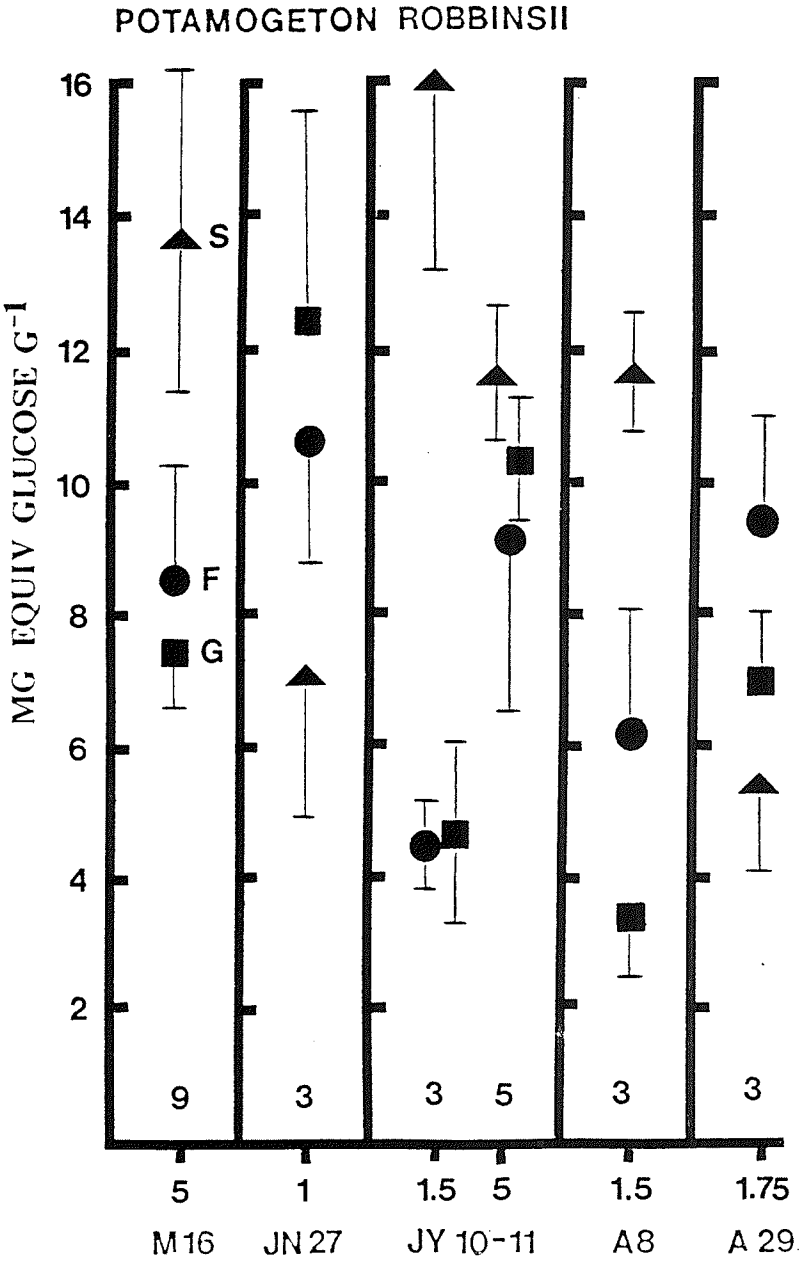
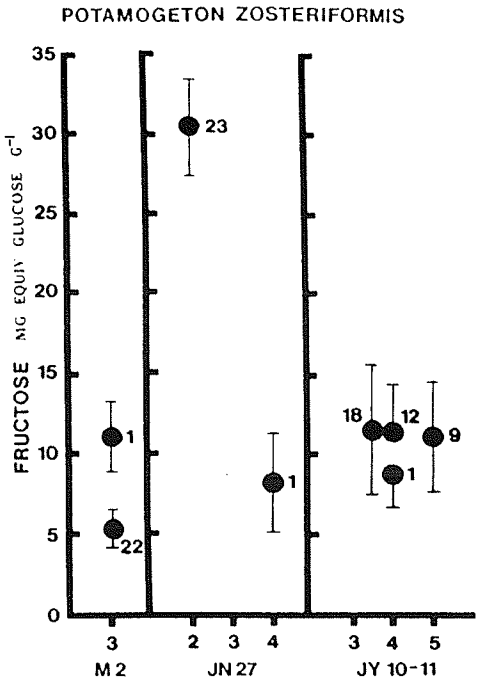
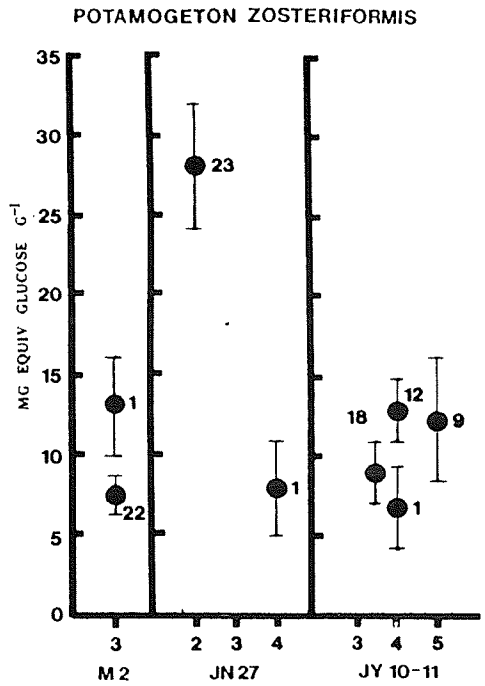

POTAMOGETON ROBBINSII
MG EQUIV GLUCOSE G^{-1}
16
14
12
10
8
6
4
2
S
F
G
9
3
3
5
3
3
5
1
1.5
5
1.5
1.75
M16
JN 27
JY 10-11
A8
A 29

Fig. 74. Fructose, glucose, and sucrose content in stems and leaves of Potamogeton zosteriformis on various sampling dates during the 1985 growing season. Vertical bars represent standard error and numbers beside circles indicate sampling site. Depth (in meters) for each collection time is shown on the horizontal axis.


POTAMOGETON ZOSTERIFORMIS
FRUCTOSE MG EQUIV GLUCOSE G⁻¹
0
5
10
15
20
25
30
35
23
1
22
1
18
12
1
9
3
M 2
2 3 4
JN 27
3 4 5
JY 10-11


POTAMOGETON ZOSTERIFORMIS
MG EQUIV GLUCOSE G⁻¹
0
5
10
15
20
25
30
35
23
1
22
1
18
12
1
9
3
M 2
2 3 4
JN 27
3 4 5
JY 10-11

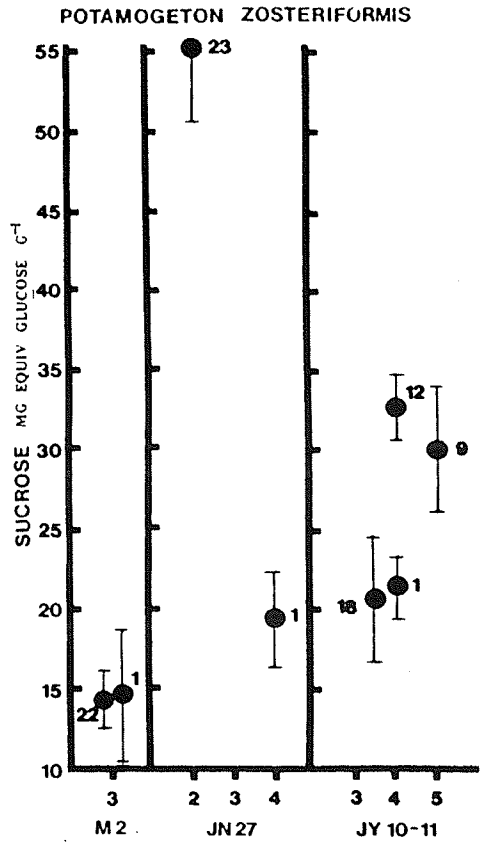

POTAMOGETON ZOSTERIFORMIS
SUCROSE MG EQUIV GLUCOSE G⁻¹
10
15
20
25
30
35
40
45
50
55
23
22
1
1
18
1
12
9
3
M 2
2 3 4
JN 27
3 4 5
JY 10-11

Fig. 75. Proportions of soluble sugars in stems and leaves of Ceratophyllum demersum on various sampling dates during the 1985 growing season. Vertical bars represent standard error. Depth (in meters) for each collection time is shown on the horizontal axis.

☐ Fructose

▨ Glucose

▩ Sucrose

▤ Melibiose/Raffinose/Stachyose

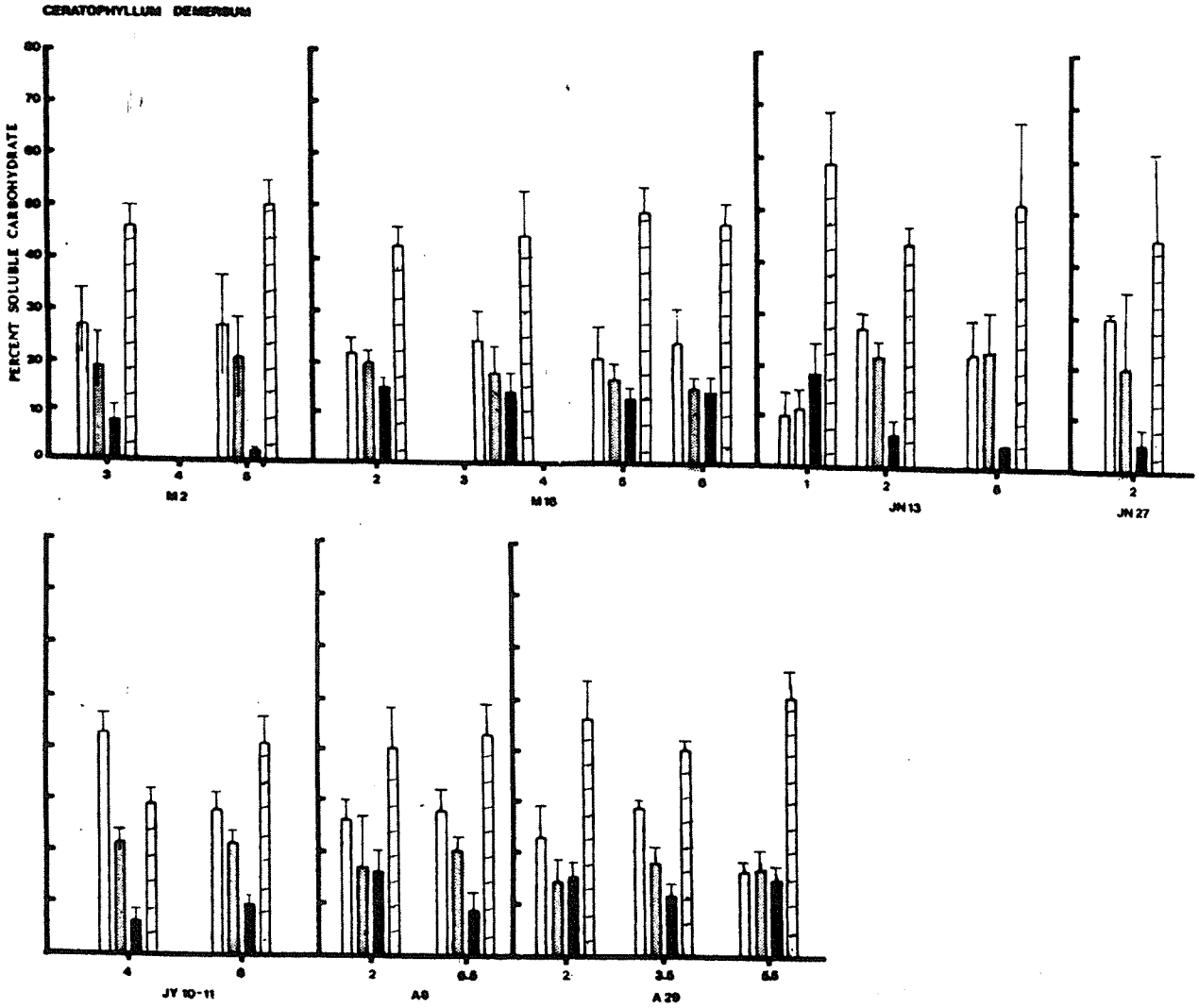
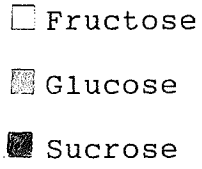

CERATOPHYLLUM DEMERSUM
PERCENT SOLUBLE CARBOHYDRATE
0
10
20
30
40
50
60
70
80
3
4
5
M 2
2
3
4
6
6
M 16
1
2
6
JN 13
2
JN 27
4
6
JY 10-11
2
5.5
A 6
2
3.5
5.5
A 29

Fig. 76. Proportions of soluble sugars in stems and leaves of Elodea canadensis on various sampling dates during the 1985 growing season. Vertical bars represent standard error. Depth (in meters) for each collection time is shown on the horizontal axis.



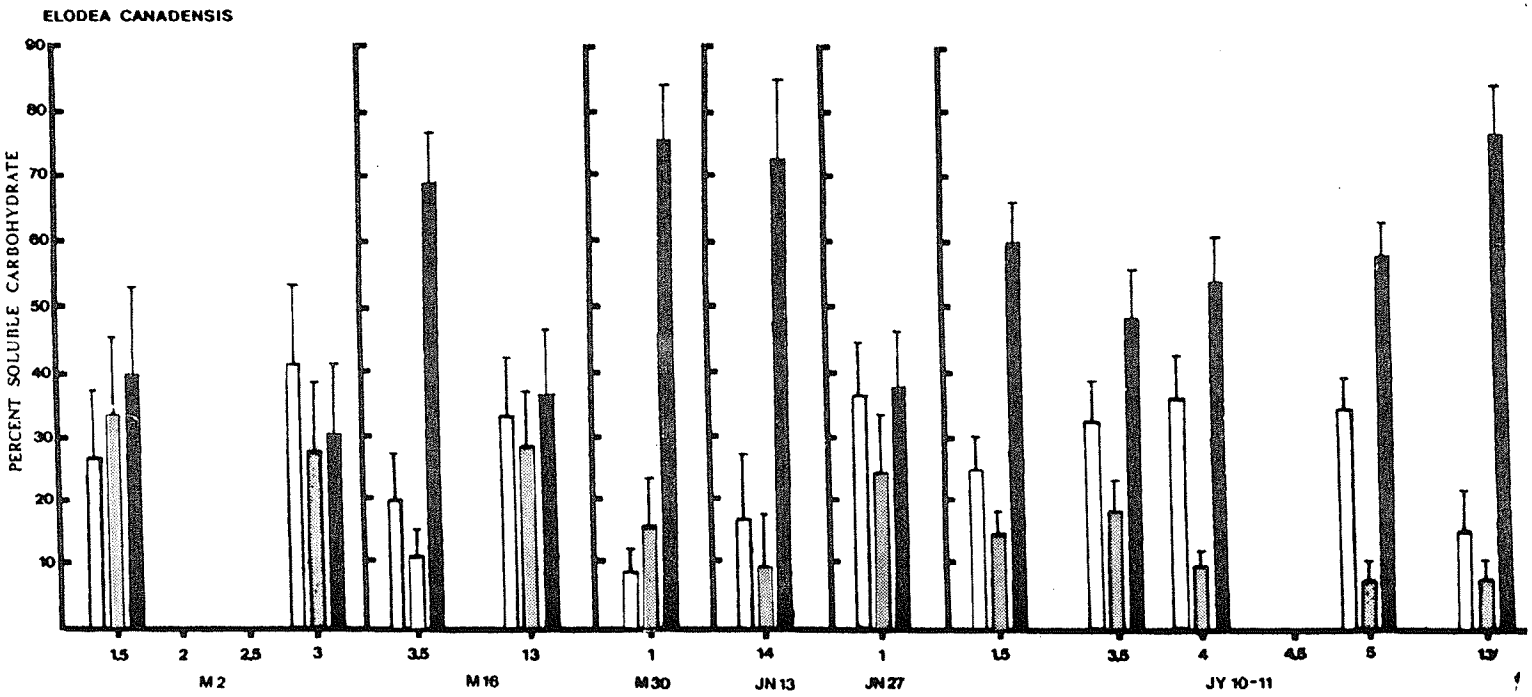
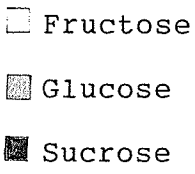

ELODEA CANADENSIS
PERCENT SOLUBLE CARBOHYDRATE
90
80
70
60
50
40
30
20
10
1.5
2
2.5
3
3.5
13
1
14
1
1.5
3.5
4
4.5
5
1.9
M 2
M 16
M 30
JN 13
JN 27
JY 10-11

Fig. 77. Proportions of soluble sugars in stems and leaves of Myriophyllum exalbescens on various sampling dates during the 1985 growing season. Vertical bars represent standard error. Depth (in meters) for each collection time is shown on the horizontal axis.



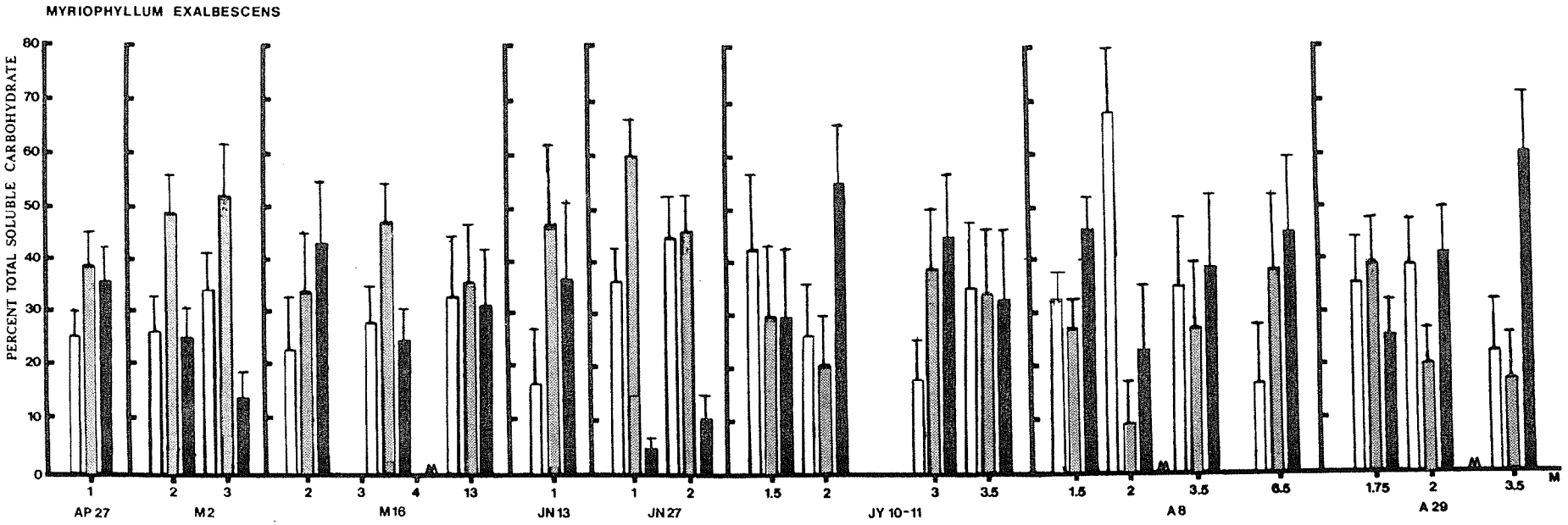
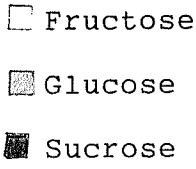

MYRIOPHYLLUM EXALBESCENS
PERCENT TOTAL SOLUBLE CARBOHYDRATE
0
10
20
30
40
50
60
70
80
1
AP 27
2
3
M2
2
3
4
M16
13
1
JN 13
1
2
JN 27
1.5
2
3
3.5
JY 10-11
1.5
2
3.5
A 8
6.5
1.75
2
A 29
3.5
M

Fig. 78. Proportions of soluble sugars in stems and leaves of Najas flexilis on various sampling dates during the 1985 growing season. Vertical bars represent standard error. Depth (in meters) for each collection time is shown on the horizontal axis.



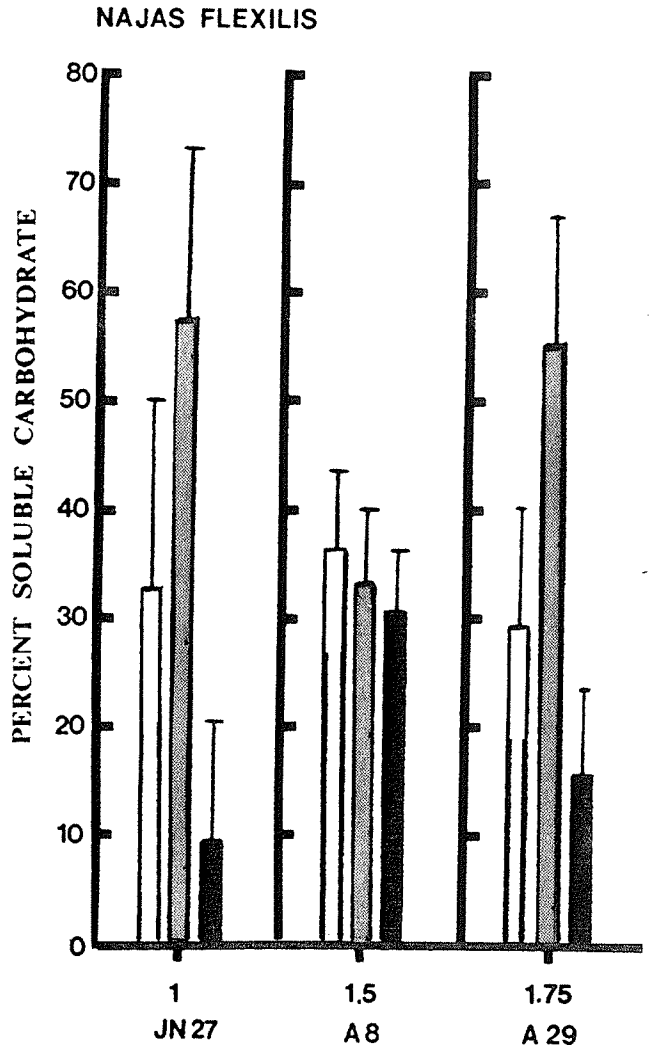
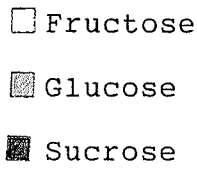

NAJAS FLEXILIS
PERCENT SOLUBLE CARBOHYDRATE
80
70
60
50
40
30
20
10
0
1
JN 27
1.5
A 8
1.75
A 29

Fig. 79. Proportions of soluble sugars in stems and leaves of Potamogeton foliosus on various sampling dates during the 1985 growing season. Vertical bars represent standard error. Depth (in meters) for each collection time is shown on the horizontal axis.



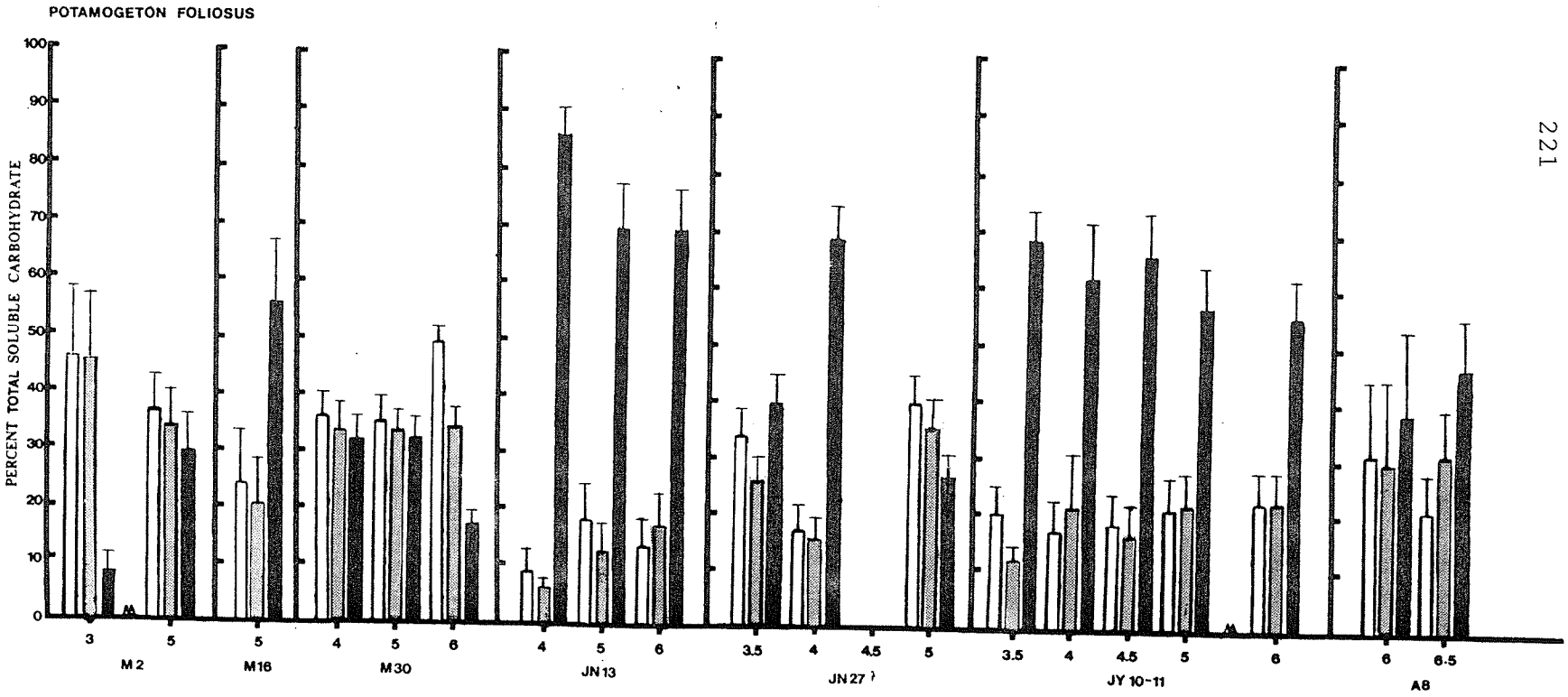
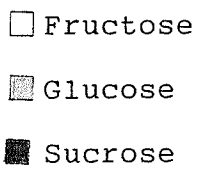

POTAMOGETON FOLIOSUS
PERCENT TOTAL SOLUBLE CARBOHYDRATE
100
90
80
70
60
50
40
30
20
10
0
3
5
M 2
5
M16
4
5
6
M30
4
5
6
JN13
3.5
4
4.5
5
JN 27
3.5
4
4.5
5
6
JY 10-11
6
6.5
A8

Fig. 80. Proportions of soluble sugars in stems and leaves of Potamogeton gramineus on various sampling dates during the 1985 growing season. Vertical bars represent standard error. Depth (in meters) for each collection time is shown on the horizontal axis.



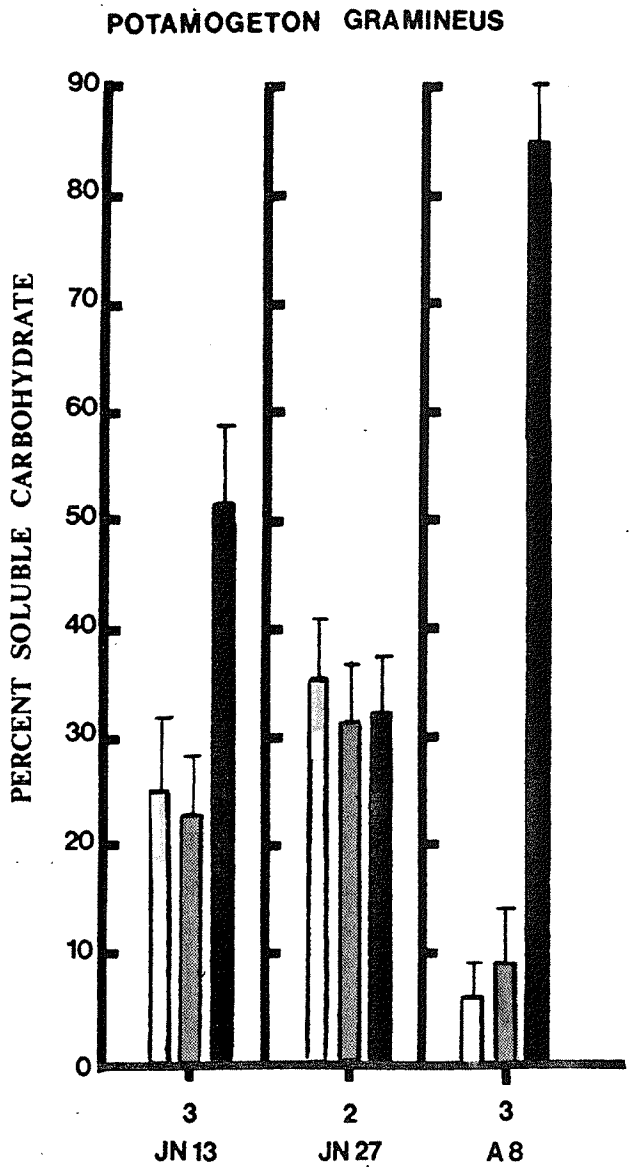
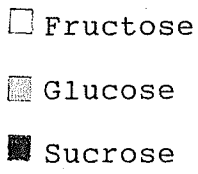

POTAMOGETON GRAMINEUS
PERCENT SOLUBLE CARBOHYDRATE
90
80
70
60
50
40
30
20
10
0
3
JN 13
2
JN 27
3
A 8

Fig. 81. Proportions of soluble sugars in stems and leaves of Potamogeton praelongus on June sampling dates during the 1985 season. Vertical bars represent standard error. Depth (in meters) is shown on the horizontal axis.



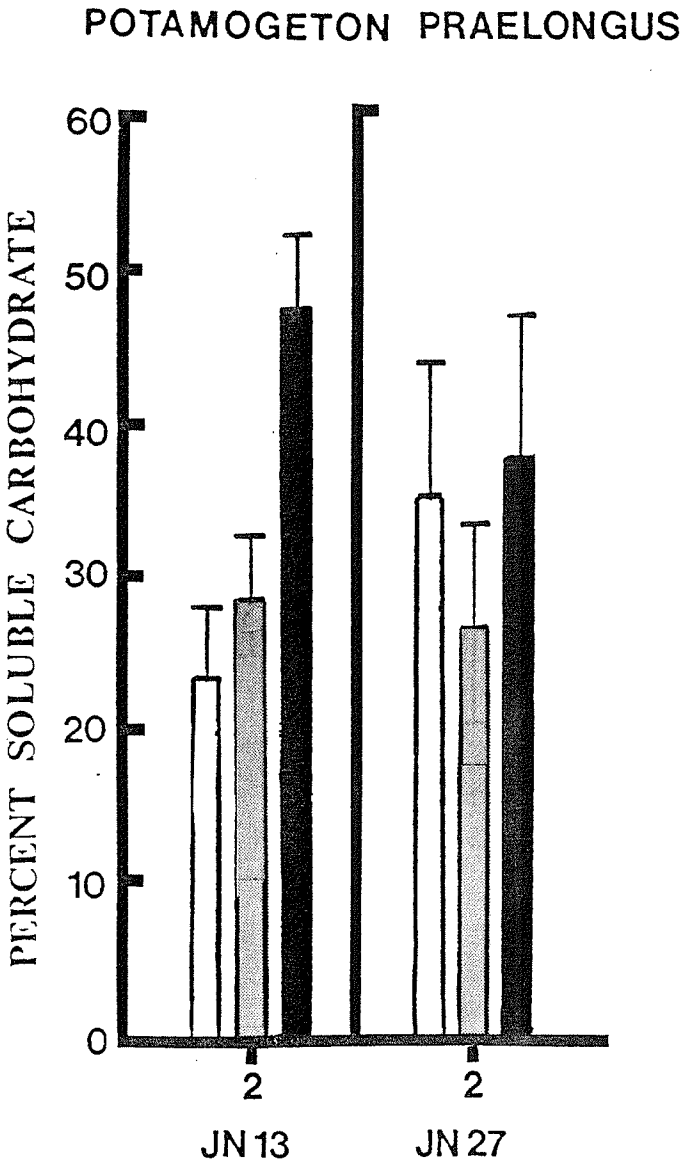
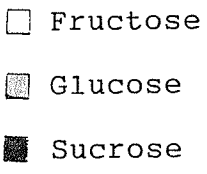

POTAMOGETON PRAELONGUS
PERCENT SOLUBLE CARBOHYDRATE
60
50
40
30
20
10
0
2
2
JN 13
JN 27

Fig. 82. Proportions of soluble sugars in stems and leaves of Potamogeton richardsonii on various sampling dates during the 1985 growing season. Vertical bars represent standard error. Depth (in meters) for each collection time is shown on the horizontal axis.



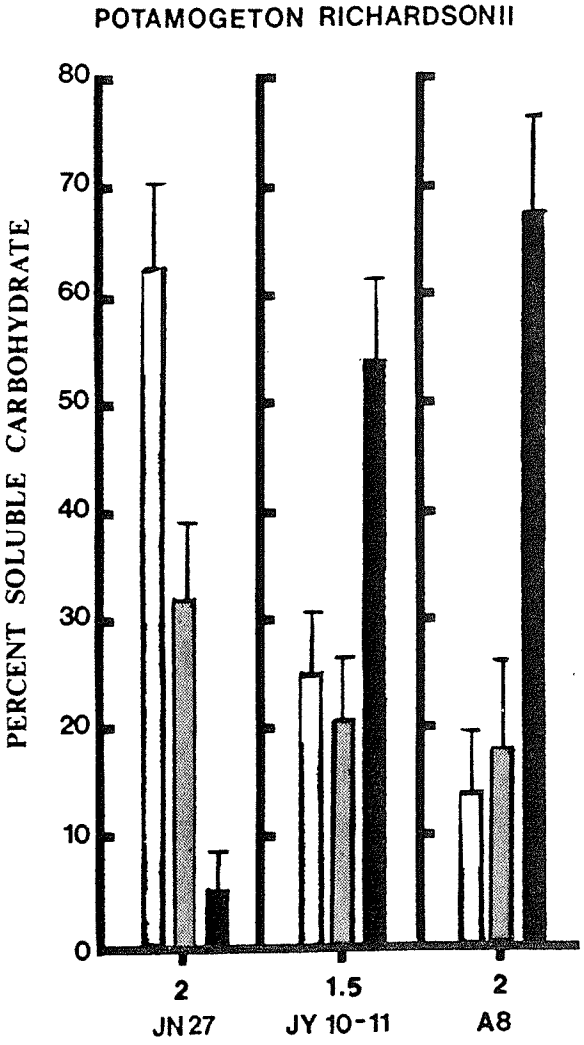
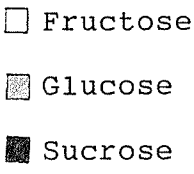

POTAMOGETON RICHARDSONII
PERCENT SOLUBLE CARBOHYDRATE
80
70
60
50
40
30
20
10
0
2
JN 27
1.5
JY 10-11
2
A8

Fig. 83. Proportions of soluble sugars in stems and leaves of Potamogeton robbinsii on various sampling dates during the 1985 growing season. Vertical bars represent standard error. Depth (in meters) for each collection time is shown on the horizontal axis.



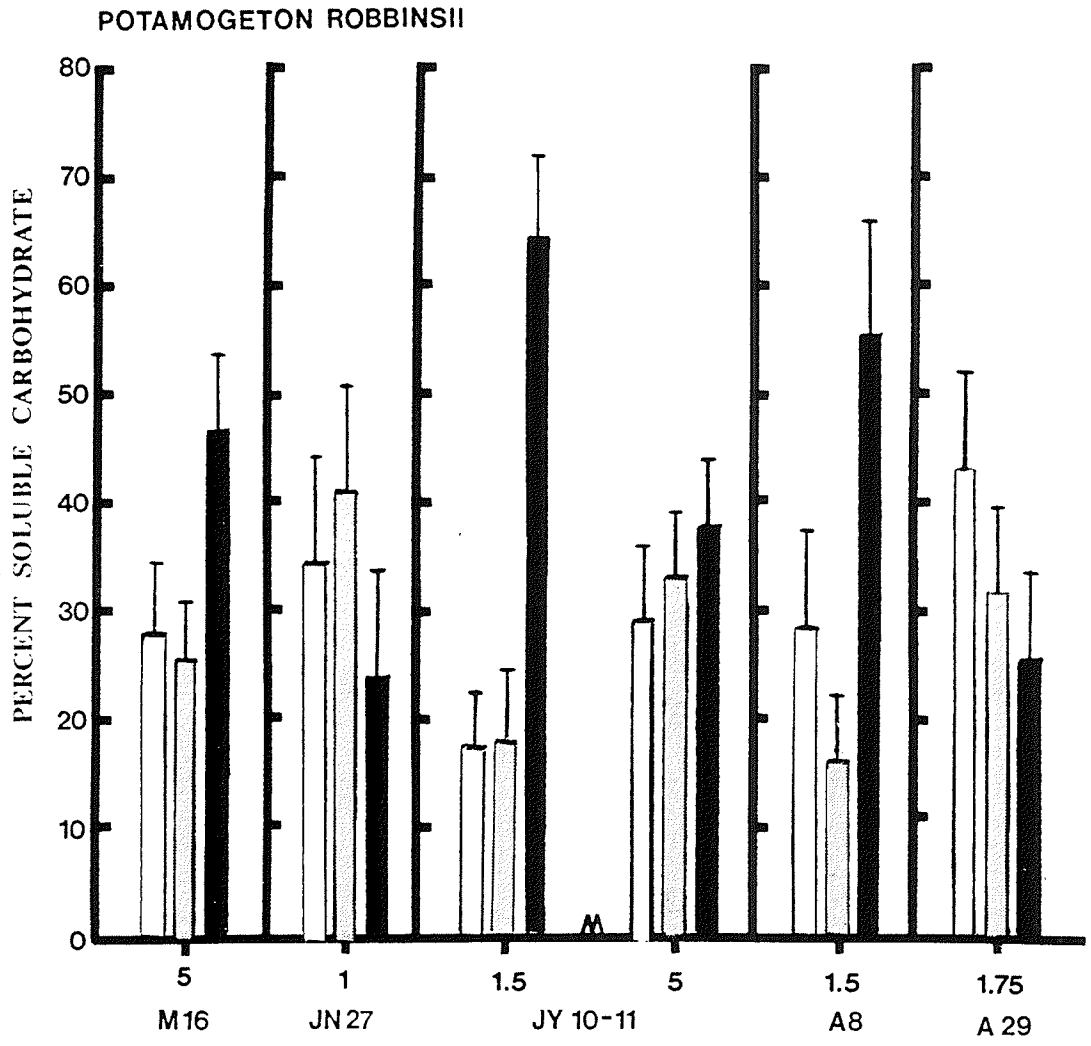
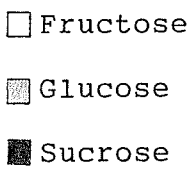

POTAMOGETON ROBBINSII
PERCENT SOLUBLE CARBOHYDRATE
80
70
60
50
40
30
20
10
0
5
M16
1
JN27
1.5
JY 10-11
5
1.5
A8
1.75
A 29

Fig. 84. Proportions of soluble sugars in stems and leaves of Potamogeton zosteriformis on various sampling dates during the 1985 growing season. Vertical bars represent standard error. Depth (in meters) for each collection time is shown on the horizontal axis.



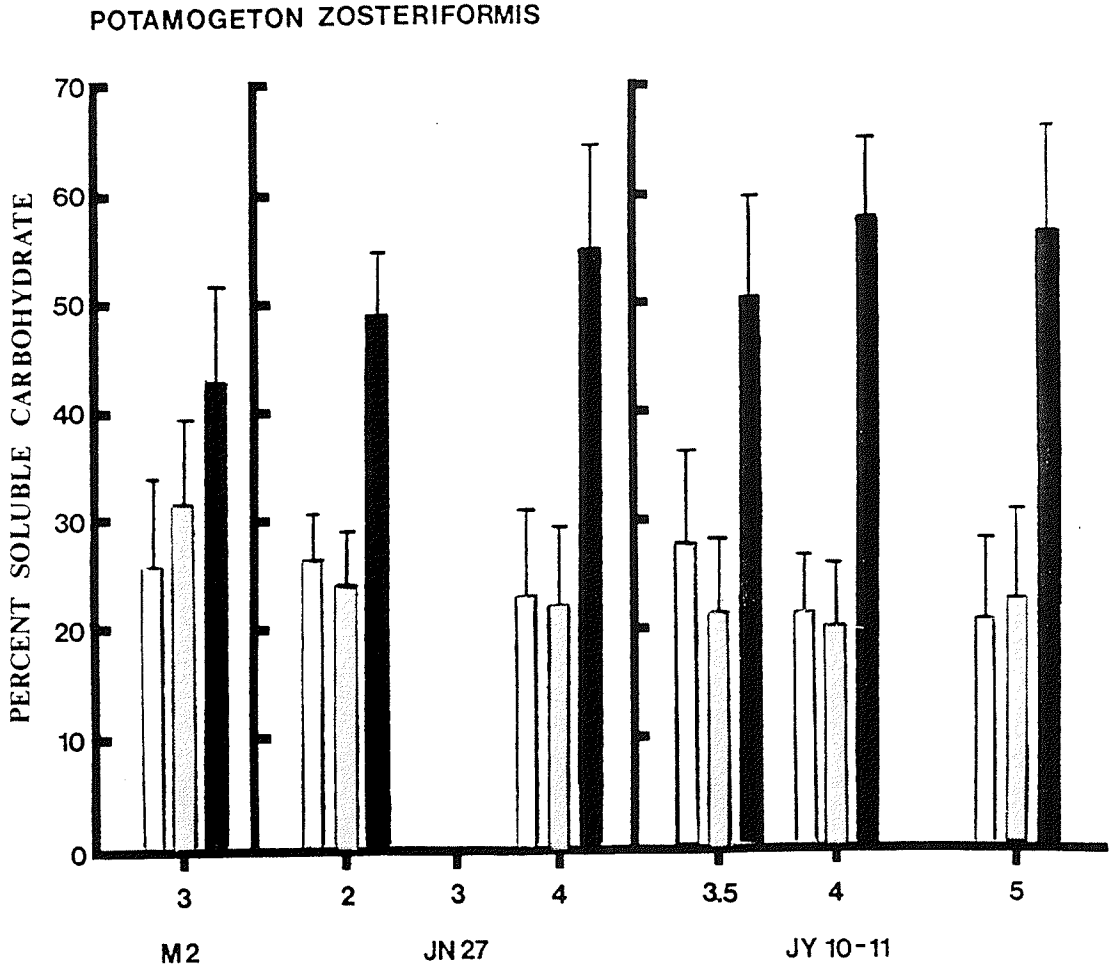

POTAMOGETON ZOSTERIFORMIS
PERCENT SOLUBLE CARBOHYDRATE
70
60
50
40
30
20
10
0
3
2
3
4
3.5
4
5
M2
JN 27
JY 10-11

Table 18. Significant differences in proportions of ethanol-soluble sugars in C.demersum during the 1985 season. 2=My 2 3=My 16 5=Jn 13 6=Jn 27 7=Jy 10-11 8=Aug 8 9=Aug 29

FRUCTOSE

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
2	11	.2671	n.s.	n.s.
3	25	.2287	n.s.	n.s.
5	10	.2132	n.s.	n.s.
6	2	.2990	n.s.	n.s.
7	9	.3454	n.s.	n.s.
8	5	.2734	n.s.	n.s.
9	17	.2304	n.s.	n.s.

GLUCOSE

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
2	11	.1937	n.s.	n.s.
3	25	.1799	n.s.	n.s.
5	10	.1898	n.s.	n.s.
6	2	.2002	n.s.	n.s.
7	9	.2156	n.s.	n.s.
8	5	.1897	n.s.	n.s.
9	17	.1678	n.s.	n.s.

SUCROSE

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
2	11	.0650	n.s.	3 9
3	25	.1440	n.s.	2
5	10	.0960	n.s.	n.s.
6	2	.0491	n.s.	n.s.
7	9	.0824	n.s.	n.s.
8	5	.1162	n.s.	n.s.
9	17	.1407	n.s.	2

Table 18.(Cont.)

MELIBIOSE/RAFFINOSE/STACHYOSE

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
2	11	.4742	n.s.	n.s.
3	25	.4473	n.s.	n.s.
5	10	.5009	n.s.	n.s.
6	2	.4517	n.s.	n.s.
7	9	.3566	n.s.	n.s.
8	5	.4207	n.s.	n.s.
9	17	.4610	n.s.	n.s.

Table 19. Significant differences in proportions of ethanol-soluble sugars in E.canadensis during the 1985 season. 2=My 2 3=My 16 4=My 30 5=Jn 13 6=Jn 27 7=Jy 10-11

FRUCTOSE

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
2	9	.3137	4	4
3	7	.2800	n.s.	n.s.
4	4	.1128	2 6 7	2 6 7
5	3	.1743	4	n.s.
6	3	.3737	4	4
7	20	.3284	4	4

GLUCOSE

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
2	9	.2926	n.s.	n.s.
3	7	.2390	n.s.	n.s.
4	4	.1814	n.s.	n.s.
5	3	.1015	n.s.	n.s.
6	3	.2390	n.s.	n.s.
7	20	.2026	n.s.	n.s.

SUCROSE

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
2	9	.3937	n.s.	n.s.
3	7	.4999	n.s.	n.s.
4	4	.7058	n.s.	n.s.
5	3	.7242	n.s.	n.s.
6	3	.3873	n.s.	n.s.
7	20	.4690	n.s.	n.s.

Table 20. Significant differences in proportions of ethanol-soluble sugars in M.exalbescens during the 1985 season. 1=Apr 27 2=My 2 3=My 16 5=Jn 13 6=Jn 27 7=Jy 10-11 8=Aug 8 9=Aug 29

FRUCTOSE

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
1	5	.2548	6	n.s.
2	16	.3053	n.s.	n.s.
3	17	.2743	n.s.	6
5	3	.1849	6 8 9	6
6	15	.4163	1 5	3 5 7
7	20	.2976	n.s.	6
8	15	.3519	5	n.s.
9	21	.3516	5	n.s.

GLUCOSE

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
1	5	.3896	n.s.	n.s.
2	16	.5162	7 8 9	3 7 8 9
3	17	.3558	n.s.	2
5	3	.4651	7 8 9	n.s.
6	15	.4959	7 8 9	7 8 9
7	20	.2900	2 5 6	2 6
8	15	.2600	2 5 6	2 6
9	21	.2690	2 5 6	2 6

SUCROSE

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
1	5	.3556	2 6	6
2	16	.1785	1 3 5 7-9	3 7-9
3	17	.3699	2 6	2 6
5	3	.3500	2 6	n.s.
6	15	.0879	1 3 5 7-9	1 3 7-9
7	20	.4124	2 6	2 6
8	15	.3881	2 6	2 6
9	21	.3920	2 6	2 6

Table 21. Proportions of sugars in roots and shoots/leaves of M.exalbescens during the 1985 season. Means with the same letter were not significantly different, as determined in SNK and Tukey's tests at alpha=0.05.

FRUCTOSE				
DATE	N	TISSUE	MEAN	
June 27	5	Roots	.4381	A
	9	Shoots/leaves	.3838	A
August 8	6	Roots	.3672	A
	9	Shoots/leaves	.3108	A
August 29	2	Roots	.3486	A
	6	Shoots/leaves	.3520	A

GLUCOSE				
DATE	N	TISSUE	MEAN	
June 27	5	Roots	.3718	A
	9	Shoots/leaves	.5259	B
August 8	6	Roots	.2895	A
	9	Shoots/leaves	.2634	A
August 29	2	Roots	.3013	A
	6	Shoots/leaves	.3870	A

SUCROSE				
DATE	N	TISSUE	MEAN	
June 27	5	Roots	.1901	A
	9	Shoots/leaves	.0903	A
August 8	6	Roots	.3434	A
	9	Shoots/leaves	.4258	A
August	2	Roots	.2181	A
	6	Shoots/leaves	.2610	A

Table 22. Significant differences in proportions of ethanol-soluble sugars in N.flexilis during the 1985 season. 6=Jn 27 8=Aug 8 9=Aug 29

FRUCTOSE

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
6	2	.3169	n.s.	n.s.
8	3	.3608	n.s.	n.s.
9	3	.2880	n.s.	n.s.

GLUCOSE

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
6	2	.5738	8	8
8	3	.3298	6 9	6 9
9	3	.5450	8	8

SUCROSE

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
6	2	.1093	8	n.s.
8	3	.3094	6	n.s.
9	3	.1670	6	n.s.

Table 23. Significant differences in proportions of ethanol-soluble sugars in P.foliosus during the 1985 season. 2=My 2 3=My 16 4=My 30 5=Jn 13 6=Jn 27 7=Jy 10-11 8=Aug 8

FRUCTOSE

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
2	18	.3609	3 5 7 8	3 5 7
3	10	.2288	2 4-6	2 4
4	12	.4213	3 5-8	3 5 7 8
5	21	.1409	2-4 6 8	2 4 6 8
6	19	.3339	3-5 7	5 7
7	50	.2070	2 4 6	2 4 6
8	11	.2761	2 4 5	4 5

GLUCOSE

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
2	18	.3368	3 5 7	3 5 7
3	10	.2019	2 4 6 8	2 4
4	12	.3354	3 5 7	3 5 7
5	21	.1385	2 4 6 8	2 4 6 8
6	19	.2959	3 5 7	5 7
7	50	.1941	2 4 6 8	2 4 6 8
8	11	.2991	3 5 7	5 7

SUCROSE

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
2	18	.3023	3 5 7	3 5 7
3	10	.5694	2 4-6 8	2 4 6
4	12	.2433	3 5-8	3 5 7
5	21	.7206	2-4 6-8	2 4 6-8
6	19	.3703	3-5 7	3 5 7
7	50	.5989	2 4-6 8	2 4-6 8
8	11	.4248	3-5 7	5 7

Table 24. Proportions of sugars in roots and shoots/leaves of P.foliosus during the 1985 season. Means with the same letter were not significantly different, as determined in SNK and Tukey'S tests at alpha=0.05.

FRUCTOSE				
DATE	N	TISSUE	MEAN	
June 27	6	Roots	.3268	A
	9	Shoots/leaves	.3719	A

GLUCOSE				
DATE	N	TISSUE	MEAN	
June 27	6	Roots	.2461	A
	9	Shoots/leaves	.3158	A

SUCROSE				
DATE	N	TISSUE	MEAN	
June 27	6	Roots	.4271	A
	9	Shoots/leaves	.3123	A

Table 25. Significant differences in proportions of ethanol-soluble sugars in P.gramineus during the 1985 season. 5=Jn 13 6=Jn 27 8=Aug 8

FRUCTOSE

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
5	3	.2450	6 8	8
6	5	.3521	5 8	8
8	6	.0659	5 6	5 6

GLUCOSE

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
5	3	.2322	8	8
6	5	.3141	8	8
8	6	.0823	5 6	5 6

SUCROSE

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
5	3	.5229	6 8	6 8
6	5	.3338	5 8	5 8
8	6	.8518	5 6	5 6

Table 26. Significant differences in proportions of ethanol-soluble sugars in P.praelongus during the 1985 season. 5=Jn 13 6=Jn 27

FRUCTOSE

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
5	6	.2472	6	6
6	15	.3689	5	5

GLUCOSE

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
5	6	.2624	6	6
6	15	.3136	5	5

SUCROSE

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
5	6	.4904	6	6
6	15	.3175	5	5

Table 27. Significant differences in proportions of ethanol-soluble sugars in P.richardsonii during the 1985 season. 6=Jn 27 7=Jy 10-11 8=Aug 8

FRUCTOSE

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
6	2	.6308	7 8	7 8
7	6	.2516	6 8	6 8
8	5	.1393	6 7	6 7

GLUCOSE

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
6	2	.3186	n.s.	n.s.
7	6	.2087	n.s.	n.s.
8	5	.1803	n.s.	n.s.

SUCROSE

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
6	2	.0507	7 8	7 8
7	6	.5397	6	6
8	5	.6804	6	6

Table 28. Significant differences in proportions of ethanol-soluble sugars in P.robbinsii during the 1985 season. 3=My 16 6=Jn 27 7=Jy 10-11 8=Aug 8 9=Aug 29

FRUCTOSE

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
3	6	.2815	9	9
6	6	.3572	7	7
7	9	.2190	6 9	6 9
8	6	.2712	9	9
9	6	.4384	3 7 8	3 7 8

GLUCOSE

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
3	6	.2667	6	n.s.
6	6	.4132	3 7 8	7 8
7	9	.2314	6	6
8	6	.1599	6 9	6 9
9	6	.3150	8	8

SUCROSE

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
3	6	.4519	6 9	6 9
6	6	.2296	3 7 8	3 7 8
7	9	.5496	6 9	6 9
8	6	.5689	6 9	6 9
9	6	.2466	3 7 8	3 7 8

Table 29. Significant differences in proportions of ethanol-soluble sugars in P.zosteriformis during the 1985 season. 2=My 2 6=Jn 27 7=Jy 10-11

FRUCTOSE

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
2	10	.2549	n.s.	n.s.
6	7	.2519	n.s.	n.s.
7	21	.2334	n.s.	n.s.

GLUCOSE

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
2	10	.3164	6 7	7
6	7	.2350	2	n.s.
7	21	.2100	2	2

SUCROSE

DATE	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
2	10	.4287	7	7
6	7	.5131	n.s.	n.s.
7	21	.5566	2	2

E. Effects of environmental variables

a. Correlation analysis

Correlation analysis was performed for soluble carbohydrate, starch, fructose, glucose, and sucrose content in C. demersum, E. canadensis, M. exalbescens, P. foliosus, and P. zosteriformis. Time, depth, light, and pH were included in the analysis (Tables 30 to 34). Environmental parameters corresponding to collection sites and times for the 5 species (Table 35) revealed a significant negative correlation between depth and light ($r=0.65$, $p<0.001$, $n=30$) (Table 36).

In C. demersum, E. canadensis, and P. foliosus, soluble carbohydrate, starch, and individual sugars were negatively correlated with depth. Negative relationships with depth were also observed for starch, fructose, and glucose in P. zosteriformis and for starch in M. exalbescens.

Soluble carbohydrate, starch, and individual sugars were positively correlated with light in C. demersum and P. foliosus with a significant ($r=0.66$, $p<0.05$, $n=10$) relationship between light and sucrose in C. demersum. The 5 parameters were negatively correlated with light in M. exalbescens.

In C. demersum, soluble carbohydrate, starch, and individual sugars were negatively correlated with pH. E. canadensis and M. exalbescens had negative relationships between starch and pH and positive relationships with pH for soluble carbohydrate and the 3 sugars. Soluble carbohydrate and sucrose were each negatively correlated with pH in P. foliosus

and P. zosteriformis, while starch, fructose, and glucose were positively related to pH. In P. zosteriformis, the negative carbohydrate - pH relationship ($r=-0.70$, $p<0.05$, $n=10$) and the positive correlation between starch and pH ($r=0.80$, $p<0.05$, $n=6$) were significant.

Starch was negatively correlated with time for C. demersum and E. canadensis. The relationship was significant for C. demersum ($r=-0.71$, $p<0.05$, $n=12$). Total soluble carbohydrate, on the other hand, had a positive relationship with time for these species. In P. zosteriformis, starch was marginally significantly positively correlated with time ($r=0.81$, $p=0.05$, $n=6$), and this relationship was also positive for M. exalbescens and P. foliosus. Total soluble carbohydrate was negatively correlated with time in these 3 species.

Fructose and glucose were each negatively correlated with time in E. canadensis, M. exalbescens, P. foliosus, and P. zosteriformis. This seasonal trend was significant for both sugars in P. foliosus (fructose - $r=-0.68$, glucose - $r=-0.66$, $p<0.02$, $n=13$), and for glucose in P. zosteriformis ($r=-1.0$, $p<0.02$, $n=3$). Fructose was negatively correlated with time in C. demersum. The relationship between sucrose and time was positive in C. demersum, M. exalbescens, and P. zosteriformis and negative in E. canadensis and P. foliosus.

Carbohydrate and starch were negatively correlated for all 5 species. Carbohydrate was positively correlated with

fructose, glucose, and sucrose in E. canadensis, M. exalbescens, and P. foliosus, with fructose and glucose in C. demersum, and with sucrose in P. zosteriformis. Of these, significant relationships were observed for fructose in C. demersum ($r=0.86$, $p<0.005$, $n=10$), glucose in M. exalbescens ($r=0.65$, p 0.05, $n=10$), and sucrose in P. foliosus ($r=0.60$, $p<0.05$, $n=13$). Negative relationships were found between carbohydrate and fructose and glucose in P. zosteriformis.

Fructose was significantly positively correlated with glucose in C. demersum ($r=0.84$, $p<0.005$, $n=10$), E. canadensis ($r=0.92$, $p<0.005$, $n=7$), and P. foliosus ($r=0.98$, $p<0.001$, $n=13$). Positive relationships between fructose and glucose were also found in M. exalbescens and P. zosteriformis. Fructose and glucose were each positively related to sucrose in C. demersum and M. exalbescens, and each of the 2 sugars was negatively related to sucrose in P. foliosus and P. zosteriformis.

b. Stepwise analysis

Relationships between metabolic parameters and environmental factors were further studied in C. demersum, E. canadensis, M. exalbescens, P. foliosus, and P. zosteriformis using stepwise multiple regression (Tables 37 and 38). With respect to soluble carbohydrate content, no variables met the 0.15 significance level for entry into the regression model for C. demersum and P. foliosus. Time and pH were included in the equation for E. canadensis ($R^2=0.88$, $p=0.005$, $n=8$). In M. exalbescens, depth was entered

(R^2=0.54, p=0.02, n=10), and pH was significant for P. zosteriformis (R^2=0.49, p=0.02, n=10).

All species except P. foliosus gave regression equations for starch. Time appeared to be an important factor, being the single variable entered into equations for C. demersum (R^2=0.50, p=0.01, n=12), M. exalbescens (R^2= 0.41, p=0.12, n=7), and P. zosteriformis (R^2=0.65, p=0.05, n=6). In E. canadensis, pH was accepted in the regression model for starch (R^2=0.64, p=0.11, n=5).

Only P. foliosus and P. zosteriformis had significant regression equations for fructose. Time was entered for P. foliosus (R^2=0.47, p=0.01, n=13), while depth and light were significant for P. zosteriformis (R^2=1.0, p<0.001, n=3).

No significant equations were found for C. demersum and E. canadensis with respect to glucose. The variables time and pH were entered into equations for M. exalbescens (R^2=0.60, p=0.04, n=10) and P. zosteriformis (R^2=1.0, p=0.02, n=3). In P. foliosus, time was accepted into the equation (R^2=0.43, p=0.02, n=13).

Time and light were accepted into the regression equation for sucrose in C. demersum (R^2=0.73, p=0.02, n=10) and P. zosteriformis (R^2=1.0, p<0.001, n=3). The variable pH was entered into the model for M. exalbescens (R^2=0.50, p=0.02, n=10) and P. foliosus (R^2=0.25, p=0.08, n=13).

c. Principal component analysis

Principal component analysis with varimax rotation was performed on seasonal soluble carbohydrate of C. demersum, E. canadensis, M. exalbescens, P. foliosus, and P. zosteriformis. Sampling times excluded from the analysis were April 27, May 30, and August 29. Starch, fructose, glucose, and sucrose were also analyzed for all of the above species except P. zosteriformis. Sampling dates excluded from starch data were April 27, May 30, June 27, and August 29, while April 27, May 30, August 8, and August 29 were omitted for analysis of the individual sugars.

Three components were retained for soluble carbohydrate content (Fig. 85) and accounted for 41.6, 38.9, and 12.2 % of the variation, respectively. The first factor had a large positive loading on P. zosteriformis (.952) and a large negative loading on M. exalbescens (-.946). The second component had a large positive value for P. foliosus (.947) and a large negative value for E. canadensis (-.910). The third component was important with respect to C. demersum (.951), while loadings on other species were much smaller.

Correlation analysis of the 3 components with depth, light, and pH (Table 39) revealed a significant positive relationship between Component 1 and depth (r=0.89, p 0.05) and a significant negative relationship between Component 1 and light (r=-0.89, p 0.05).

The 3 components retained with respect to starch content accounted for 49.8, 34.5, and 15.1 % of the variance,

respectively (Fig. 86). The first component had high positive loadings for C. demersum (.620) and M. exalbescens (.956). The second component had a high positive value for P. foliosus (.973) and a high negative value for C. demersum (-.606). The importance of the third component was greatest for M. exalbescens (.980). No significant correlations were found for the 3 starch components and the environmental parameters of depth, light, and pH (Table 40).

Principal component analysis of the variable fructose yielded 2 significant components that accounted for 51.0 and 43.2 % of the variability (Fig. 87). Component 1 had large positive loadings for M. exalbescens (.934) and P. foliosus (.909). The second component had high positive loadings on C. demersum (.882) and E. canadensis (.918). Analysis of the 2 components revealed no significant correlation with depth, light, and pH (Table 41).

The 2 components retained for glucose accounted for 74.8 and 21.0 % of the variability (Fig. 88). Component 1 had high positive loadings on M. exalbescens (.798), P. foliosus (.805), and E. canadensis (.980). Component 2 had a high positive value for C. demersum (.981) and negative readings for M. exalbescens (-.586) and P. foliosus (-.515). Correlation analysis showed that the 2 components were not significantly correlated with environmental variables (Table 42).

The first 2 components retained for sucrose content accounted for 62.4 and 26.3 % of the variability (Fig. 89).

The first component had high positive loadings for C. demersum (.937), E. canadensis (.851), and M. exalbescens (.934). The second component appeared to have similar importance for P. foliosus (.993). No significant correlations were found for the components and environmental parameters (Table 43).

Table 30. Correlation of environmental parameters and total soluble carbohydrate, starch, and soluble sugars for C.demersum. r = upper diagonal, p = lower diagonal N = 9-15

	DATE	DEPTH	LIGHT	PH	CARBO	STARCH	FRUC	GLUC	SUC
DATE	X	0.47	-0.60*	0.20	0.19	-0.71*	-0.02	0.15	0.02
DEPTH	0.075	X	-0.85*	0.49	-0.25	-0.38	-0.21	-0.10	-0.48
LIGHT	0.019	<0.001	X	-0.34	0.03	0.44	0.22	0.28	0.66*
PH	0.472	0.062	0.216	X	-0.16	-0.04	-0.43	-0.26	-0.46
CARBO	0.503	0.378	0.904	0.568	X	-0.18	0.86*	0.53	-0.13
STARCH	0.010	0.229	0.158	0.905	0.585	X	-0.21	-0.24	0.06
FRUC	0.957	0.592	0.577	0.251	0.003	0.590	X	0.84*	0.18
GLUC	0.700	0.796	0.468	0.501	0.141	0.527	0.005	X	0.46
SUC	0.965	0.196	0.050	0.218	0.736	0.858	0.636	0.206	X

* significant correlation

Table 31. Correlation of environmental parameters and total soluble carbohydrate, starch and soluble sugars for E.canadensis. N = 5-8

	DATE	DEPTH	LIGHT	PH	CARBO	STARCH	FRUC	GLUC	SUC
DATE	X	-0.23	-0.03	-0.57	0.68	-0.13	-0.12	-0.08	-0.16
DEPTH	0.579	X	-0.72*	-0.01	-0.36	-0.52	-0.43	-0.48	-0.27
LIGHT	0.944	0.044	X	-0.03	-0.13	0.58	-0.14	0.06	0.08
PH	0.144	0.987	0.944	X	0.15	-0.80	0.26	0.32	0.14
CARBO	0.064	0.382	0.758	0.725	X	-0.66	0.50	0.58	0.22
STARCH	0.836	0.374	0.303	0.106	0.222	X	0.38	0.22	0.51
FRUC	0.789	0.337	0.774	0.571	0.251	0.617	X	0.92*	0.02
GLUC	0.858	0.272	0.884	0.485	0.175	0.777	0.004	X	-0.24
SUC	0.728	0.564	0.871	0.768	0.638	0.492	0.974	0.597	X

* significant correlation

Table 32. Correlation of environmental parameters and total soluble carbohydrate, starch and soluble sugars for M.exalbescens. N = 7-10

	DATE	DEPTH	LIGHT	PH	CARBO	STARCH	FRUC	GLUC	SUC
DATE	X	-0.29	0.02	0.11	-0.44	0.64	-0.20	-0.59	0.35
DEPTH	0.420	X	-0.65*	0.23	0.73*	-0.07	0.41	0.40	0.48
LIGHT	0.951	0.041	X	-0.46	-0.41	-0.41	-0.39	-0.41	-0.57
PH	0.757	0.531	0.184	X	0.30	-0.32	0.25	0.43	0.71*
CARBO	0.198	0.016	0.236	0.407	X	-0.50	0.58	0.65*	0.55
STARCH	0.121	0.875	0.358	0.490	0.251	X	-0.18	-0.46	-0.10
FRUC	0.569	0.238	0.269	0.483	0.077	0.694	X	0.59	0.53
GLUC	0.072	0.250	0.242	0.214	0.041	0.294	0.073	X	0.36
SUC	0.318	0.159	0.086	0.023	0.096	0.837	0.117	0.303	X

* significant correlation

Table 33. Correlation of environmental parameters and total soluble carbohydrate, starch and soluble sugars for P.foliosus. N = 13

	DATE	DEPTH	LIGHT	PH	CARBO	STARCH	FRUC	GLUC	SUC
DATE	X	0.34	-0.11	-0.42	-0.11	0.26	-0.68*	-0.66*	-0.05
DEPTH	0.254	X	-0.73*	0.25	-0.05	-0.22	-0.18	-0.15	-0.16
LIGHT	0.716	0.005	X	-0.36	0.16	0.08	0.14	0.08	0.14
PH	0.159	0.410	0.220	X	-0.36	0.11	0.45	0.43	-0.50
CARBO	0.728	0.882	0.591	0.292	X	-0.04	0.12	0.11	0.60*
STARCH	0.392	0.463	0.793	0.720	0.905	X	-0.11	0.002	-0.36
FRUC	0.010	0.551	0.642	0.123	0.706	0.717	X	0.98*	-0.36
GLUC	0.015	0.618	0.793	0.140	0.724	0.996	0.001	X	-0.44
SUC	0.864	0.607	0.655	0.079	0.031	0.222	0.231	0.128	X

* significant correlation

Table 34. Correlation of environmental parameters and total soluble carbohydrate, starch and soluble sugars for P.zosteriformis. N = 3-10

	DATE	DEPTH	LIGHT	PH	CARBO	STARCH	FRUC	GLUC	SUC
DATE	X	-0.30	-0.12	-0.19	-0.12	0.81*	-0.95	-1.00*	0.99
DEPTH	0.396	X	-0.73*	-0.27	0.03	-0.27	-0.99	-0.98	0.95
LIGHT	0.734	0.016	X	-0.02	0.34	-0.40	0.21	0.48	-0.60
PH	0.601	0.454	0.945	X	-0.70*	0.80*	0.99	0.98	-0.95
CARBO	0.752	0.932	0.342	0.024	X	-0.47	-0.76	-0.92	0.96
STARCH	0.051	0.606	0.434	0.054	0.344	X	1.00	-1.00	1.00
FRUC	0.196	0.075	0.863	0.075	0.447	-	X	0.96	-0.91
GLUC	0.012	0.110	0.678	0.110	0.262	-	0.185	X	-0.99
SUC	0.073	0.194	0.593	0.194	0.177	-	0.270	0.085	X

* significant correlation

Table 35. Light (percent of surface PAR) and pH at various depths and sites in Shoal Lake during the 1985 growing season.

DATE	STATION	DEPTH(m)	LIGHT	pH
May 2	1	3.0	15	8.0
May 2	2	5.0	2.5	8.0
May 2	4	5.0	8	8.1
May 16	1	3.5	14	7.5
May 16	6	5.0	5	7.5
May 16	4	8.0	1	7.6
May 16	7	13.0	0.5	7.5
May 30	2	1.0	46	7.4
May 30	2	4.5	12	7.4
May 30	6	5.5	9	7.5
June 13	3	1.0	23	7.2
June 13	1	4.0	16	7.2
June 13	6	6.0	3	7.1
June 13	7	14.0	0.5	7.1
June 27	3	1.0	20	6.8
June 27	1	4.0	6	7.1
June 27	2	5.0	15	7.3
July 10-11	3	1.5	25	7.3
July 10-11	1	4.0	4	7.1
July 10-11	4	4.5	4	7.3
July 10-11	5	6.0	5	7.3
August 8	3	1.5	47	8.2
August 8	1	3.5	4	7.4
August 8	2	5.0	4	7.9
August 8	4	6.0	3	7.5
August 8	5	6.5	3	8.0
August 8	6	6.5	3	8.1
August 29	1	3.5	7	7.8
August 29	2	5.5	3	7.8
August 29	6	6.5	1.2	7.7

Table 36. Correlation analysis of environmental parameters. N = 30

	DATE	DEPTH	LIGHT	PH
DATE	X	-0.11	-0.06	0.04
DEPTH	0.548	X	-0.65*	0.03
LIGHT	0.753	<0.001	X	0.003
PH	0.843	0.889	0.988	X

* significant correlation

Table 37. Stepwise multiple regression equations for total soluble carbohydrate and starch content of macrophytes during the 1985 season.

Y	SPECIES	N	R^2	EQUATION
carbo	C.demersum*	15		
	E.canadensis	8	0.88	mg equiv gluc/g = 10.67(time) + 53.11(pH) - 395.85
	M.exalbescens	10	0.54	mg equiv gluc/g = 2.81(depth) + 44.02
	P.foliosus*	13		
	P.zosteriformis	10	0.49	mg equiv gluc/g = -38.08(pH) + 330.10
starch	C.demersum	12	0.50	mg starch/g = -12.46(time) + 140.64
	E.canadensis	5	0.64	mg starch/g = -143.54(pH) + 1148.06
	M.exalbescens	7	0.41	mg starch/g = 14.05(time) + 12.97
	P.foliosus*	13		
	P.zosteriformis	6	0.65	mg starch/g = 23.07(time) - 70.47

*no variables met the 0.15 significance level for entry into the model

Table 38. Stepwise multiple regression equations for soluble sugar content of macrophytes during the 1985 season.

Y	SPECIES	N	R^2	EQUATION
fruc	C.demersum*	10		
	E.canadensis*	7		
	M.exalbescens*	10		
	P.foliosus	13	0.47	mg equiv gluc/g = -2.61(time) + 25.42
	P.zosteriformis	3	0.99	mg equiv gluc/g = -3.11(depth) - 8.20(light) + 21.89
gluc	C.demersum*	10		
	E.canadensis*	7		
	M.exalbescens	10	0.60	mg equiv gluc/g = 3.98(pH) -0.85(time) - 17.72
	P.foliosus	13	0.43	mg equiv gluc/g = -2.40(time) + 24.17
	P. zosteriformis	3	1.00	mg equiv gluc/g = -1.18(time) + 0.81(pH) + 9.06
suc	C.demersum	10	0.78	mg equiv gluc/g = 0.39(time) + 14.62(light) - 1.75
	E.canadensis	7		
	M.exalbescens	10	0.50	mg equiv gluc = 5.88(pH) - 38.12
	P.foliosus	13	0.25	mg equiv gluc = -15.88(pH) + 140.10
	P.zosteriformis	3	1.00	mg equiv gluc = -17.43(light) + 1.22(time) + 14.80

* no variables met the 0.15 significance level for entry into the model

Fig. 85. Positions of macrophytes with respect to the first 3 principal components in terms of total soluble carbohydrate content.
1=C.demersum 2=E.canadensis 3=M.exalbescens
5=P.foliosus 10=P.zosteriformis

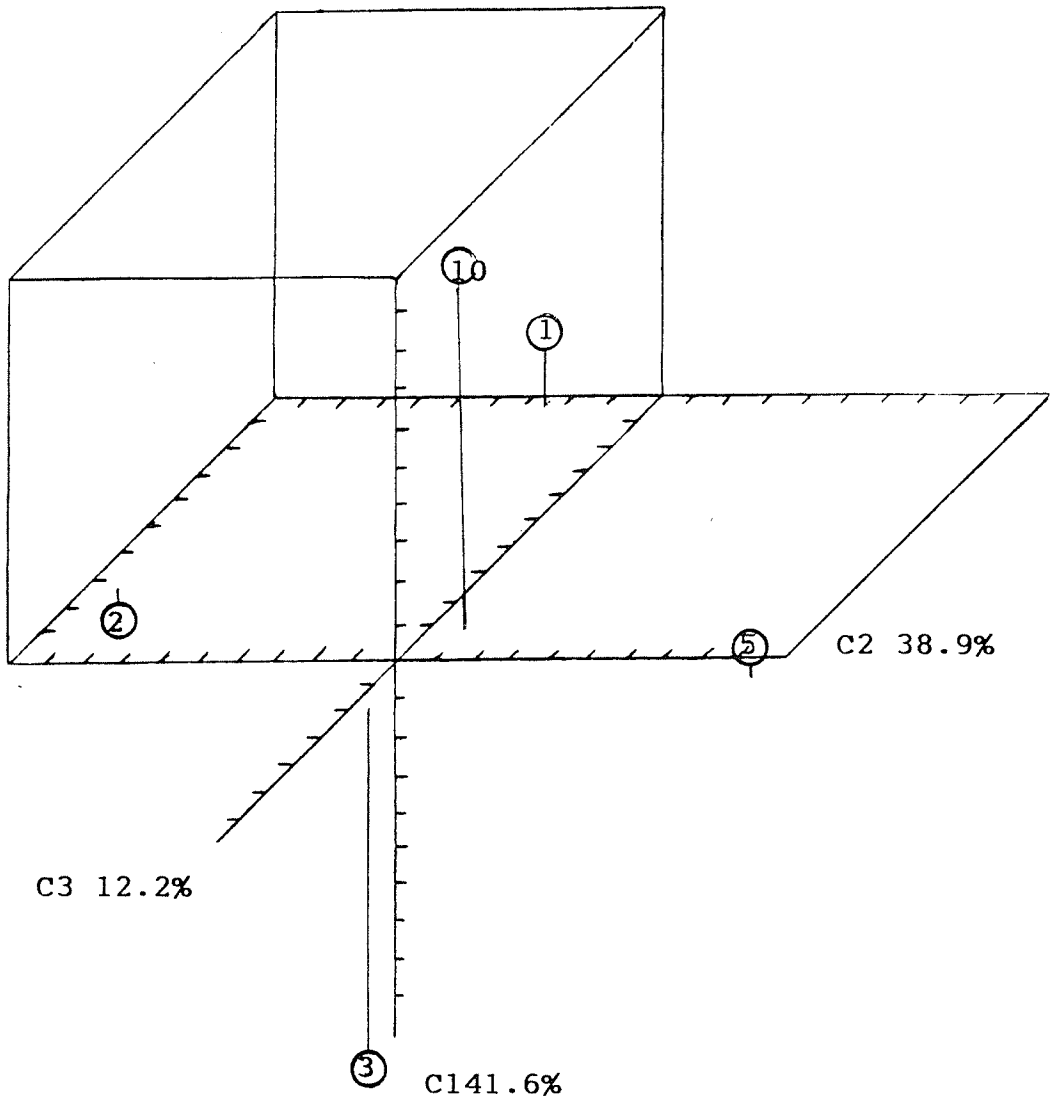

10
1
2
5
C2 38.9%
C3 12.2%
3
C141.6%

Table 39. Correlation of environmental factors with first 3 principal components for total soluble carbohydrate content.

	DEPTH	LIGHT	PH	FACT1	FACT2	FACT3
DEPTH	X	-0.66	-0.70	0.89*	0.04	-0.11
LIGHT	0.229	X	-0.02	-0.89*	-0.25	-0.44
PH	0.191	0.981	X	-0.30	0.25	0.56
FACT1	0.045	0.041	0.620	X	0.07	0.30
FACT2	0.951	0.689	0.683	0.909	X	-0.41
FACT3	0.856	0.455	0.331	0.621	0.489	X

* significant correlation

Fig. 86. Positions of macrophytes with respect to the first 3 principal components in terms of starch content. 1=C.demersum 2=E.canadensis 3=M.exalbescens 5=P.foliosus

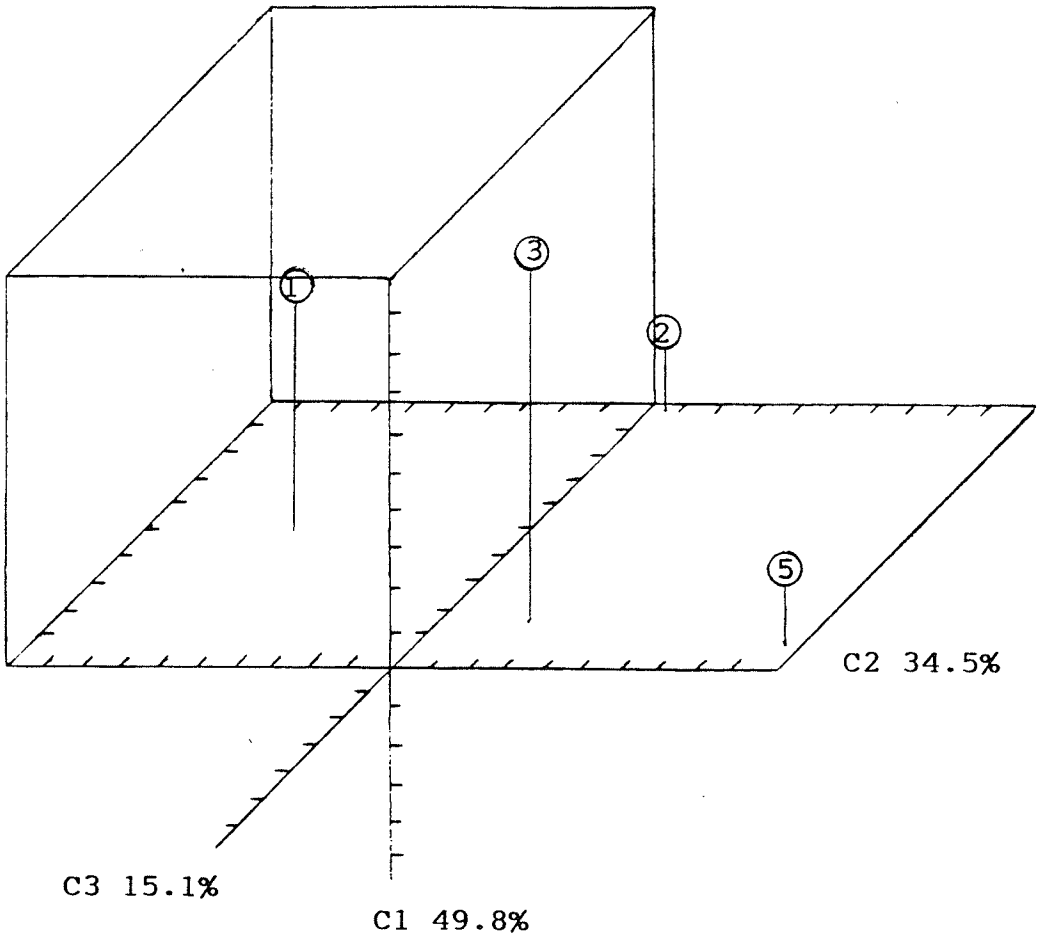

1
3
2
5
C2 34.5%
C3 15.1%
C1 49.8%

Table 40. Correlation of environmental factors with first 3 principal components for starch content.

	DEPTH	LIGHT	PH	FACT1	FACT2	FACT3
DEPTH	X	-0.73	0.44	-0.60	0.66	-0.48
LIGHT	0.268	X	-0.63	0.64	0.004	-0.02
PH	0.564	0.374	X	0.18	-0.24	-0.50
FACT1	0.400	0.361	0.815	X	-0.38	-0.39
FACT2	0.345	0.996	0.760	0.618	X	-0.51
FACT3	0.523	0.979	0.499	0.613	0.486	X

Fig. 87. Positions of macrophytes with respect to the first 2 principal components in terms of fructose content. 1=C.demersum 2=E.canadensis 3=M.exalbescens 5=P.foliosus

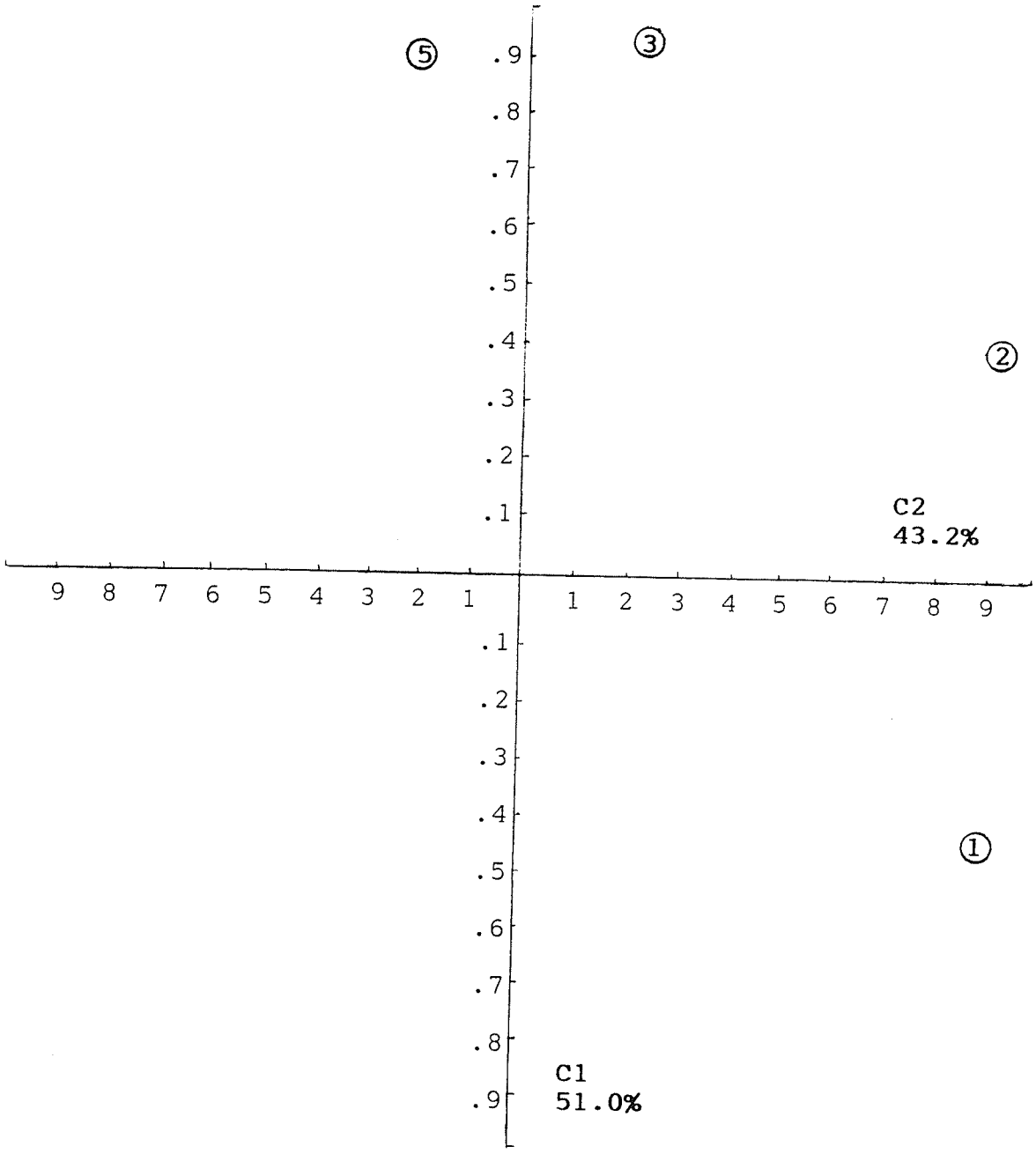

⑤
③
②
①
.9
.8
.7
.6
.5
.4
.3
.2
.1
9 8 7 6 5 4 3 2 1
1 2 3 4 5 6 7 8 9
C2
43.2%
C1
51.0%

Table 41. Correlation of environmental factors with first 2 principal components for fructose content.

	DEPTH	LIGHT	PH	FACT1	FACT2
DEPTH	X	-0.36	-0.78	0.17	0.04
LIGHT	0.643	X	-0.27	0.49	-0.01
PH	0.220	0.727	X	-0.32	-0.24
FACT1	0.830	0.510	0.682	X	-0.78
FACT2	0.960	0.988	0.761	0.220	X

Fig. 88. Positions of macrophytes with respect to the first 2 principal components in terms of glucose content. 1=C.demersum 2=E.canadensis 3=M.exalbescens 5=P.foliosus

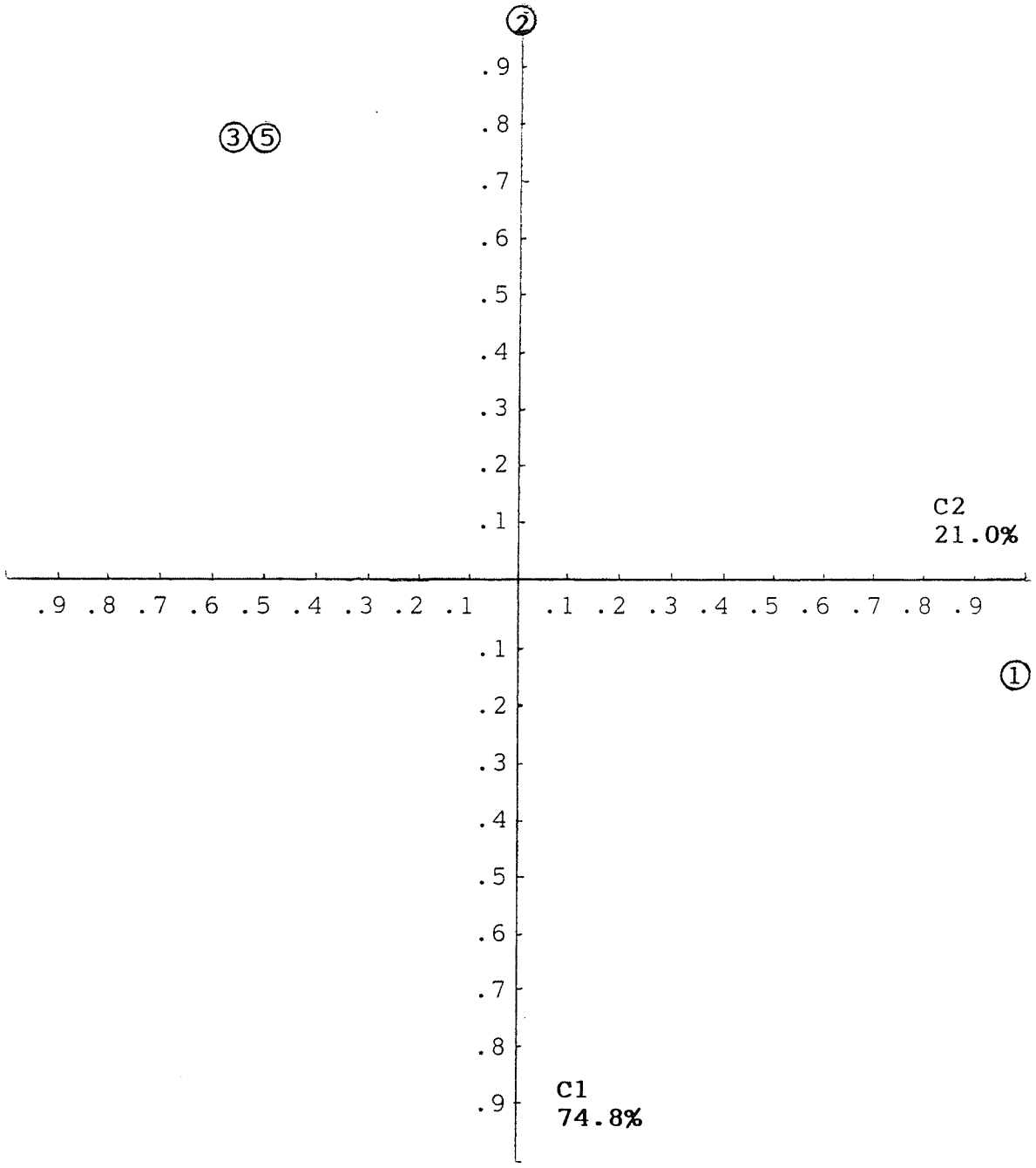

②
.9
.8
.7
.6
.5
.4
.3
.2
.1
③⑤
C2
21.0%
.9 .8 .7 .6 .5 .4 .3 .2 .1
.1 .2 .3 .4 .5 .6 .7 .8 .9
①
.1
.2
.3
.4
.5
.6
.7
.8
.9
C1
74.8%

Table 42. Correlation of environmental factors with first 2 principal components for glucose content.

	DEPTH	LIGHT	PH	FACT1	FACT2
DEPTH	X	-0.36	-0.78	0.56	-0.18
LIGHT	0.643	X	-0.27	0.46	-0.51
PH	0.220	0.727	X	-0.78	0.35
FACT1	0.435	0.535	0.222	X	-0.86
FACT2	0.819	0.486	0.650	0.140	X

Fig. 89. Positions of macrophytes with respect to the first 2 principal components in terms of sucrose content. 1=C.demersum 2=E.canadensis 3=M.exalbescens 5=P.foliosus

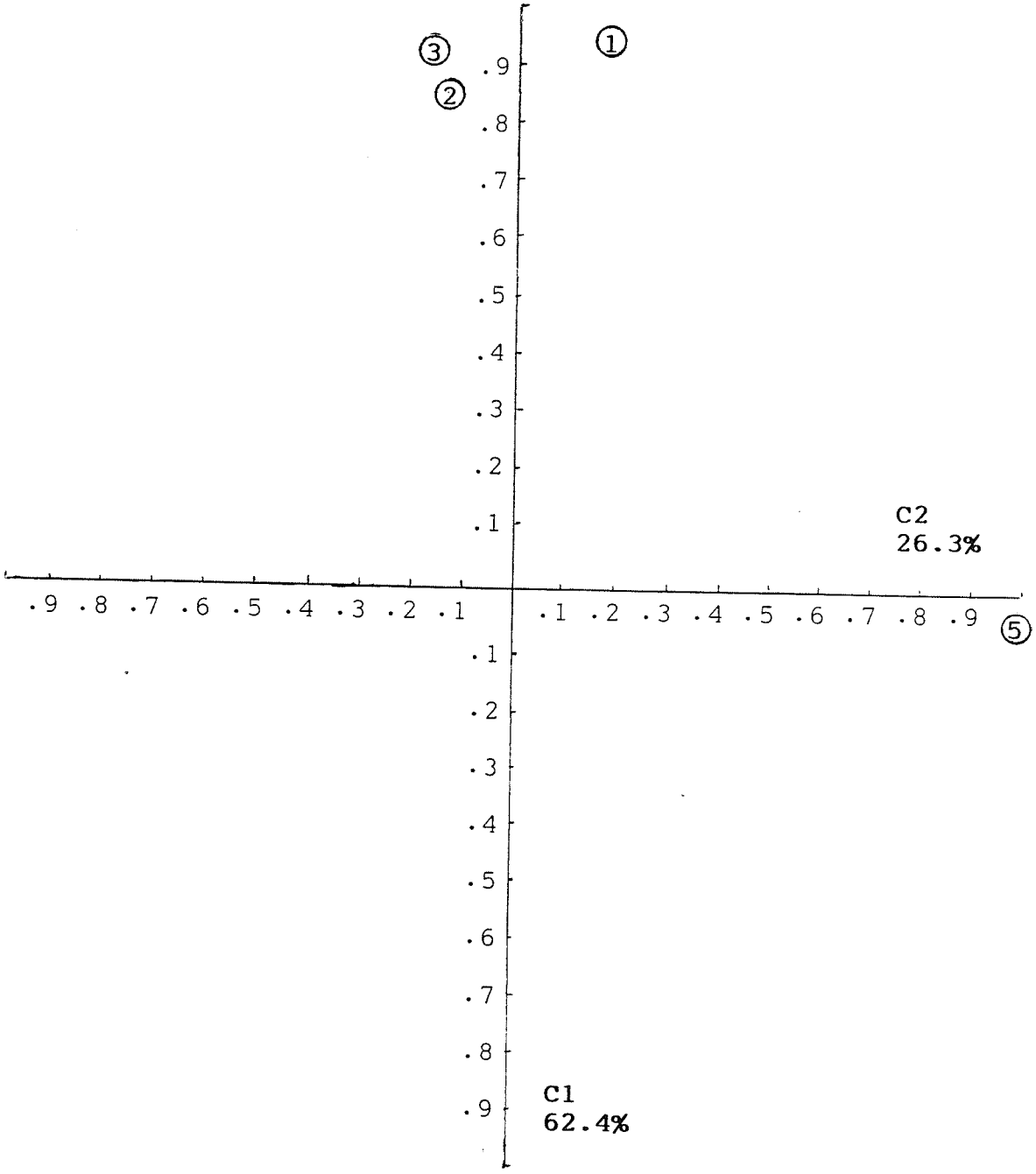

③
①
②
.9
.8
.7
.6
.5
.4
.3
.2
.1
C2
26.3%
.9 .8 .7 .6 .5 .4 .3 .2 .1
.1 .2 .3 .4 .5 .6 .7 .8 .9
⑤
.1
.2
.3
.4
.5
.6
.7
.8
.9
C1
62.4%

Table 43. Correlation of environmental factors with first 2 principal components for sucrose content.

	DEPTH	LIGHT	PH	FACT1	FACT2
DEPTH	X	-0.36	-0.78	-0.44	0.26
LIGHT	0.643	X	-0.27	0.52	-0.71
PH	0.220	0.727	X	-0.05	0.33
FACT1	0.561	0.481	0.946	X	-0.94
FACT2	0.738	0.287	0.668	0.060	X

DISCUSSION

The overall range in total soluble carbohydrate for the Shoal Lake macrophytes was large during the 1985 growing season, with a seasonal mean for each species of less than 10 % dry weight. Results agreed with a generalization made by Janauer and Englmaier (1986) that total sugar concentrations rarely exceed this limit (10 %) in aquatic plants. Values compared well with published data for some submerged macrophytes including C. demersum and E. canadensis (Best 1977; Janauer 1979; 1982a; 1982b; Janauer & Englmaier 1986). Observations of soluble carbohydrate in E. canadensis by Janauer (1981a) were similar to the lower level of the range reported for this species in the present study. The overall seasonal mean for C. demersum was higher than that found in this species by Best and Visser (1987). Soluble carbohydrate content in P. richardsonii was also higher than previously reported levels for this macrophyte (Pip & Stewart 1976). The seasonal content of soluble reserves for 6 of the species studied was greater than values observed for the same species in Shoal Lake during the 1984 growing season (Pip & Sutherland-Guy 1987). The higher levels in 1985 were at least partially attributable to the greater efficiency of the hot alcohol extraction procedure used in the present study. Carbohydrate content for all macrophytes exceeded levels reported for 3 other submerged species (Titus & Adams 1979; Best & Dassen 1987), while quantities were lower than those found in Ranunculus fluitans Lam. (Janauer 1981b;

1982b). Variation in reported values may be influenced by the degree to which seasonal, vertical, and horizontal fluctuation was taken into account in these studies. The disparity in content of total soluble carbohydrate in reports on the same species may reflect the differences in metabolic response of a particular plant to different environments.

M. exalbescens was the only species with a sufficient number of samples to allow observations of trends in carbohydrate content of organs other than shoots and leaves. Roots consistently contained significantly more soluble carbohydrate than shoots and leaves in this species over a range of 3 sampling dates. This pattern was contrasted by one P. zosteriformis sample that contained significantly more soluble carbohydrate in shoots and leaves than in roots. Titus and Adams (1979) found that total nonstructural carbohydrates in Myriophyllum spicatum L. tended to be higher in shoots than in roots during July and August of 2 consecutive seasons.

Although shoot:root ratios in submerged plants are usually higher than those of terrestrial herbaceous plants (Titus & Adams 1979), roots in M. exalbescens and perhaps other aquatics may play an important role in carbohydrate storage. Small sample size made it impossible to measure starch content of M. exalbescens roots.

Sucrose is commonly found as the predominant sugar in most terrestrial plants and this appeared to be true for many of the macrophytes in the present study. Sucrose

serves a major role in transporting glucose from source to sink regions and is the primary substrate for the biosynthesis of many plant substrates including starch (Duffus & Duffus 1984). Advantages in using this disaccharide for transport include the non-reducing nature of sucrose, its high solubility (179 g/100 ml at 0 C), and its free energy of hydrolysis (Akazawa & Okamoto 1980).

Sucrose was the primary sugar for most of the 1985 growing season in E. canadensis, P. foliosus, P. gramineus, P. richardsonii, P. robbinsii, and P. zosteriformis, and for at least one sampling date in M. exalbescens and P. praelongus. Total soluble carbohydrate was significantly ($r=0.60$, $p<0.05$, $n=13$) positively correlated with sucrose in P. foliosus. Positive correlations were also observed for total soluble carbohydrate and sucrose in E. canadensis, M. exalbescens, and P. zosteriformis. The sucrose content of E. canadensis in mid-June (72 %) was similar to levels reported for this species and June sampling time by Janauer (1981a). Sucrose was also the predominant sugar detected by Janauer in several submerged macrophytes including Potamogeton pectinatus L. (1979; 1982a; 1982b). Pip and Stewart (1976) in contrast found that fructose was the most abundant sugar in P. pectinatus and P. richardsonii.

Glucose appeared to be an important sugar during parts of the 1985 season in M. exalbescens and N. flexilis. Glucose was significantly ($r=0.65$, $p<0.05$, $n=7$) positively correlated with total soluble carbohydrate in the former species.

Other macrophytes in which glucose has been reported as a primary sugar include Callitriche obtusangula Le Gall, Myriophyllum verticillatum L., and Elodea nuttallii (Planch.) St. John (Janauer 1982b; Best & Dassen 1987).

Sugars detected in C. demersum in addition to fructose, glucose, and sucrose were melibiose, raffinose, and stachyose. A seventh component in the soluble carbohydrate fraction of this species was eluted between melibiose and a melibiose/raffinose combination in paper chromatography. This unknown represented 10 to 18 % of total soluble carbohydrate during the 1985 growing season. Best and van der Werf (1986) and Best and Visser (1987) detected 2 unidentified components that also eluted between melibiose and raffinose in GLC analysis of sugars in C. demersum. Each of these unknown accounted for approximately 10 % of total soluble carbohydrate. The unknown detected in the present study was hypothesized to be a product of the hydrolysis of stachyose, on the basis of information obtained in NMR analysis.

Individual proportions of fructose and glucose often exceeded sucrose levels in C. demersum during the 1985 season. The combined proportion of raffinose, stachyose, and melibiose (including the unknown) accounted for the major proportion of soluble sugars for all sampling dates, ranging from 33 to 50 %. The proportion of these combined sugars did not change significantly over the growing season. Best and van der Werf (1986) and Best and Visser (1987) also found that monosaccharides exceeded sucrose levels in C. demersum.

These workers reported that raffinose and melibiose accounted for 33 to 34 % of total soluble sugars. Best and Visser observed that the stachyose/raffinose concentration was relatively constant throughout the season.

The raffinose family of oligosaccharides (including stachyose) is widely distributed in plants (Dey 1980; Lewis 1984). The primary role of this group of sugars in leaves, vegetative organs, and seeds is to serve as storage carbohydrate. Stachyose is particularly important for energy storage in Hippuris vulgaris L., a macrophyte that lacks starch entirely (Janauer & Englmaier 1986). Members of the raffinose series are non-reducing like sucrose and are usually present in species where sucrose is not the major form of transport sugar (Giaquinta 1980). Stachyose has been identified as an important transport carbohydrate in many plants (Dey 1980) including C. demersum (Best & Visser 1987). Melibiose is a component of the trisaccharide raffinose and is considered to be a rare sugar in plants (Lewis 1984). This sugar accounted for more than 10% of total soluble carbohydrate in C. demersum and compared well to previously reported levels of 8% (Best & van der Werf 1986) and 7% (Best & Visser 1987) in this species.

Myo-inositol has been detected in minor quantities (generally less than 3% of total sugars) in a number of aquatic species (Janauer 1981a; 1981b; 1982a; 1982b; Best & van der Werf 1986; Janauer & Englmaier 1986; Best & Visser 1987). This alcohol sugar did not react with aniline diphenylamine

and hence was not measurable in the present study. The aldehyde or keto group of a sugar is reduced to a hydroxyl group in sugar alcohols, and consequently many techniques for sugar analysis do not reveal the presence of these compounds (Loescher 1987).

The overall range in starch content of shoots and leaves for the macrophytes was greater than the variation in soluble carbohydrate during 1985. Seasonal means for each species ranged from 37 to 118 mg/g and were higher than levels reported for several submerged species (Best 1977; Janauer 1981a; 1981b; 1982a; 1982b; Best & Dassen 1987; Best & Visser 1987) in similar quantification methods. Findings were not consistent with a generalization by Janauer and Englmaier (1986) that starch in leaves and stems of many macrophytes is less than 1 % dry weight. Best (1977) found that the starch content of C. demersum and E. canadensis was just detectable (1 %) in June-July and reached seasonal maximum levels of only 3 to 3.5 % dry weight. In the present study, the mean starch content accounted for approximately 6 % dry weight in C. demersum and 10 % dry weight in E. canadensis. Starch levels in C. demersum were more than twice as high as summer levels observed in this species by Best and Visser (1987).

Some seasonal differences in soluble carbohydrate content of macrophytes were observed during the 1985 season. Species represented by 3 or more consecutive sampling times showed a tendency for a seasonal maximum. These peaks

occurred at different times of the growing season: May 30 - June 13 in P. foliosus, June 13 in P. gramineus, June 27 - July 10-11 in P. zosteriformis, July 10-11 in C. demersum and P. robbinsii, and August 8 in E. canadensis. Soluble reserves in M. exalbescens gave a peak early in the season (April 27 - May 16) and a smaller peak on August 8. Total soluble carbohydrate had a positive correlation with time for C. demersum and E. canadensis, while negative relationships were observed for M. exalbescens, P. foliosus, and P. zosteriformis. Relationships were strongest for M. exalbescens and E. canadensis, comparing well with respective early and late seasonal peaks in these species. Among the 5 species analyzed in stepwise regression, E. canadensis was the only macrophyte in which time was entered into the equation for soluble carbohydrate when considered with the factors pH, depth, and light.

A number of workers have also observed a tendency for soluble carbohydrate accumulation at certain times of the season. Best and Visser (1987) found that soluble reserves in C. demersum reached a seasonal maximum on July 8 (between April 29 and July 22), comparable to findings for this species in the present study. Best (1977) in contrast reported that total carbohydrate content of C. demersum gave a seasonal minimum level in June of 2 consecutive years. Soluble sugars accounted for the major proportion of total reserves in the latter study, where a minimum for E. canadensis and an overall accumulation of total carbohydrate was also reported

between June and August, similar to the late seasonal peak observed in the same species in the present study. Total sugar concentration in several submerged species studied by Janauer (1982a) showed a maximum in August or September. Soluble carbohydrate content of Elodea nuttallii was higher in September than in June (Best & Dassen 1987) and shoots of Myriophyllum spicatum tended to accumulate total nonstructural carbohydrates (including starch) between June and August (Titus & Adams 1979). Pip and Stewart (1976) observed that soluble carbohydrate content of Potamogeton pectinatus and P. richardsonii was highest early in the growing season.

The positive correlation of soluble carbohydrate with time in E. canadensis and C. demersum and the negative correlation in P. foliosus presented interesting parallels with a study by Pip (1987). This worker found that total chlorophyll content increased significantly with time in the former 2 species and decreased in P. foliosus during the 1985 growing season. Increases in pigment concentrations appeared to relate to comparatively long periods of active metabolism in E. canadensis and C. demersum, while decreases in chlorophyll in P. foliosus accompanied a general seasonal loss of vitality. Changes in soluble reserves in these macrophytes may have resulted from increases or decreases in photosynthetic efficiency as affected by light-harvesting capacity. M. exalbescens and P. zosteriformis also showed a general seasonal decrease in soluble carbohydrate content, but these

species did not show defined chlorophyll differences during the season (Pip 1987). Photosynthetic efficiency may have been related to other factors in these species, such as light quality and quantity, temperature, and age of tissue. It is also important to note that the carbohydrate content of tissue is not a direct indicator of efficiency in energy conversion, due to varying respiration rates and losses of carbon through secretion.

Starch concentrations often exceeded levels of soluble sugars, with the overall mean starch:soluble carbohydrate ratio approaching or exceeding 2 in 6 of the 10 species studied. The proportion of starch in C. demersum ranged from 41 to 71% of total carbohydrate over the 1985 season and compared well with the summer mean of 62% reported for this species by Best and Visser (1987). The only other comparable proportion for a submerged species was observed in Elodea nuttallii, which had starch levels twice as high as soluble carbohydrate during parts of the year (Best & Dassen 1987). The high proportions of starch observed in the present study contrasted with the remaining reports of submerged macrophytes that suggest soluble carbohydrate is the predominant reserve substance (Best 1977; Janauer 1981a; 1981b; 1982a; 1982b; Janauer & Englmaier 1986).

There were fewer significant seasonal trends in starch than were observed for soluble carbohydrate content during 1985. This may have been due to the generally smaller sample size available for starch analysis. Starch was significantly

($r=-0.71$, $p=0.01$, $n=9$) negatively correlated with time in C. demersum and marginally significantly ($r=0.81$, $p=0.05$, $n=3$) positively correlated with time in P. zosteriformis. Starch content was negatively correlated with time in E. canadensis, while positive relationships occurred in M. exalbescens and P. foliosus. Time was entered into stepwise regression equations for starch in C. demersum, M. exalbescens, and P. zosteriformis when considered with depth, pH, and light.

The 5 species examined in correlation analysis showed an overall negative relationship between the 2 forms of reserve carbohydrate. This relationship, along with seasonal changes in proportions of total nonstructural carbohydrates suggested some degree of conversion between soluble sugars and starch in C. demersum, P. foliosus, P. zosteriformis, and P. robbinsii. Inverse relationships were less apparent in M. exalbescens and E. canadensis.

The relative abundance of individual sugars in plant tissue at a particular time has been used by some workers to explain the dynamics of carbohydrate metabolism. Best and Visser (1987) viewed the relative quantity of non-reducing sugars in C. demersum during summer as an indication that assimilate transport was the predominant process in this plant. Janauer (1981b) found low amounts of sucrose and high levels of monosaccharide in dormant apices of E. canadensis, where little transport of sugar would be expected. Best and Dassen (1987) observed that the proportion of sucrose in

leaves of Polygonum amphibium L. was higher at times of high photosynthetic activity, indicating export of assimilates. High levels of reducing sugars, on the other hand have been regarded as an indication of starch synthesis (Janauer 1981a).

Correlation analysis of some species produced no consistent relationship between individual sugars and starch content during 1985, and none of these relationships were significant. The relative abundance of sucrose and other non-reducing sugars in the species examined during the growing season did suggest that mobilization of assimilates from source regions was an important process, and that photosynthetic activity was high. The complex biochemistry of carbohydrates in plants and the possible influence of other factors upon sugar concentrations suggest that interpretations of sugar levels may oversimplify actual processes.

Negative relationships of all carbohydrate variables with water depth were more frequent than positive relationships. Correlation analysis showed that soluble carbohydrate, fructose, glucose, sucrose, and starch were all negatively correlated with depth in C. demersum, E. canadensis, and P. foliosus. Inconsistent vertical relationships with respect to soluble carbohydrate content for these species were also observed in 1984 (Pip & Sutherland-Guy 1987). These workers however found that positive relationships between carbohydrate and depth were predominant.

The lack of substantial vertical temperature fluctuation in Shoal Lake (Pip & Simmons 1986) suggested that

temperature would not be an important factor in determining photosynthetic rate in the plants studied. Light (percent surface PAR) was significantly ($r=-0.65$, $p<0.001$, $n=30$) negatively correlated with depth during the 1985 season. The tendency for macrophytes to contain lower levels of carbohydrate at greater water depth may thus have resulted from reduced photosynthetic rates at lower light intensities. Photosynthetic rates in some species have been shown to decrease with increasing depth (Wetzel 1964). Light reduction with depth was suggested to be a primary cause for the decrease in photosynthetic activity observed in lower plant portions of C. demersum (Best & Visser 1987). Light was entered into regression equations for fructose and sucrose in P. zosteriformis and sucrose in C. demersum. In principal component analysis of 5 species, the first component for total soluble carbohydrate had a significant negative relationship with light ($r=-0.89$, $p<0.05$) and a significant positive relationship with depth ($r=0.89$, $p<0.05$). This component was important with respect to P. zosteriformis and M. exalbescens.

Carbohydrate and starch content in species occurring at the 12-14 m site sometimes showed no marked differences with levels in samples collected at shallower depths. The ability of these macrophytes to maintain such efficiency at 0.5 to 1 % of surface PAR was remarkable. Extensive communities of E. canadensis, N. flexilis, P. foliosus, P. zosteriformis, M. exalbescens, and C. demersum were found at the

12-14 m site throughout the 1984 and 1985 growing seasons by Pip and Simmons (1986). These workers concluded that a combination of favorable light, temperature, and oxygen factors allowed the macrophytes to survive at such extraordinary depths.

Light attenuation in Indian Bay during the 1985 season (Appendix C) showed that sampling stations were similar with respect to water clarity. One exception was station 3, which had relatively poor light penetration. In spite of general similarities in water clarity, differences in carbohydrate content of a species between stations at the same depth were sometimes large. Such variation has also been reported by Muztar et al. (1979), Titus and Adams (1979), and Pip and Sutherland-Guy (1987). Horizontal differences show that data based on restricted sampling sites may not be representative of macrophytes in a particular lake.

Other factors in addition to light availability must influence the metabolic status of aquatic macrophytes. These factors might include temperature, water chemistry, competition, shading by periphyton, and stress imposed by grazers, disease, or edaphic conditions.

Janauer found that carbohydrate content of macrophytes may be an important indicator of the trophic status of the water body in which the plants are growing. This worker found a positive relationship between sucrose content in plant tissue and inorganic phosphorous and nitrate concentrations in lake water for Potamogeton pectinatus (1979)

and leaves of Ranunculus fluitans (1981b). Starch levels of the latter species also tended to be higher at a more eutrophic site.

In the present study, pH appeared to have a relationship to metabolic status of some species. Significant positive correlations were found between pH and sucrose content in M. exalbescens, and between pH and starch content in P. zosteriformis. The latter species also gave a significant negative relationship between total soluble carbohydrate and pH. When considered with time, depth, and light, pH was entered into the regression equation for soluble carbohydrate and starch in E. canadensis, for glucose and sucrose in M. exalbescens, sucrose in P. foliosus, and soluble carbohydrate and glucose in P. zosteriformis. Thus pH was the second most significant factor (after time) in relationship to metabolic status. Both negative and positive relationships were observed, and trends for the same metabolic parameter were inconsistent in different species.

The positive relationships compared well with observations by Fair and Meeke (1983) that photosynthetic activity in C. demersum increased with increasing pH over a pH range similar to that in Shoal Lake in 1985. The positive relationship between total soluble carbohydrate and pH in E. canadensis was interesting in view of findings by Pip (1987) that pH was positively correlated with seasonal and local chlorophyll content in this species in 1985. The tendency for nutrient content to increase with pH may have related to

changes in availability of CO_2 and bicarbonate in the lake water. The lack of consistency however suggested that other factors were operating in addition to pH.

In view of these findings, it is proposed that additional analysis of nonstructural carbohydrates in Shoal Lake macrophytes will include an examination of water chemistry parameters, to further investigate the possible role of these plants as trophic indicators.

Appendix A. Reagents

1. Soluble carbohydrate determination

Anthrone: Dissolve 300 mg anthrone and 3 g thiourea in 100 ml 75% H_2SO_4. Store in the dark and prepare fresh every 5 days.

Calibration: 0.2 mg glucose per ml water

2. Starch determination

Anthrone: Dissolve 200 mg anthrone in 100 ml cold 95% H_2SO_4. Store near 0 C and prepare fresh every 2 days.

Calibration: 1 mg glucose per ml water

Perchloric acid, 52% : Add 270 ml 72% perchloric acid to 100 ml water.

3. Paper chromatography

Developing solution: Dissolve 2 g diphenylamine and 2 ml aniline in 200 ml acetone and add 20 ml 85% H_3PO_4. Use immediately and prepare fresh as needed.

Solvent: Combine butanol, acetic acid, and water in a 52:13:35 volume proportion.

Appendix B. Mean solar energy (as PAR) incident in air and at the bottom at stations 1-7 at the time of measurement on each sampling day. Values are $\mu Es^{-1}m^{-2}$. Each value is a mean of at least 3 separate measurements, each in turn integrated over a 10 sec interval. Incident values have been rounded. (Pip 1985)

	February 20	February 26	May 2	May 16	May 30*	June 13	June 27*	July10/11	August 8	August 29
STATION 1										
Incident	1650		1575	1900	540	1600	190	2020	1700	2030
Bottom	19(3.5m)		240(3m)	273(3m)	45(4m)	22(5m)	12(4m)	77(4m)	62(3m)	131(3m)
STATION 2										
Incident			1900	-	730	-	190	2130	960	1890
Bottom			47(5m)	-	89(4m)	-	21(5m)	71(5m)	37(5m)	19(6m)
STATION 3										
Incident			1890	2075	200	2080	110	1790	2210	2160
Bottom			19(1m)	71(1m)	28(1m)	487(1m)	21(1m)	450(1m)	584(1m)	360(1m)
STATION 4										
Incident			1880	2000	1070	2200	245	1500	2130	1840
Bottom			146(5m)	19(8m)	20(6m)	18(6m)	6(6m)	58(4m)	49(6m)	8(6m)

Appendix B, continued. . .

	February 20	February 26	May 2	May 16	May 30*	June 13	June 27*	July 10/11	August 8	August 29
STATION 5										
Incident			-	-	525	-	560	1840	2000	2050
Bottom			-	-	41(6m)	-	40(5m)	99(6m)	57(6m)	37(6m)
STATION 6										
Incident	1275		1780	1830	960	1850	160	430	1820	1980
Bottom	19(4m)		109(5m)	83(5m)	86(5m)	7(6m)	24(5m)	83(4m)	57(6m)	24(6m)
STATION 7										
Incident			1710	1960	1280	1680	175	-	2230	2370
Bottom			38(10m)	28(10m)	22(10m)	42(10m)	2(10m)	-	23(10m)	17(10m)

Appendix B continued. . .

STATION 8	
Incident	1200
Bottom	17(4m)
STATION 9	
Incident	1410
Bottom	25(4m)

* heavy overcast and/or severe storm conditions

Appendix C. Light attenuation at stations 1-7 during the May-August, 1985 season. Values represent mean percentages of incident light (PAR) available at the surface. (Pip 1985)

STATION 1

Depth(m)	May 2	May 16	May 30	June 13	June 27	July 10	August 8	August 29
Air	100	100	100	100	100	100	100	100
0	77	70	73	75	81	60	58	76
0.5	66	58	59	65	76	38	35	56
1	46	34	46	50	69	34	29	33
2	21	21	28	29	32	15	7	19
3	15	14	19	16	16	11	4	7
4			8	5	6	4		

STATION 2

Depth(m)	May 2	May 30	June 27	July 10	August 8	August 29
Air	100	100	100	100	100	100
0	78	96	83	75	74	80
0.5	66	70	54	52	49	59
1	34	46	47	44	29	41
2	30	28	34	28	17	13
3	§	20	16	11	9	11
4	10	12	15	10	7	4
5	2.5		11	3	4	3
6						1.0

Appendix C continued. . .

STATION 3

Depth(m)	May 2	May 16	May 30	June 13	June 27	July 10	August 8	August 29
Air	100	100	100	100	100	100	100	100
0	79	51	79	81	74	72	72	71
0.5	63	18	41	34	49	42	47	36
1	1.0	3	14	23	20	25	26	17

STATION 4

Depth(m)	May 2	May 16	May 30	June 13	June 27	July 11	August 8	August 29
Air	100	100	100	100	100	100	100	100
0	84	86	86	81	66	87	71	57
0.5	72	60	79	65	46	65	56	50
1	52	41	65	46	38	33	41	26
2	32	19	38	29	22	14	24	10
3	21	13	17	18	14	6	13	6
4	10	7	13	11	13	4	5	4
5	8	5	8	4	6		3	2
6		4	2	0.8	2		2	0.4
7		2						
8		1.0						

Appendix C continued. . .

STATION 5

Depth(m)	May 30	June 27	July 10	August 8	August 29
Air	100	100	100	100	100
0	76	63	71	76	71
0.5	69	42	54	59	54
1	47	33	25	39	33
2	35	22	§	25	21
3	21	15	§	12	8
4	16	10	9	8	3
5	13	7	8	4	2
6	8		5	3	1.8

STATION 6

Depth(m)	May 2	May 16	May 30	June 13	June 27	July 11	August 8	August 29
Air	100	100	100	100	100	100	100	100
0	87	75	86	82	82	59	71	63
0.5	64	49	§	61	68	33	53	50
1	52	47	70	47	59	31	38	36
2	29	27	50	22	47	25	22	15
3	21	9	24	17	26	19	9	5
4	10	7	15	9	§		5	<5
5	6	5	9	3	15		<5	2
6				0.4			3	1.2

Appendix C continued. . .

STATION 7

Depth(m)	May 2	May 16	May 30	June 13	June 27	August 8	August 29
Air	100	100	100	100	100	100	100
0	82	63	79	95	-	68	71
0.5	78	46	68	82	57	49	38
1	60	33	47	55	51	31	31
2	37	17	24	40	33	16	20
3	23	7	11	25	27	10	11
4	15	4	8	16	22	5	7
5	11	3	6	§	20	<5	2
6	8	§	5	9	18	2	<2
7	5	§	4	5	16	<2	1.4
8	3	§	3	4	15	1.3	1.3
9	2.5	2	2	3	5	<1.3	1.2
10	2	1.4	1.7	2.5	1.1	1.0	0.7
12-14	0.5 →						

§ these values are not given because they were subject to abnormal variance

Appendix D. Values for pH at the surface (S) and near the bottom (B) during 1985. (Pip 1985)

Time	STATION 1		STATION 2		STATION 3		STATION 4		STATION 5		STATION 6		STATION 7		STATION 8		STATION 9	
	S	B	S	B	S	B*	S	B	S	B	S	B	S	B	S	B	S	B
February 20	7.8**7.65[2]										7.8**7.9[4]							
May 2	7.8	-	7.95	8.0[6]	8.0		8.15	8.1[5]	7.9	8.15[7]	8.2	8.15[6]	7.65	7.75[10]				
May 16	7.5	-	7.5	7.6[5]	7.5		7.5	7.6[9]	7.5	-	7.5	7.5[5]	7.6	7.5[12]	7.6			
May 30	7.35	7.3[3]	7.4	7.4[4]	7.4		7.2	7.3[6]	7.4	7.6[7]	7.2	7.5[6]	7.3	7.3[12]				
June 13	7.3	7.2[4]	7.3	-	7.2		6.9	7.0[7]	7.1	7.0[7]	7.0	7.1[6]	7.0	7.1[11]	7.0		7.1	
June 27	7.0	7.1[3]	6.9	7.3[5]	6.85		§	§	§	§	§	§	6.9	6.9[12]				
July 10/11	7.1	7.1[3]	7.2	7.2[6]	7.3		7.3	7.3[4]	7.3	7.3[7]	7.2	7.2[5]	7.2	7.2[12]				
August 8	7.8	7.4[2]	8.0	7.9[5]	8.2		8.2	7.5[7]	7.8	8.0[8]	8.1	8.1[7]	8.0	7.3[12]				
August 29	8.0	7.8[2]	7.9	7.8[4]	7.7	7.0[1]	7.5	6.9[7]	7.6	7.4[8]	7.9	7.7[8]	7.1	6.9[12]				

Additional sites: STATION 10: June 13 - S 7.0
STATION 21: May 30 - S 7.4, B[12] 7.5; June 27 - S 6.95, B[12] 6.9

* site only 1 m deep

** 0.75 m below ice surface

§ storm conditions, water got inside instruments

Superscript codes (depth below surface):

1 = 1 m	7 = 5.5 m
2 = 3 m	8 = 6 m
3 = 3.5 m	9 = 7.5 m
4 = 4 m	10 = 11 m
5 = 4.5 m	11 = 12 m
6 = 5 m	12 = 12.5 m

Appendix E. Ranges of depth and minimal seasonal light levels for macrophytes in the study area (Pip & Sutherland-Guy 1987).

Species	Depth range (m)	Minimum % of surface light
Potamogeton gramineus L.	1-2	20
P. praelongus WULFEN	1-4	2-10
P. richardsonii (BENN.) RYDB.		
P. robbinsii OAKES	1-6	1
Potamogeton foliosus RAF.	1-14	0.5
P. zosteriformis FERN.		
Najas flexilis (WILLD.) ROSTK. & SCHMIDT		
Elodea canadensis MICHX.		
Ceratophyllum demersum L.		
Myriophyllum exalbescens FERN.		

Appendix F. Biomass of individual macrophyte species harvested in quadrat samples in mid-July of 1985 in Indian Bay (Pip & Sutherland-Guy 1987).

Species	Mean dry wt., g m^{-2}
Potamogeton foliosus	49.7
P. robbinsii	47.3
P. zosteriformis	23.8
Ceratophyllum demersum	22.5
Myriophyllum exalbescens	16.1
Elodea canadensis	9.9
P. praelongus	2.7
Najas flexilis	1.0

Appendix G. Significant interspecific differences in soluble carbohydrate during the 1985 season. 1=C.demersum 2=E.canadensis 3=M.exalbescens 4=N.flexilis 5=P.foliosus 6=P.gramineus 7=P.praelongus 8=P.richardsonii 9=P.robbinsii 10=P.zosteriformis

APRIL 27

ALPHA=0.05 DF=7 MSE=19.38

SPECIES	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
3	6	73.41	5	5
5	3	96.70	3	3

MAY 2

ALPHA=0.05 DF=82 MSE=49.48

SPECIES	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
1	30	43.43	2 3 5	2 3 5
2	9	31.30	1 3 5 10	1 3 5 10
3	18	63.99	1 2 10	1 2 10
5	18	64.46	1 2 10	1 2 10
10	12	40.97	2 3 5	2 3 5

MAY 16

ALPHA=0.05 DF=90 MSE=66.79

SPECIES	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
1	36	43.78	3 5 10	3 5 10
2	9	36.35	3 5 10	3 5 10
3	18	74.90	1 2 9 10	1 2 9 10
5	15	73.02	1 2 9 10	1 2 9 10
9	6	40.18	3 5 10	3 5 10
10	12	53.40	1 2 3 5 9	1 2 3 5 9

Appendix G (Cont.)

MAY 30

ALPHA=0.05 DF=24 MSE=253.7

SPECIES	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
1	6	46.30	5	5
2	9	36.73	5	5
5	12	98.38	1 2	1 2

JUNE 13

ALPHA=0.05 DF=65 MSE=232.0

SPECIES	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
1	18	42.12	5 6 7 10	5 6 7 10
2	6	28.38	3 5 6 7 10	5 6 7 10
3	3	50.12	2 5 6 7	5 7
5	24	93.13	1 2 3 10	1 2 3 10
6	6	80.36	1 2 3	1 2
7	6	92.82	1 2 3 10	1 2 3
10	9	69.91	1 2 3 5 7	1 2 5

JUNE 27

ALPHA=0.05 DF=98 MSE=188.0

SPECIES	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
1	12	39.64	5 7 8 10	5 7 8 10
2	3	36.04	5 7 8 10	7 8 10
3	24	49.87	8 10	7 8 10
4	3	35.80	5 7 8 10	7 8 10
5	30	61.79	1 2 4 6 8	1 6 8
6	6	36.31	5 7 8 10	5 7 8 10
7	15	65.67	1 2 4 6 8	1-4 6 8
8	6	93.93	1-7 9	1-7 9
9	3	47.10	8 10	8
10	6	78.11	1-4 6 9	1-4 6

Appendix G (Cont.)

JULY 10-11

ALPHA=0.05 DF=172 MSE=338.7

SPECIES	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
1	33	54.49	8 10	8 10
2	12	57.46	8 10	8 10
3	24	42.10	8 10	5 8 10
5	51	59.21	8 10	3 8 10
6	3	55.70	8 10	n.s.
8	15	81.02	1 2 3 5 6 9	1 2 3 5 9
9	9	53.25	8 10	8 10
10	33	82.23	1 2 3 5 6 9	1 2 3 5 9

AUGUST 8

ALPHA=0.05 DF=90 MSE=52.06

SPECIES	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
1	33	45.14	2-4 6 8 9	2 3 6 8 9
2	3	90.97	1 3-6 9 10	1 3-6 9 10
3	24	61.85	1 2 4 5 8-10	1 2 4 5 8-10
4	3	35.16	1-3 5 6 8 10	2 3 6 8
5	12	45.18	2-4 6 8 9	2 3 6 8 9
6	6	64.58	1 2 4 5 8-10	1 2 4 5 8-10
8	6	86.56	1 3-6 9 10	1 3-6 9 10
9	6	31.10	1-3 5 6 8 10	1-3 5 6 8 10
10	6	51.16	2-4 6 8 9	2 3 6 8 9

AUGUST 29

ALPHA=0.05 DF=54 MSE=113.8

SPECIES	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
1	12	42.57	2	2
2	6	24.26	1 3 4 9	1 3 9
3	27	41.90	2	2
4	3	43.22	2	n.s.
9	6	44.48	2	2
10	6	33.96	2	n.s.

Appendix H. Significant interspecific differences in starch content during the 1985 season. 1=C.demersum 2=E.canadensis 3=M.exalbescens 4=N.flexilis 5=P.foliosus 6=P.gramineus 7=P.praelongus 8=P.richardsonii 9=P.robbinsii 10=P.zosteriformis

MAY 2

ALPHA=0.05 DF=29 MSE=1758.08

SPECIES	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
1	12	105.14	n.s.	n.s.
2	3	148.34	n.s.	n.s.
3	6	122.65	n.s.	n.s.
5	12	113.95	n.s.	n.s.

MAY 16

ALPHA=0.05 DF=40 MSE=942.517

SPECIES	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
1	18	73.25	n.s.	n.s.
2	3	71.89	n.s.	n.s.
3	12	70.23	n.s.	n.s.
5	9	51.33	n.s.	n.s.
9	3	100.31	n.s.	n.s.

MAY 30

ALPHA=0.05 DF=10 MSE=244.067

SPECIES	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
2	3	118.89	5	5
5	9	79.95	2	2

Appendix H (Cont.)

JUNE 13

ALPHA=0.05 DF=38 MSE=344.284

SPECIES	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
1	12	42.02	2 5 7	5 7
2	3	77.60	1 3 6 7	7
3	3	44.98	2 5 7 10	5 7
5	2	100.11	3 1 6 7	1 3 6 7 10
6	3	39.86	2 5 7 10	5 7
7	3	144.29	1 2 3 5 6 10	1 2 3 5 6 10
10	6	70.28	1 3 6 7	5 7

JUNE 27

ALPHA=0.05 DF=34 MSE=1057.55

SPECIES	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
2	3	169.27	4 7 9 10	9 10
3	9	128.76	9	9
4	3	96.55	2 8	8
5	12	145.73	9 10	9 10
7	3	91.13	2 8	8
8	3	184.01	4 7 9 10	4 7 9 10
9	3	58.68	2 3 5 8	2 3 5 8
10	6	77.17	2 5 8	2 5 8

JULY 10-11

ALPHA=0.05 DF=79 MSE=954.41

SPECIES	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
1	24	38.80	2 5 8 10	2 3 5 8 10
2	6	126.80	1 6	1 6
3	9	82.89	5	1 5
5	27	147.23	1 3 6 9	1 3 6 9 10
6	3	37.20	2 5 8 10	2 5 10
8	3	104.81	1 6	1
9	6	77.95	5	5
10	9	104.81	1 6	1 5 6

Appendix H (Cont.)

AUGUST 8

ALPHA=0.05 DF=43 MSE=1666.94

SPECIES	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
1	15	38.77	4 5 10	3 5 10
2	3	38.49	4 5 10	5 10
3	9	102.95	n.s.	1
4	3	120.93	1 2 6	n.s.
5	6	142.24	1 2 6	1 2 6
6	3	32.80	4 5 10	5 10
9	3	95.41	n.s.	n.s.
10	9	127.36	1 2 6	1 2 6

AUGUST 29

ALPHA=0.05 DF=31 MSE=1858.66

SPECIES	N	MEAN	GROUPING SNK	GROUPING TUKEY'S
1	12	52.89	10	10
2	3	57.17	10	10
3	12	84.71	10	10
9	3	82.75	10	n.s.
10	6	161.44	1 2 3 9	1 2 3

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