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Soluble Sugar Concentrations Associated with Tuber and Winter Bud Sprouting

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ABSTRACT

Many aquatic weeds rely on vegetative structures for survival and propagation, rather than seeds. American pondweed (*Potamogeton nodosus* Poiret) winter buds, and hydrilla (*Hydrilla verticillata* (L.f.) Royle, monoecious and dioecious types) tubers were allowed to sprout in water in the dark. At two-to-three day intervals individual propagules and dependent shoots were analyzed for soluble sugars. There was a significant decline in propagule fresh weight over time indicating mobilization of stored materials. Sucrose was the most abundant soluble sugar in all the propagules, but found in higher concentrations in American pondweed winter buds than in hydrilla propagules. Fructose, glucose, raffinose, and sucrose were present in American pondweed, and hydrilla. Stachyose was present in all except dioecious hydrilla and sorbitol was not detected. During sprouting, soluble sugar concentrations decreased within the original propagule and increased in shoots for hydrilla biotypes. Fructose and glucose concentrations were greater in newly formed shoots than in winter buds of American pondweed by day 14 and in hydrilla shoots versus propagules by day 22. The striking increases in concentrations of these soluble sugars in propagules and newly emergent leaf tissue suggest that starch hydrolysis is a key metabolic control point during sprouting.

Key words: hydrilla, pondweeds, physiological ecology, aquatic weeds.

INTRODUCTION

Many weedy aquatic plant species rely on vegetative structures for perennation (Sculthorpe 1967, Hutchinson 1975). Turions, tubers, and winter buds contain stored materials and are typically produced underground where they survive until they sprout when conditions become favorable for growth. Miller et al. (1976) reported that starch was the major carbohydrate present in hydrilla tubers, accounting for 47% of dry weight (dw). At 4.2% dw, sucrose was the most abundant sugar of hydrilla tubers, while other sugars comprised 0.4% dw (Miller et al. 1976). Spencer et al. (1997) reported that the N content of vegetative propagules for 3 species of pondweeds and 2 hydrilla biotypes ranged from 1.12 to 2.26%, while C content ranged from 40.3 to 42.1%. Ryan (1994) examined changes in the concentrations of soluble proteins, free amino acids, C, and N for hydrilla tubers during an overwintering period and found that C and N content decreased during this time. There were no significant trends over time for changes in the concentrations of soluble proteins, although levels of certain amino acids decreased. Tissue levels of C and N decreased for sprouted vegetative propagules incubated in darkness (Spencer and Ksander 1996). However, there is very little information on physiological changes associated with sprouting of vegetative propagules of submersed plants. For instance, the identity of the soluble sugars in propagules or the dependent plants is unknown and the timing of starch mobilization is not known. Understanding the processes associated with remobilization of stored reserves during sprouting would aid in timing the application of management techniques and perhaps the development of novel management methods (van Vierssen 1993). We report here results of an experiment that compared the levels of soluble sugars present prior to and after sprouting for American pondweed and 2 hydrilla biotypes.

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MATERIALS AND METHODS

Propagules used in this experiment were from cultures maintained at the USDA-ARS Exotic & Invasive Weeds Research Unit, Davis, California. The experiment was conducted in the spring with propagules from the previous growing season, kept at 4C until the experiment. American pondweed winter buds, sago pondweed and hydrilla (monoecious and dioecious types) tubers were placed in water in a darkened growth chamber (18C). The next day and at two to three day intervals for the next four weeks, 10 propagules of each type were retrieved. Propagules and dependent shoots were analyzed separately. Samples for sugar analysis were selected after analysis of the changes in propagule weights during the experiment: samples were taken to include the period of initial shoot extrusion and elongation. Fresh weight was determined for propagules and shoots. For analysis of soluble sugars, samples were extracted in 80% ethanol at 80C for 1 hr. The ethanolic extracts were reduced to dryness *in vacuo*, dissolved in 1.0 ml water and filtered through a 0.2 µ Nylon 66 filter. Soluble sugars were determined by HPLC as described by Aung et al. (1998) with fructose, glucose, sucrose, sorbitol, stachyose, and raffinose as standards. Statistical analysis was performed using SAS (SAS Institute 1990).

RESULTS AND DISCUSSION

Propagules sprouted between 5 and 10 days after the experiment started. Sago pondweed tubers did not sprout during this experiment and only initial values of sugars are reported (Table 1). Regression analysis showed a significant decline in

TABLE 1. MEAN CONCENTRATION (± STANDARD ERROR, N = 5) OF SOLUBLE SUGARS (MG SUGAR/G FW) FOR NON-SPROUTED SAGO PONDWEED TUBERS. VALUES IN PARENTHESIS ARE THE PERCENTAGES OF TOTAL SOLUBLE SUGARS, ROUNDED TO THE NEAREST WHOLE NUMBER.

	mg sugar/g fw					
Species	Fructose	Glucose	Raffinose	Sorbitol	Stachyose	Sucrose
Sago pondweed	0.99 ± 0.07 (3)	0.90 ± 0.15 (3)	1.24 ± 0.15 (4)	0.0 (0)	1.32 ± 0.34 (4)	27.40 ± 3.98 (86)

propagule fresh weights (fw) over time indicating consumption or mobilization of stored materials for species that sprouted (Table 2). The combined fw of propagule and shoot increased over time (Figure 1A). American pondweed produced the most shoot material relative to initial propagule size.

Qualitative and quantitative differences in soluble sugars in resting propagules of the various species were evident (Figure 1B, 1C, 1D). Fructose, glucose, raffinose, and sucrose were present in American pondweed and hydrilla (monoecious and dioecious types). Stachyose was present in all samples except dioecious hydrilla, although in low amounts, while sorbitol was not detected in any sample. Sucrose was abundant in American pondweed and was present in lower concentrations in the two hydrilla biotypes. Sucrose was the most abundant soluble sugar in all the propagules.

Following sprouting soluble sugar concentrations increased within the original propagule for American pondweed and hydrilla biotypes (Figure 1B, 1C, 1D). Soluble sugar concentrations in newly formed shoots was four times that in American pondweed winter buds by day 14 and 1 to 1.5 times that in hydrilla tubers by day 22. The striking increases in concentrations of soluble sugars in propagules and newly emergent leaf tissue suggest that the control of starch hydrolysis is a key metabolic control point during sprouting.

The sugar composition of these propagules is similar to that of other storage organs that have been investigated previously. For instance, Matthiesen and Stoller (1978) reported that mature greenhouse grown tubers of yellow nutsedge (*Cyperus esculentus* L.) sampled after storage at 2C contained sucrose as the major soluble sugar with concentrations ranging from 14 to 100% of the total sugar fraction. Glucose, fructose, and melibiose were also detected and the sugar composition varied with accession, presumably reflecting genetic variation among the samples, since they were grown in a common greenhouse. For instance, material originating in Maryland had a soluble sugar fraction of 22% fructose, 37% glucose, 14% sucrose, and 27% melibiose while a sample from California had 100% sucrose and only trace amounts of other sugars. Changes in composition during sprouting were not noted. The major soluble sugar in roots of the perennial plants chicory (*Cichorium intybus* L.) and dandelion (*Taraxacum officinale* L.) was sucrose (Cyr et al. 1990). For instance, for chicory in February, the concentration of sucrose was 154 mg/g dry weight while glucose and fructose were 36 and 9 mg/g dry weight, respectively (calculated from Figure 2 in Cyr et al. 1990). The concentration of soluble sugars declined in the root during the spring but sucrose remained dominant. In the rhizomes of bulrush (*Schoenoplectus lascustris* L.) grown outdoors in Bern, Switzerland, sucrose content reached 30 mg/g fresh weight during the winter but declined to 15 mg/g fresh weight during the growing season (Steinmann and Brändle 1984). Glucose and fructose were present in equal concentrations, at approximately 2.5 mg/g fresh weight during February and 6 mg/g fresh weight during the growing season. In all these cases, sucrose was the major sugar and the more chemically reactive reducing sugars were present in lesser amounts. In presumably dormant dioecious hydrilla tubers from Lake Ocklawaha, Florida, sucrose was also the major soluble sugar (Miller et al. 1976).

This is the first report identifying soluble sugars and detailing changes in their concentrations during sprouting of submersed aquatic plants. Many details of sprouting remain to be elucidated. For instance, are alpha-amylases and other enzymes involved in starch mobilization already formed or is their synthesis a key event in sprouting? The appearance of soluble sugars in propagules can be used as a marker for sprouting, providing an assay for treatments that might disrupt the process, such as a brief period of high temperature achievable in soil solarization, or a flux of oxygen due to the injection of hydrogen peroxide into the hydrosoil. Additional questions that might contribute to control would be an understanding of factors controlling starch mobilization during sprouting, maintaining reserves for re-growth if the shoot is excised. Research effort might profitably be directed at an understanding of the ability of hydrilla propagules to persist for years in the hydrosoil. Understanding of the ability of the propagules to remain viable, the signals for sprouting and the ability of the propagules to resist fungal infection, perhaps through soluble sugars, all may provide insights into ecologically acceptable and effective control measures.

TABLE 2. REGRESSION ANALYSIS OF THE LOGARITHM OF PROPAGULE FRESH WEIGHT (G) VERSUS TIME (DAYS).

Species	Linear regression equation	Sign.	R^2
American pondweed	FW = 50.39 - 0.0039 * Days	0.006	0.04
Hydrilla (monoecious)	FW = 53.19 - 0.0041 * Days	0.009	0.03
Hydrilla (dioecious)	FW = 32.45 - 0.0025 * Days	0.06	0.02

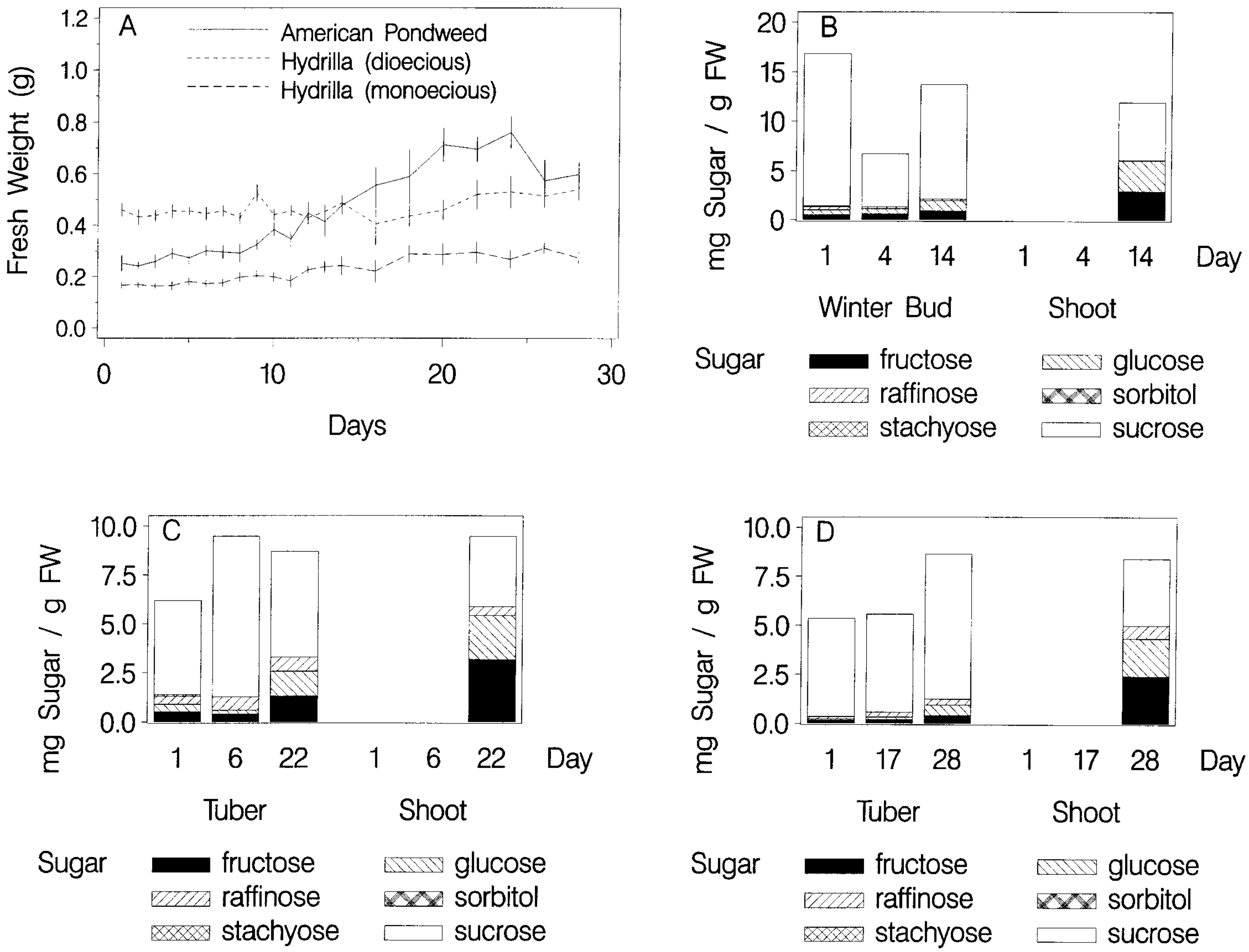

Figure 1. Characteristics of sprouted propagules: (A) changes in total fresh weight (fw) for American pondweed, dioecious hydrilla, and monoecious hydrilla propagules and new shoots, values plotted are the mean ±1 standard error (N = 10); concentrations of soluble sugars (mg sugar/g fw) for propagules and newly produced shoots on three sampling dates for American pondweed winter buds (B), monoecious hydrilla tubers (C), and dioecious hydrilla tubers (D).

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