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Effects of sediment depth and season on growth and carbohydrate allocation in *P. torreyi*

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EFFECTS OF SEDIMENT DEPTH AND SEASON ON
GROWTH AND CARBOHYDRATE ALLOCATION IN *P. TORREYI*

A Thesis
Presented to
The Faculty of Moss Landing Marine Laboratories
San Jose State University

In Partial Fulfillment
of the Requirements for the Degree
Master of Science

By
Barbara Plechner
May 1996

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A handwritten signature in black ink, appearing to read "Michael Foster", written over a horizontal line.

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ABSTRACT

THE EFFECTS OF SEDIMENT SEPTH AND SEASON ON GROWTH AND CARBOHYDRATE ALLOCATION IN *PHYLLOSPADIX TORREYI*

by Barbara Plechner

Variations in biomass, morphology, and carbohydrate (sugar and starch) reserves in the surfgrass *Phyllospadix torreyi* were examined in response to manipulations of sediment depth and changes of season. Total biomass, leaf biomass, leaf surface area, sugar concentrations and total carbohydrates varied significantly with season. These changes were typical of those observed in other seagrasses, and were probably caused by changes in light availability. Distributions of sugars shifted between above and below ground tissues on a seasonal basis, but rhizomes appeared to be the primary storage organ.

Experimental manipulations of sediment depth significantly influenced growth and carbohydrate reserves. Plants in 12 cm of sediment had less leaf area, effectively reducing photosynthetic area per plant. Thus decreases in plant biomass and carbohydrate stores may have been due to enhanced root anaerobiosis. Although surfgrass survives natural, seasonal shifts in sediment depth, these results suggest that distribution and abundance of surfgrass beds may be affected by changes in sedimentation and erosion.

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INTRODUCTION

Seagrasses are ecologically important, and subject to anthropogenic risks in the coastal environments where they reside. As a result, recent studies have focused on factors influencing the success and expansion of seagrass beds around the globe (Zimmerman et al. 1995, Williams 1990, Lanyon & Marsh 1995, McGlathery 1995, Philippart 1995). Distribution, growth rate and carbon reserves of seagrasses exhibit a wide range of seasonal variability (Dawes & Guiry 1992, Lanyon & Marsh 1995, Pirc 1989, Orth & Moore 1986, Bulthuis & Woelkerling 1983, Kerr & Stroher 1989). Many factors may account for this variation, including temperature, nutrient availability, salinity, and light intensity (Barber & Behrens 1985, McGlathery 1995, Orth & Moore 1986, Zimmerman et al. 1995, Perez et al., 1994). However, seasonal changes in sediment depth relative to seagrass rhizomes suggest variations in growth may also be related to fluctuations in sediment depth (Marba & Duarte 1994).

Growth rates may decline partly because seagrasses can occur in habitats with reducing sediments. While these plants possess the ability to transport oxygen to below ground roots and rhizomes (Roberts & McComb 1984, Arenivski & Howes 1992, Penhale & Wetzel 1983), this O₂ is photosynthetically derived, limiting root/rhizome O₂ supply to daylight hours (Smith et al. 1984). Some plants respond to anoxia by utilizing soluble sugars during fermentation at a rate comparable to those recorded during aerobiosis (Saglio 1985). However, anoxia blocks translocation of sugars, so fermentation must rely on existing internal reserves (Saglio 1985, Saglio & Pradet 1980, Saglio et al. 1980). Therefore, factors regulating the allocation of sugar between roots and shoots may be of

vital importance in controlling the ecological success of seagrasses residing in anoxic sediments (Zimmerman et al. 1985, in review).

Phyllospadix torreyi (surfgrass) is a perennial angiosperm with erect leafy shoots borne on a branched rhizome with adventitious roots securing the plant to rock (den Hartog 1970). Their ability to grow on hard substrates in exposed littoral and sublittoral environments makes surfgrasses unique from other seagrasses which generally inhabit soft bottom sediments. However, like all seagrasses, surfgrass rhizomes and blades can trap sediment, exposing plants to the potentially debilitating effects of nocturnal root anaerobiosis. In some areas along the North Pacific coast, as much as one meter of sediment has been observed surrounding plants (Phillips 1979, pers. obs.). Increased depth of anoxic sediment can potentially limit leaf area for photosynthesis, reducing oxygen supply to below ground tissues and restricting sugar mobilization. Thus, understanding temporal fluctuations in sediment depth and carbohydrate partitioning among shoots, roots, and rhizomes may be important in predicting surfgrass distributions in coastal areas subject to variation in sediment deposition. The objective of this study was to determine the effect of sediment depth on seasonal patterns of above and below ground biomass, leaf area, and distribution of sugar and starch content in leaves, roots, and rhizomes in *P. torreyi*.

Previous seasonal studies of temperate seagrasses have shown summer maxima in carbohydrate concentrations and biomass (Pirc 1989, Zimmerman et al. 1995, Perez & Romero 1994, Orth & Moore 1986). In many of these studies seasonal fluctuations in

light availability appeared to be the primary mechanism controlling changes in plant biomass (Zimmerman et al. 1995, Perez et al. 1994). Surfgrass should respond similarly, reaching maximum concentrations of carbohydrates and biomass values in summer months, which then decrease throughout winter and early spring. However, sediment depth in surfgrass populations can also vary with season, and little is known of the interaction between effects of season (light, temperature) and changes of sediment depth in coastal seagrass populations. Nonetheless, one would expect seasonal impact to be influenced by sediment dynamics. For example, carbohydrate reserves should increase in plants residing in deeper sediment to combat the prolonged effects of anoxia. Similarly, leaf area should expand in response to increased sediment, so that the meristem is closer to sediment surface to maintain leaf area for photosynthesis.

SAMPLING AREA AND METHODS

Study site description

This study was done at Stillwater Cove (36° 34' N latitude, 121° 56' W Longitude), Carmel Bay California, (Fig. 1). Research began in August 1994 and continued through July 1995. Beds of surfgrass are abundant along the shore of the cove and extend from low intertidal to the shallow subtidal zone (0 - 2m). The cove is protected from wind on all sides except the south. Surfgrass rhizomes attach directly to the Cove's sandstone substrate, and were typically covered by a layer of mostly fine to medium sand ranging from 0-26 cm deep.

Experimental manipulations of sediment depth and seasonal variation in growth

To determine the effects of sediment depth on plant biomass and carbohydrate distribution, four levels of sediment depth were examined: no burial (0 sediment covering rhizomes), 2, 6, and 12 cm of sediment above the meristem using a modification of the method described by Marba and Duarte (1994). Each level of sediment depth was independently manipulated in five replicates with one plant/replicate. This range of sediment depths was selected to represent depths measured at one meter intervals along 100 meter transects in the intertidal zones where surfgrass occurs. Sediment depths within the study site were measured each month experimental treatments were established. All plants were randomly selected and marked at a tidal height of -0.4m (below mean lower low water) to insure monthly accessibility during daylight low tides. Treatments were imposed by enclosing the roots and rhizomes of individual plants within a six inch diam. PVC cylinder, cut to a height equivalent to corresponding sediment treatments. Quarter inch holes were drilled through the sides of the cylinder at two inch intervals to permit gas exchange with the sediment. For the purpose of convenience and feasibility, rhizomes of plants removed from the field for analyses were cut to a length of 5 cm with attached shoots and roots, and always included the growing (meristematic) end of the rhizome. Plants were allowed to grow for 3-4 weeks, then collected for analyses, and the experiment repeated. Leaf length plant^{-1} , leaf surface area plant^{-1} , shoot and leaf number plant^{-1} , total biomass plant^{-1} , ratio of above/below ground biomass plant^{-1} , and

carbohydrate levels in shoots, roots, and rhizomes were measured in the laboratory using techniques described below.

Experiments were performed during winter (January and February) and spring - summer (May, June, July, and August) throughout one year (August 1994-July 1995) to evaluate the importance of month on plant response to burial. Plant response was evaluated statistically using two way ANOVA. When significant interaction was noted between main effects, one way ANOVA were performed to determine the effects of sediment depth and month separately on growth parameters and carbohydrate concentrations. Post Hoc tests (Bonferonni) of pairwise comparisons were also conducted in instances when significant differences due to sediment depth or month were observed.

Biomass measurements

All vegetation including roots and rhizomes was removed by hand from each replicate, placed in an ice-chest for transportation to the laboratory, and immediately processed. Plants were rinsed free of sediment with fresh water. Then, following the techniques outlined by Ott (1990), all leaves encrusted with calcareous red algae and bryozoans were soaked in dilute 5% hydrochloric acid for two hours and epiphytes gently scraped off with a razor blade. Plants were partitioned into leaves, roots and rhizomes, dried at 60° C for 2 days and weighed to the nearest milligram.

Leaf area

Phyllospadix leaves are uniformly linear and flat, so leaf area was estimated by length x width. Because only one side of each leaf blade is exposed to surface irradiance at any one time, length x width measurements were not doubled to include both sides of the blade in leaf area measurements.

Carbohydrate concentrations in leaves, roots, and rhizomes

Carbohydrates were removed from ground (~ 0.019g) portions of leaves, roots and rhizomes by three extraction's in 90% ethanol at 80°C for 15 min. Plant tissue was ground using a ground glass tissue homogenizer and variable speed drill. The ethanol extracts were evaporated to dryness under a stream of room temperature air and the residues dissolved in dH₂O for sugar analysis. Starch was extracted from the ethanol insoluble residue in 0.1N NaOH. Sugar and starch contents of the extracts were determined spectrophotometrically using resorcinol and anthrone assays respectively, and a sucrose standard (Zimmerman et al. 1995).

RESULTS

Biomass Measurements

With the exception of root + rhizome biomass, which did not vary significantly with sediment depth, all biomass measures varied significantly in response to sampling month and sediment depth (Fig. 2; Tables 1 & 2). All interactions between main effects were significant and one way ANOVAs were performed to test for each effect separately. Shoots generally accounted for more than 50% of total biomass, so patterns related to

sampling month and sediment depth were similar between shoot and total biomass. Shoot and total biomass were highest during July and August, and generally decreased throughout the remainder of the year (Fig. 2A,D). Likewise, patterns of shoot and total biomass were similar in response to sediment depth. Plants in two and six centimeters of sediment had significantly more biomass than those in zero and twelve centimeters of sediment (Fig. 2A,D; Bonferroni $p < 0.001$).

In contrast, root + rhizome biomass was not significantly influenced by sediment height (except in August and June) (Fig. 2B; Table 2). Root + rhizome biomass averaged approximately 1gDW plant^{-1} throughout the course of the year at all sediment depths. This trend in average weight was interrupted only once in August 1994, when the biomass of plants buried in 12cm of sediment was significantly larger than plants in all other depths (Fig. 2B; Table 2; Bonferroni $p < 0.001$).

Shoot morphology and leaf area

While no seasonal effect on shoot number plant^{-1} was evident, plants without sediment consistently produced more shoots plant^{-1} (Fig. 3A). Despite obvious effects of sediment, shoot number had little impact on leaf area plant^{-1} . However, patterns between leaf length and leaf area plant^{-1} were highly correlated ($r = 0.907$; $p < 0.001$), indicating the importance of leaf length to leaf surface area.

Significant effects of time and sediment depth were observed among measurements of leaf area (Table 2). Plants growing with 6cm of sediment had more total leaf area. In

contrast, plants growing without sediment had smaller leaf area plant⁻¹, despite a larger number of shoots (Fig. 3).

Like shoot number, leaf number seemingly had little effect on leaf surface area. In fact, temporal patterns between these parameters present sharp contrasts. Unlike leaf area where maximal values occurred in January and February, leaf number was greatest during spring (Fig. 3).

Sugar and starch concentrations

Sugar concentrations g⁻¹ FW were lowest in May and June and highest in August and July in plants with zero, two and six centimeters of sediment surrounding them (Fig. 4A). Sugar concentrations also varied significantly with sediment depth (Table 2). The most dramatic drop in sugar content occurred in plants buried in 12 cm of sediment where, with the exception of August, sugar concentrations were just above 25 μmol g⁻¹ FW (Fig. 4A). While it is not clear which sediment depth was optimal for sugar stores, it is certain that at depths of 12 cm or greater, sugar stores became extremely low (Fig. 4A).

Overall, starch was less than 50% of sugar content, making up 25-50% of the total carbohydrate pool (Fig. 4). Although starch concentrations varied significantly with month and sediment depth, no one month or sediment depth appeared optimal for starch storage (Table 2; Fig. 4B). However, like sugar content, starch levels were lowest in plants residing in 12 cm of sediment regardless of sampling month.(Fig. 5).

To determine the relative importance of leaves versus root + rhizomes as storage organs, sugar and starch concentrations were integrated over the whole plant. Monthly

changes in sugar concentrations plant^{-1} (Fig. 5A) and sugar concentrations g^{-1}FW were similar (Fig. 4A, 5A) and appear to be related to fluctuations in root-rhizome sugar content, indicating that below ground tissues function as the primary storage organs (Fig. 5A). Whole plant sugar content was greatest in August and July where concentrations of sugar were relatively equal between above and below ground plant fractions. Whole plant sugar values declined, through January and February 1995, with greater losses in leaf sugar due to decreases in leaf biomass (Fig. 5A). Sugar concentrations were lowest in spring. During this period contributions of sugar stores were greatest in leaf fractions in May (Fig. 5A). Sediment depth also seemed to influence whole plant sugar stores, with maximum accumulation of sugars in plants residing in two and six centimeters of sediment (Fig. 5A). Whole plant sugar stores and total sugar concentrations g^{-1}FW were always lowest in plants at 12 cm depth (Fig. 5A).

While whole plant starch levels were slightly higher in below ground tissues, starch content in leaf and root + rhizome fractions were relatively equal throughout the year. Whole plant starch content exhibited temporal changes like those observed in each plant fraction (data not shown). Whole plant starch content significantly dropped in January and February and returned to higher levels in spring and early summer in plants under 12 cm of sediment (Table 2, Fig 5B). Interestingly, whole plant starch levels in plants at sediment depths other than 12 cm were highest in January and February (Fig. 5B).

Sediment depths

Sediment depth in the intertidal region fluctuated on a seasonal basis, with averages ranging from eight centimeters in February to four centimeters in May (Fig. 6). While yearly averages generally remained below 10 cm across a 100 meter transect, depths exceeding 26 cm of were not unusual, especially in late summer and winter months (Fig. 7).

DISCUSSION

Despite the common occurrence of sediment depths greater than those used as maximum in this study (Fig 6,7), experimental manipulations resulted in decreased performance of plants residing in 12 cm of sediment: shoot biomass and shoot:root + rhizome ratio decreased, effectively reducing photosynthetic area plant⁻¹ (Fig 2C). Studies of *Zostera marina*, another temperate seagrass, indicate that the amount of O₂ transported and released to the sediment is directly related to the total amount of active photosynthetic tissue (Smith 1989). Plants with greater shoot biomass transport proportionately more O₂ to roots and rhizomes (Smith et al. 1984). Since root + rhizome respiration is dependent on shoot photosynthetic conditions, decreases in biomass and carbohydrate stores of plants in 12 cm of sediment may be due to enhanced root anaerobiosis (Fig 2, 4,5). However, plants with no sediment did not have the highest carbohydrate stores or biomass, indicating that some sediment is important for maximum growth of *P. torreyi*. Surfgrass, in contrast to other seagrasses, is usually found attached to hard substrates on exposed coastlines with little or no surrounding sediment. Therefore, the presence of

sediment may provide additional nutrients to the surrounding water column, improving growth potential. Previous studies of seagrasses residing in sediment suggest increased levels of nitrogen and phosphorous resulting from nutrient recycling in sediments enhance plant biomass (Short & McRoy 1984, Harlin & Thorne-Miller 1981). Thus, increased nutrient levels may explain why plants residing in 2-6cm of sediment had greater leaf area and plant biomass. Larger leaf area may also be an adaptive response to increased sediment heights as plants improve photosynthetic capacity and may be better equipped to withstand longer periods of root anaerobiosis.

Seasonal changes in plant size and carbohydrate concentrations observed in *P. torreyi* are typical of those observed in other seagrass species. (Orth & Moore 1986, Perez & Romero 1994, Kerr & Stother 1989, Pirc, 1989, Zimmerman et al. 1995). It is generally accepted that these changes are caused by fluctuations in light availability throughout the year (Dennison & Alberte 1982, Orth & Moore 1988, Zimmerman et al. 1991). Changes in light regime due to variations in turbidity, or seasonal changes in day length, effectively reduce the daily period of saturating photosynthesis (H_{sat}) and influence nightly periods of root anoxia (Smith 1989, Zimmerman 1991, 1995). In this study, biomass, leaf area, and carbohydrates amassed during enhanced photoperiods in summer, declined to minimum levels by spring (Fig. 2,3,4,5). This pattern of seasonal variation was most clearly evident in changes of biomass specific sugar content and whole plant sugar concentrations (Fig. 4,5). Temporal variations of carbohydrate levels in surfgrass suggest that the amount of carbohydrates amassed during summer months may

be important for survival of plants during winter and early spring. Mobility of carbohydrates is dependent on root + rhizome aerobiosis, which is controlled by leaf photosynthesis and ultimately Hsat (Smith 1989). Thus, the effects of shorter winter photoperiods on growth and survival of surfgrass probably depends on the size of carbohydrate reserves accumulated during summer photomaxima in both shoots and rhizomes (Saglio et al. 1984, Smith 1989, Zimmerman et al. 1995). In July and August, plants in 12 cm had significantly less sugar than plants at all other sediment depths (Fig 3, 4; Table 2) Thus, plants in 12 cm of sediment had less sugar to use during winter and early spring, resulting in reduced biomass (Fig 2, 3) and increased mortality (pers. obser.). The inability of plants in 12 cm of sediment to maximize summer sugars suggests that plants in areas prone to changes in sediment depth may have reduced distributional ranges or survival during short daylengths in winter and early spring.

In addition to changes in overall sugar content, the distribution of sugar shifted between above and below ground tissues on a seasonal basis. In January and February, sugar concentrations plant⁻¹ declined to almost half of maximum levels attained in August, and continued to decrease throughout May and June (Fig. 5A). The greatest decrease in winter was in leaf sugar due to the loss of leaf biomass observed at this time (Fig. 2A, 5A). However, winter sugar levels in roots + rhizome of *P. torreyi* were also considerably lower than in August, despite only slight changes in biomass of these tissues (Fig. 2B, 5A). Decreases in sugar content of below ground tissues are concordant with the effects of extended periods of root + rhizome anaerobiosis likely during winter months. Since anoxia

inhibits sugar transport to below ground tissues, plants must rely on existing carbohydrate reserves to fuel fermentative processes during anaerobiosis and maintain metabolic activities necessary for survival (Saglio 1985). In May, sugar concentrations plant⁻¹ were greatest in leaf fractions (Fig. 5A), indicating a shift toward new leaf production manifested by increases in leaf number (Fig. 3B) in May and June, and consistent with the opinion that young leaves serve as sinks for carbon, while older leaves serve as sources of carbon (Zimmerman et al. 1995). Leaves are also the site of sugar production, so increases in leaf sugar content should begin during spring and early summer with the advent of increased photoperiods.

Starch seemed to be an important storage component, comprising 20 - 60% of total carbohydrate pool. However, levels of starch recorded in this study were quite high and have not been observed in other seagrasses. For example, *Zostera Marina* L. was found to contain maximum starch levels in summer at only 25 Umol/g FW (Zimmerman et al. 1995) However, despite low concentrations of starch found in *Zostera Marina* L., previous studies indicate that variations in sucrose-phosphate synthase activity and use of carbon reserves in response to changes in light intensity and duration, were typical of those observed in starch storing species (Zimmerman et al. 1995). Thus increased levels of starch found in *Phyllospadix torreyi* may not be wholly uncharacteristic. Nonetheless, changes in patterns of total carbohydrates related to month and sediment depth more closely mimicked those of total sugar concentrations, suggesting that sugar is the

physiologically most important storage component in *P. torreyi* despite the abundance of starch (Fig. 4).

Surfgrass develops extensive beds on rocky shores along the North Pacific, and can experience considerable sediment fluctuation. Changes in growth patterns and carbohydrate stores in response to sediment depth observed in this study indicate that seagrasses in coastal environments subject to intense sedimentation or erosion may vary in distribution or abundance. Surfgrass should dominate coastal zones prone to periodic sedimentation. Most macroalgae require cleared patches of hard substrate or other algae for attachment, growth, and survival. The prevalence of surfgrass expansion by vegetative growth, in conjunction with its relative tolerance to sedimentation, appears to favor beds of *Phyllospadix* in sand deposition environments. However, understanding the physiological response of seagrasses to environmental variability is seemingly critical to successful expansion and preservation of seagrass habitats prone to human or natural disturbances (Zimmerman et al. 1995). In developing criteria that optimize restoration/preservation efforts, these results suggest that optimal surfgrass habitat includes 2-6 cm of sediment to maximize growth and plant productivity.

FIGURE 1. STILLWATER COVE

Table 1

Two-way ANOVA for effects of sediment depth and sampling month on shoot morphology, plant biomass measures, and carbohydrate (sugar & starch) concentrations in rhizomes, leaves and roots of *Phyllospadix torreyi* in Stillwater Cove, Pebble Beach, CA.

Treatment	d.f.	MS	F	p	Significance
<i>Shoot biomass</i>					
Month	5	5.88	64.064	< 0.001	***
Sediment height	3	8.83	96.025	< 0.001	***
Month x sediment height	15	0.92	9.812	< 0.001	***
<i>Rhizome + Root Biomass</i>					
Month	5	1.81	21.039	< 0.001	***
Sediment height	3	0.29	3.339	0.023	*
Month x sediment height	15	0.66	7.702	< 0.001	***
<i>Total biomass</i>					
Month	5	13.07	49.413	< 0.001	***
Sediment height	3	10.77	40.694	< 0.001	***
Month x sediment height	15	2.15	8.138	< 0.001	***
<i>Shoot / root + rhizome biomass</i>					
Month	5	2.21	15.472	< 0.001	***
Sediment height	3	10.01	70.113	< 0.001	***
Month x sediment height	15	1.29	9.047	< 0.001	***
<i>Leaf surface area</i>					
Month	5	35162.04	322.874	< 0.001	***
Sediment height	3	127119.36	1167.267	< 0.001	***
Month x sediment height	15	40711.57	373.832	< 0.001	***
<i>Total sugar concentration</i>					
Month	5	161976.81	310.481	< 0.001	***
Sediment height	3	315922.45	605.567	< 0.001	***
Month x sediment height	15	13049.75	25.014	< 0.001	***
<i>Total starch concentration</i>					
Month	5	2719.34	5.129	< 0.001	***
Sediment height	3	48638.66	91.739	< 0.001	***
Month x sediment height	15	9528.12	17.971	< 0.001	***
<i>Total carbohydrate concentration</i>					
Month	5	174247.50	191.243	< 0.001	***
Sediment height	3	606499.37	665.656	< 0.001	***
Month x sediment height	15	28137.41	30.882	< 0.001	***

* $p < 0.05$; *** $p < 0.001$

Table 2

One-way ANOVA for effects of sediment depth or sampling month on shoot morphology, plant biomass measurements, and carbohydrate (sugar & starch) concentrations in rhizomes, leaves and roots of *P. torreyi*.

Treatment	d.f.	MS	F	p	Significance
Shoot biomass					
Effect of sampling month at:					
0cm	5	1.32	37.296	< 0.001	***
2cm	5	0.72	5.376	0.002	*
6cm	5	4.38	29.770	< 0.001	***
12cm	5	2.18	42.334	< 0.001	***
Effect of sediment height in:					
August	3	4.85	275.900	< 0.001	***
January	3	1.62	15.859	< 0.001	***
February	3	4.53	24.579	< 0.001	***
May	3	0.80	9.263	< 0.001	***
June	3	0.39	15.929	< 0.001	***
July	3	1.15	8.407	0.001	*
Rhizome + root biomass					
Effect of sampling month at:					
0cm	5	0.37	8.568	< 0.001	***
2cm	5	0.29	1.393	0.262	NS
6cm	5	0.73	13.570	< 0.001	***
12cm	5	2.42	61.437	< 0.001	***
Effect of sediment height in:					
August	3	2.69	197.441	< 0.001	***
January	3	0.17	2.118	0.138	NS
February	3	0.40	1.410	0.277	NS
May	3	0.02	1.671	0.213	NS
June	3	0.07	10.853	< 0.001	***
July	3	0.25	2.147	0.134	NS
Total biomass					
Effect of sampling month at:					
0cm	5	2.09	16.734	< 0.001	***
2cm	5	1.64	2.726	0.044	*
6cm	5	6.92	32.340	< 0.001	***
12cm	5	8.89	74.462	< 0.001	***
Effect of sediment height in:					
August	3	9.86	344.190	< 0.001	***
January	3	2.68	8.433	0.001	*
February	3	5.26	6.611	0.004	*
May	3	0.70	6.598	0.004	*
June	3	0.61	16.538	< 0.001	***
July	3	2.43	8.019	0.002	*
Shoot:root + rhizome					
Effect of sampling month at:					
0cm	5	2.27	61.646	< 0.001	***
2cm	5	0.33	4.214	0.007	*
6cm	5	3.32	9.423	< 0.001	***

Table 2 continued 1-way ANOVA

Treatment	d.f.	MS	F	p	Significance
12cm	5	0.16	1.577	0.204	NS
Effect of sediment height in:					
August	3	3.25	37.738	< 0.001	***
January	3	2.11	13.960	< 0.001	***
February	3	7.62	25.877	< 0.001	***
May	3	2.79	20.295	< 0.001	***
June	3	0.38	12.170	< 0.001	***
July	3	0.33	2.117	0.138	NS
<i>Leaf number</i>					
Effect of sampling month at:					
0cm	5	48.76	5.682	0.001	*
2cm	5	49.85	6.654	0.001	*
6cm	5	119.79	19.488	< 0.001	***
12cm	5	128.64	15.084	< 0.001	***
Effect of sediment height in:					
August	3	61.25	11.686	< 0.001	***
January	3	221.77	30.658	< 0.001	***
February	3	395.49	54.471	< 0.001	***
May	3	184.90	15.728	< 0.001	***
June	3	200.33	34.250	< 0.001	***
July	3	177.02	20.162	< 0.001	***
<i>Leaf surface area</i>					
Effect of sampling month at:					
0cm	5	25495.06	339.524	< 0.001	***
2cm	5	6635.69	203.053	< 0.001	***
6cm	5	22999.37	231.297	< 0.001	***
12cm	5	102089.21	428.563	< 0.001	***
Effect of sediment height in:					
August	3	87920.93	277.192	< 0.001	***
January	3	97714.43	1404.074	< 0.001	***
February	3	77697.24	715.253	< 0.001	***
May	3	18534.37	284.359	< 0.001	***
June	3	26937.09	758.522	< 0.001	***
July	3	18359.55	302.310	< 0.001	***
<i>Total sugar concentration</i>					
Effect of sampling month at:					
0cm	5	62068.87	191.095	< 0.001	***
2cm	5	67330.26	52.167	< 0.001	***
6cm	5	61143.03	170.428	< 0.001	***
12cm	5	10583.90	94.031	< 0.001	***
Effect of sediment height in:					
August	3	104786.60	303.837	< 0.001	***
January	3	88887.92	69.829	< 0.001	***
February	3	73003.18	116.002	< 0.001	***
May	3	27395.40	107.360	< 0.001	***
June	3	18399.54	131.689	< 0.001	***

Table 2 continued 1-way ANOVA

Treatment	d.f.	MS	F	p	Significance
July	3	68742.58	141.150	< 0.001	***
Total starch concentration					
Effect of sampling month at:					
0cm	5	5175.30	5.875	0.001	*
2cm	5	6506.62	13.190	< 0.001	***
6cm	5	9619.45	26.974	< 0.001	***
12cm	5	10002.32	25.656	< 0.001	***
Effect of sediment height in:					
August	3	8409.87	59.561	< 0.001	***
January	3	32979.47	43.269	< 0.001	***
February	3	46120.65	61.764	< 0.001	***
May	3	4385.39	12.499	< 0.001	***
June	3	3558.55	16.573	< 0.001	***
July	3	825.31	0.855	0.484	NS
Total carbohydrate concentration					
Effect of sampling month at:					
0cm	5	88284.81	91.205	< 0.001	***
2cm	5	63224.48	48.869	< 0.001	***
6cm	5	83632.91	113.649	< 0.001	***
12cm	5	23517.54	34.954	< 0.001	***
Effect of sediment height in:					
August	3	158695.10	377.868	< 0.001	***
January	3	200257.05	141.701	< 0.001	***
February	3	229770.41	186.269	< 0.001	***
May	3	57859.08	93.285	< 0.001	***
June	3	34648.89	163.799	< 0.001	***
July	3	66621.56	44.537	< 0.001	***

* $p < 0.05$; *** $p < 0.001$; NS = not significant

Figure - 2 A,B,C,D - Mean dry weight of *Phyllospadix* at different months and sediment heights.

Figure- 3 A,B,C - Average number of shoots, leaves, and leaf area per plant of *Phyllospadix* at different months and sediment depths.

Figure - 4 A,B,C - Total sugar , starch & carbohydrate concentrations (umol/gFW) in *Phyllospadix* at different months and sediment depths

Figure - 5 A, B - Sucrose and starch concentrations in *Phyllospadix* rhizomes+ roots and leaves at different months and sediment depths.

Figure - 6- Average sediment depth (cm) in Stillwater cove during each sampling period. Measurements taken at one meter intervals across 100 m transect.

Figure - 7 - Frequency histogram of sediment depths measured at study site during each sampling period.

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