SEAGRASS PRODUCTIVITY: THE EFFECT OF LIGHT ON CARBON UPTAKE

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"SEAGRASS PRODUCTIVITY: THE EFFECT OF LIGHT ON CARBON UPTAKE"

A

THESIS

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ABSTRACT

Seagrass species are very similar. It is expected that these similarities extend to their productivity, especially their response of carbon uptake to light.

Experiments quantifying the rate of productivity estimated by ^{14}C -carbon uptake as a function of light, measured as irradiance, yielded light-response curves for six North American species.

High maximum rates, saturation irradiances, half-saturation irradiances, and the shapes of the curves were essentially the same, indicating that seagrass species share a specific type of production system. Therefore differences in their productivities are not caused by species-specific factors but environmental factors or artifacts of technique. Differences in maximum rates resulted most likely from differences in light quantity, physiological stress, or ecological roles in succession. Superimposed on the general pattern of seagrass productivity were modifications caused by environmental and ecological conditions of the habitats.

Application of models based on the Michaelis-Menton and Steele's equations yielded predictive understanding of primary production.

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INTRODUCTION

Seagrasses, marine angiosperms, exhibit some of the highest rates of primary production. The productivity of their ecosystems is correspondingly high (McRoy and McMillan, 1977), especially considering the contributions made by component primary producers other than the seagrasses such as epiphytes and benthic algae. Seagrass ecosystems are found on all but the most polar coasts and perform extremely important functions in the marine environment, such as a high production of organic matter. Seagrass ecosystems provide food, shelter, and substrates for attachment for organisms (Carr and Adams, 1973; Mann, 1972; Kita and Harada, 1962). The seagrasses themselves stabilize sediments (Ginsberg and Lowestam, 1958), help protect coastlines from storm damage (Thomas *et al.*, 1961), and increase organic matter locally through a baffling effect of seagrass leaves (Wood *et al.*, 1969). The grass beds are sites of important nutrient cycling, demanding high nutrient fluxes to support the productivity (McRoy and McMillan, 1977). Seagrass roots can extract nutrients from the sediment and pump them into the water column, therefore regaining nutrients otherwise lost to the sediment sink (McRoy and Barsdate, 1970). There are few direct grazers; most of the production goes into the formation of a detritus system which involves high microbial activity and rapid nutrient exchanges, and which transforms an often seasonal production into a constant energy source (Wood *et al.*, 1969; Fenchel, 1972). Finally, seagrass ecosystems contribute to off-shore waters as sources of organic enrichment (Menzies *et al.*, 1967; Barsdate *et al.*, 1974) and provide substrates for attachment for organisms

not resident in grass beds (Wolff, 1976).

Despite the importance of the high seagrass productivity, most of the research on it has involved isolated measurements on selected species using a variety of techniques (McRoy and McMillan, 1977). The units used most often express productivity per unit area, which is important in a community or ecosystem evaluation but gives little understanding of the potential capacity for photosynthesis that is expressed by a rate per unit weight. Few studies have yielded an understanding of the underlying mechanisms and controls and limits of productivity. This understanding is necessary for viewing the pattern of productivity for seagrasses as a general class of marine primary producers and for prediction. Without an understanding of the relationship productivity has to its forcing and limiting parameters, estimates of yields remain but there is no basis for interpreting differences in yields. Questions regarding the differences in reported rates primarily due to species differences or to environmental factors such as light, temperature, salinity and/or nutrient concentrations cannot be answered.

Light is the primary requirement for photosynthesis. For marine systems, adequate descriptions of phytoplankton production have been generated using light as the sole independent parameter (Ryther, 1956; Ryther and Yentsch, 1957; Steele, 1962). After the basic response of productivity to light was described, experimentation around environmental factors secondarily controlling productivity could be given a conceptual framework. MacIsaac and Dugdale (1972), for example, used the response to light by phytoplankton to describe nitrogen uptake, independently and as a function of photosynthesis.

Various analytical treatments have been used for assessing the effect of light on production for marine and freshwater primary production systems, especially the plankton (Ryther, 1956; Talling, 1957; Steele, 1962; Rohde, 1965; Idso and Foster, 1975; Platt, *et al.*, 1975). For seagrasses analytical treatment of the response of productivity to light is less common. Light-dependent production is described most extensively for *Zostera marina* (Burkholder and Doheny, 1968; McRoy, 1974; Short, 1975; Short and McRoy, in prep.). Jones (1968) recognized light as the single most important factor associated with primary production of *Thalassia testudinum*, a tropical seagrass, and examined its seasonal light response curves. Buesa (1975) described productivity of *Thalassia* and *Syringodium filiforme* as a function of light. Bittaker and Iverson (1976) found a linear response of *Thalassia* productivity to light. Nixon and Oviatt (1973) presented the productive response to light of *Ruppia maritima*, a temperate and tropical estuarine angiosperm.

A few studies have dealt with more indirect effects of light on productivity in seagrasses. Koch *et al.* (1974) found 200 to 450 foot-candles optimal for growth of five species in culture. Marmelstein (1966) studied the effects of photoperiod on *Thalassia*. Bachman and Barilotti (1975) reduced light over a *Zostera* bed and found a resultant reduction in turion density.

The response of seagrass productivity to light described by the body of research, except for Bittaker and Iverson (1976), is similar to the one described for other aquatic primary producers. A linear

response, where productivity increases proportionately with light, describes productivity at low light levels. This phase continues up to an apparent saturation irradiance where light is no longer limiting and productivity reaches a maximum value. Upon saturation an increase of light brings about only small increases in productivity. The expectation to this may be very high irradiances which can inhibit the maximum rate.

In this thesis I describe and compare the effect of light on productivity for six North American species from varying environments (Table 1) by measuring instantaneous productivity (using ^{14}C) as a function of irradiance, to give basis for differences, if existing, in the productivity patterns among species and to enable prediction of productivity from measurements of irradiance.

METHODS

Collection Sites

I collected six North American seagrass species from various habitats in the tropic, subtropic, and temperate environments (Table 1). These species were *Thalassia testudinum*, *Syringodium filiforme*, *Haldane wrightii*, *Ruppia maritima*, *Halophila engelmanni*, and *Phyllospadix scouleri*.

After collecting seagrasses from the field, I used the following methods to determine the effect of irradiance on the instantaneous productivity of seagrasses. Wetzel (1965) provided technical reference.

Table 1. Description of collection sites of seagrasses for productivity experiments. Environmental parameters measured at sampling time.

Locality	Latitude & Longitude	Date	T(°C)	S(‰)	pH	Species Collected	Habitat
Bahia de Mayaguez Mayaguez, P.R.	18°13'N	28,29,30, 31 May 75	2.8	35.0	8.25	<i>Thalassia</i> <i>testudinum</i>	Intertidal in bay with extensive recreation- al and industrial usage.
	67°10'W	1,2 June 75				<i>Syringodium</i> <i>filiforme</i>	
Laguna Joyuda Mayaguez, P.R.	18°7'N	30,31 May 75	-	20.0	-	<i>Halodule</i>	Shallow embayment with inlet. Much land drain- age. Possible enrichment.
	67°15'W	1,2 June 75				<i>wrightii</i>	
Redfish Bay, Texas	27°52'N	10,11,12,13,	26.5	33.0	8.4	<i>Thalassia</i>	Subtidal in shallow turbid bay.
	97°8'N	17 Aug 74	to 35.0	to 34.6	to 8.7	<i>testudinum</i> <i>Syringodium</i> <i>filiforme</i> <i>Halodule wrightii</i> <i>Ruppia maritima</i> <i>Halophila engelmanni</i>	
Izembek Lagoon, Alaska	55°0'N 163°	17 Oct 75	7.0	1.00300	3.7	<i>Ruppia</i> <i>maritima</i>	Tundra lake with dis- tant inlet to Bering Sea. Fluctuating salinity.
White Cliff Island, Alaska	55°51'N 133°30'W	7,9 Aug 75	14.0	27.0	8.3	<i>Phyllospadix</i> <i>scouleri</i>	Rocks exposed to open ocean surf.
Crane Cove, Baranof Island, Alaska	56°50'N 135°20'W	13 Aug 75	16.0	25.0	8.1	<i>Phyllospadix</i> <i>scouleri</i>	Rocks exposed to open ocean surf.
Sitka Sound, Baranof Island, Alaska	57°10'N 135°30'W	14 Aug 75	13.0	23.0	8.0	<i>Phyllospadix</i> <i>scouleri</i>	Rocks exposed to open ocean surf.

Field Experiments

I collected mats of rhizomes and roots with associated leaf bundles (turions) with shovels, or trowels if the use of SCUBA was necessary. The mats were protected as carefully as possible from direct sunlight and immediately returned to the laboratory where they were placed in flowing seawater aquaria.

I selected undamaged healthy-appearing leaf bundles attached to a small piece of rhizome with roots from the mat, cleaned the leaves of epiphytes with tissues, the rhizomes and roots of sediment and placed these plants in a clean aquarium. Most experiments were performed within 24 hr after collection.

At the time of an experiment I placed a plant in a glass-stoppered bottle (500 ml) filled with filtered seawater of known pH, salinity and temperature. Maximum temperature change during incubation was 3°C. Each bottle was injected with 5 μ c of NaH 14 CO $_3$ of known specific activity. In Texas, duplicate bottles incubated at each light level; elsewhere, triplicates incubated.

Incubation of bottles proceeded for 4 hr in natural light which was recorded by a pyrliometer as surface irradiance (100%). Light, as irradiance, was reduced successively using a series of neutral density filters admitting known percentages (1, 10, 25, 50, 75) of the surface irradiance and dark bottles (0%). In Texas, screens were used which were calibrated with a photometer to admit 43, 64 and 73% of the surface irradiance.

In Texas, I used hourly average irradiance from Brownsville (Environmental Data Service, NOAA, National Climatic Center, Asheville,

N.C.). The values represent close approximation to experimental light conditions considering the small local variation between Port Aransas and Brownsville in irradiance and weather. Skies were cloudless during the times of the experiments.

At the end of incubation plants were removed from the bottles and rinsed. Leaves were cut from rhizomes and all parts were frozen immediately in the dark.

Sample Processing

To measure the labelled carbon, plants were oxidized to CO_2 using a dry combustion technique. In preparation for oxidization each plant part was dried at 90°C for 24 hr, fumed with HCl to remove surface carbonates, homogenized by crushing or grinding, and weighed in g to four decimal points. Weighed samples were wrapped in small packets of cellulose acetate or pelletized in small pieces of ashless filter paper.

Dry combustion was done on a Packard Tri-Carb 305 sample oxidizer. Ethanolamine trapped the radioactive CO_2 . A scintillation cocktail of 15 g 2,5 diphenyloxazole, 1 g p-(bis)-(ortho-methylstryl) benzene, and 1 liter toluene was used with a methanol solvent. The radiocarbon memory of the oxidizer was reduced by running samples in order of increasing radioactivity and by burning a sufficient number of blanks between samples. Radioactivity was measured by a Beckman LS 150 scintillation counter (gain = 860, wide window ^{14}C setting) along with external standards used for quench measurements.

A second combustion technique was used for a few experiments. Each sample and a small piece of black paper were held by a platinum wire basket inside a combustion flask feeding 3 scintillation vials. The vials were filled with 15 ml of cocktail (1 part phenethylamine, 1 part methanol, 2 parts toluene and 1 packet Omniflour per liter). Oxygen flushed the combustion flask which was then sealed. Combustion was initiated by heat from an infrared lamp. After combustion ceased, N₂ flushed the flask and delivered labelled CO₂ to the vials. The radioactivity trapped by the third vial was between 2 and 17% of that in the first two vials. A Beckman LS-100C counter with external standards measured radioactivity.

Combustion efficiencies were established by combusting a labelled amino acid of known activity and comparing its activity to the same amount added to scintillation cocktail.

Productivity Calculation

After correcting for quench, background, dark uptake, combustion efficiency, and scintillation counter efficiency, the counts were converted to productivity values using the formula:

$$P = \frac{\text{DPM}_{\text{sample}} \times 1.05 \times A \times V}{\text{DPM}_{\text{ampoule}} \times T \times W} \quad (1)$$

where P = carbon uptake of leaves + roots + rhizomes in
mg C·g(dry)⁻¹·hr⁻¹.

DPM_{sample} = corrected disintegrations per minute of oxidized sample.

1.05 = correction for differential uptake of C isotopes.

A = alkalinity of water in $\text{mg C} \cdot \text{liter}^{-1}$, assuming a specific alkalinity of 0.125 (Strickland and Parsons, 1965).

V = volume of water in bottle, liters.

$\text{DPM}_{\text{ampoule}}$ = activity of labelled bicarbonate added, disintegrations per minute.

T = incubation time, hours.

W = weight of seagrass sample, grams.

Productivity in $\text{mg C} \cdot \text{g(dry)}^{-1} \cdot \text{ly}^{-1}$ was computed as follows:

$$P = \frac{P_w}{\text{IRR}} \quad (2)$$

where IRR = average irradiance falling during the incubation time in $\text{langleys} \cdot \text{hr}^{-1}$.

P_w = uptake rate in $\text{mg C} \cdot \text{g(dry)}^{-1} \cdot \text{hr}^{-1}$.

Techniques of Data Analysis

I used the calculated productivity values and corresponding irradiances in the following manners to quantify the effect of light on productivity.

Kinetic analysis

The rate of light-dependent carbon uptake (carbon uptake kinetics) was my major tool to quantify seagrass productivity. Light, as the primary requirement for photosynthesis, has the greatest influence on the rate of photosynthesis, hence productivity. The effect of light on the rate of carbon uptake, as an estimate of productivity, was

determined in the following way.

I plotted carbon uptake ($\bar{X} \pm \text{s.d.}$) versus irradiance expressed as langleys $\cdot\text{hr}^{-1}$ ($\text{ly}\cdot\text{hr}^{-1}$) or % surface irradiance (% SI). Data from individual experiments, and mean data from all experiments were plotted for each species.

I derived various constants from the curves to describe the response of productivity to light (Tables 2 and 3). The half-saturation constant for light (K_{Lt}) describes the irradiance corresponding to half the maximal uptake rate, called P_{max} (MacIsaac and Dugdale, 1972). E_{sat} is the irradiance at which the linear slope is reduced and uptake apparently begins to become saturated with light. The initial portion of the curve before saturation is approached is a first-order kinetic reaction; the rate of carbon uptake is proportional to the light. The light affinity (A) is the slope of the first-order portion of the curve, and may be used as the rate constant in kinetic equations. Absolute affinity (A_{ly}) has units $\text{mg C}\cdot\text{g}(\text{dry})^{-1}\cdot\text{ly}^{-1}$. Relative affinity ($A_{\%}$) has units $\text{mg C}\cdot\text{g}(\text{dry})^{-1}\cdot\% \text{SI}^{-1}$. I used a linear regression of all points up to the beginning of saturation to calculate the slope yielding A.

Analysis using Steele's equation

Data were computer fit by a least squares routine to Steele's equation. Steele (1962) formulated the equation to predict phytoplankton productivity as a function of light. Short (1975) applied the equation to the productivity of *Zostera*.

The equation, modified by Kremer (1975), is

$$P = P_{\max} (I/I_{\text{opt}}) \exp (1-I/I_{\text{opt}}) \quad (3)$$

where P = productivity, $\text{mg C} \cdot \text{g(dry)}^{-1} \cdot \text{hr}^{-1}$,

$P_{\max}$ = maximum productivity, $\text{mg C} \cdot \text{g(dry)}^{-1} \cdot \text{hr}^{-1}$,

I = incident irradiance, $\text{ly} \cdot \text{hr}^{-1}$,

I_{opt} = optimum irradiance where $P = P_{\max}$, $\text{ly} \cdot \text{hr}^{-1}$.

I_{opt} , $P_{\max}$, and a Chi-square goodness of fit at the 95% confidence interval were calculated.

RESULTS

All seagrass species I examined showed the general pattern of light-dependent productivity, as estimated by carbon uptake, characteristic of marine (and freshwater) primary producers. At low irradiances productivity increased proportionally with light. The first order uptake continued to an apparent saturation irradiance where uptake ceased linear dependence on light. Upon saturation by light the maximum uptake was achieved. At very high irradiances inhibition of the uptake rate can occur.

As expected, the various instantaneous uptake rates were high, over $1 \text{ mg C} \cdot \text{g(dry)}^{-1} \cdot \text{hr}^{-1}$, especially for *Ruppia*, *Halodule*, and *Halophila* (Table 4). The seagrasses from Puerto Rico, *Thalassia*, *Syringodium*, and *Halodule*, yielded the highest uptakes, approximately three times those from Texas and Alaska.

Despite differences in maximum uptake and in the rate of exponential uptake, the seagrasses from each location showed similar

Table 2. Kinetic constants describing the response of seagrass productivity, as estimated by carbon uptake, to light, measured in langleys $\cdot^{-1}$.

Light measured in langleys (ly). T = *Thalassia testudinum*, S = *Syringodium filiforme*, Hd = *Halodule wrightii*, R = *Ruppia maritima*, Hp = *Halophila engelmanni*, P = *Phyllospadix scouleri*. Blanks indicate no data.

Surface Irradiance SI (ly $\cdot$ hr $^{-1}$)	Half-Saturation Constant					Light Affinity					Saturation Irradiance				
	K_{Lt} (ly $\cdot$ hr $^{-1}$)					A_{ly} (mg C $\cdot$ g(dry) $^{-1}\cdot$ ly $^{-1}$)					E_{sat} (ly $\cdot$ hr $^{-1}$)				
	T	S	Hd	R	Hp	T	S	Hd	R	Hp	T	S	Hd	R	Hp
Puerto Rico															
81.1	31.8	30.0	24.6	-	-	139	254	1258	-	-	40.6	60.8	40.6	-	-
76.6	-	18.0	13.8	-	-	-	227	297	-	-	-	38.3	38.3	-	-
70.0	20.1	18.0	22.5	-	-	149	212	682	-	-	35.0	35.0	35.0	-	-
70.0	-	15.0	27.0	-	-	-	208	1240	-	-	-	35.0	35.0	-	-
68.1	26.1	30.0	-	-	-	230	306	-	-	-	34.1	33.8	-	-	-
63.8	18.9	21.0	-	-	-	320	206	-	-	-	31.9	31.9	-	-	-
X	24.2	20.6	21.6	-	-	210	236	869	-	-	35.4	39.2	41.6	-	-
s.d.	6.0	5.4	5.8	-	-	84	39	466	-	-	3.7	10.8	7.6	-	-
Texas															
81.4	-	52.2	49.8	41.4	17.4	-	60	168	136	171	-	59.4	59.4	52.1	52.1
79.7	37.2	38.4	47.4	39.6	-	100	79	247	217	-	51.0	58.1	58.1	51.0	-
69.1	32.4	36.6	35.4	43.2	-	113	131	232	397	-	44.2	50.4	50.4	50.4	-
68.6	45.6	45.6	51.6	55.2	21.6	62	67	174	177	197	50.0	58.3	58.3	58.3	44.2
41.7	22.2	22.2	-	27.0	21.0	170	184	-	343	473	41.7	26.7	-	30.4	26.7
X	34.2	39.0	46.2	40.8	19.8	111	104	205	254	280	46.7	50.6	56.6	48.5	40.9
s.d.	9.6	11.4	7.2	10.2	2.4	45	53	40	113	167	4.5	13.8	4.1	10.6	13.0
Alaska															
					P					P					P
24.3	-	-	-	4.3	-	-	-	-	386	-	-	-	-	6.1	-
52.3	-	-	-	-	9.9	-	-	-	-	169	-	-	-	-	13.2
46.4	-	-	-	-	7.8	-	-	-	-	174	-	-	-	-	11.4
29.4	-	-	-	-	9.6	-	-	-	-	194	-	-	-	-	15.0
18.6	-	-	-	-	6.3	-	-	-	-	339	-	-	-	-	18.6
$\bar{X}$					8.4					219					14.4
s.d.					1.7					81					3.0

Table 3. Kinetic constants describing the response of seagrass productivity, as estimated by carbon uptake, to light measured as % surface irradiance (%SI). See Table 2 for abbreviations used.

Surface Irradiance ($\text{ly}\cdot\text{hr}^{-1}$)	Half-saturation Constant					Light Affinity					Saturation Irradiance					Mean Maximum Productivity					Inhibition (* Indicates inhibition)				
	K_{Lt} (%SI)					$A_{\%I}^{-1}$ ($\text{mgC}\cdot\text{g(dry)}^{-1}\cdot\text{hr}^{-1}\cdot\%SI^{-1}$)					E_{sat} (%SI)					P_{max} ($\text{mgC}\cdot\text{g(dry)}^{-1}\cdot\text{hr}^{-1}$)									
	T	S	Hd	R	Hp	T	S	Hd	R	Hp	T	S	Hd	R	Hp	T	S	Hd	R	Hp	T	S	Hd	R	Hp
Puerto Rico																									
81.1	39	37	30	-	-	.031	.057	.283	-	-	50	75	50	-	-	4.70	6.28	17.28	-	-	-		*		
76.6	-	26	18	-	-	-	.048	.062	-	-	-	50	50	-	-	-	2.91	3.06	-	-	-		*		
70.0	-	22	39	-	-	-	.040	.241	-	-	-	50	75	-	-	-	3.47	19.01	-	-	-		*		
70.0	29	26	32	-	-	.029	.041	.132	-	-	50	50	50	-	-	1.46	2.64	8.47	-	-	-				
68.1	38	32	-	-	-	.043	.058	-	-	-	50	50	-	-	-	3.07	2.73	-	-	-		*	-		
63.8	30	33	-	-	-	.057	.037	-	-	-	50	50	-	-	-	3.17	2.18	-	-	-			-		
Texas																									
81.4	-	64	61	51	50	-	.014	.032	.031	.039	-	73	73	64	64	-	1.26	3.16	3.14	2.75	-		*		
79.7	47	48	50	50	-	.022	.018	.055	.048	-	64	73	73	64	-	1.39	1.48	4.02	3.47	-	-		*	*	-
69.1	47	53	51	61	-	.022	.025	.055	.071	-	64	73	73	73	-	1.37	1.73	4.05	5.22	-	*	*		*	-
68.6	67	67	75	81	31	.012	.013	.033	.034	.038	73	85	85	85	64	1.33	1.35	3.03	3.11	2.37	-		*	*	*
41.7	53	53	-	65	60	.020	.021	-	.040	.055	100	64	-	73	64	1.73	1.39	-	3.14	3.45	-		-		*
Alaska																									
				R	P					R	P				R	P				R	P				
24.3	-	-	-	17	-	-	-	-	0.03	-	-	-	-	25	-	-	-	1.08	-	-	-	-	-	-	*
52.3	-	-	-	-	19	-	-	-	-	0.03	-	-	-	-	25	-	-	-	1.0	-	-	-	-	-	-
46.4	-	-	-	-	17	-	-	-	-	0.02	-	-	-	-	25	-	-	-	0.81	-	-	-	-	-	-
29.4	-	-	-	-	33	-	-	-	-	0.02	-	-	-	-	50	-	-	-	1.32	-	-	-	-	-	-
18.6	-	-	-	-	34	-	-	-	-	0.02	-	-	-	-	100	-	-	-	1.16	-	-	-	-	-	-

Table 4. Comparison of Productivity data for North American seagrass species.

<u>Locality</u>	<u>Productivity</u>		<u>Reference</u>
	$\text{g(dry)} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$	$\text{mg C} \cdot \text{g(dry)}^{-1} \cdot \text{hr}^{-1}$	
<i>Thalassia testudinum</i>			
Florida	3.13		Odum, 1956
Florida	10.2		Odum, 1957
Texas	0.9-9.0		Odum & Hoskin, 1958
Puerto Rico	2.4-4.5		Odum <i>et al.</i> , 1959
Florida	0.35-1.14	0.36-1.3	Pomeroy, 1960
Florida	5.7-16.0	2.3-6.3	Odum, 1963
Florida	0.9-2.5	0.13-0.25	Jones, 1968
Florida	1.7-2.3		Zieman, 1968
Florida		1-3	Brylinsky, 1971
Cuba	9.3-12.5	1.7-2.3	Buesa, 1972
Bahamas	0.5-3		Patriquin, 1972
Barbadoes	3.1		Patriquin, 1973
Cuba	0.61-6.9		Buesa, 1974
Texas	0.6-2.7	0.01-1.08	Topham <i>et al.</i> , 1974
Florida	0.1-3.7		Zieman, 1974
Florida	1.61	0.17-0.92	Bittaker, 1975
Cuba		2.92	Buesa, 1975
Texas		0.95-1.77	Williams, this study
Puerto Rico		1.18-7.04	Williams, this study
St. Croix	2.1-2.5		Williams & Johnson, unpublished
<i>Syringodium filiforme</i>			
Florida	1.66	0.25-0.98	Bittaker, 1975
Cuba		2.91	Buesa, 1975
Texas		0.63-1.88	Williams, this study
Puerto Rico		1.58-6.30	Williams, this study
St. Croix	0.80		Williams & Johnson, unpublished

Table 4. Continued.

<u>Locality</u>	<u>Productivity</u>		<u>Reference</u>
	$\text{g(dry)} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$	$\text{mg C} \cdot \text{g(dry)}^{-1} \cdot \text{hr}^{-1}$	
<i>Halodule wrightii</i>			
Florida		1.81	Brylinsky, 1971
Florida	0.48-4.1		Dillon, 1971
Texas	0.2	0.06-0.16	Topham <i>et al.</i> , 1974
Florida	2.10	0.25-1.27	Bittaker, 1975
Cuba		4.70	Buesa, 1975
Texas		1.09-4.33	Williams, this study
Puerto Rico		1.25-20.53	Williams, this study
St. Croix	0.3		Williams & Johnson, unpublished
<i>Ruppia maritima</i>			
California	0.0-0.98		Wetzel, 1964
Rhode Island		1.75	Nixon & Oviatt, 1972
Texas		1.90-6.63	Williams, this study
Alaska		0.78-1.37	Williams, this study
<i>Halophila engelmanni</i>			
Florida	0.34	0.22-1.11	Bittaker, 1975
Cuba		4.97	Buesa, 1975
Texas		2.01-3.45	Williams, this study
<i>Zostera marina</i>			
Denmark	2-7.3	0.27-0.99	Petersen, 1913
Alaska	8	0.55	McRoy, 1966
North Carolina	0.2-1.2		Williams, 1966
Massachusetts	0.04	0.15	Conover, 1968
Rhode Island	0.4-2.9	0.15-1.1	Conover, 1968
Washington	0.6	0.16	Phillips, 1969
Alaska	3.3-3.8	0.3-0.4	McRoy, 1970
North Carolina	0.5-1.7	0.17-2.2	Dillon, 1971
Washington	0.7-4	0.44-1.9	Phillips, 1972
Alaska		1.18	McRoy, 1974
Rhode Island			Short, 1975
North Carolina	2.7	0.27-1.80	Penhale, in press

Table 4. Continued.

<u>Locality</u>	<u>Productivity</u>	<u>Reference</u>
	$\text{g(dry)} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$	$\text{mg C} \cdot \text{g(dry)}^{-1} \cdot \text{hr}^{-1}$
<i>Phyllospadix scouleri</i>		
California	1.5	Litter & Murray, 1974
Alaska	0.81-1.32	This study

half-saturation constants (K_{Lt}) and saturation irradiances (E_{sat}).

The kinetic constants derived from the light-productivity curves formed the basis for my analysis of seagrass productivity. Constants were expressed in absolute irradiance units (Table 2) or relative units of % SI (Table 3) which measure a more general adaptation to a spectrum of daily light conditions.

The contribution of root + rhizome productivity to total plant productivity was a variable percentage of the leaf productivity. In *Phyllospadix* and the Puerto Rican seagrasses the productivity of roots and rhizomes was 1 to 3% of the leaf productivity. In some plants of *Halodule* and *Syringodium* from Puerto Rico the rhizomes appeared green and the productivity correspondingly represented a high percentage of the leaf productivity, up to 18%, but generally 5 to 10%. The light curves for leaf productivity in general have the same shape as for total productivity and kinetics of carbon uptake can be described by processing only leaf samples from these plants. Light curves for root and rhizome productivity showed no characteristic pattern and indicated carbon was translocated from the leaves rather than fixed by the rhizomes. For plants having chlorophyll in the rhizome this is probably not true, but I did not investigate the kinetics of such parts. In *Ruppia* from Alaska the root and rhizome formed 7 to 37% of the leaf productivity. The roots and rhizomes of the Texas seagrasses also had productivities that represented variable percentages of the corresponding leaf productivities (mean % = 39 ± 20). Where the root and rhizome productivity was such a variable percentage of leaf productivity, the

response of productivity to light could not be extrapolated from leaf productivity alone. I do not know whether the carbon from the roots and rhizomes of such plants was translocated from the leaves or fixed in the rhizomes.

I compared the pattern of light-dependent productivity among species in each location and then compared locations which represented the tropical, subtropical and temperate environments of North America.

Tropical Environments: Puerto Rico

Seagrasses from Puerto Rico exhibited two distinct variations of the general response of carbon uptake to light (Figure 1). *Thalassia* and *Syringodium* showed an essentially identical response of a relatively slow first-order phase up to a broad plateau of maximum uptake. *Halodule* typified the second variation of the general response curve. The linear uptake, expressed in the affinity constants, was four times more rapid and upon saturation maximum uptake ($P_{\max}$) was three times greater. Inhibition also occurred more frequently. In both types of responses the linear uptake ended and saturation was approached from 50% SI or 31.9 to 40.6 $\text{ly}\cdot\text{hr}^{-1}$.

Despite differences in the initial uptake rate and in $P_{\max}$, the species had similar K_{Lt} values of 37% SI, 40, and 38 for *Thalassia*, *Syringodium*, and *Halodule* respectively. The irradiances corresponding to these percentages were 20.4 to 24.0 $\text{ly}\cdot\text{hr}^{-1}$.

The mean maximum uptakes were 2.96 $\text{mg C}\cdot\text{g(dry)}^{-1}\cdot\text{hr}^{-1}$ for *Thalassia*, 3.33 for *Syringodium*, and 11.42 for *Halodule*. The single highest rates were 7.04, 6.30 and 20.53 respectively. In *Thalassia*

Figure 1. Light-dependent productivity (means of all experiments) as estimated by carbon uptake and half saturation constants (K_{Lt}) in tropical (Puerto Rico) seagrasses: *Thalassia testudinum*, *Syringodium filiforme*, and *Halodule wrightii*.

and *Syringodium* the highest uptake occurred at 100% SI on the day of the highest irradiance ($81.1 \text{ ly}\cdot\text{hr}^{-1}$).

Thalassia and especially *Halodule* had much day to day variation in the light-response curves. *Syringodium* showed less variation (Figures 2, 3 and 4).

Subtropical Environments: Texas

Subtropical seagrasses showed the two distinct variations of the general response of carbon uptake to light described for the tropical ones (Figure 5). *Syringodium* and *Thalassia* showed an essentially identical response of a relatively slow first-order phase up to a broad region of maximum uptake. The responses of *Ruppia* and *Halophila* were essentially identical to that of *Halodule* and the three species represented the second variation of productivity as a function of light. These species initially took up carbon 2.5 times faster than *Syringodium* and *Thalassia*. Upon saturation they exhibited maximum uptake approximately 2.5 times greater than *Syringodium* and *Thalassia*. Inhibition also occurred more frequently.

The seagrasses became light-saturated at high irradiances of 27.0 to $59.4 \text{ ly}\cdot\text{hr}^{-1}$, most often greater than $48.0 \text{ ly}\cdot\text{hr}^{-1}$, which corresponded to 64 to 85% SI.

The five species had similar K_{Lt} values despite different P_{max} values and initial uptake rates. The irradiance yielding half the maximum uptake rate was 19.8 to $46.2 \text{ ly}\cdot\text{hr}^{-1}$, which corresponded to 49 to 56% SI depending on the species.

Figure 2. Daily variations ($\bar{X} \pm \text{s.d.}$) in light-dependent productivity as estimated by carbon uptake of *Thalassia* from Puerto Rico.

Figure 3. Daily variations ($\bar{X} \pm \text{s.d.}$) in light-dependent productivity as estimated by carbon uptake of *Syringodium* from Puerto Rico.

Figure 4. Daily variations ($\bar{X} \pm \text{s.d.}$) in light-dependent productivity as estimated by carbon uptake of *Halodule* from Puerto Rico.

Figure 5. Light-dependent productivity (means of all experiments) as estimated by carbon uptake in subtropical (Texas) seagrasses: *Thalassia testudinum*, *Syringodium filiforme*, *Halodule wrightii*, *Ruppia maritima*, and *Halophila engelmanni*.

Mean maximum uptake rates were $1.38 \pm 2.45 \text{ mg C} \cdot \text{g(dry)}^{-1} \cdot \text{hr}^{-1}$ for *Thalassia*, 1.35 ± 0.36 for *Syringodium*, 3.42 ± 0.84 for *Halodule*, 3.11 ± 2.45 for *Ruppia*, and 2.76 ± 0.72 for *Halophila*. Single highest rates reached were 1.77, 1.88, 4.33, 4.88, and 3.55 respectively.

Considerable day to day variation existed in the light curves (Figures 6-10).

North Temperature Environments - Alaska

Phyllospadix scouleri and *Ruppia maritima* represent the temperate seagrasses. They exhibited essentially identical light-productivity responses.

Phyllospadix scouleri

Large differences in daily surface irradiance (18.6 to $52.3 \text{ ly} \cdot \text{hr}^{-1}$) caused much variation in the shape of the response curves (Figure 11).

Saturation took 11.4 to $18.6 \text{ ly} \cdot \text{hr}^{-1}$ ($\bar{X} = 14.5 \pm 3.1$) which corresponded to 25 to 50% SI. On the day having the lowest irradiance of $18.6 \text{ ly} \cdot \text{hr}^{-1}$ on 9 August 1975 *Phyllospadix* remained in a light-limited first-order phase of uptake at all irradiances. Inhibition occurred at approximately $48.0 \text{ ly} \cdot \text{hr}^{-1}$ on the day having the highest irradiance of $52.3 \text{ ly} \cdot \text{hr}^{-1}$ on 7 August 1975.

The maximum mean uptake was $0.84 \pm 0.26 \text{ mg C} \cdot \text{g(dry)}^{-1} \cdot \text{hr}^{-1}$. The highest single uptake was 1.32. The irradiance (K_{Lt}) yielding half the maximum uptake was $8.4 \pm 1.8 \text{ ly} \cdot \text{hr}^{-1}$ or 19 to 33% SI. The general K_{Lt} for surfgrass was 20.3% SI, derived from the response curve combining data from all experiments (Figure 12). In the general response curve,

Figure 6. Daily variations ($\bar{X} \pm \text{s.d.}$) in light-dependent productivity as estimated by carbon uptake of *Thalassia* from Texas.

Figure 7. Daily variations ($\bar{X} \pm \text{s.d.}$) in light-dependent productivity as estimated by carbon uptake of *Syringodium* from Texas.

Figure 8. Daily variations ($\bar{X} \pm \text{s.d.}$) in light-dependent productivity as estimated by carbon uptake of *Halodule* from Texas.

Figure 9. Daily variations ($\bar{X} \pm \text{s.d.}$) in light-dependent productivity as estimated by carbon uptake of *Ruppia* from Texas.

Figure 10. Daily variations ($\bar{X} \pm \text{s.d.}$) in light-dependent productivity as estimated by carbon uptake of *Halophila* from Texas.

Figure 11. Daily variations ($\bar{X} \pm \text{s.d.}$) in light-dependent productivity as estimated by carbon uptake of *Phyllospadix* from Alaska.

Figure 12. Light-dependent productivity (means of all experiments $\pm$ s.d.) as estimated by carbon uptake and half-saturation constant in north temperate (Alaska) seagrass *Phyllospadix scouleri*.

the large variations in daily irradiance were incorporated by using % SI. Therefore, the area from the point where first-order uptake ended to the region of full saturation extended from 25 to 75% SI. No sharp transition from the light-limited to the light-saturated portion was seen.

Ruppia maritima

Ruppia had a rapid initial phase of uptake until light-saturated at 25% SI or $6.0 \text{ ly} \cdot \text{hr}^{-1}$. The maximum mean uptake was $1.08 \text{ mg C} \cdot \text{g(dry)}^{-1} \cdot \text{hr}^{-1}$ and occurred at 100% SI. The highest single uptake was 1.37. The irradiance yielding half the maximum uptake was $4.3 \text{ ly} \cdot \text{hr}^{-1}$ or 17% SI (Figure 13).

DISCUSSION

Techniques for Measuring Seagrass Productivity

A major problem of research concerning aquatic macrophyte productivity is the lack of a standard method of measurement. In general methods of aquatic plant productivity can be applied to seagrasses with little or no modification. Excellent reviews of aquatic plant productivity methods and their limitations are Westlake (1965) and Wetzel (1965). Wetzel and Zieman (in press) have reviewed these methods with respect to seagrasses and Bittaker and Iversen (1976) compared two of the field methods. I will devote my initial discussion to methods for measuring seagrass productivity.

Figure 13. Light-dependent productivity ($\bar{X} \pm \text{s.d.}$) as estimated by carbon uptake and half-saturation constant in north temperate seagrass (Alaska) *Ruppia maritima*. Irradiance measured as langleys $\cdot \text{hr}^{-1}$ and % surface irradiance.

Seagrasses present technical problems because they have a root and rhizome system contained in the sediment and gas-storing lacunae in the leaves. These anatomical structures impose limitations on the following methods. The simple technique of marking leaf growth with metal staples (Zieman, 1968) does not measure underground production, is subject to errors because of organic loss to herbivores, is hard to apply to seagrasses without strap-shaped leaves, and is not suitable to experimental manipulations although works well in field studies over a week in duration. The underground production of *Thalassia* has been measured by aging definite leaf scars (Patriquin, 1973). This method also does not work well for short term experimental manipulations or for many species having rhizomes without easily-recognizable leaf scars. Productivity measured by oxygen evolution is subject to errors from internal gas-recycling in the lacunae (Hartman and Brown, 1967) and low sensitivity. Diurnal studies using oxygen (Odum and Hoskin, 1958) or pH measures community metabolism and so are inappropriate for experiments specific for seagrasses alone. Any oxygen technique is also unsuitable for production measurements because of a cyclical oxygen release from seagrasses (Zieman, 1974).

I chose the radioactive carbon method because of its high sensitivity, suitability for use with all species, applicability to root and rhizome productivity measurement, and ease of handling experimental manipulations required in measuring productivity as a function of light. The assumption that radioactive bicarbonate uptake measures the carbon synthesized into living matter is subject to possible errors,

which are accepted in general until clarified by research. Photorespiration, the release of CO_2 in the light, may reduce net photosynthesis. In seagrasses Hough (1976) demonstrated this effect for two species. Carbon dioxide from respiration stored in the lacunae may be refixed internally. The diffusivity of CO_2 is greater than O_2 and may not accumulate internally (Gorski, 1929, 1935). In incubations of 4 hours or less, labelled carbon taken up was not respired and intracellular CO_2 was respired from sources not formed during the incubation (Wetzel, 1965). Carbon fixed also can be excreted as soluble organic compounds. Seagrasses can excrete up to 2% of their fixed carbon as dissolved organics (Brylinsky, 1971; Hough, 1976; Penhale and Smith, in press). Soluble organic carbons can be assimilated and fixed in addition to inorganic carbon sources. Finally seagrass tissue may absorb radiocarbon without actually fixing it.

I chose a closed bottle incubation over an *in situ* technique to insure a mass balance was maintained rather than an unquantified loss of labelled carbon to the sediment or the primary producers other than seagrasses. Reduced water flow over *Zostera* caused a reduction in measured productivity (Conover, 1968). This effect may influence results from a closed bottle experiment, especially for the surfgrass *Phyllospadix* which grows in areas of high-energy water flows. The effect of removing the roots and rhizomes from the anoxic conditions of the sediment may not be serious if the seagrasses pump oxygen into the sediments (Wetzel, pers. com.). Despite shortcomings in a closed bottle radioactive carbon technique I consider it preferable to other techniques for measuring instantaneous productivity in seagrasses.

Irradiance and Productivity

The high seagrass productivity I measured compares well with existing productivity data (Table 4). The Puerto Rican plants produced fastest, and the rates decreased progressively for more northern plants. A decrease in productivity for temperate species compared with subtropical and tropical species was noticed by McRoy and McMillan (1977). I found this trend appearing within one species (*Ruppia*) from subtropical to far northern habitats. However when the rates for 100% SI were normalized for irradiance (eq. 2) *Ruppia* showed no difference (95% confidence interval, α -type error) in maximum productivity between two different environments. Likewise there was no difference in productivity between *Phyllospadix* from Alaska and *Thalassia* and *Syringodium* from Puerto Rico. Incubation temperatures in Alaska and Puerto Rico were within optimums for the species (Phillips, 1960; McRoy, 1966; Zieman, 1974) and data indicate a similar Q_{10} relationship for seagrass species (Jones, 1968; Short, 1975). Therefore the effect of temperature on productivity was not considered to cause the differences in rates between temperate and tropical environments. The difference in productivity between plants from tropical or subtropical and temperate environments may be attributed to the difference in irradiance available to the plants. The productivity in Texas was significantly different from that in Puerto Rico for *Thalassia*, *Syringodium*, and *Halodule*, despite normalization for irradiance. I suggest the lower productivity of Texas seagrasses possibly is caused by ecological stress experienced in habitats that are at the northern limit of the species distribution.

The stress is primarily temperature; low winter and high summer temperatures prevent optimal growth (Phillips, 1960; Den Hartog, 1970; Zieman, 1974). In the tropics water temperature is maintained within temperature optimums by tradewind-driven circulation. The argument that tropical seagrass species are more productive than more temperate ones is not valid. Rather, tropical environmental conditions such as light quantity are more propitious to high productivity.

Another indication that the plants in Texas are experiencing ecological stress that could reduce maximum productivity is that they have higher half-saturation values and light-saturate at higher irradiances than in the tropics. It takes more light to achieve half the maximum uptake for plants at the northern limit to their geographical range. Saturating at higher irradiances would allow an extended first-order phase where production is directly proportional to incoming light.

The Response of Carbon Uptake to Irradiance

The seagrasses responded to light in the typical manner of marine primary producers (Steemann-Nielsen, 1975) and of seagrasses specifically (McRoy, 1974; Buesa, 1975). A light-limited phase of carbon uptake approximated first-order kinetic reactions up to an apparent saturation irradiance beyond which a maximum uptake ($P_{\max}$) was achieved. Inhibition occurred at high irradiances. Subtropical and tropical species required high irradiances for saturation (50% SI and greater). The temperate species usually saturated at irradiance 40% SI.

While there was considerable day to day variation in light-dependent productivity, clear patterns appeared when irradiance was

expressed as a percentage of the surface irradiance, which incorporated the differences in daily irradiance. Marine plants respond photosynthetically to a discrete quantity of light energy (irradiance). However, the quantity of light varies daily and seasonally and the plants adapt to these changes (Steemann-Nielsen, 1975; Short and McRoy, in prep.). Variations will be a range of irradiance about an average condition. Percent SI corresponds to this range. Except for very low irradiances compared to the average, the response of photosynthesis to light may be described using average irradiances (Steemann-Nielsen, 1975). The effect of low irradiances is easily seen when the corresponding productivity curve is compared to the one for the average condition. Within an environment seasonal adaptations will preserve the shape of the response curve but the range of irradiance corresponding to a % SI will change. Using % SI allows comparison of light curves from environments having different incoming irradiances. Relative irradiance allows normalization for adaptations to local conditions of irradiance. For example, at $40 \text{ ly} \cdot \text{hr}^{-1}$ *Thalassia* from Puerto Rico begins to saturate; however, at the same irradiance *Phyllospadix* from Alaska is photo-inhibited.

The basic pattern was the typical response of marine primary producers. More significantly, there was a characteristic seagrass response. In each climatic region I sampled, the different seagrass species exhibited striking similarities in significant details of their productive response to light. Furthermore the relationship of species to each other in one environmental region (subtropical) was the same in a different environmental region (tropical). Presumably a basic seagrass production system acts as the common denominator for the response.

If this is correct differences in productivity of the species are not caused by species-specific factors but rather environmental conditions and/or artifacts of techniques used to measure productivity.

Kinetic Constants Describing the Basic Seagrass Productive Response

The half-saturation constant is significant in indicating a characteristic seagrass response of productivity to light. In each environment there was a remarkable concurrence of K_{Lt} values among the different species, despite the situations where linear uptake rates (A) or maximum productivity (P_{max}) differed. Similar K_{Lt} values express similar relationships among species of the saturated uptake phase under enzymatic control to the light-limited uptake under photochemical control. Non-intersection of the different response curves indicates the species do not compete for light. In phytoplankton systems intersection of response curves indicated different competitive advantages for species under different conditions (Dugdale, 1967; Eppley *et al.*, 1969).

The half-saturation constant is derived from P_{max} . The controls and limits of P_{max} are not known although temperature and nutrients are likely to be important. To compare species, using a 'constant' derived from a variable (P_{max}) under as yet unqualified controls and limits reveals a weakness in theoretical and practical considerations. In spite of this weakness I think K_{Lt} is a useful empirical method for comparing species, especially considering the striking concurrence of K_{Lt} . Establishing the control of P_{max} will clarify the theoretical problem. It is possible that the control of P_{max} is the same for all seagrass species in one environment.

The irradiance (E_{sat}) at which uptake is no longer linear with respect to light and saturation begins is also essentially identical among species in each environmental region, despite cases of differing linear uptake rates. The interpretation is that the species all require the same quantity of light to initiate a fully operative production system, one no longer light-limited, another indication of a basically similar photo-system.

Variations of Light-Dependent Seagrass Productivity

Superimposed on the basic pattern of light-dependent seagrass productivity are variations effected by physical and biological conditions of the environment. Physical conditions, such as available light and length of the growing season, cause the differences in the productive response from environment to environment. These conditions modify the saturation irradiance (E_{sat}) and P_{max} , but do not change the basic shape of the response curve. Biological factors, such as a species' ecological growth strategy, modify the shapes of the curves within an environment by changing the linear rate of uptake, P_{max} , and sensitivity to very high irradiance. In the tropics and subtropics where species follow one of two main ecological growth strategies (colonizer or climax), two distinct non-competitive productive responses resulted. These responses correspond to the adventitious or colonizer species and to the climax species.

I will discuss how such variations are exemplified in each type of environment. However, the importance remains that the variations

are of one production system and are caused by environmental and ecological factors rather than species-specific factors.

Tropical and subtropical environments: Puerto Rico and Texas

Disregarding K_{Lt} and E_{sat} , which are similar, the productivity of tropical and subtropical species *Thalassia*, *Syringodium*, *Halodule*, *Ruppia*, and *Halophila*, showed two distinct types of responses. *Thalassia* and *Syringodium* demonstrated an essentially identical response in their light-dependent productivity. Buesa (1975) also found this similarity. I have interpolated his data for kinetic analysis and found the resulting constants for the Cuban plants to be very similar to the Puerto Rican plants (Table 5).

Halodule, *Ruppia*, and *Halophila* exhibited the second type of response. The linear uptake (A) and P_{max} were two to four times greater than that of *Thalassia* and *Syringodium*. The species characterized by the second type of response were also more sensitive to high irradiance, indicated by more frequent inhibition. The other three species showed a narrower range of irradiance yielding maximum uptake compared to the broad plateau region of maximum uptake of *Thalassia* and *Syringodium*. *Thalassia* and *Syringodium* can adapt their maximum productivity more easily to varying irradiances. *Halodule*, *Ruppia*, and *Halophila* also attained higher instantaneous productivity than *Thalassia* and *Syringodium* in Cuba (Buesa, 1975) and Florida (Bittaker, 1975).

The type of light response a species showed is indicative of its ecological role in seagrass succession patterns. Rapid uptake in low light and high maximal rates suggest a pioneering or colonizer-type role,

Table 5. Comparison of kinetic constants describing the response of carbon uptake to light in seven seagrass species and in kelp. See Table 2 for abbreviations used. Z=*Zostera marina*, K=kelp.

Location	K _{Lt} (%SI)					A _% (mgC·g(dry) ⁻¹ ·hr ⁻¹ ·%SI ⁻¹)					E _{sat} (%SI)					P _{max} (mgC·g(dry) ⁻¹ ·hr ⁻¹)					Inhibition (*Indicates inhibition)				
	T	S	Hd	Rp	Hp	T	S	Hd	Rp	Hp	T	S	Hd	Rp	Hp	T	S	Hd	Rp	Hp	T	S	Hd	Rp	Hp
Puerto Rico	37	40	38	-	-	0.047	0.046	0.196	-	-	50	50	50	-	-	2.96	3.33	11.42	-	-				*	
Cuba (Buesa, 1975)	33	38	-	-	-	0.026	0.035	-	-	-	58	78	-	-	-	2.92	2.89	-	-	-	*				
Texas	50	54	56	52	49	0.023	0.022	0.057	0.042	0.053	64	73	73	73	64	1.38	1.36	3.42	3.11	2.76			*	*	*
Florida (Jones, 1968)	26	-	-	-	-	0.011	-	-	-	-	31	-	-	-	-	0.036	-	-	-	-	*				
Rhode Island (Nixon and Oviatt, 1973)	-	-	-	20	-	-	-	-	0.036	-	-	-	-	40	-	-	-	-	1.75	-					
	K	P	Rp	Z		K	P	Rp	Z		K	P	Rp	Z		K	P	Rp	Z		K	P	Rp	Z	
Alaska	-	-	-	16	-	-	-	-	0.025	-	-	-	-	25	-	-	-	-	1.08	-					
(Williams, in prep.)	-	-	20.3	-	-	-	-	0.019	-	-	-	-	25	-	-	-	-	0.84	-	-					
(McRoy, 1974)	-	16	-	-	-	-	0.031	-	-	-	-	25	-	-	-	-	1.00	-	-	-					
	-	-	-	-	12.5	-	-	-	-	-	-	-	-	-	25	-	-	-	-	1.18					*

one ready to take advantage of a favorable environmental condition, even if brief.

The typical seagrass succession pattern is described by structural changes in species composition from species with small growth forms to those with larger stout forms (Den Hartog, 1977; Figure 14). Seagrass species may be subdivided on the basis of growth forms into at least six categories (Den Hartog, 1967). Species with small growth forms, including the genera *Halodule* and *Halophila*, form the parvozosterid and halophilid categories. Categories of species with larger growth forms are magnozosterids (including the genus *Zostera*) and syringodiids (including the genus *Syringodium*). Enhalids and amphibolids include species with the largest growth forms.

Halodule is known as a seagrass colonizer (Den Hartog, 1970, 1971, 1977). It occurs in places less suitable to other seagrasses and quickly establishes and stabilizes the bottom after disturbances such as boat rutting or storms. If appropriate conditions develop, *Thalassia* eventually colonizes and becomes more important.

Ruppia, while not having a definite position in a seagrass successional scheme and being in a family (Najadaceae) of freshwater and brackish angiosperms, functions in the marine system as a seagrass. *Ruppia* is able to bloom and rapidly colonize areas opened by a change in the physical parameters of the environment (Wetzel, 1964; Nixon and Oviatt, 1973; Welsh, 1975). I found *Ruppia* growing in a tundra lake with a remote ocean inlet near Cold Bay, Alaska one autumn and no evidence of its growth two summers later. I have seen it growing in hypersaline, high temperature isolated spray pools and as a permanent

Scheme of the succession series leading to the *Posidonia oceanica* association. Progressive developments are indicated by thick arrows, regressive developments by thin arrows.

Scheme of the succession series leading to the *Thalassia testudinum* association.

Scheme of a succession series leading via a seagrass community to a forest of giant kelp.

Scheme of a succession series in which seagrasses form the only plant community.

Figure 14. Schemes of seagrass succession series. Figure from Den Hartog (1977).

species in more typical grass bed situations.

The ecology of *Halophila* is not well-known; however, it is also a colonizing and adventitious species (Den Hartog, 1970, 1977). It can also occur in gaps in climax seagrass communities. In the Pacific, a *Halophila* species may be the first to colonize. *Halophila* also dominates in places unsuitable for other species.

Syringodium plays as yet an unknown role in the successional pattern. These data on productivity suggest it should be considered a climax species, having the same type of light-dependence as *Thalassia*, which is well-established as a climax species (Patriquin and Knowles, 1972; Bittaker, 1975; Den Hartog, 1977). I observed in the Caribbean Sea (U.S. and British Virgin Islands and Puerto Rico) that many of the mixed-species grass beds were dominated in terms of density by *Syringodium* whose biomass could equal that of *Thalassia*. I suggest that the classical zonation pattern describing *Syringodium* growing deeper than *Thalassia* (Phillips, 1960; Moore, 1963) is not caused by a difference in the primary response of their productivity to light. An intolerance of *Syringodium* to high light has been the suggested cause (Humm, 1956; Buesa, 1974) but these data showed no such intolerance, despite exposure to irradiances higher than those of Buesa. Buesa (1975) did find *Syringodium* to have a lower compensation energy and to photosynthesize better with blue light than *Thalassia*. If light is the prime factor causing *Syringodium* to grow deeper than *Thalassia*, it is expressed through these differences between the two species' response to light quality, and not in the kinetic response.

North temperate environments: Alaska

In the north temperate environment, the response of productivity to light was essentially identical for all species. I consider this support for the hypothesis that seagrasses have a common type of production system. *Phyllospadix* and *Ruppia* began saturation with light at 25% SI and had similar K_{Lt} values. *Ruppia* had a slightly greater maximum uptake and slightly higher affinity for light than *Phyllospadix* but the difference was not striking enough to label two distinct types of responses. The results of McRoy's (1974) kinetic analysis of *Zostera marina* fell into the pattern for temperate seagrasses I described for *Phyllospadix* and *Ruppia*, although *Zostera* showed more inhibition (Figure 15). The similarity of the three species is remarkable considering the radically different habitats of surf-swept rocks, a brackish tundra lake, and a dense lagoonal grass bed, and considering the experiments were performed in different seasons.

Ruppia and *Phyllospadix* (Den Hartog, 1977) are known as colonizer or adventitious species, while *Zostera* may act as a climax as well as a colonizer species. The species colonizing after the destruction of *Zostera* beds on the U.S. Atlantic coast during the wasting disease of the 1930's was eelgrass, *Zostera* (Cottam and Munro, 1954; Rasmussen, 1977). The two distinct variations of light-dependent productivity seen in the tropical and subtropical plants, a probable result of ecological factors, were not observed in the temperate species. In the temperate zone where species generally occupy distinct niches the evolution of two types of productive response probably did not occur while in the tropics the selective pressure of a competitive co-existence of up to

Figure 15. Light-dependent productivity (means of all experiments) and half-saturation constants in north temperate (Alaska) seagrasses and kelp: *Phyllospadix scouleri*, *Ruppia maritima*, *Zostera marina* (after McRoy, 1974). Kelp after Williams and McRoy (in prep.).

five species perhaps resulted in the two distinct variations I observed.

The ability of one species, *Ruppia*, to demonstrate two productive responses (the colonizer-type in subtropics and the temperate type) is further support for ascribing differences in productive responses to environmental factors, rather than species-specific factors.

Phyllospadix is replaced by canopy-forming kelp and can persist only in areas such as the lower eulittoral and upper sublittoral where canopy-formers do not survive (Den Hartog, 1977). In such areas *Phyllospadix* prevents the establishment of smaller kelp species which are common in the same depth zone wherever *Phyllospadix* does not grow (Black, 1974). In southeast Alaska these kelp species are *Laminaria* and *Alaria*. I performed light-carbon uptake experiments on these species (Williams and McRoy, in prep.) and found response curves and kinetic constants similar to those for *Phyllospadix* (Figure 15; Table 5). This result, indicating the productivity of *Phyllospadix* does not outcompete kelp for irradiance, indirectly supports Black's finding that it is the surfgrass's rhizome system which physically prevents kelp establishment.

I did not expect the production system of brown algae to be similar to that of a vascular seagrass, yet half-saturation constants for kelp compared well with those of *Phyllospadix* and other temperate species. This may be evidence for interpreting half-saturation constants as indicators of environmental 'fitness'. The kelp and the seagrasses are equally well-adapted to the light regime they receive.

I applied a kinetic analysis to data from Rhode Island (Nixon and Oviatt, 1973) for another comparison of temperate *Ruppia*. The linear uptake, saturation irradiance, and P_{max} were intermediate between Texas

and Alaska plants, but the half-saturation constant was similar to the Alaskan *Ruppia* (Table 5). I mentioned early in the discussion that the difference in maximum productivity between Texas and Alaska was a result of the increased light available in Texas. A low saturation irradiance enables the plant to achieve maximum uptake even at low irradiances, which would be advantageous to a temperate plant with an annual growth ecology. The tropical species are exposed to only small variations in the seasonal irradiance and therefore by having extended first-order phases can respond well to such small variations.

Productivity Patterns: Evidence for Process Succession

The theory of succession (Margalef, 1968; Odum, 1969) describes an orderly, directed, predictable process of community or ecosystem development and resultant modification of the physical environment. The result of succession is a stabilized ecosystem with a store of information accumulated in feedback mechanisms. Although succession has been described most frequently in structural terms such as changes in species composition, changes in functional aspects occur also. McRoy (pers. com.) has termed the changes in functional processes, reflected in structural changes and occurring over a gradient of ecosystem development, as process succession. He viewed the slowness of *Zostera* ecosystems to recover after the wasting disease of the 1930's, despite the high growth rates of the plants, to be a result of process succession. The recovery was dependent on the development of the slowest process in the system, which was decomposition (McRoy and Bridges, 1975).

Recovery from disturbance of *Thalassia* beds is the analogous situa-

tion for the North American tropics and subtropics. *Thalassia*, like *Zostera*, is a climax species and depends, for example, on the oxidation-reduction conditions in the sediment be maintained within a narrow range by the seagrass community (Zieman, 1976). Recovery of *Thalassia* beds appears not to be timed to rapid growth but rather to the slow development of processes, such as those expressed by oxidation-reduction conditions.

Further support for process succession is found in the development of feedback mechanisms in nutrient cycles. In old field succession, colonizing plants depend primarily on nitrogen fixation yet as succession advances inhibition of nitrification increases proportionally, assuring nitrogen accumulation (Rice *et al.*, 1960; Rice, 1971; Rice and Pancholy, 1972, 1973 and 1974). The inhibition is biological feedback in the form of root exudates or leaf leachates. In seagrass beds process succession of nutrient cycles along a gradient of plant development from external nutrient sources to increasingly internal, or system-controlled, ones also occurs. Capone and Taylor (unpublished manuscript) found more nitrogen fixation at the edge of *Thalassia* beds where presumably sparse plant growth could not build up the organic nitrogen levels possible in the dense center of the bed where the detritus system is developed better. Patriquin (1972) found gradients of reducing conditions corresponding to gradients of seral development in Caribbean grass beds. Reduction conditions were probably indicative of sulfur cycle processes.

Productivity processes also undergo succession. Biomass and primary production generally increase. More importantly, the ratio of primary

production to total biomass drops. As the seagrass community succeeds the smaller species (halophilids and parvozosterids) are replaced by larger ones (enhalids and amphibolids, magnozosterids and syringodiids). These larger species can attain higher standing stocks and areal production. It is these larger species, represented by *Thalassia* and *Syringodium*, which also have the lower instantaneous productivities than the smaller ones such as *Halodule*, *Ruppia*, and *Halophila*, which appear early in succession. Therefore as succession progresses in seagrass beds, the ratio of primary production to biomass is lowered.

Prediction of Seagrass Productivity

By quantifying the relationship of productivity to its major forcing function, light, these data may be used to predict productivity from measurements of light. Platt *et al.* (1975) provided an excellent review and discussion of the strengths and limitations of the extensive types of productivity predictions that have been made for phytoplankton. Predictions of seagrass productivity are few (Short, 1975) largely due to lack of basic understanding of the photosynthetic response of seagrasses to light.

McRoy (1974) suggested prediction of *Zostera* productivity using what is commonly known as the Michaelis-Menton kinetic equation. He found this equation can empirically describe the hyperbolic light-productivity curve in *Zostera* for irradiances below 50% SI. The equation is

$$P = \frac{P_{\max} \cdot I}{K_{Lt} + I}$$

where P = uptake rate ($\text{mg C} \cdot \text{g(dry)}^{-1} \cdot \text{hr}^{-1}$),

P_{max} = maximum uptake rate,

I = *in situ* irradiance (% SI or $\text{ly} \cdot \text{hr}^{-1}$),

K_{Lt} = irradiance where $P = 1/2 P_{\text{max}}$.

The K_{Lt} and P_{max} values I found may be used in this expression. The results of these kinetic experiments suggest that in any location the establishment of one seagrass species' K_{Lt} will establish K_{Lt} for any other seagrass growing in the area. P_{max} must also be established. In the temperate regions P_{max} found for one species will probably be a good approximation for all species growing there. In the subtropics and tropics a P_{max} for colonizer species (halophilids and parvozosterids) and a P_{max} for climax species (magnozosterids, syringodiids, enhalids, and amphibolids) must be established separately. P_{max} for colonizer species will most frequently occur at irradiances less than 100% SI, while P_{max} for climax species is likely to occur at surface irradiances, and the experimental design for measuring P_{max} should reflect this.

Prediction using the Michaelis-Menton relationship assumes that light is the single factor limiting productivity. In nature probably more than one factor limits productivity. Experiments, such as I performed, repeated under different temperature, salinity, and nutrient conditions would evolve a family of curves to add degrees of predictability to the formulation. In addition, insight into the factors controlling P_{max} would be gained. I discussed the theoretical qualification of using a variable (P_{max}) to generate a constant (K_{Lt}), but I do not know how serious a limitation this is to using the expression. It is certainly worthy of consideration.

The Michaelis-Menton equation will not describe photo-inhibition. In subtropical and tropical climax species and in the temperate species I examined this is not a serious limitation. For subtropical and tropical colonizer species the expression may not be appropriate for predictive purposes.

Steele (1962) developed a formulation (eq. 3) which incorporated a term for photo-inhibition. Short (1975) and Short and McRoy (in prep.) used Steele's equation to predict *Zostera* productivity with good success; I had less success (Table 6). Steele's equation did not predict the majority of the observed inhibition and with few exceptions predicted the irradiance (I_{opt}) yielding the maximum productivity to be greater than the measured surface irradiance. A main feature of Steele's equation is that seasonal adaptations to light are expressed through I_{opt} . If I_{opt} is greater than the actual surface irradiance, the plants may have been adapted to a previous period of higher average surface irradiance. Short (1975) found evidence for a period of 30 days for *Zostera* to adapt to a different average irradiance. Jones (1968) also observed seasonal adaptations of productivity to irradiance in *Thalassia*. Where I_{opt} was predicted to be unreasonably, even orders of magnitude, greater than the surface irradiance, the corresponding predicted P_{max} was much higher than any range of actual rates. On a day when a plant does not reach saturation and uptake is proportional to light, such a prediction may be expected. I did not find Steele's equation consistently predicting very high I_{opt} for days when the seagrasses were not saturated. I expected very high I_{opt} to occur in the *Phyllospadix* data for the low irradiance days; it did not. For *Thalassia* and *Syringodium* from Texas

Table 6. Comparison of observed productivity data with that predicted by Steele's equation.

Date	Surface Irradiance ($\text{ly}\cdot\text{hr}^{-1}$)	Observed Mean P_{max} ($\text{mgC}\cdot\text{g}(\text{dry})^{-1}\cdot\text{hr}^{-1}$)	Corresponding Predicted Point	Inhibition (*indicates inhibition)	Optimal Irradiance ($\text{ly}\cdot\text{hr}^{-1}$)	Predicted P_{max} ($\text{mgC}\cdot\text{g}(\text{dry})^{-1}\cdot\text{hr}^{-1}$)	Predicted Inhibition (*indicates predicted inhibition)	CHI-Square Goodness of Fit
Puerto Rico								
<i>Thalassia testudinum</i>								
28 May 75	68.1	3.07	2.79		19596.0	296.72		3.0
29 May 75	47.9	3.17	3.07		60.8	3.08		2.9
31 May 75	81.1	4.70	4.01		16301.0	388.41		3.9
1 June 75	70.0	1.46	1.50		77.1	1.51		0.6
<i>Syringodium filiiforme</i>								
28 May 75	68.1	2.73	2.69	*	59.2	2.72		2.4
29 May 75	47.9	2.18	2.74		174.0	3.97		1.7
30 May 75	76.6	2.91	2.94		125.7	3.27		1.3
31 May 75	81.1	6.28	6.56		15778.2	471.94		1.2
1 June 75	70.0	2.64	2.69		151.7	3.49		1.1
2 June 75	70.0	3.47	3.24		95.6	3.38		2.1
<i>Halodule wrightii</i>								
30 May 75	76.6	3.06	2.63	*	5.4	2.77	*	3.1
30 May 75	81.1	17.23	17.31		96.6	17.57		5.3
1 June 75	70.0	8.47	7.32		102.4	7.79		13.1
2 June 75	70.0	19.01	14.54	*	61.7	14.73		15.2
Cuba								
<i>Thalassia testudinum</i>								
Buesa, 1975	24.0	2.15	1.94	*		1.94	*	0.1
Buesa, 1975	21.6	4.20	2.75	*		2.91		2.1

Table 6. Continued

Date	Surface Irradiance ($\text{ly}\cdot\text{hr}^{-1}$)	Observed Mean P_{max} ($\text{mgC}\cdot\text{g}(\text{dry})^{-1}\cdot\text{hr}^{-1}$)	Corresponding Predicted Point	Inhibition (*indicates inhibition)	Optimal Irradiance ($\text{ly}\cdot\text{hr}^{-1}$)	Predicted P_{max} ($\text{mgC}\cdot\text{g}(\text{dry})^{-1}\cdot\text{hr}^{-1}$)	Predicted Inhibition (*indicates predicted inhibition)	CHI-Square Goodness of Fit
Texas								
<i>Thalassia testudinum</i>								
10 Aug 74	68.6	1.33	1.14		49859.4	305.08		0.5
11 Aug 74	69.1	1.37	1.25	*	114.0	1.39		1.5
12 Aug 74	41.7	1.73	1.70		46949.4	705.64		0.9
17 Aug 74	79.7	1.39	1.49	*	192.6	2.01		1.1
<i>Syringodium filiforme</i>								
10 Aug 74	68.6	1.35	1.27		916.8	413.81		0.2
11 Aug 74	69.1	1.73	1.56	*	181.7	2.21		1.0
12 Aug 74	41.7	1.39	1.54		300.8	4.69		1.3
13 Aug 74	81.4	1.26	1.23		59728.2	331.18		1.2
17 Aug 74	79.7	1.48	1.56		1109.4	8.59		0.2
<i>Halodule wrightii</i>								
10 Aug 74	68.6	3.03	2.09	*	221.8	3.81		2.2
11 Aug 74	69.1	4.05	4.34		3316.2	78.25		1.4
13 Aug 74	81.4	3.16	2.01	*	51387.6	638.49		1.5
17 Aug 74	79.7	4.02	2.82	*	22011.6	393.44		2.3
<i>Ruppia maritima</i>								
10 Aug 74	68.6	3.11	2.31	*	67.6	2.33		3.6
11 Aug 74	69.1	5.22	4.55	*	441.6	12.51		5.1
12 Aug 74	41.7	3.14	3.27		29986.2	865.45		1.8
13 Aug 74	81.4	3.14	1.84	*	30582.0	348.77		0.2
17 Aug 74	79.7	3.47	2.01	*	150.5	3.06		2.3

Table 6. Continued

Date	Surface Irradiance ($\text{ly}\cdot\text{hr}^{-1}$)	Observed Mean P_{max} ($\text{mgC}\cdot\text{g}(\text{dry})^{-1}\cdot\text{hr}^{-1}$)	Corresponding Predicted Point	Inhibition (*indicates inhibition)	Optimal Irradiance ($\text{ly}\cdot\text{hr}^{-1}$)	Predicted P_{max} ($\text{mgC}\cdot\text{g}(\text{dry})^{-1}\cdot\text{hr}^{-1}$)	Predicted Inhibition (*indicates predicted inhibition)	CHI-Square Goodness of Fit
Texas (cont'd)								
<i>Halophila engelmanni</i>								
10 Aug 74	68.6	2.37	2.34	*	54.6	2.41	*	0.5
12 Aug 74	41.7	3.45	3.06	*	58.9	3.23		2.4
13 Aug 74	81.4	2.75	3.13		32598.0	461.71		2.3
Alaska								
<i>Ruppia maritima</i>								
17 Oct 75	24.3	1.08	1.05		19.8	1.07		0.7
<i>Phyllospadix scouleri</i>								
7 Aug 75	52.3	1.00	0.82	*	28.8	0.82	*	0.3
9 Aug 75	18.6	1.16	2.52		106.5	2.52		0.7
13 Aug 75	46.4	0.81	0.70		355.8	0.70	*	0.6
14 Aug 75	29.4	1.32	1.12		40.6	1.12		0.4

very high I_{opt} values were reasonable from the shape of the light curves, which could be fit as straight lines on some days. In the rest of the data very high I_{opt} values indicated Steele's equation may not be a good predictor. The fault may be too much scatter in the data, causing a straight line to be the best least-squares fit and suggesting no saturation occurred, which would yield a very high I_{opt} .

SUMMARY AND CONCLUSIONS

I found high productivity (0.81 to $17.31 \text{ mg C} \cdot \text{g(dry)}^{-1} \cdot \text{hr}^{-1}$) in six North American seagrass species. Productivity increased on a north to south geographical gradient, corresponding to an increase in irradiance. Despite similar irradiance available to the plants in Texas and Puerto Rico the maximum rates were significantly different and I have suggested this is a result of physiological stress, primarily temperature, the plants experienced in Texas, near the northern limit of their distribution.

The response of productivity to light in these seagrasses was characterized by a phase of linear, first-order kinetic reaction at low irradiances where uptake was proportional to light. At an apparent saturation irradiance uptake was no longer limited by light; after saturation occurred maximum uptake was reached. At high irradiances inhibition occurred.

Certain details of the general response were the same for species growing in the same climatic region, such as the saturation irradiance and half-saturation constant. This is evidence for the existence of a common seagrass production system. In addition the light curves did

not intersect, suggesting the species were not in direct competition for light. And in the majority of the situations the light curves were essentially identical.

In the tropics and subtropics, represented by plants from Puerto Rico and Texas, two distinct variations of the basic seagrass light-dependent productivity occurred. The colonizer species *Halodule*, *Ruppia*, and *Halophila* showed more rapid linear uptake, higher maximum productivity, and more frequent inhibition than the climax species *Thalassia* and *Syringodium*. As *Syringodium* was essentially identical to *Thalassia* light quantity is probably not the primary factor restricting *Syringodium* to deeper waters than *Thalassia*.

The temperate species *Phyllospadix* and *Ruppia* had almost identical light-dependent productivity, and their response was very similar to that described for *Zostera* (McRoy, 1974). The temperate plants saturated much sooner than the tropical and subtropical plants.

I conclude that seagrasses have the same basic type of production system and base my conclusion on the similarities in the response of their productivities to light, such as general shape of their light curves, saturation irradiance, and half-saturation constants. The implication follows that differences in maximum productivity are not a result of species-specific factors but environmental factors such as differing available irradiance, stress to physiological tolerances, or ecological factors such as growth strategy and role in succession. Within its geographical range one species, *Ruppia*, showed two adaptations of the fundamental pattern of light-dependent productivity for two different types of habitats. I suggest that where species co-exist at

least two non-competitive types of productive strategies will occur, one for colonizer species (halophilids and parvozosterids), the other for climax species (magnozosterids and syringodiids, and/or amphibolids and enhalids). These strategies are expressions of process succession in seagrass ecosystems.

Understanding of productivity ideally dependent on light allows prediction from light measurements. The Michaelis-Menton kinetic equation and Steele's equation are only two of the many possible models to use for prediction of productivity.

A major lacking in the understanding of seagrass productivity is the control of maximum productivity. Light, temperature, salinity, nutrients, and position in the seagrass successional pattern are sure to interact to influence the maximum productivity. Families of response curves for each variable would increase the usefulness of predictive analyses, and should form the next conceptual step in understanding seagrass productivity.

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APPENDIX A

IRRADIANCE AND CARBON UPTAKE DATA CORRECTED FOR
DARK UPTAKE

APPENDIX A. Irradiance and carbon uptake data corrected for dark uptake.

Location Species Date	Irradiance $\text{ly}\cdot\text{hr}^{-1}$	% Surface Irradiance	Leaf ($\text{mgC}\cdot\text{g}(\text{dry})^{-1}\cdot\text{hr}^{-1}$)	Root ($\text{mgC}\cdot\text{g}(\text{dry})^{-1}\cdot\text{hr}^{-1}$)	Leaf & Root ($\text{mgC}\cdot\text{g}(\text{dry})^{-1}\cdot\text{hr}^{-1}$)	Leaf ($\text{mgC}\cdot\text{g}(\text{dry})^{-1}\cdot\text{ly}^{-1}$)	Root ($\text{mgC}\cdot\text{g}(\text{dry})^{-1}\cdot\text{ly}^{-1}$)	Leaf & Root ($\text{mgC}\cdot\text{g}(\text{dry})^{-1}\cdot\text{ly}^{-1}$)	$\frac{\text{Root uptake}}{\text{Leaf uptake}} \times 100$
Puerto Rico									
<i>Thalassia testudinum</i>									
28 May 1975	0.7	1	0.06	0.02	0.07	0.0009	0.0002	0.0011	27
		1	0.07	0.00	0.06	0.0010	0.0001	0.0009	0
	17.0	25	0.08	0.00	0.08	0.0012	0.0000	0.0012	0
		25	0.54	0.58	1.12	0.0079	0.0085	0.0164	7
	34.1	50	1.91	0.07	1.98	0.0281	0.0010	0.0294	4
		50	2.03	--	--	0.0298	--	--	--
		50	2.41	0.00	2.41	0.0354	0.0000	0.0354	0
	51.1	75	1.47	0.00	1.47	0.0215	0.0000	0.0215	0
		75	1.34	0.00	1.34	0.0170	0.0000	0.0170	0
		75	1.53	0.04	1.57	0.0225	0.0006	0.0231	3
	68.1	100	3.57	0.17	3.74	0.0524	0.0023	0.0548	5
		100	2.97	0.13	3.10	0.0435	0.0017	0.0453	4
		100	1.30	1.07	2.37	0.0191	0.0158	0.0348	83
29 May 1975	0.6	1	0.07	0.00	0.07	0.0011	0.0000	0.0011	0
		1	0.25	0.00	0.26	0.0040	0.0001	0.0041	2
		1	0.12	0.00	0.12	0.0019	0.0000	0.0019	0
	16.0	25	0.99	--	--	0.0155	--	--	--
		25	1.16	0.01	1.17	0.0181	0.0002	0.0183	1
		25	0.93	--	--	0.0145	--	--	91
	31.9	50	4.46	0.01	4.47	0.0698	0.0001	0.0699	0
		50	1.81	0.00	1.81	0.0283	0.0001	0.0284	0
		50	2.52	0.00	2.52	0.0394	0.0000	0.0394	0
	47.9	75	2.50	--	--	0.0392	--	--	--
		75	2.02	--	--	0.0317	--	--	--
		75	2.08	0.01	2.09	0.0327	0.0001	0.0328	0
	63.8	100	3.82	0.08	3.90	0.0599	0.0012	0.0611	2
		100	2.15	0.03	2.18	0.0337	0.0004	0.0341	1
		100	3.41	0.04	3.44	0.0435	0.0006	0.0540	1

APPENDIX A. (continued)

Location Species Date	Irradiance	% Surface irradiance	Leaf	Root	Leaf & root	Leaf	Root	Leaf & root	Root uptake Leaf uptake	x 100
31 May 1975	0.8	1	0.01	0.00	0.01	0.0001	0.0000	0.0002	7	
		1	0.06	0.02	0.07	0.0007	0.0002	0.0009	30	
		1	0.08	--	--	0.0010	--	--	--	
	20.3	25	0.83	--	--	0.0102	--	--	--	
		25	0.64	0.03	0.67	0.0079	0.0004	0.0083	5	
		25	0.67	--	--	0.0082	--	--	--	
	40.6	50	1.37	0.19	1.57	0.0169	0.0024	0.0193	14	
		50	1.45	--	--	0.0178	--	--	--	
		50	2.03	--	--	0.0251	--	--	--	
	60.8	75	1.27	--	--	0.0156	--	--	--	
		75	1.50	0.06	1.56	0.0185	0.0007	0.0191	4	
		75	1.04	--	--	0.0128	--	--	--	
	81.1	100	1.21	--	--	0.0149	--	--	--	
		100	3.54	3.51	7.04	0.0436	0.0433	0.0869	99	
		100	2.20	0.17	2.36	0.0271	0.0020	0.0291	7	
1 June 1975	0.7	1	0.02	0.01	0.03	0.0003	0.0001	0.0004	33	
		1	0.04	0.02	0.06	0.0005	0.0003	0.0008	52	
		1	0.04	0.01	0.05	0.0005	0.0001	0.0007	26	
	17.5	25	0.54	0.02	0.57	0.0077	0.0004	0.0081	5	
		25	0.55	0.06	0.61	0.0079	0.0008	0.0087	11	
		25	0.44	0.07	0.51	0.0063	0.0010	0.0073	16	
	35.0	50	1.40	0.29	1.69	0.0200	0.0041	0.0241	20	
		50	0.45	--	--	0.0065	--	--	--	
		50	1.12	--	--	0.0160	--	--	--	
	52.5	75	1.90	--	--	0.0272	--	--	--	
		75	1.28	--	--	0.0182	--	--	--	
		75	1.57	--	--	0.0224	--	--	--	
	70.0	100	1.76	0.16	1.93	0.0252	0.0023	0.0275	9	
		100	1.19	0.08	1.27	0.0170	0.0011	0.0181	7	
		100	1.02	0.16	1.18	0.0146	0.0023	0.0169	16	
Puerto Rico <i>Syringodium filiforme</i> 28 May 1975	0.7	1	0.03	0.00	0.03	0.0004	0.0000	0.0004	0	
		1	0.00	0.00	0.00	0.0000	0.0000	0.0000	0	
		1	0.01	0.00	0.01	0.0001	0.0000	0.0001	7	
	17.0	25	0.86	0.02	0.88	0.0126	0.0002	0.0129	2	
		25	0.90	0.00	0.90	0.0132	0.0000	0.0132	0	
		25	1.11	0.01	1.12	0.0163	0.0001	0.0164	1	

APPENDIX A. (continued)

Location Species Date	Irradiance	% Surface irradiance	Leaf	Root	Leaf & root	Leaf	Root	Leaf & root	Root uptake Leaf uptake	X 100
29 May 1975	34.1	50	2.04	0.07	2.10	0.0299	0.0010	0.0309	3	
		50	2.82	0.00	2.82	0.0414	0.0000	0.0414	0	
		50	3.57	0.07	3.64	0.0290	0.0006	0.0296	2	
	51.1	75	2.82	0.02	2.84	0.0414	0.0003	0.0417	1	
		75	2.59	0.02	2.60	0.0380	0.0002	0.0382	1	
		75	3.54	0.01	3.55	0.0521	0.0001	0.0522	0	
	68.1	100	1.57	0.01	1.58	0.0230	0.0001	0.0232	1	
		100	2.75	0.03	2.78	0.0404	0.0005	0.0409	1	
	0.6	1	0.00	0.00	0.00	0.0000	0.0000	0.0000	0	
		1	0.00	0.00	0.00	0.0010	0.0000	0.0010	0	
		1	0.00	0.01	0.01	0.0000	0.0001	0.0001	0	
	16.0	25	1.13	0.01	1.14	0.0177	0.0001	0.0178	0	
		25	0.23	0.00	0.23	0.0036	0.0000	0.0036	0	
		25	0.91	0.00	0.91	0.0143	0.0000	0.0143	0	
	31.9	50	1.04	0.01	1.04	0.0163	0.0001	0.0164	1	
		50	2.49	0.05	2.53	0.0390	0.0007	0.0397	2	
		50	1.77	0.01	1.78	0.0277	0.0002	0.0279	1	
	47.9	75	0.29	--	--	0.0045	--	--	--	
		75	2.38	0.02	2.40	0.0373	0.0004	0.0377	1	
		75	2.00	0.01	2.10	0.0314	0.0001	0.0316	0	
	63.8	100	3.50	0.00	3.50	0.0549	0.0000	0.0549	0	
		100	2.39	0.02	2.41	0.0374	0.0003	0.0377	1	
		100	2.25	0.02	2.28	0.0353	0.0004	0.0357	1	
30 May 1975	0.8	1	0.02	0.00	0.02	0.0003	0.0000	0.0003	0	
		1	0.03	0.00	0.03	0.0004	0.0000	0.0004	0	
		1	0.06	0.01	0.07	0.0008	0.0001	0.0009	12	
	19.2	25	0.88	0.02	0.91	0.0115	0.0003	0.0118	3	
		25	0.41	0.01	0.42	0.0053	0.0001	0.0054	2	
		25	1.35	0.02	1.37	0.0177	0.0002	0.0179	1	
	38.3	50	1.71	--	--	0.0223	--	--	--	
		50	2.42	0.06	2.48	0.0316	0.0007	0.0324	2	
		50	2.82	0.04	2.32	0.0297	0.0005	0.0302	2	
	57.5	75	2.75	0.02	2.77	0.0359	0.0003	0.0362	1	
		75	1.90	0.04	1.93	0.0248	0.0005	0.0253	2	
		75	2.73	0.09	2.82	0.0356	0.0012	0.0368	3	
	76.6	100	2.17	0.05	2.22	0.0283	0.0006	0.0290	2	
		100	3.54	0.05	3.59	0.0462	0.0006	0.0468	1	

APPENDIX A. (continued)

Location Species Date	Irradiance	% Surface irradiance	Leaf	Root	Leaf & root	Leaf	Root	Leaf & root	Root uptake Leaf uptake	X 100
31 May 1975	0.8	1	0.20	0.00	0.20	0.0025	0.0000	0.0025	0	
		1	0.24	0.00	0.24	0.0029	0.0000	0.0029	0	
		1	0.05	0.00	0.05	0.0007	0.0000	0.0007	20	
	20.3	25	1.59	0.07	1.66	0.0196	0.0008	0.0204	4	
		25	1.65	0.02	1.67	0.0239	0.0002	0.0241	1	
		25	1.02	0.00	1.01	0.0125	0.0001	0.0125	0	
	40.6	50	3.73	0.02	3.76	0.0460	0.0003	0.0463	1	
		50	2.15	0.00	2.15	0.0265	0.0001	0.0265	0	
	60.8	75	5.44	0.08	5.52	0.0671	0.0010	0.0681	1	
		75	5.63	0.08	5.72	0.0694	0.0010	0.0704	1	
	81.1	100	6.19	0.07	6.26	0.0764	0.0008	0.0772	1	
		100	6.23	0.07	6.30	0.0768	0.0009	0.0777	1	
1 June 1975	0.7	1	0.01	0.00	0.01	0.0001	0.0000	0.0001	0	
		1	0.02	0.00	0.02	0.0004	0.0002	0.0006	0	
		1	0.04	0.00	0.04	0.0006	0.0000	0.0006	0	
	17.5	25	0.50	0.00	0.50	0.0072	0.0002	0.0072	0	
		25	1.11	0.01	0.12	0.0159	0.0001	0.0160	1	
		25	0.40	0.01	0.41	0.0057	0.0001	0.0058	1	
	35.0	50	1.65	--	--	0.0236	--	--	--	
		50	1.39	0.00	1.93	0.0276	0.0001	0.0275	0	
		50	2.12	0.02	2.14	0.0304	0.0002	0.0306	1	
	52.5	75	2.28	0.02	2.30	0.0326	0.0003	0.0329	1	
		75	2.76	0.06	2.82	0.0394	0.0009	0.0403	2	
		75	1.57	0.02	1.58	0.0224	0.0002	0.0226	1	
	70.0	100	2.39	0.06	2.45	0.0342	0.0008	0.0351	2	
		100	2.78	0.04	2.82	0.0400	0.0006	0.0406	1	
2 June 1975	0.7	1	0.15	0.00	0.15	0.0022	0.0000	0.0022	1	
		1	0.08	0.00	0.08	0.0011	0.0001	0.0012	5	
		1	0.05	0.00	0.05	0.0007	0.0000	0.0007	1	
	17.5	25	2.03	0.08	2.11	0.0290	0.0011	0.0302	4	
		25	1.15	0.02	1.17	0.0164	0.0002	0.0167	1	
		25	2.39	0.01	2.40	0.0341	0.0001	0.0342	0	
	35.0	50	1.87	0.12	1.98	0.0267	0.0017	0.0283	6	
		50	1.88	0.06	1.94	0.0269	0.0009	0.0279	3	
		50	2.27	0.04	2.31	0.0324	0.0006	0.0330	2	

APPENDIX A. (continued)

Location Species Date	Irradiance	% Surface irradiance	Leaf	Root	Leaf & root	Leaf	Root	Leaf & root	Root uptake Leaf uptake	x 100
	52.5	75	2.60	0.01	2.61	0.0371	0.0002	0.0373	1	
		75	2.53	0.01	2.54	0.0361	0.0002	0.0363	0	
		75	2.77	0.02	2.79	0.0396	0.0003	0.0399	1	
	70.0	100	2.54	0.01	2.54	0.0362	0.0001	0.0363	0	
		100	4.49	0.06	4.55	0.0613	0.0009	0.0622	1	
		100	3.21	0.10	3.31	0.0459	0.0014	0.0473	3	
Puerto Rico <i>Halodule wrightii</i> 30 May 1975	0.8	1	0.02	0.00	0.02	0.0002	0.0000	0.0002	7	
	19.2	25	1.41	0.04	1.45	0.0185	0.0005	0.0189	3	
		25	3.02	0.07	3.09	0.0394	0.0009	0.0403	2	
		25	0.79	0.21	0.99	0.0103	0.0027	0.0130	26	
	38.3	50	2.83	0.23	3.06	0.0369	0.0031	0.0400	8	
		50	2.39	--	--	0.0312	--	--	--	
		50	3.40	--	--	0.0443	--	--	--	
	57.5	75	1.92	0.24	2.16	0.0251	0.0031	0.0282	12	
		75	4.15	--	--	0.0542	--	--	--	
		75	2.09	--	--	0.0273	--	--	--	
	76.6	100	3.93	0.19	4.11	0.0513	0.0024	0.0537	5	
		100	1.31	0.40	1.35	0.0171	0.0005	0.0176	3	
31 May 1975	0.8	1	0.04	0.00	0.04	0.0005	0.0000	0.0005	0	
		1	0.13	0.00	0.11	0.0017	0.0000	0.0017	0	
		1	0.24	0.00	0.24	0.0030	0.0000	0.0003	0	
	20.3	25	9.62	0.18	9.80	0.1186	0.0023	0.1209	2	
		25	4.68	0.16	4.84	0.0577	0.0020	0.0597	3	
	40.6	50	12.97	1.45	14.42	0.1599	0.0179	0.1778	11	
		50	12.98	0.62	13.60	0.0071	0.0076	0.1677	5	
	60.8	75	11.07	0.87	11.96	0.1366	0.0108	0.1474	8	
		75	16.84	2.86	19.70	0.2076	0.0352	0.2429	17	
	81.1	100	14.28	0.71	15.00	0.1761	0.0088	0.1849	5	
		100	19.91	0.62	20.53	0.2455	0.0077	0.2532	3	
		100	15.99	0.16	16.16	0.1972	0.0020	0.1992	1	
1 June 1975	0.1	1	0.12	0.03	0.15	0.0017	0.0004	0.0022	26	
		1	0.04	0.03	0.07	0.0006	0.0004	0.0010	65	
		1	0.17	0.01	0.18	0.0024	0.0001	0.0025	5	

APPENDIX A. (continued)

Location Species Date	Irradiance	% Surface irradiance	Leaf	Root	Leaf & root	Leaf	Root	Leaf & root	Root uptake Leaf uptake	X 100
2 June 1975	17.5	25	2.45	0.07	2.52	0.0340	0.0010	0.0361	3	
		25	2.41	0.08	2.49	0.0345	0.0011	0.0356	3	
		25	4.21	0.36	4.57	0.0602	0.0051	0.0652	8	
	35.00	50	4.95	0.44	5.40	0.0708	0.0064	0.0771	9	
		50	8.50	0.62	9.12	0.1214	0.0089	0.1303	7	
		50	4.91	0.44	5.36	0.0701	0.0063	0.0765	9	
	52.5	75	1.30	0.93	2.23	0.0185	0.0133	0.0319	72	
		75	0.40	0.50	0.91	0.0057	0.0072	0.0130	25	
		75	7.52	1.27	8.79	0.1074	0.0182	0.1256	17	
	70.0	100	8.13	0.74	8.87	0.1161	0.0106	0.1267	9	
		100	7.23	0.64	7.86	0.1033	0.0091	0.1124	9	
		100	8.37	0.41	8.68	0.1181	0.0058	0.1239	5	
	0.7	1	0.20	--	--	0.0029	--	--	--	
		1	0.21	0.03	0.24	0.0030	0.0004	0.0034	13	
		1	0.15	0.01	0.16	0.0021	0.0001	0.0022	4	
	17.5	25	3.12	0.34	3.46	0.0446	0.0049	0.0495	11	
		25	9.29	--	--	0.1327	--	--	--	
		25	8.06	0.54	8.60	0.1152	0.0076	0.1228	7	
	35.0	50	14.87	1.24	16.11	0.2125	0.0177	0.2302	8	
		50	13.69	0.59	14.28	0.1955	0.0085	0.2040	4	
		50	5.25	0.40	5.65	0.0750	0.0057	0.0807	8	
	52.5	75	16.70	0.60	17.30	0.2385	0.0086	0.2471	4	
		75	17.69	1.75	19.44	0.2528	0.0250	0.2777	10	
		75	18.43	1.86	20.29	0.2633	0.0266	0.2899	10	
	70.0	100	9.11	0.50	9.61	0.1301	0.0071	0.1372	5	
		100	10.71	0.73	11.43	0.1529	0.0104	0.1633	7	
Texas <i>Thalassia testudinum</i> 10 August 1974	43.9	64	0.56	0.21	0.76	0.0081	0.0030	0.0111	37	
		64	0.23	0.03	0.26	0.0034	0.0005	0.0038	14	
	50.1	73	0.81	0.35	1.16	0.0118	0.0051	0.0169	44	
		73	0.58	0.22	0.80	0.0085	0.0032	0.0117	37	
	58.3	85	0.83	0.00	0.83	0.0120	0.0001	0.0119	0	
	68.6	100	0.68	0.65	1.33	0.0099	0.0095	0.0194	96	

APPENDIX A. (continued)

Location Species Date	Irradiance	% Surface irradiance	Leaf	Root	Leaf & root	Leaf	Root	Leaf & root	Root uptake Leaf uptake	X 100
11 August 1974	28.3	41	0.35	0.09	0.43	0.0050	0.0012	0.0063	25	
		41	0.24	0.08	0.32	0.0035	0.0012	0.0047	35	
	44.2	64	0.67	0.10	0.77	0.0098	0.0014	0.0111	14	
		64	1.47	0.48	1.96	0.0213	0.0071	0.0284	33	
	50.4	73	0.68	0.35	1.03	0.0098	0.0051	0.0149	52	
		73	0.85	0.42	1.28	0.0123	0.0061	0.0185	50	
	69.1	100	0.98	0.27	1.25	0.0142	0.0039	0.0181	28	
		100	0.70	0.26	0.96	0.0101	0.0038	0.0139	38	
	17.1	41	0.31	0.02	0.34	0.0075	0.0006	0.0081	8	
		41	0.15	0.02	0.17	0.0036	0.0005	0.0041	15	
12 August 1974	26.7	64	1.14	0.42	1.56	0.0275	0.0100	0.0375	37	
		64	0.93	0.24	1.18	0.0224	0.0058	0.0282	26	
	30.4	73	0.79	0.20	0.99	0.0189	0.0049	0.0238	26	
		73	1.31	0.14	1.44	0.0313	0.0032	0.0346	10	
	41.7	100	1.38	0.39	1.77	0.0332	0.0094	0.0425	28	
		100	1.52	0.16	1.68	0.0364	0.0038	0.0402	10	
	32.7	41	0.13	0.11	0.24	0.0017	0.0013	0.0030	79	
		41	0.41	0.23	0.64	0.0052	0.0029	0.0080	55	
17 August 1974	51.0	64	1.18	0.36	1.54	0.0149	0.0045	0.0193	30	
		64	0.78	0.46	1.24	0.0098	0.0058	0.0155	59	
	58.2	73	0.76	0.08	0.84	0.0095	0.0011	0.0106	11	
		73	1.60	0.25	1.86	0.0201	0.0032	0.0233	16	
	79.7	100	1.05	0.41	1.47	0.0132	0.0052	0.0184	39	
		100	0.93	0.30	1.23	0.0116	0.0038	0.0154	33	
	43.9	64	0.47	0.19	0.66	0.0068	0.0028	0.0096	41	
		64	0.37	0.10	0.47	0.0054	0.0014	0.0068	26	
Texas <i>Syringodium filiforme</i> 10 August 1974	50.1	73	0.94	0.07	1.01	0.0137	0.0010	0.0147	8	
	58.3	85	0.75	0.43	1.17	0.0109	0.0062	0.0171	57	
	68.6	100	0.87	0.34	1.21	0.0127	0.0050	0.0177	40	
		100	0.97	0.53	1.49	0.0141	0.0077	0.0217	54	

APPENDIX A. (continued)

Location Species Date	Irradiance	% Surface irradiance	Leaf	Root	Leaf & root	Leaf	Root	Leaf & root	Root uptake Leaf uptake	X 100
11 August 1974	28.3	41	0.28	0.00	0.28	0.0041	0.0000	0.0041	0	
		41	0.56	0.00	0.56	0.0082	0.0000	0.0082	0	
	44.2	64	1.10	0.21	1.31	0.0160	0.0030	0.0190	19	
		73	1.74	0.13	1.88	0.0252	0.0019	0.0271	8	
	50.4	73	1.40	0.18	1.58	0.0203	0.0026	0.0229	13	
		100	0.73	0.41	1.41	0.0106	0.0059	0.0165	56	
	69.1	100	1.02	0.50	1.52	0.0148	0.0072	0.0219	49	
12 August 1974	17.1	41	0.23	0.07	0.29	0.0055	0.0016	0.0071	29	
		41	0.17	0.06	0.24	0.0042	0.0015	0.0057	36	
	26.7	64	0.71	0.20	0.90	0.0169	0.0047	0.0216	28	
		64	1.41	0.36	1.77	0.0338	0.0086	0.0424	25	
	30.4	73	1.22	0.30	1.52	0.0293	0.0071	0.0364	24	
		73	0.96	0.22	1.18	0.0230	0.0054	0.0284	23	
	41.7	100	1.14	0.48	1.62	0.0273	0.0116	0.0389	42	
		100	0.86	0.29	1.15	0.0207	0.0069	0.0277	33	
	13 August 1974	33.4	41	0.24	0.09	0.33	0.0030	0.0011	0.0041	36
41			0.33	0.12	0.44	0.0040	0.0014	0.0055	35	
52.1		64	0.31	0.02	0.34	0.0038	0.0003	0.0041	32	
		64	0.62	0.28	0.91	0.0077	0.0035	0.0111	45	
59.4		73	1.06	0.24	1.30	0.0131	0.0029	0.0160	22	
		73	0.60	0.22	0.82	0.0073	0.0027	0.0100	37	
81.4		100	1.23	0.65	1.88	0.0151	0.0080	0.0230	53	
		100	0.57	0.06	0.63	0.0070	0.0008	0.0078	11	
17 August 1974		32.7	41	0.24	0.10	0.34	0.0030	0.0013	0.0043	42
	41		0.50	0.23	0.72	0.0062	0.0029	0.0091	46	
	51.0	64	0.87	0.23	1.10	0.0109	0.0029	0.0133	27	
		64	0.70	0.52	1.22	0.0088	0.0065	0.0153	74	
	58.2	73	0.95	0.37	1.31	0.0119	0.0046	0.0165	39	
		73	0.72	0.31	1.04	0.0091	0.0040	0.0130	44	
	79.7	100	1.25	0.23	1.48	0.0157	0.0029	0.0186	18	
Texas										
<i>Halodule wrightii</i>										
10 August 1974	43.9	64	0.05	0.64	0.68	0.0007	0.0093	0.0100	89	
	50.1	73	1.12	0.78	1.90	0.0164	0.0113	0.0277	69	

APPENDIX A. (continued)

Location Species Date	Irradiance	% Surface irradiance	Leaf	Root	Leaf & root	Leaf	Root	Leaf & root	$\frac{\text{Root uptake}}{\text{Leaf uptake}} \times 100$
11 August 1974	58.3	85	1.57	1.21	2.78	0.0230	0.0176	0.0406	77
		85	2.12	1.16	3.28	0.0308	0.0170	0.0478	55
	68.6	100	1.87	0.76	2.63	0.0272	0.0111	0.0384	41
		100	1.02	0.08	1.09	0.0148	0.0011	0.0159	7
	28.3	41	0.47	0.31	0.78	0.0068	0.0044	0.0112	66
		41	0.86	0.46	1.32	0.0125	0.0066	0.0191	53
	44.2	64	1.22	1.21	2.43	0.0177	0.0175	0.0352	99
		64	1.95	1.90	3.85	0.0282	0.0275	0.0557	97
	50.4	73	2.96	0.92	3.88	0.0428	0.0133	0.0561	31
		73	2.40	1.15	3.55	0.0347	0.0167	0.0514	48
	69.1	100	2.28	1.69	3.97	0.0330	0.0245	0.0575	74
		100	2.73	1.39	4.12	0.0395	0.0201	0.0596	51
13 August 1974	33.4	41	0.32	0.11	0.43	0.0039	0.0013	0.0052	33
		41	0.36	0.13	0.49	0.0044	0.0016	0.0060	36
	52.1	64	1.13	0.71	1.84	0.0139	0.0087	0.0226	62
		64	1.06	0.54	1.61	0.0130	0.0067	0.0197	51
	59.4	73	1.85	0.31	3.16	0.0227	0.0161	0.0389	71
		100	1.82	0.67	2.49	0.0224	0.0082	0.0306	37
17 August 1974	32.7	41	0.62	0.25	0.87	0.0078	0.0032	0.0110	41
		41	0.38	0.14	0.52	0.0048	0.0018	0.0066	37
	51.0	64	1.33	1.06	2.39	0.0168	0.0133	0.0300	79
		64	1.56	0.61	2.17	0.0196	0.0077	0.0273	39
	58.2	73	2.88	1.46	4.33	0.0361	0.0183	0.0544	51
		73	2.46	1.25	3.71	0.0309	0.0157	0.0466	51
	79.7	100	2.55	0.70	3.25	0.0320	0.0088	0.0408	27
		100	2.50	1.18	3.68	0.0314	0.0148	0.0462	47
Texas <i>Ruppia maritima</i> 10 August 1974	43.9	64	1.43	0.79	2.22	0.0209	0.0115	0.0324	55
		64	1.35	0.48	1.83	0.0197	0.0071	0.0268	36
	50.1	73	1.15	0.37	1.52	0.0168	0.0054	0.0222	32
		73	2.12	0.26	2.38	0.0309	0.0038	0.0348	12
	58.3	85	1.20	0.17	1.37	0.0175	0.0025	0.0200	14
		85	2.61	2.22	4.84	0.0381	0.0324	0.0705	85

APPENDIX A. (continued)

Location Species Date	Irradiance	% Surface irradiance	Leaf	Root	Leaf & root	Leaf	Root	Leaf & root	$\frac{\text{Root uptake}}{\text{Leaf uptake}} \times 100$
	68.6	100	1.79	0.20	1.99	0.0261	0.0029	0.290	11
11 August 1974	28.3	41	0.52	0.19	0.71	0.0075	0.0028	0.0103	37
		41	0.67	0.27	0.94	0.0097	0.0039	0.0136	41
	44.2	64	2.36	0.78	3.14	0.0341	0.0113	0.0455	33
		64	2.23	0.49	2.72	0.0323	0.0070	0.0394	22
	50.4	73	2.71	1.08	3.80	0.0392	0.0157	0.0549	40
		73	6.53	0.10	6.63	0.0945	0.0015	0.0960	2
	69.1	100	1.93	0.92	2.85	0.0279	0.0133	0.0412	48
		100	3.69	1.18	4.88	0.0534	0.0171	0.0706	32
12 August 1974	17.1	41	0.42	0.18	0.60	0.0101	0.0044	0.0145	43
		41	0.43	0.06	0.48	0.0103	0.0013	0.0116	13
	26.7	64	1.96	0.68	2.64	0.0471	0.0163	0.0634	35
		64	1.98	0.37	2.35	0.0475	0.0088	0.0563	18
	30.4	73	2.24	0.70	2.94	0.0537	0.0168	0.0705	31
		100	1.68	0.51	2.20	0.0404	0.0122	0.0526	30
	41.7	100	2.84	1.23	4.07	0.0681	0.0295	0.0976	43
		100	2.84	1.23	4.07	0.0681	0.0295	0.0976	43
13 August 1976	33.4	41	0.38	0.15	0.53	0.0047	0.0019	0.0066	40
		41	0.53	0.17	0.71	0.0066	0.0021	0.0087	32
	52.1	64	1.16	0.43	1.59	0.0142	0.0053	0.0195	37
		64	1.43	0.88	2.30	0.0175	0.0108	0.0283	61
	59.4	73	2.11	1.03	3.14	0.0259	0.0126	0.0386	49
		73	0.17	0.43	0.60	0.0021	0.0052	0.0074	47
	81.4	100	1.64	0.90	2.54	0.0201	0.0111	0.0312	55
		100	1.42	0.94	2.36	0.0175	0.0115	0.0290	66
17 August 1974	32.7	41	0.47	0.02	0.49	0.0059	0.0003	0.0061	5
		41	0.72	0.03	0.74	0.0090	0.0004	0.0094	4
	51.0	64	1.51	1.03	2.54	0.0190	0.0130	0.0319	68
		64	2.48	0.99	3.47	0.0311	0.0125	0.0436	40
	79.7	100	1.25	1.15	2.40	0.0156	0.0145	0.0301	92
		100	1.21	0.98	2.19	0.0152	0.0123	0.0275	81

APPENDIX A. (continued)

Location Species Date	Irradiance	% Surface irradiance	Leaf	Root	Leaf & root	Leaf	Root	Leaf & root	Root uptake Leaf uptake	X 100
Texas										
<i>Halophila engelmanni</i>										
10 August 1974	43.8	64	1.24	0.51	1.75	0.0180	0.0074	0.0255	41	
		64	2.61	0.45	3.06	0.0380	0.0066	0.0446	17	
	50.1	73	1.61	0.53	2.13	0.0234	0.0077	0.0311	33	
		73	1.46	1.11	2.56	0.0212	0.0162	0.0374	76	
	58.3	85	1.42	0.70	2.12	0.0207	0.0103	0.0310	50	
		85	2.12	0.50	2.62	0.0310	0.0072	0.0382	23	
	68.6	100	1.61	0.57	2.18	0.0235	0.0083	0.0318	35	
		100	1.32	1.25	2.56	0.0192	0.0182	0.0374	93	
12 August 1974	17.1	41	0.91	0.29	1.20	0.0217	0.0070	0.0287	32	
		41	0.50	0.07	0.56	0.0119	0.0016	0.0135	14	
	26.4	64	2.22	1.22	3.45	0.0533	0.0293	0.0827	55	
		64	2.05	1.40	3.44	0.0491	0.0335	0.0826	68	
	30.4	73	2.39	1.00	3.39	0.0573	0.0240	0.0812	42	
		73	1.79	1.10	2.89	0.0430	0.0263	0.0692	61	
	41.7	100	1.53	0.48	2.01	0.0367	0.0115	0.0482	31	
		100	2.22	0.97	3.19	0.0531	0.0233	0.0765	44	
13 August 1974	33.4	41	0.56	0.22	0.78	0.0069	0.0027	0.0096	40	
		41	0.20	0.01	0.21	0.0025	0.0002	0.0027	5	
	52.1	64	1.68	1.12	2.80	0.0207	0.0138	0.0345	67	
		64	1.41	0.63	2.04	0.0174	0.0077	0.0251	44	
	59.4	73	2.19	1.37	3.55	0.0269	0.0168	0.0436	63	
		73	1.39	0.29	1.68	0.0170	0.0036	0.0206	21	
	81.4	100	2.09	0.66	2.75	0.0257	0.0081	0.0338	32	
	Alaska									
<i>Phyllospadix scouleri</i>										
7 August 1975	0.5	1	0.02	0.00	0.02	0.0004	0.0000	0.0004	0	
		1	0.03	0.00	0.03	0.0006	0.0000	0.0006	0	
		1	0.01	0.00	0.01	0.0002	0.0000	0.0002	0	
	13.1	25	0.37	0.01	0.38	0.0071	0.0002	0.0073	2	
		25	0.49	--	--	0.0094	--	--	--	
		25	0.54	0.01	0.55	0.0103	0.0002	0.0105	2	
	26.2	50	0.79	0.05	0.84	0.0151	0.0010	0.0161	7	
		50	0.58	0.01	0.59	0.0111	0.0002	0.0113	3	
		50	0.85	0.03	0.88	0.0163	0.0006	0.0169	3	

APPENDIX A. (continued)

Location Species Date	Irradiance	% Surface irradiance	Leaf	Root	Leaf & root	Leaf	Root	Leaf & root	<u>Root uptake</u> <u>Leaf uptake</u>	X 100
9 August 1975	39.2	75	0.80	0.01	0.81	0.0153	0.0002	0.0155	1	
		75	0.97	0.01	0.98	0.0186	0.0002	0.0188	1	
		75	0.99	0.01	1.00	0.0189	0.0002	0.0191	1	
	52.3	100	0.50	0.00	0.50	0.0096	0.0000	0.0096	1	
		100	0.47	0.00	0.47	0.0090	0.0000	0.0090	1	
		100	0.69	0.01	0.39	0.1312	0.0000	0.1312	2	
	0.2	1	0.02	0.00	0.02	0.0009	0.0001	0.0010	8	
		1	0.01	0.00	0.01	0.0005	0.0001	0.0006	17	
		1	0.01	0.00	0.02	0.0008	0.0001	0.0009	14	
	4.7	25	0.42	0.02	0.44	0.0225	0.0009	0.0234	4	
		25	0.50	0.00	0.50	0.0268	0.0002	0.0270	1	
		25	0.38	0.00	0.38	0.0203	0.0001	0.0204	0	
	9.3	50	0.10	0.36	0.46	0.0054	0.0193	0.0247	57	
		50	0.53	0.03	0.55	0.0282	0.0014	0.0296	5	
	14.0	75	0.87	0.03	0.90	0.0467	0.0018	0.0485	4	
		75	0.73	0.02	0.75	0.0393	0.0010	0.0402	2	
	18.6	100	0.01	0.16	1.17	0.0542	0.0084	0.0626	16	
		100	0.87	0.06	0.93	0.0467	0.0033	0.0500	7	
		100	0.89	0.07	0.96	0.0479	0.0036	0.0515	8	
13 August 1975	0.5	1	0.01	0.00	0.01	0.0001	0.0000	0.0001	0	
		1	0.00	0.00	0.00	0.0000	0.0000	0.0000	0	
		1	0.01	0.01	0.02	0.0003	0.0002	0.0005	71	
	11.6	25	0.47	0.01	0.48	0.0100	0.0003	0.0103	3	
		25	1.08	0.01	1.09	0.0232	0.0002	0.0234	1	
		25	0.65	--	--	0.0141	--	--	--	
	23.2	50	0.80	0.01	0.82	0.0173	0.0002	0.0176	1	
		50	0.43	0.01	0.44	0.0094	0.0002	0.0095	2	
		50	1.01	0.01	1.02	0.0217	0.0003	0.0220	1	
	34.8	75	0.74	0.01	0.75	0.0159	0.0003	0.0161	2	
		75	0.66	0.00	0.67	0.0143	0.0001	0.0143	1	
		75	1.03	0.05	1.09	0.0223	0.0012	0.0234	5	

APPENDIX A. (continued)

Location Species Date	Irradiance	% Surface irradiance	Leaf	Root	Leaf & root	Leaf	Root	Leaf & root	<u>Root uptake</u> <u>Leaf uptake</u>	X 100
14 August 1975	46.4	100	1.37	0.02	1.39	0.0296	0.0004	0.0300	1	
		100	0.72	0.01	0.73	0.0155	0.0003	0.0157	2	
		100	0.65	0.00	0.65	0.0141	0.0001	0.0142	1	
	0.3	1	0.02	0.00	0.02	0.0006	0.0001	0.0006	13	
		1	0.00	0.00	0.00	0.0000	0.0000	0.0000	0	
		1	0.01	0.00	0.01	0.0004	0.0001	0.0005	14	
	7.4	25	0.34	0.01	0.35	0.0115	0.0005	0.0120	4	
		25	0.32	0.00	0.32	0.0108	0.0000	0.0108	0	
		25	0.29	0.00	0.29	0.0176	0.0000	0.0176	0	
	14.1	50	0.88	0.00	0.88	0.0299	0.0000	0.0299	0	
		50	0.79	0.00	0.79	0.0268	0.0000	0.0268	0	
		50	0.84	0.00	0.84	0.0287	0.0001	0.0286	0	
	22.1	75	1.09	0.00	1.09	0.0371	0.0001	0.0372	0	
		75	0.61	0.00	0.61	0.0207	0.0001	0.0208	0	
		75	1.02	0.00	1.02	0.0346	0.0001	0.0347	0	
	29.4	100	1.01	0.00	1.01	0.0345	0.0000	0.0345	0	
		100	1.29	0.03	0.74	0.0437	0.0011	0.0449	3	
		100	0.88	0.01	0.89	0.0299	0.0003	0.0302	1	
Alaska <i>Ruppia maritima</i> 17 October 1974	0.2	1	0.08	0.01	0.09	0.0031	0.0005	0.0036	15	
1		0.14	0.00	0.14	0.0056	0.0000	0.0056	0		
2.4	10	0.28	0.00	0.28	0.0116	0.0000	0.0116	0		
	10	0.33	0.02	0.35	0.0135	0.0009	0.0145	7		
6.1	25	0.58	0.06	0.65	0.0240	0.0027	0.0267	11		
	25	0.77	0.05	0.82	0.0318	0.0021	0.0339	7		
12.2	50	0.58	0.19	0.77	0.0239	0.0077	0.0316	32		
24.3	100	1.00	0.37	1.37	0.0412	0.0151	0.0563	37		
	100	0.67	0.11	0.78	0.0278	0.0045	0.0323	16		

APPENDIX B

IRRADIANCE AND CARBON UPTAKE DATA; OBSERVED UPTAKE
AND UPTAKE PREDICTED BY STEELE'S EQUATION

APPENDIX B. Irradiance and carbon uptake data; observed uptake and uptake predicted by Steele's equation.

Location Species Date	Irradiance $\text{ly}\cdot\text{hr}^{-1}$	% Surface Irradiance	Observed Uptake $\text{mgC}\cdot\text{g}(\text{dry})^{-1}\cdot\text{hr}^{-1}$	Predicted Uptake $\text{mgC}\cdot\text{g}(\text{dry})^{-1}\cdot\text{hr}^{-1}$	Optimal Irradiance $\text{ly}\cdot\text{hr}^{-1}$	Predicted Maximum Uptake $\text{mgC}\cdot\text{g}(\text{dry})^{-1}\cdot\text{hr}^{-1}$	Chi-square Goodness of fit
Puerto Rico							
<i>Thalassia testudinum</i>							
28 May 1975	0.7	1	0.07	0.03	19596.0	296.70	3.0
		1	0.06	0.03			
	17.0	25	0.07	0.70			
		25	1.12	0.70			
	34.1	50	1.98	1.40			
		50	2.40	1.40			
	51.1	75	1.47	2.10			
		75	1.16	2.10			
		75	1.57	2.10			
	68.1	100	3.74	2.79			
		100	3.10	2.79			
		100	2.37	2.79			
29 May 1975	0.6	1	0.07	0.09	60.8	3.08	2.9
		1	0.26	0.09			
		1	0.12	0.09			
	15.9	25	1.17	1.69			
	31.9	50	4.47	2.60			
		50	1.81	2.60			
		50	2.52	2.60			
	47.9	75	2.09	3.00			
	63.8	100	3.90	3.07			
		100	2.18	3.07			
		100	3.44	3.07			
31 May 1975	0.8	1	0.01	0.04	16301.0	388.40	3.9
		1	0.07	0.04			
	20.3	25	0.67	1.00			
	40.6	50	1.57	2.00			
	60.8	75	1.56	3.01			
	81.1	100	7.04	4.01			
		100	2.36	4.01			

APPENDIX B. (continued)

Location Species Date	Irradiance	% Surface Irradiance	Observed Uptake	Predicted Uptake	Optimal Irradiance	Predicted Maximum Uptake	Chi-square Goodness of fit
1 June 1975	0.7	1	0.02	0.04	77.1	1.51	0.6
		1	0.05	0.04			
		1	0.05	0.04			
	17.5	25	0.57	0.74			
		25	0.61	0.74			
		25	0.51	0.74			
	35.0	50	1.69	1.18			
	70.0	100	1.93	1.50			
		100	1.27	1.50			
		100	1.18	1.50			
Puerto Rico <i>Syringodium filiforme</i> 28 May 1975	0.7	1	0.05	0.08	59.2	2.72	2.4
		1	0.00	0.08			
		1	0.01	0.08			
	17.0	25	0.88	1.60			
		25	0.90	1.60			
		25	1.12	1.60			
	34.1	50	2.10	2.39			
		50	2.82	2.39			
		50	3.64	2.39			
	51.1	75	2.84	2.69			
		75	2.60	2.69			
		75	3.55	2.69			
	68.1	100	1.58	2.69			
		100	2.78	2.69			
29 May 1975	0.6	1	0.00	0.04	174.0	3.97	1.7
		1	0.00	0.04			
		1	0.00	0.04			
	16.0	25	1.14	0.90			
		25	0.23	0.90			
		25	0.91	0.90			
	31.9	50	1.05	1.65			
		50	2.53	1.65			
		50	1.78	1.65			

APPENDIX B. (continued)

Location Species Date	Irradiance	% Surface Irradiance	Observed Uptake	Predicted Uptake	Optimal Irradiance	Predicted Maximum Uptake	Chi-square Goodness of fit
30 May 1975	47.9	75	2.40	2.52	125.7	3.27	1.3
		75	2.01	2.52			
	63.8	100	3.50	2.74			
		100	2.41	2.74			
		100	2.28	2.74			
	0.8	1	0.02	0.05			
		1	0.03	0.05			
		1	0.06	0.05			
	19.2	25	0.91	1.16			
		25	0.42	1.16			
		25	1.37	1.16			
	38.3	50	2.48	2.00			
		50	2.32	2.00			
	57.5	75	2.77	2.57			
		75	1.93	2.57			
		75	2.82	2.57			
	76.6	100	2.22	2.94			
		100	3.59	2.94			
31 May 1975	0.8	1	0.20	0.07	15778.2	471.94	1.7
		1	0.24	0.07			
		1	0.05	0.07			
	20.1	25	1.66	1.65			
		25	1.67	1.65			
		25	1.01	1.65			
	40.6	50	3.76	3.29			
		50	2.15	3.29			
	60.8	75	5.52	4.93			
		75	5.72	4.93			
	81.1	100	6.26	6.56			
		100	6.30	6.56			

APPENDIX B. (continued)

Location Species Date	Irradiance	% Surface Irradiance	Observed Uptake	Predicted Uptake	Optimal Irradiance	Predicted Maximum Uptake	Chi-square Goodness of fit
1 June 1975	0.7	1	0.01	0.04	15.17	3.49	1.1
		1	0.02	0.04			
		1	0.07	0.04			
	17.5	25	0.50	0.94			
		25	1.11	0.94			
		25	0.40	0.94			
	35.0	50	1.93	1.68			
		50	2.14	1.68			
	52.5	75	2.30	2.25			
		75	2.82	2.25			
		75	1.58	2.25			
	70.0	100	2.45	2.69			
		100	2.82	2.69			
2 June 1975	0.7	1	0.15	0.07	95.6	3.39	2.1
		1	0.08	0.07			
		1	0.05	0.07			
	17.5	25	2.11	1.40			
		25	1.17	1.40			
		25	2.40	1.40			
	35.0	50	1.93	2.34			
		50	1.94	2.34			
		50	2.31	2.34			
	52.5	75	2.61	2.92			
		75	2.54	2.92			
		75	2.79	2.92			
	70.0	100	2.54	3.24			
		100	4.53	3.24			
		100	3.31	3.24			

APPENDIX B. (continued)

Location Species Date	Irradiance	% Surface Irradiance	Observed Uptake	Predicted Uptake	Optimal Irradiance	Predicted Maximum Uptake	Chi-square Goodness of fit
Puerto Rico <i>Halodule wrightii</i> 30 May 1975	0.8 19.2	1 25 25 25 50 75 100 100	0.00 1.45 3.09 0.99 3.06 2.16 4.11 1.35	0.10 1.88 1.88 1.88 2.63 2.77 2.59 2.59	5.4	2.77	3.1
31 May 1975	0.8 20.3 40.6 60.8 81.1	1 1 1 25 25 50 50 75 75 100 100 100	0.01 0.11 1.23 9.80 4.84 14.42 13.60 11.96 19.70 15.00 20.53 16.16	0.40 0.40 0.40 8.11 8.11 13.15 13.15 16.00 16.00 17.31 17.31 17.31	96.6	17.57	5.3
1 June 1975	0.7 17.5 35.0 52.5	1 1 1 25 25 25 50 50 50 75 75 75	0.15 0.07 0.18 2.52 2.49 4.57 5.40 9.12 5.36 2.23 0.91 8.79	0.14 0.14 0.14 3.05 3.05 3.05 5.15 5.15 5.15 6.51 6.51 6.51	102.4	7.80	13.0

APPENDIX B. (continued)

Location Species Date	Irradiance	% Surface Irradiance	Observed Uptake	Predicted Uptake	Optimal Irradiance	Predicted Maximum Uptake	Chi-square Goodness of fit
	70.0	100	8.87	7.32			
		100	7.86	7.32			
		100	8.68	7.32			
2 June 1975	0.7	1	0.24	0.45	61.7	14.72	15.2
		1	0.16	0.45			
	17.5	25	3.46	8.54			
		25	8.61	8.54			
	35.0	50	16.11	12.87			
		50	14.28	12.87			
		50	5.65	12.87			
	52.5	75	17.30	14.54			
		75	19.44	14.54			
		75	20.29	14.54			
	70.0	100	9.61	14.60			
		100	11.43	14.60			
Texas							
<i>Thalassia testudinum</i>							
10 August 1974	43.9	64	0.76	0.73	49859.4	305.08	0.5
		64	0.26	0.73			
	50.0	73	1.16	0.83			
		73	0.80	0.83			
	58.3	85	0.82	0.97			
	68.6	100	1.33	1.34			
11 August 1974	28.3	41	0.43	0.73	114.0	1.39	1.5
		41	0.32	0.73			
	44.2	64	0.77	1.00			
		64	1.96	1.00			
	50.4	73	1.03	1.08			
		73	1.28	1.08			
	69.1	100	1.25	1.25			
		100	1.95	1.25			

APPENDIX B. (continued)

Location Species Date	Irradiance	% Surface Irradiance	Observed Uptake	Predicted Uptake	Optimal Irradiance	Predicted Maximum Uptake	Chi-square Goodness of fit
12 August 1974	17.1	41	0.34	0.70	46949.4	705.64	0.9
		41	0.17	0.70			
	26.7	64	1.56	1.09			
		64	1.18	1.09			
	30.4	73	0.99	1.24			
		73	1.44	1.24			
	41.7	100	1.77	1.70			
		100	1.68	1.70			
17 August 1974	32.7	41	0.24	0.78	192.6	2.01	1.1
		41	0.64	0.78			
	51.0	64	1.54	1.11			
		64	1.24	1.11			
	58.1	73	0.84	1.22			
		73	1.86	1.22			
	79.9	100	1.47	1.49			
		100	1.23	1.49			
Texas <i>Syringodium filiforme</i> 10 August 1974	43.9	64	0.66	0.81	916.8	413.81	0.2
		64	0.47	0.81			
	50.1	73	1.01	0.92			
	58.3	85	1.17	1.08			
	68.6	100	1.21	1.27			
		100	1.49	1.27			
11 August 1974	28.3	41	0.26	0.80	181.7	2.21	1.0
		41	0.52	0.80			
	44.2	64	1.31	1.14			
	50.4	73	1.88	1.26			
		73	1.58	1.26			
	69.1	100	1.14	1.56			
		100	1.52	1.56			

APPENDIX B. (continued)

Location Species Date	Irradiance	% Surface Irradiance	Observed Uptake	Predicted Uptake	Optimal Irradiance	Predicted Maximum Uptake	Chi-square Goodness of fit
12 August 1974	17.1	41	0.29	0.69	300.8	4.69	1.3
		41	0.24	0.69			
	26.7	64	0.90	1.04			
		64	1.77	1.04			
	30.4	73	1.52	1.67			
		73	1.18	1.67			
	41.7	100	1.62	1.54			
		100	1.15	1.54			
13 August 1974	33.4	41	0.33	0.50	59728.2	331.18	1.2
		41	0.44	0.50			
	52.1	64	0.34	0.79			
		64	0.91	0.79			
	59.4	73	1.30	0.90			
		73	0.82	0.90			
	81.4	100	1.88	1.23			
		100	0.63	1.23			
17 August 1974	32.7	41	0.34	0.67	1109.4	8.59	0.2
		41	0.72	0.67			
	51.0	64	1.10	1.03			
		64	1.22	1.03			
	58.2	73	1.31	1.16			
		73	1.04	1.16			
	79.7	100	1.48	1.56			
Texas <i>Halodule wrightii</i> 10 August 1974	43.9	64	0.68	1.68	221.5	3.81	2.2
		73	1.90	1.87			
	58.3	85	2.78	2.09			
		85	3.28	2.09			
	68.6	100	2.68	2.35			
		100	1.09	2.35			

APPENDIX B. (continued)

Location Species Date	Irradiance	% Surface Irradiance	Observed Uptake	Predicted Uptake	Optimal Irradiance	Predicted Maximum Uptake	Chi-square Goodness of fit
11 August 1974	28.3	41	0.78	1.80	3316.2	78.25	1.4
		41	1.32	1.80			
	44.2	64	2.43	2.80			
		64	3.85	2.80			
	50.4	73	3.88	3.19			
		73	3.55	3.19			
	69.1	100	3.97	4.34			
		100	4.12	4.34			
13 August 1974	33.4	41	0.43	1.13	51387.6	638.49	1.5
		41	0.49	1.13			
	52.1	64	1.84	1.76			
		64	1.61	1.76			
	59.4	73	3.16	2.01			
	81.4	100	2.49	2.75			
17 August 1974	32.7	41	0.87	1.58	22011.6	393.44	2.3
		41	0.52	1.58			
	51.0	64	2.39	2.47			
		64	2.17	2.47			
	58.2	73	4.33	2.82			
		73	3.71	2.82			
	79.7	100	3.25	3.86			
		100	3.68	3.86			
Texas							
<i>Ruppia maritima</i>							
10 August 1974	43.9	64	2.22	2.15	67.6	2.33	3.6
		64	1.83	2.15			
	50.1	73	1.52	2.24			
		73	2.38	2.24			
	58.3	85	1.37	2.31			
		85	4.84	2.31			
	68.6	100	1.99	2.33			
		100	1.90	2.33			

APPENDIX B. (continued)

Location Species Date	Irradiance	% Surface Irradiance	Observed Uptake	Predicted Uptake	Optimal Irradiance	Predicted Maximum Uptake	Chi-square Goodness of fit
11 August 1974	28.6	41	0.71	2.05	441.6	12.51	5.1
		41	0.94	2.05			
	44.2	64	3.14	3.08			
		64	2.72	3.08			
	50.4	73	3.80	3.46			
		73	6.63	3.46			
	69.1	100	2.85	4.55			
		100	4.88	4.55			
12 August 1974	17.1	41	0.60	1.34	29986.2	865.45	1.8
		41	0.48	1.34			
	26.7	64	2.64	2.09			
		64	2.35	2.09			
	30.4	73	2.94	2.39			
	41.7	100	2.20	3.27			
		100	4.07	3.27			
13 August 1974	33.4	41	0.53	1.03	30582.0	348.77	2.4
		41	0.71	1.03			
	52.1	64	1.59	1.61			
		64	2.30	1.61			
	59.4	73	3.14	1.84			
		73	0.60	1.84			
	81.4	100	2.54	2.52			
		100	2.36	2.52			
17 August 1974	32.7	41	0.49	1.45	150.5	3.06	2.3
		41	0.74	1.45			
	51.0	64	2.54	2.01			
		64	3.47	2.01			
	79.7	100	2.40	2.60			
		100	2.19	2.60			

APPENDIX B. (continued)

Location Species Date	Irradiance	% Surface Irradiance	Observed Uptake	Predicted Uptake	Optimal Irradiance	Predicted Maximum Uptake	Chi-square Goodness of fit
Texas							
<i>Halophila engelmanni</i>							
10 August 1974	43.9	64	1.75	2.35	54.6	2.41	0.5
		64	3.06	2.35			
	50.1	73	2.13	2.40			
		73	2.56	2.40			
	58.3	85	2.12	2.40			
		85	2.62	2.40			
	68.6	100	2.18	2.34			
		100	2.56	2.34			
	17.1	41	1.20	1.91	58.9	3.23	2.4
		41	0.56	1.91			
12 August 1974	26.7	64	3.45	2.53			
		64	3.44	2.53			
	30.4	73	3.39	2.70			
		73	2.89	2.70			
	41.7	100	2.01	3.06			
		100	3.10	3.06			
13 August 1974	missing						
Alaska							
<i>Phyllospadix scouleri</i>							
7 August 1975	0.5	1	0.02	0.04	28.8	0.82	0.3
		1	0.03	0.04			
		1	0.01	0.04			
	13.1	25	0.67	0.64			
		25	0.55	0.64			
	26.2	50	0.84	0.82			
		50	0.59	0.82			
		50	0.88	0.82			
	39.2	75	0.81	0.78			
		75	0.98	0.78			
		75	1.00	0.78			
	52.3	100	0.50	0.66			
		100	0.47	0.66			
		100	0.70	0.66			

APPENDIX B. (continued)

Location Species Date	Irradiance	% Surface Irradiance	Observed Uptake	Predicted Uptake	Optimal Irradiance	Predicted Maximum Uptake	Chi-square Goodness of fit
9 August 1975	0.2	1	0.02	0.01	106.5	2.52	0.7
		1	0.01	0.01			
		1	0.02	0.01			
	4.7	25	0.44	0.29			
		25	0.50	0.29			
		25	0.38	0.29			
	9.3	50	0.13	0.55			
		50	0.55	0.55			
	14.0	75	0.90	0.79			
		75	0.75	0.79			
	18.6	100	1.16	1.01			
		100	0.93	1.01			
		100	0.96	1.01			
13 August 1975	0.5	1	0.00	0.02	355.8	0.70	0.6
		1	0.00	0.02			
		1	0.11	0.02			
	11.6	25	0.47	0.45			
		25	0.60	0.45			
	23.2	50	0.81	0.65			
		50	0.44	0.65			
		50	0.57	0.65			
	34.8	75	0.74	0.70			
		75	0.66	0.70			
		75	0.60	0.70			
	46.4	100	0.77	0.68			
		100	0.72	0.68			
		100	0.62	0.68			
14 August 1975	0.3	1	0.03	0.02	40.6	1.12	0.4
		1	0.01	0.02			
		1	0.03	0.02			
	7.4	25	0.36	0.46			
		25	0.32	0.46			
		25	0.53	0.46			

APPENDIX B. (continued)

Location Species Date	Irradiance	% Surface Irradiance	Observed Uptake	Predicted Uptake	Optimal Irradiance	Predicted Maximum Uptake	Chi-square Goodness of fit
	14.7	50	0.89	0.77			
		50	0.80	0.77			
		50	0.85	0.77			
	22.7	75	1.10	0.96			
		75	0.62	0.96			
		75	1.03	0.96			
	29.4	100	1.02	1.07			
		100	1.32	1.07			
		100	0.89	1.07			
Alaska							
<i>Ruppia maritima</i>							
17 October 1974	0.2	1	0.09	0.03	19.8	1.07	0.6
		1	0.14	0.03			
	2.4	10	0.28	0.31			
		10	0.35	0.31			
	6.1	25	0.65	0.65			
		25	0.82	0.65			
	12.2	50	0.77	0.96			
	24.3	100	1.37	1.05			
		100	0.78	1.05			