

# Seasonal Biomass and Carbohydrate Allocation in Waterhyacinth<sup>1</sup>

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## ABSTRACT

Seasonal biomass and carbohydrate allocation in waterhyacinth [*Eichhornia crassipes* (Mart.) Solms.] were evaluated to identify potential physiological weaknesses in the growth of the plant. Waterhyacinths were grown in outdoor tanks at Vicksburg, MS. Monthly plant samples (June 1987 through November 1988) were separated into leaves, petioles, membranes, stem-bases, stolons, roots, and inflorescences to evaluate the seasonal changes in free sugars, starch, TNC, and dry weight for each plant structure. Maximum plant biomass occurred in early to mid-

September, and root size was related to the onset of flowering. Blooming rachises were strong carbohydrate sinks containing the highest level of free sugars (22.8%) found in the entire plant. Waterhyacinths stored maximum carbohydrates in stem-bases during the September to October period, with starch and sucrose being the main components of the carbohydrate reserves. Average stem-base weight was only 5% of total plant weight, but stem-bases contained up to 14% of free sugars, 20% of TNC, and 40% of starch found in the entire plant in the fall.

*Key words:* *Eichhornia crassipes*, dry weight, carbohydrate reserves, free sugars, starch, TNC.

<sup>1</sup>Part of this data was previously published in the US Army Corps of Engineers Aquatic Plant Control Research Program annual proceedings, Misc. Papers A-88-5 and A-89-1. Received for publication July 27, 1989 and in revised form November 13, 1989.

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## INTRODUCTION

A better understanding of aquatic macrophyte growth cycles and identification of physiological weaknesses in those cycles are needed to improve the effectiveness of control techniques. A physiological weakness may occur

during the growth cycle when a plant is least likely to recover following the application of a control method. Application of control tactics during this period is more likely to provide maximum overall effectiveness.

Carbohydrate allocation has been used to identify physiological weak points in the life cycles of terrestrial species. In forage and turf species, weak points were identified in order to protect and maintain the plant vigor of early spring growth (Wilson and Robson 1970; Smith 1973, 1975; Booyset and Nelson 1975). Conversely, in weed control aspects, these physiological weaknesses have been used as control points to suppress spring growth or eradicate target plants. One control technique is to disrupt the normal source-to-sink translocation of carbohydrates that precedes winter dormancy. For example, mowing of shoots in the fall prevents accumulation of below-ground carbohydrates in perennials by interrupting translocation of carbohydrates from shoots to roots and rhizomes. Without sufficient carbohydrate reserves, plants are more susceptible to winter injury or death, and spring growth is diminished. Spring growth, when underground reserves are low, is also a critical period during which a control method, such as repeated mowing, is most effective for controlling perennial weeds (Klingman et al. 1975; Peters and Lowance 1978).

Perennial aquatic plants may also rely on stored carbohydrate reserves for survival through winter and initiation of spring growth. In addition, recovery from periods of stress caused by temperature fluctuations, drought, nutrient depletion, diseases, and control tactics may also be dependent on carbohydrate reserves. Weldon and Blackburn (1968) showed that chemical control of alligatorweed [*Alternanthera philoxeroides* (Mart.) Griseb.] was most effective when treatments coincided with low levels of total nonstructural carbohydrates (TNC) in underground stems. The authors concluded that herbicide applications on alligatorweed at that time prevented replenishment of carbohydrate reserves and resulted in more effective control.

Linde et al. (1976) identified a relationship between carbohydrate reserves and growth cycle events in cattail (*Typha glauca* Godr.). When the pistillate spike was lime green in color and the staminate spike appeared dark green, carbohydrate reserves were at their lowest level in the plant. The color of the pistillate and staminate spikes marked the optimum time for appropriate control measures.

Kimbel and Carpenter (1981) tested the hypothesis that harvesting disrupted seasonal patterns of TNC storage in Eurasian watermilfoil (*Myriophyllum spicatum* L.). For example, an autumn harvest may have disrupted carbohydrate partitioning from shoots to roots, thereby diminishing the following year's growth. Eleven months posttreatment, TNC concentrations were significantly lower in a harvested plot than in a control plot.

While considerable information exists on the biology of waterhyacinth [*Eichhornia crassipes* (Mart.) Solms.], few data are available regarding carbohydrate allocation in this species (Pesacreta and Luu 1988). The few reports of carbohydrate content in waterhyacinth have largely dealt with

whole-plant carbohydrates as an indicator for the potential of methane gas production or animal feed (Penfound and Earle 1948; Boyd 1969; Tucker 1981a and 1981b; Tucker and DeBusk 1981).

The objective of this study was to evaluate the seasonal allocation of dry weight and carbohydrates in the various plant structures of waterhyacinth. Based on this information, potential physiological weaknesses in the growth cycle of this plant are suggested. Although data were analyzed for every plant structure, this paper presents results from selected structures related to the carbohydrate and survival status of the plant. In addition, some data from other plant structures are presented for informational purposes.

## MATERIALS AND METHODS

Waterhyacinth populations were initiated from uniformly sized ramets and cultured outdoors in three tanks (240 x 76 x 76 cm) at Vicksburg, MS (32°20'N, 90°50'W). A 10% Hoagland solution (Hoagland and Arnon 1950) was used as a nutrient source, except during June and mid-July 1988, when a 20% solution was used to alleviate nutrient deficiency symptoms. Plants were grown for several months prior to sampling for biomass and carbohydrate determination. Uncrowded, open-water conditions were maintained by removing plants from part of the water surface area, every 3 to 4 weeks, to allow room for continuous vegetative reproduction. Following removal of plants, the nutrient solution was replaced in all tanks. Monthly plant samples were obtained from June 1987 to November 1988. A 0.25 m<sup>2</sup> frame was placed in the waterhyacinth stand at a point which estimated the actual proportion of young and mature plants in the population at the time of sampling. Plants enclosed within the frame were collected and separated into different structures: stem-bases, roots, inflorescences, stolons, leaves (laminae), petioles, and membranes. Membranes are thin sheets of tissue which surround the leaf - stem, and stem - stolon junctions, and envelop young, preemergent ramets. Leaves and petioles were separated by age classes of young, mature, and old categories. Young leaves included the top two leaves of each plant; old leaves were those with partially yellow blades and necrotic tissue; and mature leaves were all others. During February and March, samples consisted of only stem-bases, since the existing plant mass was comprised of living stem-bases and dead material.

Plant samples were dried in a forced-air oven at 58 C to constant dry weight and ground to pass a 1 mm screen in a Cyclone Sample Mill (Udy Corp., Boulder, CO) prior to carbohydrate analyses. Total nonstructural carbohydrates (starch, hydrolyzed sugars, reducing sugars) were determined by a modification of the procedure of Swank et al. (1982). Extracts for TNC were incubated for 15 min at 55 C with one unit of amyloglucosidase (Sigma Chemical Corp. No. A3042) per ml to achieve complete starch hydrolysis before assaying for reducing sugars (Nelson 1944). Free sugars (hydrolyzed and reducing) were determined on extracts not incubated with amyloglucosidase. Sugar species of reserve carbohydrates were identified by thin-

layer chromatography (TLC) based on the methods of Lato et al. (1968), with minor modifications (Streeter and Bosler 1976).

The percent distribution of dry weight for each plant structure is expressed as the percentage of dry weight in that plant structure/total plant dry weight. Carbohydrate concentration is expressed as grams per 100 g dry weight.

A completely randomized design with three replicates (three tanks) was used. Data were analyzed to (1) compare levels of carbohydrates and dry weights among plant parts in each month, and (2) to evaluate seasonal changes in these parameters for each plant part. Therefore, treatments were different plant parts and different sampling dates.

A separate experiment was performed to ascertain the change of carbohydrates during and after blooming. In this study, blooming and wilted (5- to 7-day-old) inflorescences were sampled on six dates and divided into three different parts: rachises, florets, and peduncles. At each sampling date, 27 blooming and 27 wilted inflorescences were randomly collected. Data were analyzed as a randomized block design, with 6 sampling dates as 6 blocks, and 6 inflorescence parts as 6 treatments.

Measured parameters of both experiments included concentration of carbohydrates (free sugars, starch, and TNC) and dry weight distribution in different plant structures. The Bayesian Least Significant Difference test (Smith 1978; Steel and Torrie 1980) was used to separate the effects of treatment means.

## RESULTS AND DISCUSSION

### Pattern of Growth and Biomass Production

The seasonal biomass production of waterhyacinth grown under the experimental conditions of this study is depicted in Figure 1. In March, the amount of biomass was small and consisted of a few stem-bases, surrounded by masses of necrotic tissue. As the weather warmed in April, young ramets emerged from overwintering stem-bases, and biomass slowly increased. Biomass continued to in-

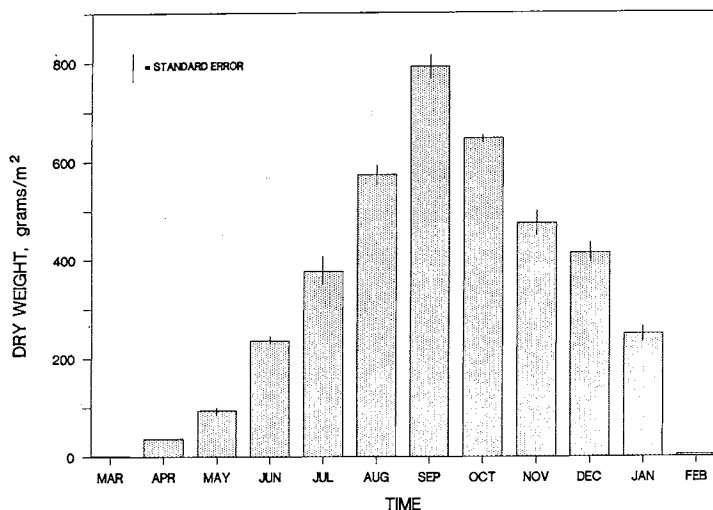


Figure 1. Mean dry weight mass of waterhyacinth on a seasonal basis.

crease during May and June, a period marked by maximum vegetative reproduction. Ramets were 5 to 15 cm in diameter, less than 15 cm tall, and had leaves with bulbous petioles during this period.

In July, plants were approximately 20 cm in height and possessed a mixture of bulbous leaves, located at low positions on the stem, and nonbulbous leaves, at higher positions on the stem. Although ramets were still being produced, the rate of production had slowed (data not shown). Crowded conditions began to occur at this time due to the growth of individual plants and ramet production.

By August, most plants were 25 to 30 cm tall and biomass was more than 2 times the June biomass. Crowded conditions resulted in the shading and senescence of many lower leaves. In mid-August, plants exhibited an extremely slow rate of young ramet production prior to flowering. Even under uncrowded conditions along the open-water side of the mat, plants produced very few ramets, and these were large and slow to develop. In late August and throughout September, most plants reached maturity and were >30 cm tall, ramet production slowed, and flowers were in full bloom. Maximum waterhyacinth biomass occurred in early to mid-September.

A general senescence of old, tall leaves in October produced openings in the waterhyacinth canopy that allowed for the formation of new, short leaves. As a consequence of this process, plant height ranged from 15 to 25 cm and biomass declined. Also, a second peak of ramet production (less than in spring) was observed during this post-blooming period.

Old leaves continued to senesce (and biomass declined) during November and December, and many plants, 15 to 20 cm in height, were present. The onset of cold weather triggered a general senescence of all plants in January, and a substantial reduction of biomass occurred by February.

### Seasonal Allocation of Biomass and Carbohydrates in Plant Structures

*Leaves, petioles, and membranes.* For brevity, biomass and carbohydrate data for leaves, petioles, and membranes are not shown; however, a summary of the seasonal trends for these parameters is provided. In addition, ranges of biomass and carbohydrate levels for leaves, petioles, and membranes are presented in Table 1.

The dry weight proportions of young leaves and petioles were smallest in September/October, and greatest from April through July. The period of high biomass in young structures reflected the period of active ramet production in the spring.

Mature leaf proportions were greatest in the spring and early summer, and smallest in the fall. The high spring/summer biomass resulted from a waterhyacinth population that consisted of many large-leaved plants. In contrast, the low fall biomass was due to a high proportion of old and senescing leaves in the population. Highest biomass of mature petioles occurred in mid-summer due to elongation of the petiole in response to crowded conditions.

Biomass of old leaves and petioles was greatest in October, when the population contained a higher proportion

TABLE 1. LOW AND HIGH VALUES OF DRY WEIGHTS AND CARBOHYDRATES (FREE SUGARS, STARCH, AND TNC) IN LEAVES, PETIOLES, AND MEMBRANES OF WATERHYACINTY FOR 3 REPLICATES.

Parts <sup>1</sup>	% Total Plant		% Free Sugars ± SE			% Starch ± SE		% TNC ± SE	
	Dry Weight ± SE <sup>2</sup>								
YL	1.2 ± 0.1	12.6 ± 1.0	2.3 ± 0.1	6.3 ± 0.4	0.1 ± 0.1	2.1 ± 0.3	2.8 ± 0.1	7.9 ± 0.2	
YP	1.3 ± 0.2	5.9 ± 0.5	1.8 ± 0.0	5.9 ± 0.5	0.0 ± 0.1	1.7 ± 0.5	2.3 ± 0.0	7.6 ± 0.8	
ML	5.8 ± 0.7	27.7 ± 0.1	3.4 ± 0.1	8.9 ± 0.1	0.3 ± 0.2	4.2 ± 0.2	4.1 ± 0.2	11.8 ± 0.5	
MP	9.5 ± 1.5	45.3 ± 4.4	3.0 ± 0.2	8.3 ± 0.7	0.2 ± 0.0	5.0 ± 1.3	3.3 ± 0.1	13.9 ± 2.1	
OL	1.7 ± 0.3	8.8 ± 0.2	3.4 ± 0.0	7.3 ± 0.1	0.2 ± 0.0	3.4 ± 1.5	3.7 ± 0.1	9.8 ± 2.2	
OP	2.2 ± 0.3	23.6 ± 1.2	2.8 ± 0.1	7.9 ± 0.4	0.3 ± 0.1	2.5 ± 0.4	3.4 ± 0.1	10.7 ± 0.7	
MB	1.3 ± 0.1	5.4 ± 0.1	2.8 ± 0.1	5.0 ± 0.1	0.2 ± 0.0	0.8 ± 0.1	3.2 ± 0.2	5.9 ± 0.1	

<sup>1</sup>Plant parts: young leaf (YL), young petiole (YP), mature leaf (ML), mature petiole (MP), old leaf (OL), old petiole (OP), and membrane (MB).

<sup>2</sup>Standard error of the means.

of old plants, and least in May, when many young plants were present. Seasonal biomass distribution of leaves and petioles in different age classes reflect shifts in the growth stages and characteristics of waterhyacinth populations.

The proportion of membranes was significantly greater in April and May, when the waterhyacinth population consisted of many young plants. These diminutive plants had small proportions of other plant structures resulting in a greater proportion of membranes (since membranes are located at every connection between leaf-stem, stolon-stem, or ramet-stolon). Although small in proportion, membranes may play an important role in ramet development. As new ramets emerge, each is wrapped entirely in the tube-like membrane filled with mucin, which acts as a protective envelope.

No clear seasonal patterns of carbohydrate concentration were found in young leaves, old leaves, and old petioles. However, seasonal trends of carbohydrate concentration were observed in mature leaves, as well as young and mature petioles. Young, spring petioles were generally smaller and less verdant than petioles produced in autumn. These factors may have contributed to the increased carbohydrate content found in young, fall petioles. Mature leaves and petioles had highest concentrations of carbohydrates around October. The high levels of carbohydrates in mature leaves and petioles during these cool months suggest that waterhyacinths were vigorously photosynthesizing to accumulate carbohydrates used for fall vegetative reproduction, and for food reserves in stem-bases.

No clear seasonal trends in starch concentrations were observed in membranes; however, levels of free sugars and TNC were significantly greater in membranes from August through November. This increase in free sugars was probably due to the high proportion of young membranes that were formed along with young fall ramets.

**Roots.** The proportion of biomass allocated to roots ranged from 8.1 to 38.8% of total plant weight (Figure 2). No distinct seasonal patterns were noted in proportion of biomass allocated to roots; however, root mass was clearly related to flowering and the availability of nutrients.

In flowering plants, root weight often exceeded 23% (23.0-38.8%) of total plant weight (shoot/root ratio < 3.3), while in non-flowering plants root biomass was always less than 23% (8.1-22.3%), yielding a shoot/root ratio > 3.3. This root mass/flowering relationship is in agreement with our field observations. Blooming plants in Texas and

Louisiana exhibited large, robust root systems, whereas plants in the vegetative stage had much shorter root systems.

Center and Spencer (1981) reported a shoot/root ratio for waterhyacinth from Lake Alice, Florida that ranged from 2.0 to 2.5 from mid-March to mid-December. This ratio was much lower during winter months and declined to 0.2 in mid-February. Other researchers (Moorhead et al. 1988) showed that mean waterhyacinth shoot/root ratio was 1.93 (1.64 to 2.46) for plants grown in a fertilized reservoir and 1.14 (0.79 to 1.67) for plants grown in an unfertilized reservoir in central Florida. In general, shoot/root ratios reported from other studies were smaller than those reported in our study. The fact that other researchers included the stem-base/rhizome complex as part of the root mass fraction may explain some of these discrepancies.

When a 20% Hoagland solution was used to alleviate nutrient deficiency symptoms on the plants (June and mid-July 1988), root growth and flowering were suppressed (Figure 2). In contrast, root growth was stimulated, roots became extremely long (> 70 cm), and flowers were abundant, when plants were grown in 5% Hoagland solution at this same time in adjacent culture tanks. Similarly, Richards (1982) and Watson and Brochier (1988) noted that low nutrient conditions induced inflorescence formation in waterhyacinth; while Moorhead et al. (1988) found more waterhyacinth root growth in an unfertilized reservoir than in a fertilized reservoir.

Root systems play an important role in the overall hormonal physiology of terrestrial plants, perhaps serve as centers for hormone synthesis, and distribute these hormones to various plant structures (Torrey 1976). Roots are major sites for cytokinin synthesis, and this hormone influences the partitioning of photoassimilates between shoots and roots (Gersani et al. 1980). It is possible that roots play a similar role in waterhyacinth and that root mass is related to factors triggering the flowering process in this plant.

Root carbohydrate levels remained relatively constant on a seasonal basis. Concentrations averaged 4.0% for free sugars, 0.4% for starch, and 4.5% for TNC (Figure 2).

**Inflorescences.** Dry weight proportions of inflorescences ranged from 0.5 to 10.1%, while carbohydrate concentrations averaged 5.9% for free sugars, 0.9% for starch, and 7.0% for TNC (data not presented).

The decreased ability of waterhyacinth to produce ramets after flowering stimulated our interest in investigat-

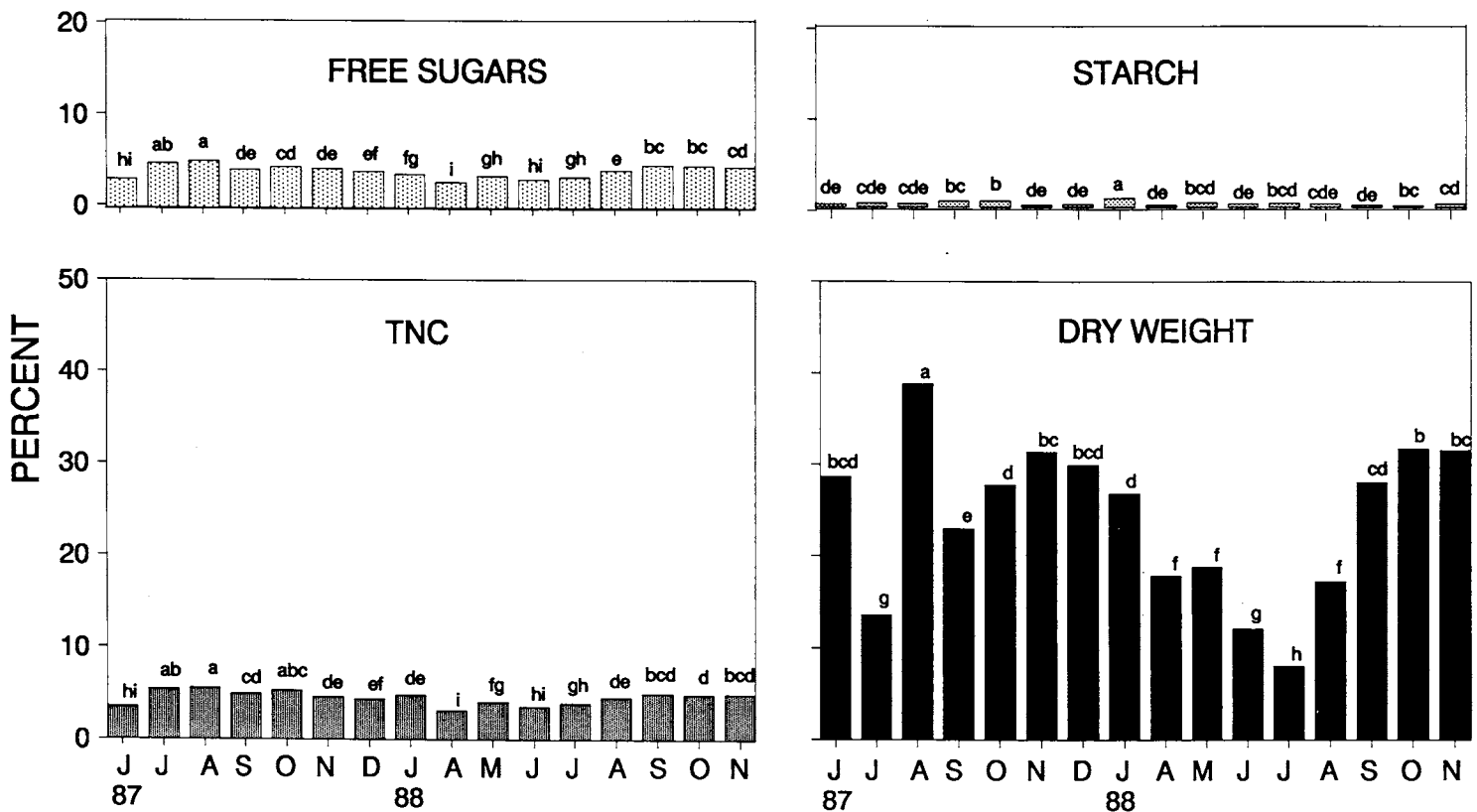


Figure 2. Seasonal distribution of free sugars, starch, total non-structural carbohydrates (TNC), and dry weight in roots. Different letters within a subfigure indicate significant differences at the 5% level according to Bayesian Least Significant Difference Test.

ing the distribution of carbohydrates among inflorescence structures during and after blooming. Generally, inflorescence structures contained low levels of starch and high levels of free sugars. Starch concentration was highest (3.2%) in blooming rachises and lowest (0.5%) in old florets (Figure 3). Blooming rachises contained the highest average level of free sugars (22.8%) found in the inflorescence, as well as in the entire plant. These high levels of free sugars indicate that blooming rachises are strong carbohydrate sinks during the flowering process. Free sugars and TNC decreased significantly in the rachises following inflorescence wilt; however, no change in carbohydrate levels occurred in peduncles over this same period. This suggests that carbohydrates may move from the rachis to the stem, via the peduncle, following flower wilt. This movement may act as an energy conservation mechanism, whereby the remaining carbohydrates in the rachis are translocated toward other energy demanding sinks (e.g. meristematic tissues of ramets or flowers).

**Stolons.** The proportion of biomass allocated to stolons ranged from 1.1 to 5.5% (Figure 4) with an average of 3.3% plant weight. The highest stolon weight, 5.5% in April 1988, corresponded to uncrowded growing conditions of early spring.

The concentration of carbohydrates in stolons ranged from 2.7 to 13.5% for free sugars, from 0.2 to 5.0% for starch, and from 2.9 to 18.3% for TNC. The increase of free sugars and TNC in stolons was concurrent with the accumulation of carbohydrates in stem-bases during the

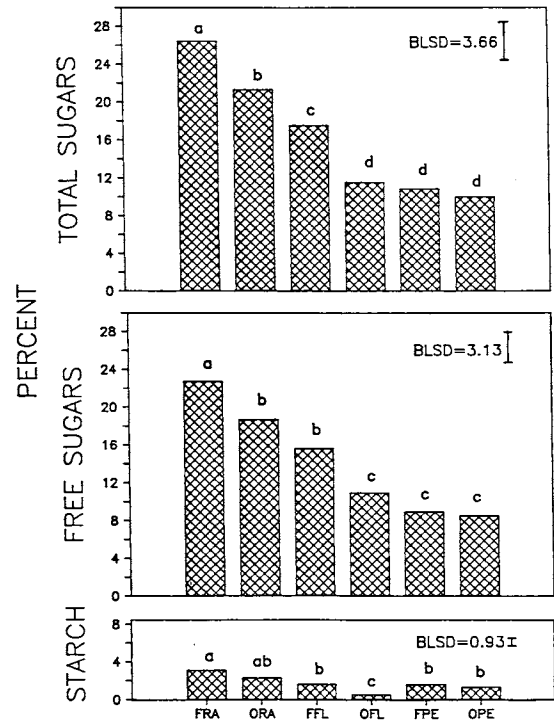


Figure 3. Carbohydrate distribution in various inflorescence structures. Flowering rachis (FRA), old rachis (ORA), flowering floret (FFL), old floret (OFL), flowering peduncle (FPE), and old peduncle (OPE). Different letters within a subfigure indicate significant differences at the 5% level according to Bayesian Least Significant Difference Test.

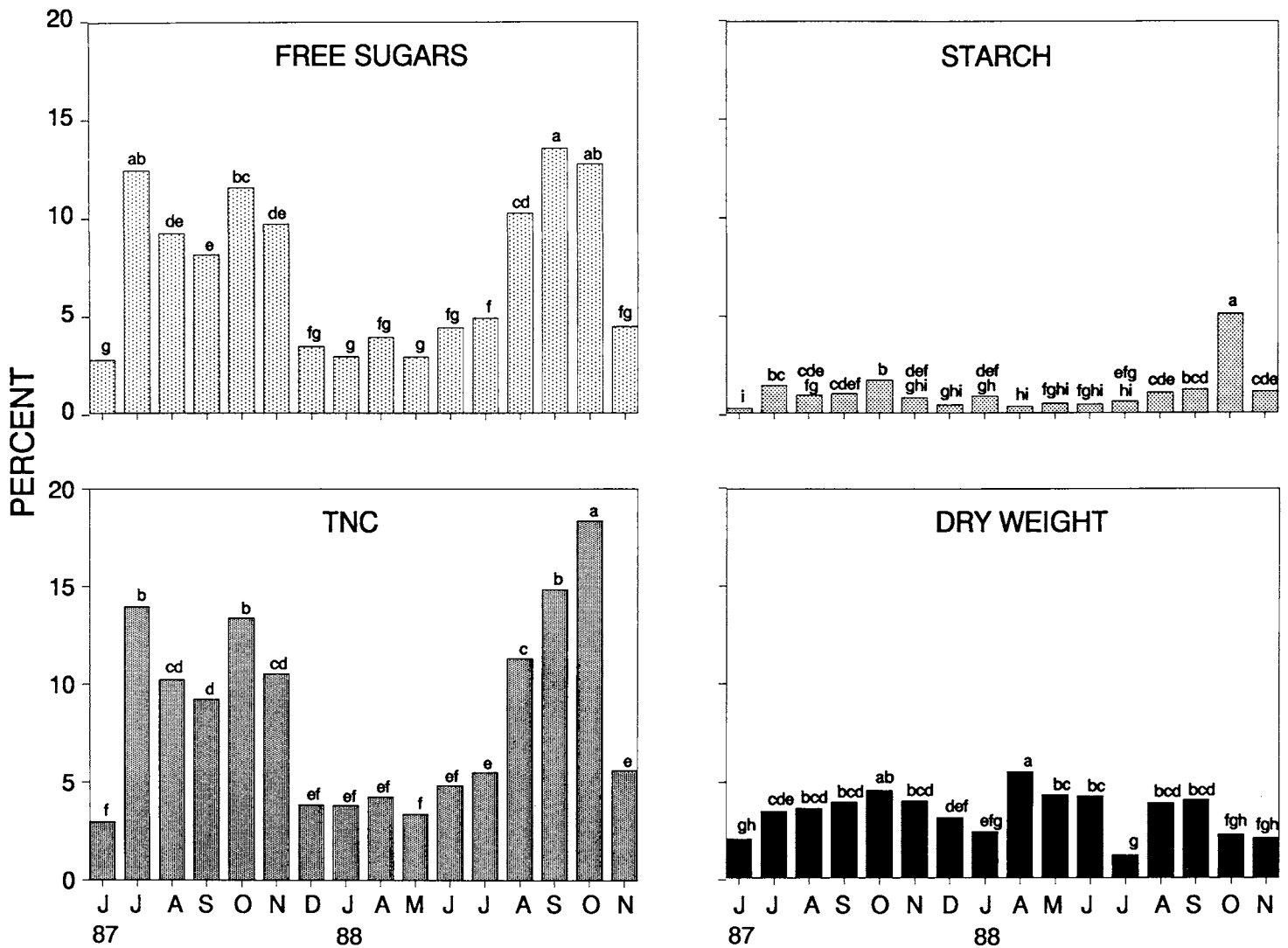


Figure 4. Seasonal distribution of free sugars, starch, total non-structural carbohydrates (TNC), and dry weight in stolons. Different letters within a subfigure indicate significant differences at the 5% level according to Bayesian Least Significant Difference Test.

fall (as discussed later). Though stolons contained lower starch levels compared with stem-bases, there was an increase of stolon starch from late summer to mid-fall (Figure 4). This trend implies that stolons play a role in the storage of carbohydrate reserves. In addition, stolons contained high levels of free sugars in September/October, suggesting that stolons may function as temporary storage sites, as well as conducting corridors for translocating sugars from mature stem-bases to developing ramets. A similar response in wheat under water stress was reported by Drossopoulos et al. (1987). Stems and roots became temporary sites for sucrose accumulation in wheat a few days before the emergence of inflorescences. Later this accumulated sucrose was moved to support the development of inflorescences and seeds.

*Stem-bases.* The dry weight proportions of stem-bases (Figure 5) were generally small (2.2 to 5.4%), with an average of 4.3% of total plant weight. Exceptions occurred in February and March, when overwintering stem-base pro-

portions were 15.8 and 17.6% of total plant weight, respectively. This large biomass proportion was due to frost-burn and death of many other plant parts over the winter.

The concentration of carbohydrates in stem-bases ranged from 2.5 to 20.8% for free sugars, from 0.2 to 11.8% for starch, and from 3.4 to 31.5% for TNC (Figure 5). A trend of increasing carbohydrate levels in stem-bases began in July/August and peaked in September/October. This increased storage of carbohydrate reserves in stem-bases during the fall prepared the plants for winter survival. In the fall, even though stem-base proportion was < 5% of total plant weight, the stem-bases contained nearly 14% of free sugars, 20% of TNC, and 40% of starch found in the entire plant (Table 2). Results from TLC showed that starch and sucrose were the main component of stem-base carbohydrate reserves in winter. Fructose and glucose were also detected in stem-bases. The reduction of stem-base carbohydrate reserves which followed the October peak was the result of two factors: increasing amounts of

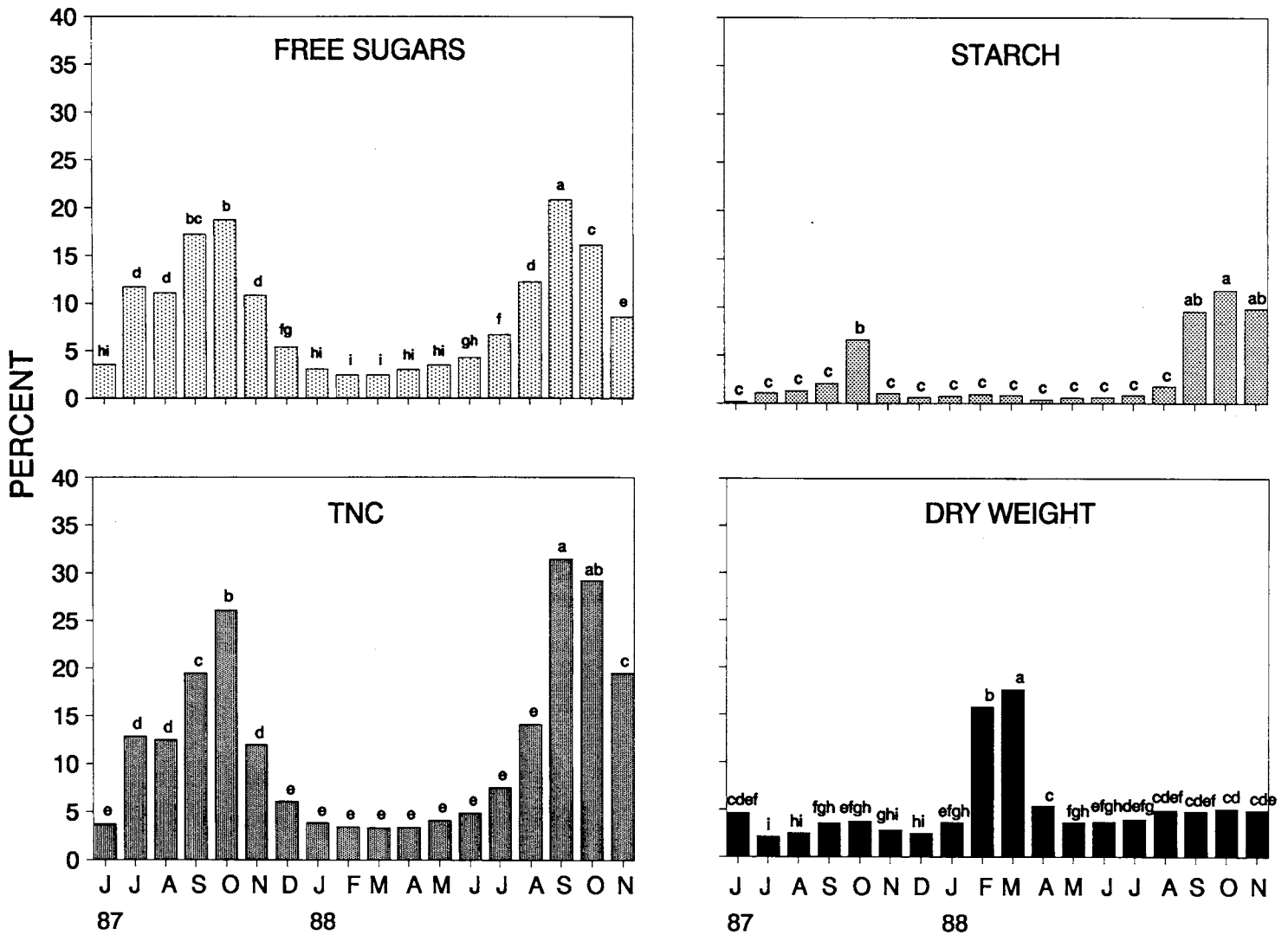


Figure 5. Seasonal distribution of free sugars, starch, total non-structural carbohydrates (TNC), and dry weight in stem-bases. Different letters within a subfigure indicate significant differences at the 5% level according to Bayesian Least Significant Difference Test.

TABLE 2. THE PERCENTAGE OF CARBOHYDRATES (FREE SUGARS (FREE), STARCH (STAR), TOTAL NON-STRUCTURAL (TNC)), AND THE PERCENT DISTRIBUTION OF DRY WEIGHT (DW), AND QUANTITIES OF CARBOHYDRATES (QFREE, QSTAR, QTNC) AMONG DIFFERENT PLANT STRUCTURES (P) IN OCTOBER, 1988.

P <sup>1</sup>	FREE	STAR	TNC	DW	QFREE	QSTAR	QTNC
YL	6.3 de <sup>2</sup>	0.7 bc	7.1 cd	1.2 f	1.3 f	0.6 c	1.2 g
YP	5.9 efg	1.0 bc	7.0 cd	1.5 f	1.4 ef	1.1 c	1.3 fg
ML	7.9 c	2.3 bc	10.5 c	5.8 d	7.6 d	10.5 bc	8.1 de
MP	7.5 cd	2.9 bc	10.7 c	9.6 c	11.9 c	20.8 b	13.6 cd
OL	4.8 fgh	0.2 c	5.1 d	8.9 c	7.2 d	1.4 c	6.0 efg
OP	4.3 h	0.3 bc	4.7 d	23.6 b	17.0 b	8.2 bc	14.9 bc
SB	16.1 a	11.8 a	29.2 a	5.1 de	13.7 c	40.8 a	19.9 ab
RT	4.7 gh	0.2 c	4.8 d	31.8 a	25.0 a	3.5 c	20.7 a
SL	12.7 b	5.1 b	18.4 b	2.2 f	4.7 de	8.7 bc	5.5 efg
MB	5.1 efg	0.2 c	5.3 d	2.6 ef	2.2 ef	0.3 c	1.8 fg
IN	6.0 ef	0.5 bc	6.6 cd	7.6 cd	7.8 d	3.9 c	6.9 ef
BLSD	1.3	4.7	4.8	2.8	3.3	14.4	5.6

<sup>1</sup>Plant structures: young leaf (YL), young petiole (YP), mature leaf (ML), mature petiole (MP), old leaf (OL), old petiole (OP), stem-base (SB), root (TR), stolon (SL), membrant (MB), and inflorescence (IN).

<sup>2</sup>Means within a column followed by the same letter are not statistically different at 5% level, according to Bayesian Least Significant Difference (BLSD) test.

necrotic tissue surrounding the stem-base/rhizome complex; and increasing abundance of young ramets in the population.

In summary, information on seasonal biomass and carbohydrate allocation demonstrates the important role of stem-bases in the winter survival of waterhyacinth. Potential weak points in the growth cycle of waterhyacinth include: the period shortly before mid-September or mid-October when plants are actively translocating carbohydrates to stem-bases; and in early spring when weather is warm enough for young ramet emergence and carbohydrates in the stem-bases are low. This information may be important for the management of waterhyacinth in its northern range of adaptation.

#### ACKNOWLEDGEMENTS

This research was conducted under the US Army Corps of Engineers Aquatic Plant Control Research Program, Environmental Laboratory, US Army Engineer Waterways Experiment Station. Permission was granted by the Chief of Engineers to publish this information. We thank Cindy Waddle and Cindy Teeter for laboratory assistance in this study, and Drs. C. J. Nelson and W. G. Spollen for technical advice on the thin-layer chromatography procedures.

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