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Carbon Partitioning in Eelgrass[1]

Regulation by Photosynthesis and the Response to Daily Light-Dark Cycles

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Diel variations in rates of C export, sucrose-phosphate synthase (SPS) and sucrose synthase (SS) activity, and C reserves were investigated in *Zostera marina* L. (eelgrass) to elucidate the environmental regulation of sucrose formation and partitioning in this ecologically important species. Rates of C flux and SPS activity increased with leaf age, consistent with the ontogenic transition from sink to source status. Rates of C export and photosynthesis were low but quantitatively consistent with those of many terrestrial plant species. The V_{max} activity of SPS approached that of maize, but substrate-limited rates were 20 to 25% of V_{max}, indicating a large pool of inactive SPS. SPS was unresponsive to the day/night transition or to a 3-fold increase in photosynthesis generated by high [CO_2] and showed little sensitivity to inorganic phosphate. Consequently, regulation of eelgrass SPS appeared similar to starch- rather than to sugar-accumulating species even though eelgrass accumulates sucrose. Leaf [sucrose] was constant and high throughout the diel cycle, which may contribute to the down-regulation of SPS. Root sucrose synthase activity was high but showed no response to nocturnal anoxia. Root [sucrose] also showed no diel cycle. The temporal stability of [sucrose] confers an ability for eelgrass to buffer the effects of prolonged light limitation that may be key to its survival and ecological success in environments subject to periods of extreme light limitation and chaotic daily variation in light availability.

Seagrasses are critically important sources of primary production and habitat structure in estuaries and coastal marine environments (Mann, 1982). The ability to tolerate permanently flooded (usually anoxic) sediments allows seagrasses to exploit benthic marine habitats unavailable to other macrophytes (Smith et al., 1984, 1988). Anoxia tolerance in the temperate seagrass *Zostera marina* L. (eelgrass) involves structural features that provide photosynthetically derived O_2 to below-ground tissues (root and rhizome), thereby restricting root anoxia to the night and to periods of light-limited photosynthesis (Smith et al., 1984). Roots remain viable and carry out protein synthesis at reduced rates while anaerobic as long as there is sufficient Suc present to drive fermentation at a C consumption rate that is only 65% of that under aerobiosis (Smith et al., 1988). Eelgrass roots do not exhibit a Pasteur effect in response to anoxia (Smith, 1989). Anaerobiosis in the root/rhizome also blocks Suc translocation in eelgrass, thereby limiting the Suc pool present in below-ground tissues at the onset of anoxia (R.C. Zimmerman, unpublished data). Thus, metabolic processes that regulate the formation, export, and mobilization of Suc in eelgrass may both determine internal patterns of resource allocation and control the ecological success of this and other seagrass species.

The dynamics of Suc formation and translocation have been examined extensively in terrestrial crop species, especially maize (Huber et al., 1985; Stitt, 1994). Leaf Suc levels often oscillate more than 6-fold between dawn and dusk as Suc is formed in response to photosynthesis and exported subsequently to sink tissues like roots, developing fruits, or immature leaves (Kalt-Torres and Huber, 1987; Stitt et al., 1988). Maize roots, for example, depend on daily resupply of Suc to maintain essential levels of respiration, protein synthesis, and nutrient assimilation (Massiminio et al., 1981).

Rates of Suc export from source leaves have been linked principally to the activity of SPS (EC 2.4.1.14) (Stitt 1994). The activity of this enzyme is regulated by a variety of mechanisms that differ among species in response to developmental stage and environmental conditions (Rufty et al., 1983; Huber et al., 1985, 1989a; Kerr and Huber, 1987; Stitt and Quick, 1989; Nguyen-Quoc et al., 1990). The transition from sink to source in developing leaves is characterized by a marked increase in SPS activity (Giaquinta, 1979). In group I species (e.g. maize, barley [Huber et al., 1989a]), SPS shows strong light activation of V_{max} and Pi inhibition. In group II species (e.g. spinach, sugar beet, broad bean), light alters some kinetic properties of SPS that become apparent at substrate-limiting concentrations (Huber et al., 1989a; Stitt and Quick, 1989). SPS activity is also sensitive to Pi inhibition in group II. Groups I and II accumulate primarily Suc, the levels of which respond dramatically to light/dark transitions. Group III species (soybean, pea, tobacco), however, show virtually no light

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Abbreviations: ANOVA, analysis of variance; $CO_{2(diss)}$, dissolved CO_2; F-6-P, Fru-6-P; G-6-P, Glc-6-P; P_m, light-saturated rate of photosynthesis; PPF, photosynthetic photon flux; SPS, Suc-P synthase; SS, Suc synthase.

activation of SPS activity and minimal response to Pi (Huber et al., 1989a). Group III species accumulate primarily starch, and the soluble sugar levels change little with light/dark transitions (Huber et al., 1989a)

Rates of Suc import in sink tissues can be related to the activity of SS (EC 2.4.1.13), which carries out the initial catabolic step in sucrolysis (Sung et al., 1988; Stitt, 1994). Activity of SS is high in developing storage organs such as sugar beet taproots and maize kernels, shows up-regulation in response to anoxia in maize, soybean, and rice, and is down-regulated in leaves during the transition from sink to source (Giaquinta, 1979; Springer et al., 1986; Nguyen-Quoc et al., 1990; Xue et al., 1991). The absence of functional SS in the endosperm of developing maize kernels of *Shrunken* mutants prevents phloem unloading of Suc and reduces starch content within the kernels, producing the collapsed phenotype upon dehydration (Schwartz 1960).

In comparison to terrestrial crop species, very little is known about the regulatory dynamics of Suc formation and allocation in natural populations, particularly among aquatic species such as the seagrasses. The goal of this study was to investigate the dynamics of Suc source and sink regulation in the temperate seagrass *Z. marina* in relation to light availability, photosynthesis, and the nocturnal period of root anoxia. Eelgrass must survive in highly variable light environments that limit rates of photosynthesis and lead to long daily periods of root anoxia (Zimmerman et al., 1991, 1994). Thus, the temporal dynamics of carbon partitioning between shoots and below-ground tissues may be critical for determining the geographic distribution, colonization depth, and ecological success of seagrasses in environments that typically exhibit extreme variations in light availability.

MATERIALS AND METHODS

Rates of Photoassimilate Export and SPS Activity

Vegetative *Zostera marina* L. plants were collected by hand (scuba) from a natural population growing subtidally (5–7 m deep) at Del Monte Beach, in Monterey Bay, CA (36°30′40″ N, 121°52′30″ W) and transplanted into 4-L plastic pots filled with anoxic sediment collected from the eelgrass meadow. The pots were placed in outdoor tanks plumbed with running seawater and covered with neutral density screens to simulate the natural submarine light environment of the eelgrass meadow (25% of surface PAR, maximum midday PPF ≅ 500 μmol quanta m^{-2} s^{-1}).

Photoassimilate export rates were measured by changes in mass and Suc content of photosynthetic leaves over time (Terry and Mortimer, 1972). Mass accumulation was measured as changes in leaf weight while plants were exposed to natural sunlight at a PPF between 500 and 1000 μmol quanta m^{-2} s^{-1}, well above photosynthetic saturation (Dennison and Alberte, 1982; Zimmerman et al., 1991, 1994). Screening was adjusted throughout the day to ensure light saturation of photosynthesis without risking photoinhibition from prolonged exposure to high PPF (>1500 μmol quanta m^{-2} s^{-1}). Three replicate discs (5 mm diameter, 2–4 mg) were removed from the lateral margin of each leaf from four plants (four to five leaves per plant) 10 cm below the tip in the early morning, and the plants were incubated at photosynthesis-saturating PPF for 4.5 to 5 h. Three discs were then removed from the opposite margin of each leaf at the end of the incubation period. All discs were dried at 60°C for 24 h and weighed to a precision of ±0.3% (10 μg) using a microbalance. Discs gained approximately 100 μg during the incubation period. Soluble carbohydrates (Suc + Fru + Glc) were extracted from the homogenized discs in hot ethanol and assayed using anthrone and a Suc standard (Yemn and Willis, 1954).

Maximum rates of photosynthetic C assimilation (^{14}C) were determined immediately after the 4.5- to 5-h incubation period using 2-cm leaf segments taken proximally to the disc removal zone. Leaf segments (100 mg fresh weight) were placed in glass scintillation vials filled with 20 mL of air-saturated 0.2-μm-filtered seawater and 1 μCi of [^{14}C]bicarbonate. The vials were clipped to a vertically positioned disc rotating at 6 rpm in a running seawater bath (15°C) and incubated for 1 h at a PPF of 500 μmol quanta m^{-2} s^{-1} provided by a quartz-halogen lamp. Incorporation of ^{14}C was determined by liquid scintillation counting of tissue homogenized in NCS (Amersham) and acidified with HCl to volatilize inorganic ^{14}C. Quench correction was performed according to the sample channels ratio. Photosynthetic rates were converted to rates of carbohydrate accumulation assuming that all fixed C was assimilated into carbohydrate at a ratio of 0.425 g C g^{-1} CH_2O (Terry and Mortimer, 1972). The rate of assimilate export was calculated as the difference between the measured rates of photosynthesis and mass (carbohydrate) accumulation.

Enzyme Activity

The tissue remaining above and below the disc removal zone of each leaf was used for determination of SPS activity. Crude extracts were prepared by grinding fresh tissue segments in chilled extraction buffer (50 mM Hepes, 15 mM $MgCl_2$, 2% [w/v] PEG-20, 0.02% [v/v] Triton X-100, 20 mM ascorbate, 10 mM DTT, 2% [w/v] polyvinylpolypyrrolidone, pH 6.5; grind ratio = 10 mL g^{-1} fresh weight). The extraction slurry was centrifuged (1 min at 1480*g*) and the supernatant was subsequently desalted under centrifugation (1 min at 1480*g*) on a column of Sephadex G-25 equilibrated with extraction buffer (no polyvinylpolypyrrolidone) at pH 7.5. The desalted extracts were assayed immediately for SPS activity at 37°C over a 10-min time course. Reactions were terminated by alkalinization with 1 N KOH and boiling for 10 min. Suc and Suc-P formed by enzyme activity in vitro were quantified spectrophotometrically (488 nm) using a resorcinol assay (Huber and Israel, 1982). Enzyme activity of each tissue sample was calculated from the time rate of change in Suc concentration.

V_{max} assays were performed at pH 7.5 using substrate concentrations of 10 mM UDP-Glc, 17 mM F-6-P, and 50 mM G-6-P. Substrate-limiting assays were performed at pH 7.5 using 3 mM UDP-Glc, 2 mM F-6-P, 10 mM G-6-P, and 5 mM Pi to prevent artificial substrate activation of down-regulated enzyme, which is necessary for examining light acti-

vation of SPS (Stitt et al., 1988; Huber et al., 1989a). Sensitivity to [Pi] (0–6 mM) was evaluated at limiting concentrations of UDP-Glc, F-6-P, and G-6-P.

Diel Patterns of SPS and SS Activity

Diel changes in activity of shoot SPS and root SS were investigated using mature vegetative plants collected as above and maintained in outdoor running seawater tanks screened to provide a natural pattern of solar insolation. Leaf No. 3 (No. 1 = youngest) was removed from each of five replicate shoots at noon, sunset, midnight, dawn, and the following noon. The V_{max} activity of root SS (synthase direction) was assayed as described for SPS using one root bundle of the youngest emergent pair on each plant, except that Fru replaced F-6-P in the reaction buffer. Carbohydrates were extracted from sibling root bundles in hot ethanol and assayed with resorcinol.

Effect of Elevated Photosynthesis on SPS Activity and Leaf [Suc] Levels

Entire mature leaves were excised from 10 shoots just before sunrise. Five leaves were placed in an open 5-L plastic container filled with seawater bubbled with CO_2 to increase the concentration of $CO_{2(diss)}$ to 1.8 mM. The $[CO_{2(diss)}]$ was controlled by periodic bubbling with CO_2 to maintain seawater pH between 6.0 and 6.2. Five other leaves were placed in an identical open container filled with seawater at normal $[CO_{2(diss)}]$ (0.01 mM) and pH (8.0). Both containers were placed in a controlled-environment chamber to maintain temperature (15–16°C) and provided with photosynthesis-saturating PPF (150 μmol quanta m^{-2} s^{-1}). The open chambers were mixed by magnetic stirrers to prevent diffusion limitation of photosynthesis and accumulation of O_2 in the incubation medium. Leaves were removed from the containers after 2 h. A section was removed from each leaf for polarographic determination of photosynthesis (O_2) at incubation $[CO_{2(diss)}]$ (1.8 or 0.01 mM). Another section was removed for determination of Suc content as described above. The remainder of each leaf was assayed for SPS activity (V_{max} and substrate-limited) as described above.

RESULTS

Rates of Photoassimilate Export and SPS Activity

Changes in carbohydrate content of leaves were small but measurable relative to the initial size of the carbohydrate pool (Fig. 1a). Young leaves (leaf Nos. 1 and 2) consistently gained carbohydrate in the light, whereas older leaves (leaf Nos. 4 and 5) generally lost carbohydrate even though rates of C fixation were independent of leaf age (Fig. 1b). This is consistent with the principle that young leaves generally function as C sinks, whereas older leaves (e.g. Nos. 4 and 5) act as C sources. Leaf No. 3 appeared to be in transition between sink and source status. The V_{max} activity of SPS increased with leaf age, almost in mirror image to the pattern for sugar accumulation,

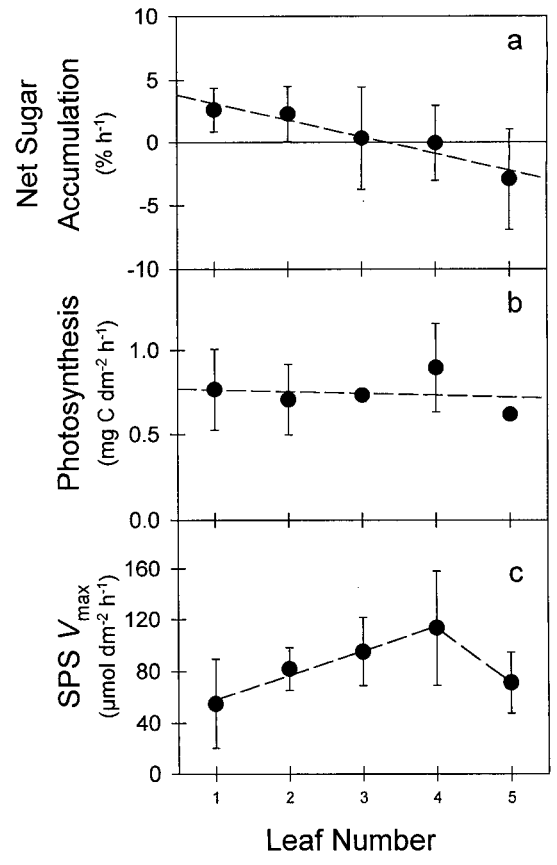

Figure 1. Effect of age on rates of net sugar accumulation (a), ^{14}C photosynthesis (b), and SPS activity (V_{max}) (c) in intact leaves of *Z. marina*. The youngest leaves (No. 1) were less than 10 d old, and the oldest leaves (No. 5) were at least 10 weeks old. Error bars indicate one sample SD of the mean (n = 4) for each leaf number. Dashed lines represent the line of best fit determined by linear regression to the mean values for all leaf types.

except that activity was consistently low in the oldest, generally senescent leaves (No. 5, Fig. 1c).

Rates of carbohydrate export from individual leaves (Fig. 2a), although low, were quantitatively consistent with the overall relationship to photosynthesis shown for other species (data from Huber et al., 1985), generally falling inside the 99% confidence intervals of the regression analysis (overall r^2 = 0.76). Substrate-limited SPS activity in eelgrass generally fell outside the 99% confidence intervals generated by linear regression of SPS activity against rates of export in crop plants (Fig. 2b). Thus, eelgrass SPS activity is slightly higher than would be predicted from export rates. Anomalously high SPS activity was most apparent in young leaves (Nos. 1 and 2) that appeared to be C sinks (carbohydrate accumulators), which may reflect a developmental gradient within young leaves as the distal portions make the transition from C sinks to sources.

Diel Variation in Enzyme Activity and Sugar Content

Leaf SPS showed no significant diel pattern that could be described as light activation, either in terms of V_{max} or

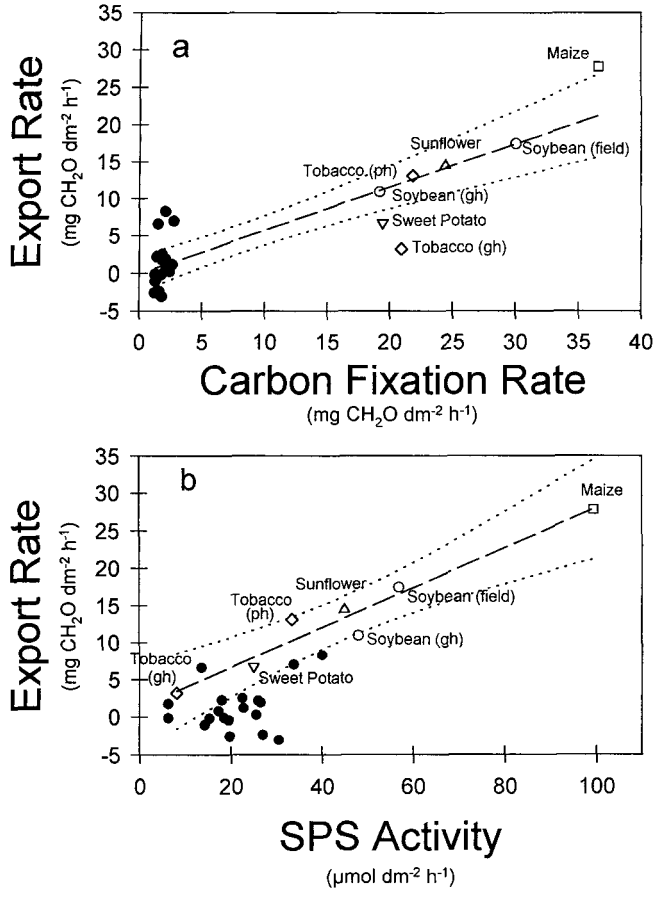

Figure 2. Export rate from photosynthetic leaves of *Z. marina* plotted as a function of C fixation rate (a) and substrate-limited activity of SPS (b). ●, Data collected from eelgrass. Data from other plant species identified in the figure were taken from Huber et al. (1985). Least-squares linear regression and 99% confidence intervals are indicated by solid and dashed lines, respectively.

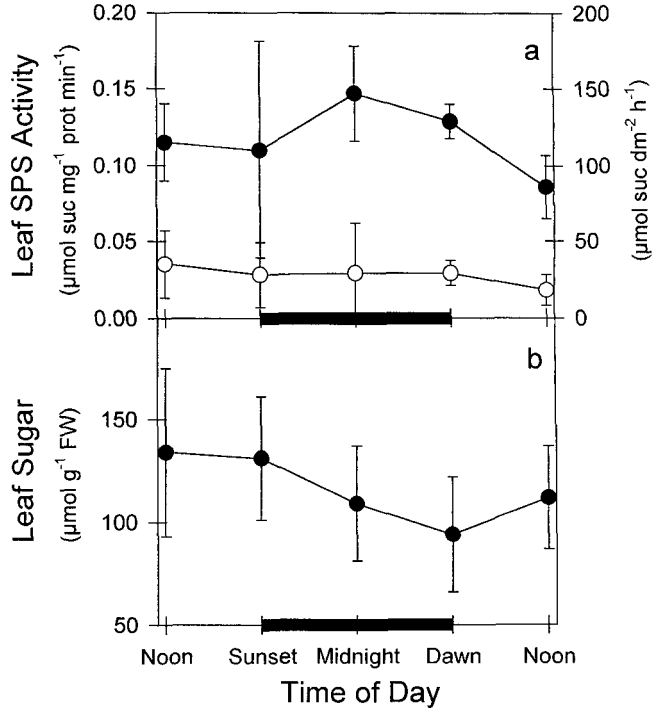

Figure 3. a, Diel pattern of SPS activity in eelgrass leaves. ●, V_{max} activities; ○, substrate-limited rates. b, Diel pattern in leaf Suc content. In both cases, error bars indicate ±1 SD of the mean of five leaves for each sampling period. The nocturnal period is indicated by black bars along the time axis. FW, Fresh weight.

substrate-limited activity (Fig. 3a). Substrate-limited rates were approximately 25% of V_{max} throughout the diel cycle. The apparent 25% decline in leaf sugar content during the dark period was consistent with nocturnal respiration and/or Suc export in the absence of net synthesis, but temporal differences were not statistically significant as determined by ANOVA (Fig. 3b). The in vitro impact of [Pi] on substrate-limited SPS activity was small but measurable (Fig. 4). SPS activity was reduced to 60% of the control ([Pi] = 0 mM) rate in the presence of 1 mM Pi. SPS activity, however, was not measurably sensitive to additional increases in [Pi] above 1 mM.

As for leaf SPS, there was no diel pattern in root SS activity (Fig. 5a). Significant differences detected by ANOVA ($P < 0.01$, $F = 6.80$, df = 4,20, $MS_{Time} = 2631$, $MS_{within} = 387$) resulted from low SS activity in roots from the first noon sampling period, as determined by Newmann-Keuls post-hoc analysis of the time series. The highest values of SS activity were measured the following noon, indicating that the differences detected by ANOVA did not result from the day/night cycle. Roots contained less than 10% of the sugar content of the leaves (normalized to fresh weight) and showed no statistically significant variation over the day/night cycle (Fig. 5b).

Effect of Elevated Photosynthesis on SPS Activity and Leaf [Suc] Levels

The P_m of eelgrass leaves responded dramatically to [$CO_{2(diss)}$]. The P_m was 3-fold higher at 1.8 mM $CO_{2(diss)}$ (pH 6.0) than in normal seawater (0.01 mM $CO_{2(diss)}$, pH 8;

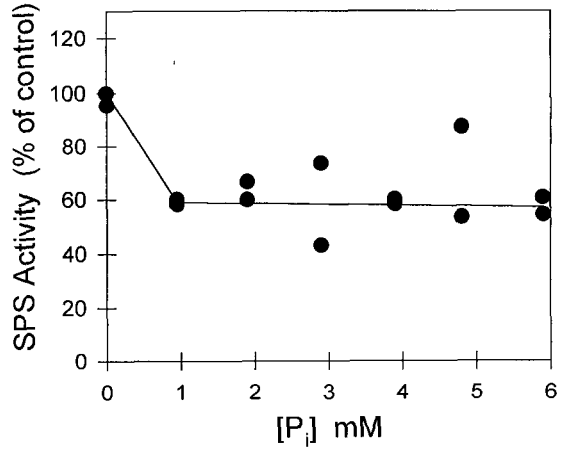

Figure 4. Impact of [Pi] on substrate-limited activity of SPS extracted from *Z. marina*. Placement of the trend line through the data was determined by visual inspection.

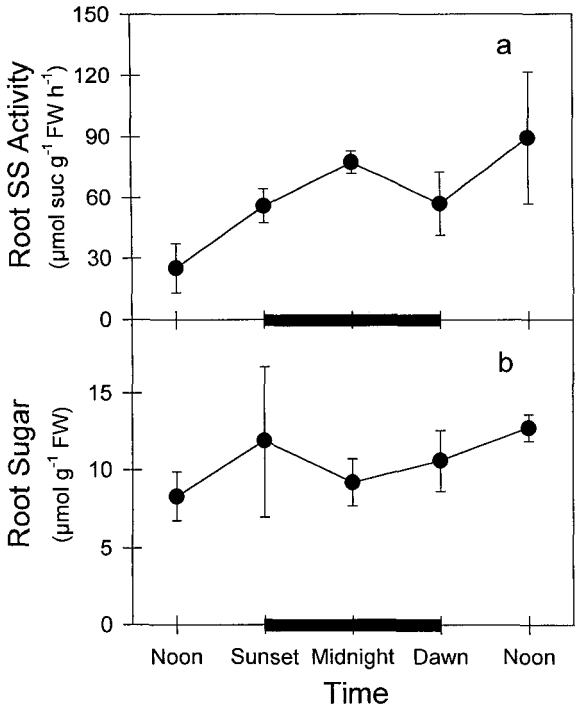

Figure 5. a, Diel pattern of SS activity in eelgrass roots. b, Diel pattern in root sugar content. Error bars indicate ±1 SD of the mean of three roots for each sampling period. The nocturnal period is indicated by black bars along the time axis. FW, Fresh weight.

Table I). In contrast, respiration was unaffected by [$CO_{2(diss)}$]. The high rate of P_m produced a 43% increase in Suc content of leaves incubated in 1.8 mM $CO_{2(diss)}$, relative to control leaves. Although the increase in Suc clearly resulted from elevated rates of photosynthesis in 1.8 mM $CO_{2(diss)}$, it was accomplished without a significant increase in the substrate-limited activity of SPS, whether expressed on a fresh-weight basis or as a percent of V_{max} (Table I).

DISCUSSION

Rates of seagrass photosynthesis are typically only 20% of those reported for macrophytic algae such as *Ulva lactuca* and *Macrocystis integrifolia* and less than 10% of that reported for maize (Drew, 1978; Mazzella et al., 1981; Dennison and Alberte, 1982; Smith et al., 1983; Sand-Jensen and Gordon, 1984; Huber et al., 1989a; Zimmerman et al., 1991, 1995). This probably results from relatively inefficient utilization of HCO_3^- (Beer, 1989; Durako, 1993). Despite low photosynthetic rates in *Z. marina*, the transition from C sink to source in leaf Nos. 1 through 4 was accompanied by a doubling in SPS activity (V_{max}), linking the development of C export capacity in maturing leaves to an increase in SPS. Furthermore, the relationships between C fixation rate, substrate-limited SPS activity, and C export in eelgrass are consistent statistically with the patterns reported for terrestrial crop plants (Huber et al., 1985; Stitt and Quick, 1989; Stitt, 1994).

Lack of SPS activation by light or photosynthesis and minimal sensitivity to [Pi] suggest that regulation of eelgrass SPS may be more similar to that of group III species (soybean, pea, tobacco, cucumber, melon, *Arabidopsis thalina*) than to that of group I or group II species such as maize, barley, and spinach (Huber et al., 1989b), in which SPS activity is sensitive to light activation and Pi inhibition (Rufty et al., 1983; Sicher and Kremer, 1984; Kalt-Torres and Huber, 1987; Stitt et al., 1988; Huber et al., 1989b). In group III species that do not undergo light activation of SPS, substrate-limited rates of SPS activity approach 80 to 90% of V_{max}, suggesting that 80 to 90% of the SPS pool remains active throughout the day/night cycle (Huber et al., 1989a). Substrate-limited rates of eelgrass SPS activity, however, were only 20 to 25% of V_{max}, suggesting that less than half of the SPS pool was activated even when photosynthesis rates were increased 3-fold. The low level of active SPS in eelgrass, however, was adequate for Suc production, as indicated by the 50% higher level of Suc in leaves incubated at 1.8 mM $CO_{2(diss)}$. It is not clear why eelgrass leaves maintain such a large pool of inactive SPS, but control of Suc synthesis and C partitioning involves more than manipulation of bulk enzyme abundance (Stitt, 1994).

Although the stability of Suc pools within eelgrass leaves is also consistent with what is observed in group III starch accumulators, >90% of the carbohydrate pool in eelgrass leaves is present as Suc rather than starch (Zimmerman et

Table I. *Light-saturated photosynthesis (P_m), dark respiration (R), SPS activity, and sugar content of Z. marina leaves incubated under high (1.8 mM) and normal (0.01 mM) concentrations of $CO_{2(diss)}$*

Values are presented as means of five samples for each treatment with SDs in parenthesis. Substrate-limited SPS activity is listed as a function of fresh weight and as a percentage of V_{max}. *t*, Results of Student's *t* test. df, Degrees of freedom. P, The probability that the means are not significantly different. Significance levels (Sig.): n.s., not significant at $P \leq 0.05$; *, significant at $P \leq 0.05$; **, significant at $P \leq 0.01$.

Treatment	P_m	R	SPS Activity			[Suc]
			V_{max}	Substrate limited	Substrate limited	
	μmol O_2 g^{-1} fresh wt h^{-1}		μmol Suc g^{-1} fresh wt h^{-1}		% of V_{max}	μmol g^{-1} fresh wt
High $CO_{2(diss)}$	103 (45)	13 (7)	130 (20)	29 (14)	23 (12)	77 (12)
Normal $CO_{2(diss)}$	35 (10)	16 (5)	161 (54)	30 (13)	16 (5)	54 (12)
t	3.34	0.95	1.21	0.09	0.77	3.03
df	8	8	8	8	8	8
P	0.01	0.37	0.13	0.46	0.45	0.02
Sig.	**	n.s.	n.s.	n.s.	n.s.	*

al., 1989, 1995). In Suc-accumulating species from group I and group II, Suc levels can vary as much as 5-fold over the day in response to photosynthetic production, and as much as 90% of the net C fixed is exported from the leaf (Rufty et al., 1983; Sicher and Kremer, 1984; Kalt-Torres and Huber, 1987). Suc levels in eelgrass leaves were 50 to 100% higher than those reported for maize, but only 60% of the C fixed was exported during the 5-h incubation period. Given that eelgrass photosynthesis is only 10% of that in maize, the daily Suc flux from an eelgrass leaf is only about 4% of the flux from a maize leaf and may not require up-regulation of SPS.

Nocturnal export rates in maize drop in proportion to the declining levels of Suc remaining in the leaves (Kalt-Torres et al., 1987). Nocturnal export from eelgrass leaves, however, is blocked by anoxia of below-ground tissue (R.C. Zimmerman, unpublished data). Nocturnal respiratory depletion of eelgrass leaf Suc was so small as to be statistically insignificant. Constantly high Suc levels in eelgrass leaves may also prevent a diel cycle in SPS activity. Daytime accumulation of Suc to levels 50% below those observed in eelgrass reduce SPS activity in maize after midday (Stitt et al., 1988).

Activity of SS does not undergo a diel cycle or exhibit light activation in crop plants similar to SPS (Kalt-Torres and Huber, 1987). Expression of SS, however, is induced in response to anoxia (Freeling and Bennett, 1985; McCarty et al., 1986; Xue et al., 1991). Unlike many higher plant species, eelgrass roots do not exhibit a dramatic shift in the types or abundance of proteins synthesized under anaerobiosis (Smith et al., 1988; Smith, 1989; Kraemer and Alberte, 1995), and many of the anoxia stress proteins, including alcohol dehydrogenase and SS, are expressed constitutively at high levels in eelgrass (Smith et al., 1988). Root SS activity, however, decreases with root age and increases in response to extended cycles of reduction in daily photosynthetic periods (Kraemer and Alberte, 1995; R.C. Zimmerman, unpublished data), suggesting that eelgrass roots possess some capacity for acclimation to prolonged daily anoxia.

Eelgrass SPS activity and C reserves did not cycle with the same dramatic amplitude or frequency observed in group I or II species. Although this homeostasis clearly reflects the low rates of photosynthesis, respiration, and export characteristic of eelgrass leaves, the maintenance of high Suc levels indicates that *Z. marina* cannot be aligned unambiguously with starch-accumulating group III species either.

Suc pools that remain large relative to demand may be ecologically important for buffering the negative effects of daily fluctuations in light availability typical of eelgrass environments (Zimmerman et al., 1994). One day of low irradiance produces C limitation in maize roots that depresses respiration and nutrient uptake for 3 d or more after plants are returned to high irradiance, but the C pool in eelgrass roots is sufficient to meet the requirements of anaerobic metabolism for at least 3 d in the absence of any translocation (Massiminio et al., 1981; Smith et al., 1988; Smith, 1989; Kraemer and Alberte, 1995). The lack of a Pasteur effect in eelgrass roots also may be important for extended anoxia tolerance. Extreme light limitation and prolonged anoxia of 3 to 5 d duration occur commonly in seagrass meadows (Zimmerman et al., 1991, 1994, 1995). Consequently, a large Suc buffer, rather than the rapid conversion of fixed C into growing biomass, may determine the ecological success of seagrasses in environments characterized by unpredictable light availability and periods of prolonged root anoxia.

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