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Effects of irradiance, temperature, and nutrients on growth dynamics of seagrasses: A review

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Abstract

Productivity of seagrasses can be controlled by physiological processes, as well as various biotic and abiotic factors that influence plant metabolism. Light, temperature, and inorganic nutrients affect biochemical processes of organisms, and are considered as major factors controlling seagrass growth. Minimum light requirements for seagrass growth vary among species due to unique physiological and morphological adaptations of each species, and within species due to photo-acclimation to local light regimes. Seagrasses can enhance light harvesting efficiencies through photo-acclimation during low light conditions, and thus plants growing near their depth limit may have higher photosynthetic efficiencies. Annual temperatures, which are highly predictable in aquatic systems, play an important role in controlling site specific seasonal seagrass growth. Furthermore, both thermal adaptation and thermal tolerance contribute greatly to seagrass global distributions. The optimal growth temperature for temperate species range between 11.5 °C and 26 °C, whereas the optimal growth temperature for tropical/subtropical species is between 23 °C and 32 °C. However, productivity in persistent seagrasses is likely controlled by nutrient availability, including both water column and sediment nutrients. It has been demonstrated that seagrasses can assimilate nutrients through both leaf and root tissues, often with equal uptake contributions from water column and sediment nutrients. Seagrasses use HCO_3^- inefficiently as a carbon source, thus photosynthesis is not always saturated with respect to DIC at natural seawater concentrations leading to carbon limitation for seagrass growth. Our understanding of growth dynamics in seagrasses, as it relates to main environmental factors such as light, temperature, and nutrient availability, is critical for effective conservation and management of seagrass habitats.

Keywords: Growth dynamics; Nutrient availability; Production; Seagrass; Temperature; Underwater irradiance

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1. Introduction

Seagrass meadows are among the most productive plant communities, providing habitat and food for a variety of marine organisms (Heck and Westone, 1977; McRoy and McMillan, 1977; Orth et al., 1984; Summerson and Peterson, 1984; Huh and Kitting, 1985). Although many factors may influence seagrass growth, productivity is mainly regulated by underwater irradiance, temperature, and nutrient availability (Phillips et al., 1983; Wetzel and Penhale, 1983; Dennison et al., 1993; Dunton, 1994; Lee and Dunton, 1996). Seagrass photosynthesis, and thereby, their growth, survival, and depth distribution are directly linked to underwater irradiance (Dennison et al., 1993; Cabello-Pasini et al., 2003), and seagrass loss has been reported worldwide because of reductions in underwater light (Cambridge and McComb, 1984; Giesen et al., 1990; Dennison et al., 1993; Onuf, 1994; Short and Wyllie-Echeverria, 1996). Reduced underwater irradiance may be caused by epiphytic and planktonic algal accumulations from excess anthropogenic nutrients, increased sediment run-off, and resuspension of bottom sediments (Orth and Moore, 1983; Cambridge et al., 1986; Onuf, 1994).

Seagrass productivities usually exhibit distinct seasonal variations, with rates increasing during spring and summer and decreasing during fall and winter (Vermaat et al., 1987; Dunton, 1994; Lee and Dunton, 1996; Lee et al., 2005). As temperature significantly affects the biochemical processes involved in photosynthesis and respiration, it is considered a major factor controlling seasonal seagrass growth (Tutin, 1942; Phillips et al., 1983; Lee and Dunton, 1996; Lee et al., 2005). However, water temperature and irradiance often correlate and exhibit similar seasonal trends, and thus, it can be difficult to separate these two environmental parameters with regard to seagrass growth and production (Kaldy and Dunton, 2000; Kaldy, 2006).

Because of their high productivity, seagrasses should be able to assimilate large amounts of inorganic nutrients. Thus, nutrient availability may play a significant role in regulating seagrass production in areas where light is plentiful. Nutrient enrichment studies have shown that additions of inorganic nutrients can stimulate seagrass growth, suggesting nutrient limitation for plant production (Orth, 1977; Harlin and Thorne-Miller, 1981; Iizumi et al., 1982; Dennison et al., 1987; Short et al., 1990; Pérez et al., 1991; Murray et al., 1992; Williams and Ruckelshaus, 1993; Lee and Dunton, 2000).

While nutrients can limit seagrass growth, excessive water column nutrient enrichment can promote increased light attenuation due to epiphytic growth and phytoplankton blooms, resulting in significant seagrass decline (Orth and Moore, 1983; Silberstein et al., 1986; Giesen et al., 1990; Tomasko and Lapointe, 1991; Short et al., 1995). In most cases, however, nutrient enrichment in sediments enhances seagrass growth with no observable adverse effects (Bulthuis and Woelkerling, 1981; Agawin et al., 1996; Alcoverro et al., 1997; Udy and Dennison, 1997; Lee and Dunton, 2000). Therefore, although seagrasses can access nutrient from both the water column and sediments, effects of nutrient availability on seagrass production may vary depending on the nutrient sources. In this comprehensive review, we present and synthesize the current literature on light, temperature and nutrient effects on seagrass physiology and growth.

2. Irradiance and seagrass production

2.1. Minimum light requirement for seagrass growth

Growth of seagrasses depends on the quantity and quality of light available for photosynthesis (Zieman and Wetzel, 1980). Therefore, reductions of underwater light, due to anthropogenic and natural disturbances, often result in large-scale seagrass die-off (Short and Wyllie-Echeverria, 1996). Underwater light intensity is attenuated exponentially with water depth according to the Lambert–Beer equation ($I_z = I_0 \cdot e^{-Kd \cdot Z}$), wherein light attenuation with increasing water depth is associated with absorption and scattering processes due to dissolved substances, phytoplankton, non-algal particulate matter, and water itself (Weidemann and Bannister, 1986; McPherson and Miller, 1987; Roesler et al., 1989; Gallegos et al., 1990).

As seagrasses often grow in distinct bands from the intertidal zone to depths at which plants receive minimum irradiance for survival, minimum light requirements for these plants have usually been determined as percent light at maximal depth limit using K_d, the light attenuation coefficient (Duarte, 1991; Dennison et al., 1993). However, minimum light requirements of seagrasses (2–37% surface irradiance, SI; Table 1) are much higher than those of macroalgae and phytoplankton (about 1–3% SI; Strickland, 1958; Luning and Dring, 1979; Sand-Jensen, 1988; Duarte, 1991; Markager and Sand-Jensen, 1992; Dennison et al., 1993). As each seagrass species has unique physiological and morphological adaptations to light availability, the minimal light requirements should vary among different seagrasses (Dennison et al., 1993). This is consistent with a number of studies that have demonstrated variability in minimum light requirements within species (Table 1). For example, the minimum light requirement for *Zostera marina* in a Danish embayment was 11% SI, whereas the estimated light requirement for same species in Netherlands was 29.4% SI (Table 1; Dennison et al., 1993; Olesen and Sand-Jensen, 1993). This variability within species is likely attributed to photo-acclimation to local light regimes. The light requirements of submersed plants are tightly coupled with plant morphology (Middelboe and Markager, 1997). A minimum light requirement for rosette-type freshwater angiosperms, which has higher root:shoot ratios, was much greater than caulescent angiosperms (Sheldon and Boylen, 1977; Middelboe and Markager, 1997). *Halophila* spp. usually have the greatest depth limit, and consequently the lowest minimum light requirement among seagrasses (Table 1). In contrast to other species, which have strap-shaped leaves, *Halophila* spp. have petiolate leaves along rhizomes or on distal nodes of erect stems (Kuo and den Hartog, 2006). It is likely that petiolate leaves, with elliptic or ovate blades, are more efficient at harvesting light than linear or lanceolate leaves. Moreover, *Halophila* spp. usually have low root:shoot ratios (*Halophila ovalis* had lowest root:shoot ratio among 7 South-east Asian seagrasses; Terrados et al., 1999b). Therefore, the morphological characteristics of *Halophila* spp. are likely reflected in their minimum light requirement.

The light requirements in % SI will vary with latitude (Duarte and Kalff, 1987; Middelboe and Markager, 1997). For example, the required light (as % SI) for submerged angiosperms in freshwater lakes increases with increasing latitude (Duarte and Kalff, 1987; Middelboe and Markager, 1997). Since ambient surface light is lower in temperate regions (relative to tropics), required light in terms of % SI should be higher in temperate species. However, the minimum light requirements for temperate and tropical species were comparable (means as 16 and 18% SI, respectively; Table 1). Additionally, the relationship between minimum required light and latitude in seagrasses exhibits a weak positive relationship or a negative relationship with latitudes (Table 1). These results imply that light requirements in seagrasses can become acclimated to local light conditions. Thus, seagrass productivity may not change proportionally with local light conditions, and consequently, underwater light availability may not always be a good indicator of seagrass productivity.

2.2. Photosynthesis and irradiance

Light requirements for seagrass growth and survival have often been expressed as % surface irradiance (% SI; Duarte, 1991; Dennison et al., 1993). As the level of surface irradiance varies both spatially and temporally, there is a concern when using estimates of % SI to determine minimum light requirements for a given species. Minimum light requirements may also be determined by establishing the relationship between underwater irradiance and photosynthetic production using photosynthesis–irradiance (*P–I*) curves (Kenworthy and Haunert, 1991; Morris and Tomasko, 1993; Herzka and Dunton, 1997), which may provide valuable information for light requirements necessary to sustain optimal growth (Dunton and Tomasko, 1994). *P–I* curves can be divided into three regions; 1) a light limited region in which photosynthetic rates linearly increase with increasing irradiance, 2) a light-saturated region in which photosynthesis is independent of irradiance, and 3) a photoinhibited region in which photosynthesis decreases with further increases in irradiance. The curve can provide estimates for the initial slope (α; photosynthetic quantum efficiency), the light-saturated photosynthetic rate (P_{max}), saturating irradiance for photosynthesis (I_k) where α intersects P_{max} (P_{max}/α), compensation irradiance (I_c) where net photosynthesis is zero, and photoinhibition irradiance (I_i) where photosynthesis decreases with further increases in irradiance. I_k and I_c can be used to determine light requirements based on daily light saturation period (H_{sat}), and the daily light compensation period

Table 1
Minimum light requirements of various seagrass species distributed worldwide

Species	Location	Latitude	Minimum light requirement (%)	Source
Temperate				
Amphibolis antaractica	Waterloo Bay, Australia	27°S	24.7	Dennison et al. (1993)
Heterozostera tasmanica	Waterloo Bay, Australia	27°S	20.2	Dennison et al. (1993)
	Chile	30°S	17.4	Dennison et al. (1993)
	Spencer Gulf, Australia	32°–35°S	4.4	Dennison et al. (1993)
	Victoria, Australia	38°S	5	Dennison et al. (1993)
	Port Phillip Bay, Australia	38°06′S	5	Bulthuis (1983a)
	Mean		10.4	
Posidonia oceanica	Malta	35°N	9.2	Dennison et al. (1993)
	Fraile Island, Murcia, Spain	37°N	10–16	Ruiz and Romero (2001)
	Port Lligat, Spain	40°–42°N	11.5	Olesen et al. (2002)
	Medas Island, Spain	42°N	7.8	Dennison et al. (1993)
	Mean		10.9	
Posidonia angustifolia	Waterloo Bay, Australia	27°S	24.7	Dennison et al. (1993)
Posidonia ostenfeldii	Waterloo Bay, Australia	27°S	24.7	Dennison et al. (1993)
Posidonia sinuosa	Waterloo Bay, Australia	27°S	24.7	Dennison et al. (1993)
Ruppia maritima	Brazil	32°S	8.2	Dennison et al. (1993)
Ruppia megacarpa	Wilson Inlet, Australia	34°–35°S	24	Carruthers and Walker (1999)
Zostera noltii	Cadiz Bay, Spain	36°30′N	2	Peralta et al. (2002)
Zostera marina	Japan	35°N	18.2	Dennison et al. (1993)
	Denmark	54°–57°N	20.6	Dennison et al. (1993)
	Western Long Island Sound, USA	41°N	13	Koch and Beer (1996)
	Eastern Long Island Sound, USA	41°N	12	Koch and Beer (1996)
	Woods Hole, USA	41°N	18.6	Dennison et al. (1993)
	Netherlands	51°N	29.4	Dennison et al. (1993)
	Roskilde, Denmark	55°N	19.4	Dennison et al. (1993)
	Aarhus Bight, Denmark	56°N	11	Olesen and Sand-Jensen (1993)
	Kattegat, Denmark	57°N	20.1	Dennison et al. (1993)
	Mean		18	
Tropical/subtropical				
Cymodocea nodosa	Malta	35°N	7.3	Dennison et al. (1993)
	Ebro Delta, Spain	40°S	10.2	Dennison et al. (1993)
	Alfacs Bay, Spain	40°–42°N	4.4	Olesen et al. (2002)
	Mean		7.3	
Halodule wrightii	Laguna Madre, USA	27°21′N	18	Dunton (1994)
	Laguna Madre, USA	27°21′N	15–20	Burd and Dunton (2001)
	Indian River Lagoon, USA	27°30′N	24–37	Kenworthy and Fonseca (1996)
	Indian River Lagoon, USA	27°30′N	20	Steward et al. (2005)
	Corpus Christi Bay, USA	27°49′N	18	Dunton (1994)
	Corpus Christi Bay, USA	27°49′N	20	Czerny and Dunton (1995)
	San Antonio Bay, USA	28°15′N	18	Dunton (1994)
	Florida, USA	25°–30°N	17.2	Dennison et al. (1993)
	Mean		20.7	
Halophila decipiens	Cuba	23°N	8.8	Dennison et al. (1993)
Halophila decipiens	St. Croix, USA	17°N	4.4	Dennison et al. (1993)
Halophila engelmanni	Cuba	23°N	23.7	Dennison et al. (1993)
Syringodium filiforme	Cuba	23°N	19.2	Dennison et al. (1993)
	Florida, USA	25°–30°N	18.3	Dennison et al. (1993)
	Florida, USA	25°–30°N	17.2	Dennison et al. (1993)
	Indian River Lagoon, USA	27°02′N	24–37	Kenworthy and Fonseca (1996)
	Mean		23.1	
Thalassia testudinum	Puerto Rico	18°N	24.4	Dennison et al. (1993)
	Cuba	23°N	23.5	Dennison et al. (1993)
	Florida Bay, USA	25°N	13	Fourqurean and Zieman (1991)
	Corpus Christi Bay, USA	27°49′N	20	Czerny and Dunton (1995)
	Corpus Christi Bay, USA	27°49′N	>14	Lee and Dunton (1997)
	Florida, USA	25°–30°N	15.3	Dennison et al. (1993)
	Mean		18.4	

(H_{comp}), respectively (Dennison and Alberte, 1982, 1985; Zimmerman et al., 1994).

Photosynthetic parameters often show seasonal variability (Dennison, 1987; Herzka and Dunton, 1997; Alcoverro et al., 1998). In *Z. marina* and *Thalassia testudinum*, P_{max}, dark respiration (R_d), α, I_k and I_c were lowest in winter, increased with higher water temperature in the early spring and peaked in summer (Dennison, 1987; Herzka and Dunton, 1997). Pérez and Romero (1992) also found higher P_{max} and I_k values during summer (in comparison to winter values) for *Cymodocea nodosa*. Moreover, I_k and I_c of *Posidonia oceanica* showed significantly higher values during warmer months (Alcoverro et al., 1998). Seasonality in photosynthetic parameters is likely controlled by changes in water temperature (Marsh et al., 1986; Herzka and Dunton, 1997; Masini and Manning, 1997). In *Heterozostera tasmanica* and *Z. marina*, the initial slopes (α) were relatively constant with increasing temperature, whereas saturation irradiance (I_k), and compensation irradiance (I_c) increased with increasing temperatures (Bulthuis, 1983b; Marsh et al., 1986). These increases in I_k and I_c reflect changes in P_{max} and dark respiration rates in response to higher temperatures. Masini and Manning (1997) also reported increased I_k and I_c values with increased water temperatures for *Posidonia* spp. and *Amphibolis* spp. Since I_c often increases with temperature, more light is necessary at higher temperatures to allow for positive carbon balance.

While seasonal variance is found for *P–I* parameters influenced by temperature, inter- and intra-specific differences are also found (Tables 2 and 3). These variances may reflect differences in photosynthetic processes or methodologies employed (Dunton and Tomasko, 1994). Most *P–I* measurements have been conducted in laboratories using leaf segments without non-photosynthetic tissues. Non-photosynthetic below-ground tissues can account for more than 50% of the total seagrass biomass, and must be supported by photosynthetically derived carbon and oxygen (Smith et al., 1984; Powell et al., 1989; Dunton, 1990; Caffrey and Kemp, 1991; Fourqurean and Zieman, 1991; Ralph et al., 1992; Agostini et al., 2003). Therefore, whole plant respiratory oxygen demand is greater than the respiratory demand for photosynthetic tissues only, and thus I_c and I_k measurements for intact plants will be considerably higher than values measured using leaves alone (Table 3). Therefore, compensation irradiance estimated using leaf segments is of limited use in predicting whole plant carbon balance (Dunton and Tomasko, 1994). Laboratory experiments also tend to severely underestimate I_c and I_k (Dunton and Tomasko, 1994; Herzka and Dunton, 1997), in comparison of *in situ* and laboratory-derived photosynthetic parameters, higher values of I_c, I_k, and low relative quantum yields based on *in situ* shoot and whole plant incubations have been reported for seagrasses (Fourqurean and Zieman, 1991; Dunton and Tomasko, 1994; Herzka and Dunton, 1997). Thus, the application of *P–I* models to assess seagrass light requirements is complicated by variability due to various methodologies used in *P–I* construction (Herzka and Dunton, 1997).

A single species growing under different environmental conditions also have been shown to possess varying light requirements (Table 2; Dennison, 1987; Masini and Manning, 1997; Ruiz and Romero, 2003). Plants collected near their maximum depth limits have higher photosynthetic efficiencies (α) and lower light requirements for saturated photosynthesis than plants growing in shallower waters (Masini and Manning, 1997). Seagrasses can enhance light harvesting efficiencies through photo-acclimation during low light conditions (West, 1990; Olesen and Sand-Jensen, 1993; Abal et al., 1994; Philippart, 1995; Olesen et al., 2002), thus plants growing near their depth limit may have higher photosynthetic efficiencies. Lower I_c and I_{sat} and greater photosynthetic efficiencies have also been observed in seagrasses inhabiting inner harbors, where light availability is reduced through high turbidities, in comparison to less turbid outer harbor stations (Ruiz and Romero, 2003). The plants in the inner harbor were likely subjected to light-limitation, and thus changes in photosynthetic parameters are possibly photo-acclimatization responses allowing seagrasses to maximize carbon fixation under light limited conditions (Dennison, 1987; Fourqurean and Zieman, 1991; Pérez and Romero, 1992; Herzka and Dunton, 1997; Alcoverro et al., 1998; Ruiz and Romero, 2003).

2.3. Growth rate and irradiance

Consistent with the *P–I* relationship, a seagrass growth response to light is described by a hyperbolic function with saturation kinetics (Olesen and Sand-Jensen, 1993; Vermaat and Verhagen, 1996; Peralta et al., 2002). For example, eelgrass growth rate was highest between 100 and 150 μmol photons m^{-2} s^{-1}, with light compensated-growth between 19 and 47 μmol photons m^{-2} s^{-1} (Olesen and Sand-Jensen, 1993). These saturation and compensation irradiances levels for growth resembled I_k and I_c values determined from *P–I* curves for eelgrass (Tables 2 and 3). Leaf growth rate of *Zostera noltii*, as a function of underwater irradiance, also revealed an asymptotic relationship (Vermaat and Verhagen, 1996). Leaf growth rates were fairly constant above 5 mol photons m^{-2} d^{-1},

Table 2

Photosynthesis–irradiance parameters reported for various seagrass species including the light-saturated photosynthetic rate (P_{max}), compensation irradiance (I_c), saturation irradiance (I_k), photosynthetic quantum efficiency (α), and growing and/or measuring conditions

Species	Tissue	P_{max} (μmol O_2 g^{-1} dw h^{-1})	I_c (μmol m^{-2} s^{-1})	I_k (μmol m^{-2} s^{-1})	α (μmol O_2 g^{-1} dw h^{-1})	Condition	Source
Temperate							
Amphibolis antarctica	Whole plant	31.3–46.9	17–23	32–40	0.039–0.054^{a}	Temperature (13–23 °C)	Masini and Manning (1997)
Amphibolis griffithii	Whole plant	2.42±0.18^{a}	20±0.9	70±2.4	0.035±0.003^{a}	Gross P_{max}	Masini et al. (1995)
	Whole plant	31.3–109.4	15–17	25–56	0.039^{a}	Temperature (13–23 °C)	Masini and Manning (1997)
Phyllospadix torreyi	Above-ground	26.0^{d}	5^{k}	36^{k}		Intertidal	Drew (1979)
Posidonia australis	Whole plant	0.84±0.07^{a}	25±1.2	90±4.1	0.009±0.001^{a}	Gross P_{max}	Masini et al. (1995)
	Whole plant	25.0–62.5	17–20	35–50	0.015–0.024^{a}	Temperature (13–23 °C)	Masini and Manning (1997)
Posidonia oceanica	Above-ground	240.6	37	257	0.323	Yearly and tissue age means	Alcoverro et al. (1998)
	Above-ground	12.5–96.9				Variable pH, AZ inhibitor	Invers et al. (1999)
	Above-ground	28.1–125.0				Variable pH, control	Invers et al. (1999)
	Above-ground	218.4	21		1.431	Average water temp. (20 °C)	Enríquez et al. (1995)
	Above-ground	106.9	12.01±3.8	44.2±17.4	2.188±0.094	Control, May	Ruiz et al. (2001)
	Above-ground	213.8	4.3±1.9	44.5±10.8	4.688±0.031	Fish farm station (HA), May	Ruiz et al. (2001)
	Above-ground	211.3	5.38±1.56	38.6±8.56	5.313±0.625	Fish farm station (HB), May	Ruiz et al. (2001)
	Above-ground	188.1	3.88±2.17	66.4±11.8	2.813±0.031	Control, Aug.	Ruiz et al. (2001)
	Above-ground	328.1	2.57±2.18	74.3±11.3	4.375±0.063	Fish farm station (HA), Aug.	Ruiz et al. (2001)
	Above-ground	337.5	2.03±4.32	72.2±22.6	4.688±0.313	Fish farm station (HB), Aug.	Ruiz et al. (2001)
	Above-ground	110–175	3.1–5.4		3.9–5.0	0.7–15.6 m depth	Olesen et al. (2002)
	Above-ground	215.3	12.8±1.7	72.5±5.1	2.969±0.313	Control (1993, 60 d)	Ruiz and Romero (2001)
	Above-ground	141.9	1.97±1.83	12.3±3.2	14.063±10.0	16.7% of SI (1993, 60 d)	Ruiz and Romero (2001)
	Above-ground	92.2	0.68±0.42	2.45±0.7	37.500±23.125	10.4% of SI (1993, 60 d)	Ruiz and Romero (2001)
	Above-ground	80.0	7.2±1.6	19±4.7	4.063±0.625	Control (1995, 20 d)	Ruiz and Romero (2001)
	Above-ground	340.6	14.2±2.79	228.7±20.2	3.125±1.531	Control (1995, 50 d)	Ruiz and Romero (2001)
	Above-ground	390.6	15±1	191.8±14	2.031±0.094	Control (1995, 90 d)	Ruiz and Romero (2001)
	Above-ground	96.3	8.12±1.18	22.5±3.7	4.063±0.313	16.7% of SI (1995, 20 d)	Ruiz and Romero (2001)
	Above-ground	226.9	7.44±1.08	65.7±7.3	3.438±0.313	16.7% of SI (1995, 50 d)	Ruiz and Romero (2001)
	Above-ground	160.9	1.5±0.07	20.9±0.31	7.500±0.094	16.7% of SI (1995, 90 d)	Ruiz and Romero (2001)
	Above-ground	161.9	0.46±1.8	20.9±7.8	7.719	Inner harbor	Ruiz and Romero (2003)
	Above-ground	221.3	1.08±1.5	23.2±6.81	9.531	Intermediate harbor	Ruiz and Romero (2003)
	Above-ground	273.1	3.6±3.4	75.9±18.8	3.594	Outer harbor	Ruiz and Romero (2003)
	Above-ground	264.1	4.5±3	113.1±50.1	2.313	Reference station	Ruiz and Romero (2003)
	Above-ground	8.1^{d}	4^{k}	26^{k}		5 and 33 m depth	Drew (1979)
Posidonia sinuosa	Whole plant	0.89±0.12^{a}	24±1.6	55±3.2	0.016±0.002^{a}	Gross P_{max}, 2 m depth at 18 °C	Masini et al. (1995)
	Whole plant	1.11±0.19^{a}	24±2.3	59±3.7	0.019±0.003^{a}	Gross P_{max}, 4 m depth at 18 °C	Masini et al. (1995)
	Whole plant	65.0	22±1.9	62±9.1	0.015±0.002^{a}	Uniform light field, Gross P_{max}	Masini et al. (1995)
	Whole plant	77.8	31±3.7	91±8.3	0.012±0.001^{a}	Attenuated light field, Gross P_{max}	Masini et al. (1995)
	Whole plant	37.2–76.6	22–28	37–56	0.014–0.019^{a}	Temperature (13–23 °C)	Masini et al. (1995)
	Whole plant	18.8–37.5	20–25	38–55	0.015^{a}	Temperature (13–23 °C)	Masini and Manning (1997)
Ruppia maritima	Above-ground	426.3	23		1.922	Average water temp. (20 °C)	Enríquez et al. (1995)

(continued on next page)

Table 2 (*continued*)

Species	Tissue	P_{max} (μmol O_2 g^{-1} dw h^{-1})	I_c (μmol m^{-2} s^{-1})	I_k (μmol m^{-2} s^{-1})	α (μmol O_2 g^{-1} dw h^{-1})	Condition	Source
Zostera carpriconi	Above-ground	4.2[e]	45	182		Leaf segments, artificial seawater	Flanigan and Critchley (1996)
	Above-ground	179.4		195±45		Intertidal, winter	Schwarz (2004)
	Above-ground	167.5		242±21		Subtidal, winter	Schwarz (2004)
Zostera marina	Above-ground	0.5–1.7[c]		100–290	0.0035[c]	Seasonal variations	Zimmerman et al. (1995)
	Above-ground	0.20±0.03[b]		27±5	0.010[b]	Control	Zimmerman et al. (1997)
	Above-ground	0.30–0.78[b]		27–82	0.011[b]	CO_2 enrichment	Zimmerman et al. (1997)
	Above-ground	0.40[b]	12	125	0.0021[b]	Leaf No. 1, Base	Mazzella and Alberte (1986)
	Above-ground	0.24[b]	7	40	0.0053[b]	Leaf No. 1, Apex	Mazzella and Alberte (1986)
	Above-ground	0.36[b]	25	115	0.0022[b]	Leaf No. 2, Base	Mazzella and Alberte (1986)
	Above-ground	0.22[b]	14	85	0.0024[b]	Leaf No. 2, Middle	Mazzella and Alberte (1986)
	Above-ground	0.23[b]	13	55	0.0041[b]	Leaf No. 2, Apex	Mazzella and Alberte (1986)
	Above-ground	0.26[b]	33	80	0.0024[b]	Leaf No. 3, Base (+epi.)	Mazzella and Alberte (1986)
	Above-ground	0.23[b]	21	80	0.0023[b]	Leaf No. 3, Base (−epi.)	Mazzella and Alberte (1986)
	Above-ground	0.23[b]	9.1	80	0.0023[b]	Leaf No. 3, Middle (+epi.)	Mazzella and Alberte (1986)
	Above-ground	0.19[b]	6.6	80	0.0020[b]	Leaf No. 3, Middle (−epi.)	Mazzella and Alberte (1986)
	Above-ground	0.22[b]				Leaf No. 3 Base (+epi.), early Aug.	Mazzella and Alberte (1986)
	Above-ground	0.23[b]				Leaf No. 3 Middle (+epi.), early Aug.	Mazzella and Alberte (1986)
	Above-ground	0.59[b]				Leaf No. 3 Apex (+epi.), early Aug.	Mazzella and Alberte (1986)
	Above-ground	0.17[b]				Leaf No. 3 Base (+epi.), late Aug.	Mazzella and Alberte (1986)
	Above-ground	0.50[b]				Leaf No. 3 Middle (+epi.), late Aug.	Mazzella and Alberte (1986)
	Above-ground	0.25[b]				Leaf No. 3 Apex (+epi.), late Aug.	Mazzella and Alberte (1986)
	Above-ground	0.47[b]	10	100		1.3 m depth	Dennison and Alberte (1982)
	Above-ground	0.32[b]				5.5 m depth	Dennison and Alberte (1982)
	Above-ground	14.2[d]	6[k]	50[k]		10 m depth	Drew (1979)
	Whole plant	156.3–193.8	85	450	0.156–0.250	NO_3^- enrichment	Touchette (1999)
	Above-ground	0.055±0.0026[b]	0.9	7	9.1[b]	Variable temp. 0 °C	Marsh et al. (1986)
	Above-ground	0.095±0.0060[b]	1	16	6.2[b]	Variable temp. 5 °C	Marsh et al. (1986)
	Above-ground	0.15±0.018[b]	3	36	4.5[b]	Variable temp. 10 °C	Marsh et al. (1986)
	Above-ground	0.33±0.057[b]	8	90	4.0[b]	Variable temp. 15 °C	Marsh et al. (1986)
	Above-ground	0.32±0.031[b]	17	78	5.2[b]	Variable temp. 20 °C	Marsh et al. (1986)
	Above-ground	0.44±0.051[b]	13	102	5.0[b]	Variable temp. 25 °C	Marsh et al. (1986)
	Above-ground	0.45±0.093[b]	19	99	5.6[b]	Variable temp. 30 °C	Marsh et al. (1986)
	Above-ground	0.30±0.044[b]	36	120	3.5[b]	Variable temp. 35 °C	Marsh et al. (1986)
	Above-ground	3–6.5[i]	30–35	250	0.008[i]	Young leaf segments	Jiménez et al. (1987)
	Above-ground	8.44±0.04[b]	12.0±2.5	210±20.2	0.0038±0.0002[b]	Low sulfide	Goodman et al. (1995)
	Above-ground	0.54±0.03[b]	42.5±9.0	220±19.8	0.0028±0.0003[b]	Medium sulfide	Goodman et al. (1995)
	Above-ground	0.33±0.02[b]	60.0±10.1	198.±22.5	0.0020±0.0003[b]	High sulfide	Goodman et al. (1995)
	Above-ground	214.1	40		0.156	Average water temp. (20 °C)	Enríquez et al. (1995)
	Above-ground				0.78±0.06	Initial	Holmer and Bondgaard (2001)
	Above-ground	130–190			0.84±0.09	Control (full-oxygenated water)	Holmer and Bondgaard (2001)
	Above-ground	55–130			0.25±0.03	Low oxygen	Holmer and Bondgaard (2001)

	Above-ground	25–90			0.56±0.01	Low sulfide	Holmer and Bondgaard (2001)
	Above-ground	20–80				High sulfide	Holmer and Bondgaard (2001)
	Above-ground	0.7–2.4[c]		50–200	0.09–0.029[c]	Lagoon, seasonal	Cabello-Pasini et al. (2002)
	Above-ground	0.5–1.8[c]		10–350	0.05–0.062[c]	Open coast, seasonal	Cabello-Pasini et al. (2002)
Zostera noltii	Whole plant	71–236[f]	98–300	222–390	0.23–0.63[f]	Seasonal variations	Vermaat and Verhagen (1996)
	Above-ground	3–6.5[i]	30–35	350	0.008[i]	Young leaf segments	Jiménez et al. (1987)
	Above-ground	378.8	56		1.425	Average water temp. (20 °C)	Enríquez et al. (1995)
	Above-ground			175	0.042±0.003[e]	Seasonal	Silva and Santos (2004)
Tropical/subtropical							
Cymodocea nodosa	Above-ground	93.8				Water flow >0.64 m s^{-1}	Koch (1994)
	Above-ground	27.2–75.0	0.07–50.6	25.9–165.9	0.281–1.219	10 °C	Terrados and Ros (1995)
	Above-ground	60.6–237.2	18.1–32.1	77.8–231.2	0.625–1.219	20 °C	Terrados and Ros (1995)
	Above-ground	59.1–438.1	26.0–116.4	135.1–400.9	0.156–0.159	30 °C	Terrados and Ros (1995)
	Above-ground	62.5–228.1				Variable pH, AZ inhibitor	Invers et al. (1999)
	Above-ground	150.0–290.6				Variable pH, control	Invers et al. (1999)
	Above-ground	262.2	61		1.444	Average water temp. (20 °C)	Enríquez et al. (1995)
	Above-ground	165–250	5.7–10.7			0.4–3.8 m depth	Olesen et al. (2002)
	Above-ground	21.8[d]	4[k]	38[k]		0.3 and 33 m depth	Drew (1979)
Cymodocea rotundata	Above-ground	169.7–261.3	12.5–37.1		0.625–3.125	Seasonal	Agawin et al. (2001)
Cymodocea serrulata	Whole plant	0.476±0.135[g]				0.5 m depth	Hena et al. (2001)
	Whole plant	0.292±0.030[g]				2.0 m depth	Hena et al. (2001)
Enhalus acoroides	Above-ground	40.9–196.3	2.5–26.0		0.313–6.250	Seasonal	Agawin et al. (2001)
Halodule uninervis	Above-ground	0.12[b]	20–40	50		Variable depth	Beer and Waisel (1982)
Halodule wrightii	Whole plant	456–651	48–66	245–429	1.5–2.3	*In situ*, Blackjack peninsula	Dunton (1996)
	Whole plant	203–652	48–164	147–652	0.6–2.2	*In situ*, East Flats	Dunton (1996)
	Whole plant	140–1104	37–177	189–453	0.5–2.4	*In situ*, seasonal	Dunton and Tomasko (1994)
	Whole plant	441±80	111±21	349±27	1.3±0.2	Field (28–30 °C)	Dunton and Tomasko (1994)
	Above-ground	421±21	22±2	101±4	4.2±0.3	Lab (29 °C)	Dunton and Tomasko (1994)
Halophila engelmannii	Above-ground		10–60	432–504		Seasonality, salinity	Dawes et al. (1987)
Halophila johnsonii	Above-ground	10–510	2–14	14–41	5–13	Salinity (0–60 PSU)	Torquemada et al. (2005)
	Above-ground	125–480	2–10.5	25–52	6.2–11.8	Temp. (15–25 °C)+Salinity (30, 50 PSU)	Torquemada et al. (2005)
	Above-ground	310–720	2–7.2	28–65	9–18	pH (5–8.2)+Salinity (30, 50 PSU)	Torquemada et al. (2005)
Halophila stipulacea	Above-ground	40[b]	20–40	100		Variable depth	Beer and Waisel (1982)
	Whole plant	9.0[d]	2[k]	20[k]		0.5 m depth	Drew (1979)

(continued on next page)

Table 2 (*continued*)

Species	Tissue	P_{max} (µmol O_2 g^{-1} dw h^{-1})	I_c (µmol m^{-2} s^{-1})	I_k (µmol m^{-2} s^{-1})	α (µmol O_2 g^{-1} dw h^{-1})	Condition	Source
Syringodium filiforme	Whole plant	200–220	125–140	370	0.6–0.7	*In situ*, Gross P_{max}	Major and Dunton (2000)
	Whole plant	180–305	10–25	144	1.3–2.0	Lab, Gross P_{max}	Major and Dunton (2000)
Thalassia hemprichii	Above-ground	141.3–330.3	8.3–31.9		0.02–0.17	Seasonal	Agawin et al. (2001)
Thalassia testudinum	Above-ground	352.6			2.605	Basal leaf segment	Enríquez et al. (2002)
	Above-ground	349.0			2.622	Apical leaf segment	Enríquez et al. (2002)
	Whole plant	77.6 ± 25.2		49.3 ± 10.0	1.62 ± 0.30	Age (0.25 months), Gross P_{max}	Kaldy and Dunton (1999)
	Whole plant	58.1 ± 4.7	73.0 ± 7.6	94.6 ± 19.6	0.67 ± 0.08	Age (2 months), Gross P_{max}	Kaldy and Dunton (1999)
	Whole plant	222.9 ± 9.4	30.0 ± 4.3	119.1 ± 16.3	2.05 ± 0.25	Age (6 months), Gross P_{max}	Kaldy and Dunton (1999)
	Whole plant	224.1 ± 13.7	36.0 ± 9.7	137.9 ± 10.6	1.65 ± 0.07	Age (9 months), Gross P_{max}	Kaldy and Dunton (1999)
	Whole plant	215.3 ± 16.5	56.0 ± 9.0	218.6 ± 48.6	1.14 ± 0.19	Age (15 months), Gross P_{max}	Kaldy and Dunton (1999)
	Whole plant	480.0		438	1.097	P/I Model 2	Fourqurean and Zieman (1991)
	Whole plant	348.8		407	0.819	P/I Model 3	Fourqurean and Zieman (1991)
	Whole plant	346.9		357	0.971	P/I Model 5	Fourqurean and Zieman (1991)
	Whole plant	320.6		426	0.789	P/I Model 6	Fourqurean and Zieman (1991)
	Above-ground	100.0				Water flow >0.25 m s^{-1}	Koch (1994)
	Above-ground	270	44	110	2.45	Corpus Christi Bay	Herzka and Dunton (1997)
	Above-ground	208	36	87	2.44	Lower Laguna Madre	Herzka and Dunton (1997)
	Whole plant	195	107	281	0.7	*In situ*, Lower Laguna Madre	Herzka and Dunton (1997)
	Above-ground	141.9	39		1.969	Egmout Key, shallow	Dawes and Tomasko (1988)
	Above-ground	197.2	45		2.156	Egmout Key, deep	Dawes and Tomasko (1988)
	Above-ground	190.0	32		3.219	Anclote Key, shallow	Dawes and Tomasko (1988)
	Above-ground	81.3	24		3.031	Anclote Key, deep	Dawes and Tomasko (1988)
Thalassodendron ciliatum	Above-ground	30–50[j]		1.5–5[k]		0.5–33 m depth	Parnik et al. (1992)

a. µg O_2 µg chl^{-1} h^{-1}; b. µmol O_2 mg chl^{-1} min^{-1}; c. µmol O_2 g^{-1} fw min^{-1}; d. µg C cm^{-2} h^{-1}; e. µmol O_2 m^{-2} s^{-1}; f. µg O_2 g^{-1} AFD min^{-1}; g. mg O_2 g^{-1} fw h^{-1}; h. µg C mg^{-1} dw h^{-1}; i. mg C g^{-1} dw h^{-1}; j. µmol CO_2 kg^{-1} dw s^{-1}; k. W m^{-2}.

Table 3
Average values of P–I parameters for temperate and tropical/subtropical seagrass species

Species	Tissue	$P_{\max}$ (μmol O_2 g^{-1} dw h^{-1})	I_c (μmol m^{-2} s^{-1})	I_k (μmol m^{-2} s^{-1})
Temperate				
Amphibolis antarctica	Whole plant	37.5	19	36
Amphibolis griffithii	Whole plant	58.4	18±2	49±21
Posidonia australis	Whole plant	34.7	21.5±3.5	66±24
Posidonia oceanica	Leaf segment	199.3±18.9	7.8±1.8	73.3±16.1
Posidonia sinuosa	Whole plant	58.5±9.8	24.8±1.3	60.6±6.5
Ruppia maritima	Leaf segment	426.3	23	
Zostera carpriconi	Leaf segment	173.5±6.0	45	206±18.2
Zostera marina	Leaf segment	119.9±31.1	21.7±4.1	116.0±17.2
	Whole plant	175	85	450
Zostera noltii	Leaf segment	378.8	44.3±11.8	262.5±87.5
	Whole plant		175.5	341.5
Tropical/subtropical				
Cymodocea nodosa	Leaf segment	174.1±28.5	35.1±11.2	149.2±45.3
Cymodocea rotundata	Leaf segment	223.4	24.1	
Enhalus acoroides	Leaf segment	127.5	14.1	
Halodule uninervis	Leaf segment		30	50
Halodule wrightii	Leaf segment	421	22	101
	Whole plant	424±51.3	89.5±11.3	337.5±5.8
Halophila engelmannii	Leaf segment		30	468
Halophila johnsonii	Leaf segment	307.8±55.3	5.7±0.5	35.8±3.5
Halophila stipulacea	Leaf segment		30	100
Syringodium filiforme	Whole plant	215.0±5.0	75.5±57.5	257.0±113.0
Thalassia hemprichii	Leaf segment	237.2	19.9	
Thalassia testudinum	Leaf segment	210.0±32.7	36.7±3.2	98.5±11.5
	Whole plant	248.9±40.7	60.4±13.9	252.9±47.0

but growth dropped markedly below that irradiance. Manipulated light conditions, using shading screens on *Z. noltii* beds, revealed significant changes in plant growth (Peralta et al., 2002). For growth in these plants, estimated values for compensating and optimum daily integrated irradiances were 0.8 and 16.9 mol photons m^{-2} d^{-1}, respectively (which corresponded to 2% and 34% of the SI). Furthermore, the relationship between plant growth rate and daily integrated photon irradiance followed a saturation model which included photoinhibition, with maximum growth rates of *Z. noltii* occurring at intermediate light levels (42% SI or 20.6 mol photons m^{-2} d^{-1}), and decreased at 100% SI (Peralta et al., 2002). A linear growth response to light availability also has been reported from outdoor mesocosm experiments on *Z. marina* (Short et al., 1995). This linear response, which is in contrast to hyperbolic functions with light saturation levels, suggests that plants in that study used all available light (up to full sunlight) to increase productivity (Short et al., 1995).

2.4. Role of daily light periods in seagrass growth

Underwater photon flux density (PFD) has been represented as daily integrated irradiance for light availability (Zimmerman et al., 1994; Herzka and Dunton, 1998; Lee et al., 2005), but integrated irradiance may not be a reliable predictor of seagrass production (Zimmerman et al., 1994). Since photosynthetic rates can be saturated at irradiances higher than I_k, a daily production integral may not increase proportionally with increasing integrated irradiances. The duration of PFDs above light compensation points and light saturation points is represented by H_{comp} and H_{sat}, respectively (Dennison and Alberte, 1982, 1985). Since compensation irradiance represents the minimum light for plant survival, H_{comp} has been used to predict the minimum light requirement and/or the maximum depth limit for seagrasses. As saturation irradiance represents the light conditions for maximum photosynthesis, H_{sat} has been used to predict carbon balance and daily or yearly integrated production (Dennison and Alberte, 1982, 1985; Zimmerman et al., 1994; Herzka and Dunton, 1998). Thus, the lengths of H_{sat} and H_{comp} have been closely correlated with growth and survival of seagrasses (Dennison and Alberte, 1982, 1985; Zimmerman et al., 1994; Herzka and Dunton, 1998). *In situ* light manipulation in *Z. marina* beds revealed no appreciable growth responses unless changes in light were accompanied by differences in daily light periods (Dennison and Alberte, 1982, 1985). This suggests that daily light periods (H_{sat} and H_{comp}), rather than absolute light intensity, are important features controlling seagrass photosynthesis and growth (Dennison and Alberte, 1982, 1985).

H_{sat} ranged from 9.2 to 12.8 h (H_{comp} was between 11.2 and 12.4) in shallow *Z. marina* beds in Great Harbor, MA, while H_{sat} ranged from 6.4 to 9 h in deeper beds (Table 4; Dennison and Alberte, 1982, 1985). When eelgrass growth was plotted as a function of H_{sat}, the rate of growth showed saturation-type responses; with H_{sat} values exceeding 10 h did not enhance eelgrass growth (Dennison and Alberte, 1985). However, eelgrass leaf growth significantly decreased when H_{sat} values fell below 10 h (Dennison and Alberte, 1985). Deeper eelgrass beds had shorter H_{sat} (<6 h) resulting in low daily carbon gains, and elevated plant mortalities. These results suggest that an H_{sat} value of 6 h is minimum for eelgrass growth and survival (Dennison and Alberte, 1985). Additionally, an H_{sat} of 10 h was suggested as a suitable indicator of sufficient light for eelgrass growth. H_{sat} for persistent *P. oceanica* and *Z. marina* beds were approximately 10 h (Table 4; Zimmerman et al., 1995; Koch and Beer, 1996). In a persistent *T. testudinum* bed in southern Texas, monthly average H_{sat} ranged between 4 and 10 h (Table 4; Herzka and Dunton, 1998), and when H_{sat} was limited to 4 h in June, *T. testudinum* entered into a severe negative carbon balance. Nevertheless, significant production of *T. testudinum* in Florida Bay has been reported at depths (3 to 5 m) where the daily H_{sat} period was zero (Fourqurean and Zieman, 1991). Since photosynthesis can continue when light levels are below I_k, substantial carbon fixation rates were observed at depths where H_{sat} period was 0 h. Therefore, H_{sat} values provide a good approximation of daily production, however there may be situations where it is inappropriate (Fourqurean and Zieman, 1991). Since *T. testudinum* has higher I_k values compared to *P. oceanica* and *Z. marina*, H_{sat} for *T. testudinum* were usually shorter than those at the *P. oceanica* and *Z. marina* (Table 4).

In the H_{sat} model for daily production, gross photosynthesis can be calculated by multiplying P_{max} with H_{sat}, and net photosynthesis can be determined by subtracting respiration from gross photosynthesis (Dennison, 1987; Zimmerman et al., 1994; Herzka and Dunton, 1998). The H_{sat} model assumes zero production during periods when underwater irradiance is lower than I_k; thus, it can lead to an underestimation of production (Henley, 1993; Zimmerman et al., 1994; Herzka and Dunton, 1998). The H_{sat} model has been used to examine growth depth limits, light requirements, carbon balances, and productivities for several seagrass species (Dennison and Alberte, 1982, Fourqurean and Zieman, 1991; Dunton, 1994; Herzka and Dunton, 1998). High correlations between net photosynthesis and *in situ* growth rates have been observed for *Z. marina* (Dennison, 1987). Zimmerman et al. (1994) suggested that accurate integrated production can be predicted using the H_{sat} model when the daily H_{sat} period was calculated from continuous PFD measurements. These results indicate that a simple model using *P–I* parameters and H_{sat} can be used to predict seagrass productivity. However, the H_{sat} model may significantly underestimated production of *T. testudinum* when daily underwater PFD was less than 15 mol photons m^{-2} d^{-1} (Herzka and Dunton, 1998). The 15 mol photons m^{-2} d^{-1} represents an average instantaneous PFD of 300 μmol photons m^{-2} s^{-1}, which is close to *in situ* I_k of *T. testudinum* in southern Texas. Therefore, the H_{sat} model may fail to accurately predict seagrass production when plants are not light-saturated during a significant portion of the daily photoperiod (Herzka and Dunton, 1998).

2.5. Effects of light reduction on seagrass growth

Seagrasses may exhibit several physiological and morphological responses to light reduction. The magnitude and time required to initiate a response may depend on species, light intensity and duration, and interactions between environmental conditions (*e.g.* temperature and nutrient availabilities; Bulthuis, 1983a,b; Gordon et al., 1994; Van Lent et al., 1995; Abal, 1996; Grice et al., 1996; Longstaff and Dennison, 1999). In *Halophila pinifolia*, physiological responses to light reductions include changes in amino acid content, chlorophyll (chl) levels, and $\delta^{13}C$ occurred well before morphological changes are observed (*e.g.* biomass, shoot density, and canopy height; Longstaff and Dennison, 1999). Photoadaptive responses in seagrasses to reductions in irradiance have been reflected in seagrasses through decreases in plant size, shoot density, biomass, leaf production rates and chl composition (including *a*:*b* ratios and chl content; Wiginton and McMillan, 1979; Dennison and Alberte, 1982, 1985; Neverauskas, 1988; Tomasko and Dawes, 1989; Abal et al., 1994; Lee and Dunton, 1997; Peralta et al., 2002). Lower leaf biomass and size are early plant responses to light reduction (Gordon et al., 1994; Lee and Dunton, 1997), for example, leaf biomass in *T. testudinum* declined more rapidly than below-ground biomass following light reductions (Lee and Dunton, 1997). Changes in leaf biomass from shading is a product of etiolation and defoliation, which are common responses in both terrestrial and submersed plants to lower light conditions (Addicott and Lyon, 1973; Backman and Barilotti, 1976; Neverauskas, 1988; Gordon et al., 1994;

Table 4
The lengths of daily light periods (H_{comp} and H_{sat}) reported for various seagrass species, and growing and/or measuring conditions

Species	Location	I_c (μmol photons m^{-2} s^{-1})	H_{comp} (hour)	I_k (μmol photons m^{-2} s^{-1})	H_{sat} (hour)	Condition(s)	Source
Amphibolis griffithii	Warnbro Sound, Australia		8.1±0.3		5.2±0.7	Top of canopy, July	Carruthers and Walker (1997)
	Warnbro Sound, Australia		4.3±0.5		0.3±0.2	Base of canopy, July	Carruthers and Walker (1997)
	Warnbro Sound, Australia		13.6±0.1		11.6±0.2	Top of canopy, December	Carruthers and Walker (1997)
	Warnbro Sound, Australia		9.4±0.2		5.2±0.3	Base of canopy, December	Carruthers and Walker (1997)
Posidonia oceanica	Fraile Island, Spain			72.5±5.1	10.6±0.23	Control, June 1993	Ruiz and Romero (2001)
	Fraile Island, Spain			12.3±3.2	12±0.2	16.7% SI, June 1993	Ruiz and Romero (2001)
	Fraile Island, Spain			2.45±0.7	12.6±0.22	10.4% SI, June 1993	Ruiz and Romero (2001)
	Fraile Island, Spain			19±4.7	8.5±0.5	Control, May 1995	Ruiz and Romero (2001)
	Fraile Island, Spain			22.5±3.7	8.7±0.25	16.7% SI, May 1995	Ruiz and Romero (2001)
	Fraile Island, Spain			228.7±20.2	9.5±0.28	Control, June 1995	Ruiz and Romero (2001)
	Fraile Island, Spain			65.7±7.3	11.1±0.12	16.7% SI, June 1995	Ruiz and Romero (2001)
	Fraile Island, Spain			191.8±14	9.5±0.28	Control, August 1995	Ruiz and Romero (2001)
	Fraile Island, Spain			20.9±0.31	12.7±0.25	16.7% SI, August 1995	Ruiz and Romero (2001)
	Levante Bay, Spain			20.9±7.8*	10.5±0.56*	Inner Harbor	Ruiz and Romero (2003)
	Levante Bay, Spain			23.2±6.81*	10.3±0.5*	Intermediate Harbor	Ruiz and Romero (2003)
	Levante Bay, Spain			75.9±18.8*	9.5±0.42*	Outer harbor	Ruiz and Romero (2003)
	Fraile Island, Spain			113.1±50.1*	9.8±0.4*	Reference station	Ruiz and Romero (2003)
Thalassia testudinum	Laguna Madre, USA			297	8.0±0.5	May	Herzka and Dunton (1998)
	Laguna Madre, USA			297	4.0±0.9	June	Herzka and Dunton (1998)
	Laguna Madre, USA			297	10.0±0.2	July	Herzka and Dunton (1998)
	Laguna Madre, USA			281	7.6±0.4	August	Herzka and Dunton (1998)
	Laguna Madre, USA			281	6.6±0.4	September	Herzka and Dunton (1998)

(continued on next page)

Table 4 (*continued*)

Species	Location	I_c (μmol photons m^{-2} s^{-1})	H_{comp} (hour)	I_k (μmol photons m^{-2} s^{-1})	H_{sat} (hour)	Condition(s)	Source
	Florida Bay, USA		13.5		10.38	1 m depth	Fourqurean and Zieman (1991)
	Florida Bay, USA		13.2		8.8	2 m depth	Fourqurean and Zieman (1991)
	Florida Bay, USA		12.6		0	3 m depth	Fourqurean and Zieman (1991)
	Florida Bay, USA		11.9		0	4 m depth	Fourqurean and Zieman (1991)
	Florida Bay, USA		11.5		0	5 m depth	Fourqurean and Zieman (1991)
	Laguna Madre, USA	80	7.55±0.50	315	2.75±0.87	Field	Dunton (1994)
	Laguna Madre, USA	80	7.55±0.50	101	6.88±0.57	Lab	Dunton (1994)
	Corpus Christi Bay, USA	80	7.90±0.10	315	3.6±0.46	Field	Dunton (1994)
	Corpus Christi Bay, USA	80	7.90±0.10	101	7.6±0.47	Lab	Dunton (1994)
	San Antonio Bay, USA	80	6.0	315	2.1	Field	Dunton (1994)
	San Antonio Bay, USA	80	6.0	101	5.3	Lab	Dunton (1994)
Zostera marina	Great Harbor, USA	10	12.4	100	9.2	Shallow station	Dennison and Alberte (1982)
	Great Harbor, USA	10	11.2	100	6.4	Deep station	Dennison and Alberte (1982)
	Great Harbor, USA			100	12.8	Shallow station, June	Dennison and Alberte (1985)
	Great Harbor, USA			100	12.1	Shallow station, August	Dennison and Alberte (1985)
	Great Harbor, USA			100	9	Deep station, June	Dennison and Alberte (1985)
	Great Harbor, USA			100	8.8	Deep station, August	Dennison and Alberte (1985)
	Great Harbor, USA			100	13.1	Shallow, June	Dennison et al. (1987)
	Great Harbor, USA			100	10.4	Deep, June	Dennison et al. (1987)
	Great Harbor, USA			100	12	Shallow, August	Dennison et al. (1987)
	Great Harbor, USA			100	8.3	Deep, August	Dennison et al. (1987)
	Keil Cove, USA				10.8±1.9	0.5 m depth	Zimmerman et al. (1995)
	Paradise Cove, USA				10.3±2.3	0.5 m depth	Zimmerman et al. (1995)
	Long Island Sound, USA			150	13	Seasonal	Koch and Beer (1996)

Lee and Dunton, 1997). During the active growing season, loss of leaf tissue may negatively impact photosynthetic carbon fixation and oxygen production (including the transport of oxygen to below-ground tissues; Lee and Dunton, 1997, 2000; Connell et al., 1999).

Non-structural carbohydrates are usually high in rhizome tissues and serve as energy reserves for plants during low photosynthetic periods (Dawes and Lawrence, 1980; Durako and Moffler, 1985; Lee and Dunton, 1996; Cabello-Pasini et al., 2002). Significant decreases in tissue carbohydrates, due to underwater light reduction, have been reported in *T. testudinum* (Lee and Dunton, 1997). For seagrasses, aerobic metabolism in below-ground structures directly depends on above-ground O_2 production (Smith et al., 1984). Thus, below-ground tissues will occasionally undergo anaerobic conditions during low photosynthetic periods caused by low light. When below-ground tissues respire anaerobically, carbon demand increases to meet the changing metabolic requirements, which in turn further decrease carbohydrate reserves (Lee and Dunton, 1997).

At reduced light conditions, seagrass performance can be enhanced through a number of photo-acclimative responses that maximize the efficiency of light harvesting (West, 1990; Olesen and Sand-Jensen, 1993; Abal et al., 1994; Philippart, 1995; Olesen et al., 2002). The acclimative responses may be achieved through increased pigment content and greater leaf area per unit leaf biomass (increasing light absorption efficiencies; Enríquez et al., 1994; Lee and Dunton, 1997; Olesen et al., 2002). Increased chl content and decreased chl *a*:*b* ratio in seagrass leaf tissues have been reported in response to light reductions (Wiginton and McMillan, 1979; Dennison and Alberte, 1982, 1985; Abal et al., 1994; Lee and Dunton, 1997). Wavelengths absorbed by chl *a* decrease more rapidly than those absorbed by chl *b* as water depth increases (Weidemann and Bannister, 1986; McPherson and Miller, 1987). Thus, rapid increases in chl *b* levels relative to chl *a* (leading to lower chl *a*:*b* ratios), would allow for more efficient use of available wavelengths during reduced light conditions (Lee and Dunton, 1997). Studies of the photo-acclimatory responses of seagrass morphology to depth and shading have shown that above-ground biomass and shoot density tended to decrease with increasing depth and/or shading (Dennison and Alberte, 1986; Lee and Dunton, 1997; Longstaff et al., 1999; Olesen et al., 2002). Reductions in shoot densities and above-ground biomass during low light conditions are possibly an effective acclimation response to reduce self-shading within the canopy (Olesen et al., 2002; Enríquez and Pantoja-Reyes, 2005).

3. Temperature and seagrass growth

3.1. Effects of temperature on growth patterns

Growth rates in seagrasses exhibit clear seasonal trends, with increasing growth during spring and summer, and decreasing growth during fall and winter (Orth and Moore, 1986; Vermaat et al., 1987; Macauley et al., 1988; Dunton, 1990; Thom, 1990; Lee and Dunton, 1996). It has been suggested that these seasonal growth patterns are regulated by insolation and temperature or *via* an interaction of both (Wetzel and Penhale, 1983; Dunton, 1994; Lee and Dunton, 1996). Because irradiance and temperature are related, it is difficult to separate these effects. Although surface irradiance exhibits distinct seasonal trends, underwater PFD can show a high degree of variation with no clear seasonality (Dunton, 1994; Zimmerman et al., 1994; Lee and Dunton, 1996). Therefore, based on studies involving water temperature with seasonal growth patterns, numerous researchers consider temperature a primary factor controlling seasonal growth (Setchell, 1929; Tutin, 1942; Phillips et al., 1983; Bulthuis, 1987; Lee and Dunton, 1996). In *T. testudinum* (from Corpus Christi Bay, Texas), there was a strong correlation between water temperature and productivity, wherein leaf productivities increased with increasing temperatures (from 23 °C to 29 °C), with no high temperature growth inhibition (Lee and Dunton, 1996). However, poor correlations arise between seasonal water temperatures and seagrass productivities when all seasonal data are combined (Sand-Jensen and Borum, 1983; Lee et al., 2005). Elevated temperatures during fall and spring may enhanced seagrass productivities (*e.g. Syringodium filiforme* and *T. testudinum*), but high temperatures during summer can reduced seagrass productivities (Barber and Behrens, 1985). That is, biomass accumulation and water temperatures are positively correlated during spring and fall when water temperatures are lower than optimal. However, a negative correlation during summer months can develop due to high temperature growth inhibitions. Therefore, the seasonal patterns between productivity and water temperature maybe offset, and as a consequence, leaf production is poorly correlated with water temperature when annual data is considered (Barber and Behrens, 1985; Lee et al., 2005).

Growth of temperate seagrasses (*e.g.*, *Z. marina*) shows seasonal variations, but different patterns from those reported for tropical species (Kenworthy et al., 1982; Dennison, 1987; Lee et al., 2005). In Korea, *Z. marina* growth is highest during spring, however rapid reductions in biomass and growth have been observed during the summer (Lee et al., 2005). Optimal temperature for eelgrass growth in this area is between 15 and 20 °C, with growth inhibitions developing at temperatures above 20 °C. Exposure to high water temperatures promotes increases in respiration relative to photosynthesis, and consequently, leads to reductions in photosynthesis-to-respiration ratios (P:R ratios; Marsh et al., 1986). Therefore, growth in some seagrasses can be limited by seasonally high water temperatures during summer months (Wetzel and Penhale, 1983; Evans et al., 1986; Marsh et al., 1986; Lee et al., 2005).

In areas where summer water temperatures are considerably higher than the optimal growth temperatures, seagrasses may exhibit a bimodal growth pattern (*e.g. Z. marina* in lower latitudes; Kenworthy et al., 1982; Dennison, 1987; Lee et al., 2005). As stated previously, optimal growth temperatures of *Z. marina* usually ranged between 15 °C and 20 °C (Table 5). Therefore, *Z. marina* at lower latitudes will be exposed to optimal water temperatures during both spring and fall, and reductions in eelgrass growth will be observed during summer months due to high temperature stress (resulting in a bimodal seasonal growth pattern). Similarly, eelgrass leaf production on the coast of Korea was highest in the spring (temperatures between

Table 5

Temperature ranges at the study sites and the optimal temperature for growth of temperate and tropical/subtropical seagrass species

Species	Location	Latitude	Water temp. range (°C)	Optimal temp. (°C)	Source
Temperate					
Amphibolis Antarctica	Shark Bay, Australia	24°–26°S	18–26	26	Walker and McComb (1988)
Phyllospadix torreyi	Bodega Head, California, USA	38°20′N	12–21	13	Drysdale and Barbour (1975)
Posidonia australis	Shark Bay, Australia	24°–26°S	18–26	19	Walker and McComb (1988)
Posidonia oceanica	Calvi Bay, France (10 m depth)	42°N	13–25.5	18	Bay (1984)
	Calvi Bay, France (30 m depth)	42°N	12.5–22.0	13	Bay (1984)
Zostera asiatica	Akkeshi Bay, Japan	43°01′N	−0.7–16.0	12.6	Watanabe et al. (2005)
Zostera capensis				15–20	Edgecumbe (1980)
Zostera japonica	Dadae Bay, Korea	34°43′N	7.2–25.4	22	Lee et al. (2006)
	Yaquina Bay, USA	44°N	9–12	11.5	Kaldy (2006)
Zostera marina	Akkeshi Bay, Japan	43°01′N	−1.6–18.4	16.1	Watanabe et al. (2005)
	San Quintin Bay, Mexico (Transect I)	30°29′N	17.4–22.9	17.6	Ibarra-Obando and Huerta-Tamayo (1987)
	San Quintin Bay, Mexico (Transect I and II)	30°29′N	17.4–22.9	19.8	Ibarra-Obando and Huerta-Tamayo (1987)
	Koje Bay, Korea	34°N	8.3–26.9	20	Lee et al. (2005)
	Kosung Bay, Korea	34°N	1.6–31.8	16	Lee et al. (2005)
	Dadae Bay, Korea	34°43′N	7.2–25.4	17	Lee et al. (2006)
	Lagoon of Venice, Italy	45°N	6–30	20–24	Sfriso and Ghetti (1998)
	Åland Islands, Finland	60°21′N	7.0–16.5	13.0	Boström et al. (2004)
	Åland Islands, Finland	60°09′N	3.0–16.5	16.5	Boström et al. (2004)
	York River, USA	37°N	0–30	16	Moore et al. (1996)
	Vellerup Vig, Denmark	55°N	5–23	16.5	Sand-Jensen (1975)
Tropical/subtropical					
Cymodocea nodosa	Bay of Piran, Yugoslavia (2 m depth)	44°N	9.4–24.5	24.5	Peduzzi and Vukovič (1990)
	Bay of Piran, Yugoslavia (4 m depth)	44°N	9.4–24.5	24.5	Peduzzi and Vukovič (1990)
	Bay of Piran, Yugoslavia (6 m depth)	44°N	9.4–24.5	24.5	Peduzzi and Vukovič (1990)
Halodule uninervis	Shark Bay, Australia	25°53′S	14.5–30.5	23–26	Masini et al. (2001)
Halophila ovalis	Swan/Canning Estuary, Australia	31°–32°S		25	Hillman et al. (1995)
Syringodium filiforme	Tampa Bay, USA	27°N	11.9–32.3	23–29	Barber and Behrens (1985)
	Indian River, USA	28°N		28	Gilbert and Clark (1981)
	Indian River Lagoon, USA	27°32.2′N	9–32	32	Fry and Virnstein (1988)
Thalassia testudinum	Laguna Madre, USA		15–30	30	Kaldy and Dunton (2000)
	Corpus Christi Bay, Texas	27°49′N	13–30	29	Lee and Dunton (1996)
	Puerto Morelos, Mexico (Lagoon)	20°51′N	26.2–30.7	30.1	Van Tussenbroek (1995)
	Puerto Morelos, Mexico (Coast)	20°51′N	26.2–30.7	28.6	Van Tussenbroek (1995)
	Puerto Morelos, Mexico (Back-reef)	20°51′N	26.2–30.7	28.6	Van Tussenbroek (1995)
	Tampa Bay, USA	27°N	11.9–32.3	23–31	Barber and Behrens (1985)
	Biscayne Bay, USA	25°N	19.0–35.5	28–31	Zieman (1975)
	Charlotte Harbor, USA	26°50′N	14–33	30	Tomasko and Hall (1999)
	Jamaica	17°–18°N	27.3–29.9	29.4	Greenway (1974)

15 and 20 °C), and then decreased with increasing temperatures. Leaf production showed another peak, when eelgrass plants were re-exposed to optimal water temperature during the fall (Lee et al., 2005). However, eelgrass at higher latitudes (*e.g.* Akkeshi Bay, Japan) showed only unimodal growth patterns (Watanabe et al., 2005).

The thermal adaptations of seagrasses contribute to their global distribution and seasonal growth dynamics (McRoy and McMillan, 1977; Wetzel and Penhale, 1983; Marsh et al., 1986; Lee et al., 2005). Because temperate seagrass species are usually exposed to lower water temperatures (relative to tropical/subtropical species), they may be adapted to lower water temperatures and have limited tolerance to high temperatures. Therefore, optimal growth temperatures of temperate seagrass species are much lower than those of tropical/subtropical species (Table 5). Optimal growth temperatures for temperate species ranged from 11.5 °C to 26 °C, whereas the temperatures for tropical/subtropical species ranged from 23 °C to 32 °C (Table 5).

3.2. Effects of temperature on photosynthesis

The effects of temperature on photosynthesis have often been examined using *P–I* curves (Bulthuis, 1987;

Table 6
Optimal temperatures for photosynthesis of temperate and tropical/subtropical seagrass species

Species	Location	Latitude	Water temp. range (°C)	Optimal temp. (°C)	Source
Temperate					
Amphibolis antarctica	Perth, Australia	31°59′S	13–23	23	Masini and Manning (1997)
Amphibolis griffithii	Perth, Australia	31°59′S	13–23	23	Masini and Manning (1997)
Heterozostera tasmanica	Victoria, Australia	38°S	5–40	30	Bulthuis (1983b)
Phyllospadix torreyi	California, USA (intertidal)	34°16′N	10–23	23	Drew (1979)
Posidonia australis	Perth, Australia	31°59′S	13–23	23	Masini and Manning (1997)
Posidonia oceanica	Malta	35°51′N	11–36	32	Drew (1978)
	Malta	35°51′N	12–32	32	Drew (1979)
Posidonia sinuosa	Princess Royal Harbor, Australia	35°03.2′S	13–24	18–23	Masini et al. (1995)
	Perth, Australia	31°59′S	13–23	18–23	Masini and Manning (1997)
Ruppia maritima	Chesapeake Bay, USA	37°25′N	1–28	28	Wetzel and Penhale (1983)
	Chesapeake Bay, USA	37°16′N	8–30	23	Evans et al. (1986)
Zostera marina	Chesapeake Bay, USA	37°25′N	1–28	22	Wetzel and Penhale (1983)
	Chesapeake Bay, USA	37°16′N	8–30	19	Evans et al. (1986)
	Newport River estuary, USA	34°N	15–29	22	Penhale (1977)
	Izembek Lagoon, USA (subtidal)	55°N	0–40	30	Biebl and McRoy (1971)
	Izembek Lagoon, USA (intertidal)	55°N	0–40	35	Biebl and McRoy (1971)
	California, USA	34°16′N	4–21	21	Drew (1979)
	Bahia Todos Santos, Mexico (lagoon)	31°45′N	16–22	17	Cabello-Pasini et al. (2002)
	Bahia Todos Santos, Mexico (open coast)	31°45′N	16–22	21	Cabello-Pasini et al. (2002)
	Great Harbor, USA	40°31.5′N	0–20	16–20	Dennison (1987)
	Great Harbor, USA	40°31.5′N	0–35	25–30	Marsh et al. (1986)
Tropical/subtropical					
Cymodocea nodosa	Malta	35°51′N	11–36	32	Drew (1978)
	Malta	35°51′N	11–36	30	Drew (1979)
	Alfaques Bay, Spain	40°N	8–32	32	Pérez and Romero (1992)
	Mar Menor lagoon, Spain	37°N	10–30	30	Terrados and Ros (1995)
Cymodocea rotundata	Santiago Islands, The Philippines	16°27′03″N	24–33	27	Agawin et al. (2001)
Enhalus acoroides	Santiago Islands, The Philippines	16°27′03″N	24–33	27	Agawin et al. (2001)
Halophila decipiens	Anclote Key, USA	28°08′44″N	10–30	30	Dawes et al. (1989)
Halophila johnsonii	Haulover Park, Biscayne Bay, USA	25°55′N	15–35	35	Torquemada et al. (2005)
	Indian River estuary, USA	27°28′40″N	10–30	30	Dawes et al. (1989)
Halophila ovalis	Taylor's Bay, Australia	33°50′S	10–40	25–30	Ralph (1998)
Halodule wrightii	Laguna Madre, USA	27°21′N	12–30	30	Dunton and Tomasko (1994)
	San Antonio Bay, USA	28°15′N	17–28	28	Dunton (1996)
	Corpus Christi Bay, USA	27°49′N	17–29	25	Dunton (1996)
Thalassia hemprichii	Santiago Islands, The Philippines	16°27′03″N	24–33	27	Agawin et al. (2001)
Thalassia testudinum	Corpus Christi Bay, USA	27°49′N	15–31	29	Herzka and Dunton (1997)
	Lower Laguna Madre, USA	26°08′N	15–31	27	Herzka and Dunton (1997)
	Lower Laguna Madre, USA	26°08′05″N	10–32	31	Herzka and Dunton (1998)

Herzka and Dunton, 1997). $P_{\max}$, I_k, I_c, and respiration rates usually increase with increasing water temperature (Bulthuis, 1983b; Dennison, 1987; Marsh et al., 1986; Pérez and Romero, 1992; Herzka and Dunton, 1997; Masini and Manning, 1997; Moore et al., 1997). As expected, the optimal temperatures for seagrass growth and photosynthesis are often higher for tropical/subtropical species than temperate species (Table 6).

The optimum temperature for photosynthesis can vary with underwater irradiance (Bulthuis, 1987). For example, the optimum temperature for photosynthesis decreased from 30 °C to <5 °C, as irradiance decreased from 955 to 37 μmol photons m^{-2} s^{-1} in *H. tasmanica* (Bulthuis, 1987). This implies that seagrasses growing in low light conditions have lower optimum temperatures for photosynthesis than plants in high light conditions. Plants at higher temperatures likely need more light to maintain positive carbon balances than those at lower temperatures. Thus, photosynthetic production in seagrasses is more susceptible to high water temperatures at reduced light conditions. Consequently, reductions in underwater light may be more harmful to seagrasses during summer rather than winter (Hillman et al., 1989).

As photosynthesis is only one of many factors determining growth in seagrasses, the optimal temperature for photosynthesis should not be confused with the optimal temperature for growth (Bulthuis, 1987). The role of temperature on seagrass growth is considerably more complicated than its effect on photosynthesis. The importance of temperature on nutrient availability and uptake, leaf senescence, nutrient partitioning within the plants, and respiration will contribute to the optimal temperature for seagrasses (Marsh et al., 1986; Bulthuis, 1987; Herzka and Dunton, 1997; Lee and Dunton, 1999b). Both respiration and photosynthesis increase with increasing water temperatures, but respiration usually increases more than photosynthesis at progressively higher temperatures, thus leading to a reduction in net photosynthesis (Bulthuis, 1983b; Dennison, 1987; Marsh et al., 1986; Pérez and Romero, 1992; Herzka and Dunton, 1997; Masini and Manning, 1997). From the available data, the optimum temperatures for both growth and photosynthesis were variable with seagrass species, but the optimum temperatures for growth were usually lower than those for photosynthesis (Table 7).

Seagrasses in shallow or intertidal zones are exposed to a variety of environmental extremes, including high

Table 7

Average values of optimal temperatures for growth and photosynthesis of temperate and tropical/subtropical seagrass species

Species	Optimal temp. (°C)	
	Growth	Photosynthesis
Temperate		
Amphibolis antarctica	26	23
Amphibolis griffithii		23
Heterozostera tasmanica		30
Phyllospadix torreyi	13	23
Posidonia australis	19	23
Posidonia oceanica	15.5±2.5	32
Posidonia sinuosa		20.5
Ruppia maritima		25.5±2.5
Zostera asiatica	12.6	
Zostera capensis	17.5	
Zostera japonica	18.5±3.5	
Zostera marina	15.3±1.6	23.3±1.8
Tropical/subtropical		
Cymodocea nodosa	24.5	31.0±0.5
Cymodocea rotundata		27
Enhalus acoroides		27
Halophila decipiens		30
Halophila johnsonii		32.5±2.5
Halophila ovalis	25	27.5
Halodule wrightii		27.7±1.5
Halodule uninervis	24.5	
Syringodium filiforme	28.7±1.8	
Thalassia hemprichii		27
Thalassia testudinum	29.1±0.3	29.0±1.2

solar radiation and wide temperature fluctuations. As there is a rapid decline in photosynthesis when *in situ* temperature exceeds the optimum temperature, elevated temperatures in shallow areas will have significant impact on seagrass photosynthesis and productivity (Bulthuis, 1987; Ralph, 1998; Seddon and Cheshire, 2001). Pulse amplitude modulated (PAM) fluorometers have been used to measure the effects of thermal stress on chlorophyll *a* fluorescence (Ralph, 1998; Seddon and Cheshire, 2001; Campbell et al., 2006). Photosynthetic efficiencies can decrease at extreme temperatures (Ralph, 1998; Seddon and Cheshire, 2001). For example, effective quantum yields ($\Delta F/F_m'$) and maximum quantum yields (F_v/F_m) of *H. ovalis* were similar and relatively stable over a fairly wide range of temperatures. However, at extreme temperatures (40 °C or 10 °C), substantial decreases were noted in both $\Delta F/F_m'$ and F_v/F_m (Ralph, 1998). This dramatic decline in F_v/F_m at extreme temperatures was linked to chronic inhibition of photosynthesis, as indicated by F_o and F_m responses being completely quenched during excessive temperature challenges. These plants were unable to recover from extreme temperature treatments, suggesting irreversible damage to photosynthetic structures (Ralph, 1998). The dramatic declines in F_v/F_m, due to chronic inhibition of photosynthesis by heat stress have also been reported in seven tropical seagrass species (Campbell et al., 2006). The photosynthetic responses to elevated temperature in this experiment also suggest that photosynthesis likely underwent irreversible damage from short-term or episodic changes in seawater temperatures (as high as 40–45 °C; Campbell et al., 2006).

4. Nutrients and seagrass growth

4.1. Inorganic nutrients for seagrass growth

To maintain growth, primary producers such as seagrasses require inorganic carbon and nutrients. Most marine macrophytes can utilize both CO_2 and HCO_3^- for photosynthetic carbon reduction (Beer, 1989; Durako, 1993; Larkum and James, 1996; Beer and Rehnberg, 1997; Invers et al., 2001). There are millimolar concentrations of dissolved inorganic carbon (DIC) in seawater which is approximately three orders of magnitude greater than concentrations of inorganic N or P (Short et al., 1985; Pérez et al., 1991; Lee and Dunton, 2000). While a number of elements are essential for plant growth, we are usually concerned with the few that are likely to limit plant growth in natural systems. Nutrients that most commonly limit seagrass growth are N and P (Duarte, 1990; Romero et al., 2006). Carbon constitutes approximately 30–40% of seagrass tissue dry weight, whereas N and P account for 1–4%, and 0.1–1.0% of tissue dry weight, respectively (Duarte, 1990; Pérez-Lloréns and Niell, 1993; Fourqurean et al., 1997; Lee and Dunton, 1999b; Terrados et al., 1999b). Variability in C content of seagrass leaves is much less than N or P (Duarte, 1990). This lower variability in C levels relative to N or P suggests that C limited growth is rare in seagrasses (Short et al., 1985; Pérez et al., 1991; Lee and Dunton, 2000).

Seagrasses can assimilate inorganic nutrients through both above- and below-ground tissues (Iizumi and Hattori, 1982; Thursby and Harlin, 1982, 1984; Short and McRoy, 1984; Stapel et al., 1996; Pedersen et al., 1997; Terrados and Williams, 1997; Lee and Dunton, 1999b; Gras et al., 2003; Nielsen et al., 2006). Major inorganic N sources available to seagrasses include NO_3^- and NH_4^+ in the water column, and NH_4^+ in sediment pore waters. Higher leaf uptake rates have been reported for NH_4^+ in comparison to NO_3^- in several seagrasses (Short and McRoy, 1984; Terrados and Williams, 1997; Lee and Dunton, 1999b). Assimilation of NO_3^-, by plant tissues, is influenced by the availability of photosynthate and/or stored C, and thus is energetically costly (Thacker and Syrett, 1972; Lara et al., 1987; Turpin, 1991). Therefore, seagrasses would benefit from the uptake of reduced forms of N (*i.e.* NH_4^+; Lee and Dunton, 1999b). The main P source is PO_4^{3-}, and occurs in the water column as well as sediments. With the exception of areas characterized by high river input, water column nutrient concentrations are usually low (typically <3 μM for NO_3^- and NH_4^+, and <2 μM for PO_4^{3-}; Tomasko and Lapointe, 1991; Hemminga et al., 1995; Ruiz and Romero, 2003; Lee et al., 2005). In sediment pore water, however, nutrient concentrations are much higher than the overlying water column (Dennison et al., 1987; Lee and Dunton, 1999b; Terrados et al., 1999a; Lee et al., 2005; Kaldy, 2006). Concentrations of pore water NH_4^+ usually range from <20 μM to 1000 μM, whereas concentration of PO_4^{3-} can exceed 20 μM in sediment pore waters (Udy and Dennison, 1997; Touchette and Burkholder, 2000; Lee et al., 2005). Because of higher nutrient concentrations in sediment compared to overlying water, pore waters are often considered a main source of nutrients for seagrasses (Iizumi and Hattori, 1982; Short and McRoy, 1984; Zimmerman et al., 1987).

However, some studies have demonstrated higher nutrient uptake affinities in leaves in comparison to roots (Pedersen et al., 1997; Lee and Dunton, 1999b). Seagrass leaves are usually exposed to considerably lower nutrient concentrations. Therefore, seagrass leaves may have developed the ability to assimilate nutrients under lower concentrations. With this in mind, nutrient uptake may also saturate at lower concentrations in leaf tissues (Stapel et al., 1996; Lee and Dunton, 1999b). Conversely, nutrient uptake by roots exhibits saturation at much higher nutrient concentrations than those observed in leaves. Nutrient uptake kinetics in seagrass tissues reflects plant adaptations to life in water column with low nutrients and relatively high nutrients in sediment pore water. Thus, although there are significant differences in nutrient concentration between pore water and water column, an equal contribution of water column and sediment nutrients in plant nutrient acquisition has been suggested by various researchers (Iizumi and Hattori, 1982; Short and McRoy, 1984; Zimmerman et al., 1987; Pedersen and Borum, 1992; Stapel et al., 1996; Terrados and Williams, 1997; Lee and Dunton, 1999b). Iizumi and Hattori (1982) demonstrated that approximately 55% of the total N requirement for *Z. marina* growth was supplied as sediment NH_4^+. In another study using a numerical model, root contributions to NH_4^+ uptake accounted for roughly 60% of total N (Zimmerman et al., 1987). In *T. testudinum*, root NH_4^+ uptake from sediments accounted for 50% of total plant N uptake, with leaf NO_3^- and NH_4^+ assimilation accounting for the remaining N (Lee and Dunton, 1999b).

The respective contributions of leaf and root nutrient uptake may vary as a function of nutrient concentrations in the water column and sediment (Zimmerman et al., 1987). However, in *T. testudinum*, proportional uptake of N from leaves and roots were not significantly different between sites which were markedly different with respect to sediment nitrogen concentrations (Lee and Dunton, 1999b). Biomass allocations, produced by different nutrient conditions, probably caused this discrepancy. Seagrasses allocate more biomass into below-ground tissues under low sediment nutrient availability. In contrast, more biomass in above-ground tissues can occur when nutrients are readily available, thus allowing for greater carbon fixation (Lee and Dunton, 1999a). Therefore, in high sediment nutrient conditions, leaf nutrient acquisition may increase due to larger leaf biomass. Consequently, contributions of leaf and root nutrient uptake, from the water column and sediments, to total nutrient acquisition may not change with sediment nutrient conditions (Lee and Dunton, 1999b).

4.2. Nutrient limitation and plant responses to nutrient enrichments

Increasing *in situ* nutrient availability by nutrient enrichment has been used to examine nutrient-limited growth in seagrasses (Orth 1977; Harlin and Thorne-Miller, 1981; Iizumi et al., 1982; Dennison et al., 1987; Short et al., 1990; Pérez et al., 1991; Murray et al., 1992; Agawin et al., 1996; Udy and Dennison, 1997; Lee and Dunton, 2000). When supplying N and/or P to nutrient-limited plants, increases in biomass, productivities, and shoot size are typical responses (Bulthuis et al., 1992; Agawin et al., 1996; Udy and Dennison, 1997; Lee and Dunton, 2000). However, seagrass growth is not always limited by ambient nutrient concentrations, as increased nutrient availability sometimes has limited effect on seagrass growth (Bulthuis and Woelkerling, 1981; Dennison et al., 1987; Lee and Dunton, 2000).

Increased sediment nutrients have also led to increased plant productivities through physiological changes including maximum rate of photosynthesis, photosynthetic efficiency, and/or increased chl concentrations (Agawin et al., 1996; Lee and Dunton, 1999a). Increased photosynthetic performance and chl concentrations, following nutrient enrichment of a nutrient-limited population, suggest an interaction between photosynthetic carbon fixation and nutrient availability. Increased seagrass tissue N, as a result of N enrichment, has been observed in different seagrasses (Bulthuis et al., 1992; Erftemeijer et al., 1994; Alcoverro et al., 1997; Udy and Dennison, 1997; Lee and Dunton, 1999a). The assimilation of inorganic N requires C skeletons for incorporating ammonium into amino acids (Turpin et al., 1990; Huppe and Turpin, 1994). Carbon skeletons and reduction energy for N uptake and assimilation can be supplied by photosynthetic processes. Therefore, increased nutrient availability may induce photosynthetic C fixation and metabolism (Agawin et al., 1996; Lee and Dunton, 1999a). Increased productivity and biomass of leaves, as a result of nutrient enrichment, is the most common plant response when living in nutrient-limited environments (Orth, 1977; Bulthuis and Woelkerling, 1981; Agawin et al., 1996; Alcoverro et al., 1997; Udy and Dennison, 1997; Lee and Dunton, 2000). These increases in leaf production and biomass may be associated with increases in C fixation necessary to meet the increased C demand during N reduction and assimilation.

Although seagrasses can use inorganic nutrients from the water column, elevated water column nutrient levels can adversely affect seagrasses through the stimulation of phytoplanktonic, epiphytic and macroalgal productivities (Harlin and Thorne-Miller, 1981; Short, 1987; Coleman and Burkholder, 1994; Short et al., 1995; Wear et al., 1999). Blooms of competing primary producers, caused by water column nutrient enrichment, can lead to reductions in light available to seagrasses (Harlin and Thorne-Miller, 1981; Van Montfrans et al., 1984; Borum, 1985; Giesen et al., 1990; Tomasko and Lapointe, 1991; Van

Lent et al., 1995; Wear et al., 1999). Additionally, Burkholder et al. (1992, 1994) demonstrated that water column NO_3^- enrichment promoted eelgrass decline through a direct physiological response unrelated to algal light attenuation. Lack of an inhibition mechanism for sustained NO_3^- uptake by eelgrass leaves likely caused internal imbalances in carbohydrates (Burkholder et al., 1992).

Short et al. (1990) investigated the role of P and N in the primary production of a tropical seagrass *S. filiforme* using long-term nutrient enrichment experiments. Substantial increase in seagrass growth, biomass, and tissue P levels after P enrichment likely reflected P limitation for these plants growing in tropical carbonate sediments. Pérez et al. (1991) also showed P limitation in *C. nodosa* growth in carbonate sediments. In their study, increased sediment P levels resulted in increased seagrass tissue P content, shoot growth, biomass and density, and reduced tissue N:P ratios (Pérez et al., 1991). Short (1987) demonstrated that sediment geochemistry in seagrass beds is important in determining the limiting nutrient to seagrass growth. Seagrasses growing in terrigenous sediment are usually nitrogen-limited, whereas seagrasses growing in biogenic carbonate sediments are often phosphorus-limited due to binding of phosphate in the carbonate sediments (Short et al., 1990; Pérez et al., 1991; Fourqurean et al., 1992a,b; Koch et al., 2001).

4.3. *In situ nutrient concentrations and nutrient availability*

Because of high nutrient uptake affinities in leaves and possible detrimental effects of high water column nutrient concentrations on seagrass growth (Orth and Moore, 1983; Silberstein et al., 1986; Giesen et al., 1990; Tomasko and Lapointe, 1991; Pedersen et al., 1997; Lee and Dunton, 1999b; Wear et al., 1999), seagrass production may not correlate well with water column nutrients. Seagrass production dynamics, as related to sediment nutrient availability, is generally well documented, but comparably less is known about the effects of *in situ* water column nutrient availability on seagrass growth. From available data in literature, productivities of seagrasses were not significantly correlated with water column nutrient concentrations (except for *Z. marina* production with water column P; Table 8). Productivity of *Z. marina* was strongly correlated with water column P levels, suggesting possible P limitation for *Z. marina* growth in some areas.

Significantly smaller eelgrass leaves and lower leaf productivities have been reported when sediment pore water NH_4^+ concentrations dropped below 100 μM. Thus a pore water NH_4^+ concentration of 100 μM have been suggested as a threshold for N limitation in *Z. marina* (Short, 1983; Dennison et al., 1987), and is consistent with saturation levels reported for NH_4^+ uptake in *Z. marina* roots (Iizumi and Hattori, 1982; Thursby and Harlin, 1982). For *T. testudinum*, plant growth did not vary with sediment NH_4^+ concentration from 100 μM to 2000 μM (Lee and Dunton, 2000). The lack of a plant response to changes in sediment NH_4^+ suggests that pore water NH_4^+ concentrations of 100 μM may provide an adequate pool of inorganic N for *T. testudinum* growth. Although sediment nutrient concentrations in some seagrass beds are indicative of nutrient growth limitation, *in situ* nutrient levels should not be confused with nutrient availability. Relationships between seagrass leaf productivities and sediment nutrient concentrations did not exhibit strong positive correlations (Table 8). These weak correlations imply that *in situ* nutrient concentration is not a good indicator of nutrients available for growth. As with water column P, sediment P also exhibited significant correlations with productivity of *Z. marina*, suggesting P-limited growth for *Z. marina* in some locations (Table 8). Typically, P limitation for seagrass growth occurs in carbonate sediments (Short et al., 1990; Pérez et al., 1991; Fourqurean et al., 1992a, b; Koch et al., 2001); however, P limitation has also been reported in temperate bays with siliceous sediments (Fourqurean and Cai, 2001; Johnson et al., 2006). Therefore, these results imply that P limitation for seagrass growth is also common in temperate seagrass beds with terrigenous sediments.

Sediment nutrients (*e.g.* NH_4^+ and PO_4^{3-}) are often supplied by remineralization (Jørgensen, 1977, 1982; Hines and Lyons, 1982; Boon et al., 1986; Holmer and Nielsen, 1997). *In situ* sediment nutrient concentrations represent a balance between inorganic nutrient production and consumption. Both regeneration of inorganic nutrients in sediments and turnover rates of nutrient pools are important factors that determine the degree of nutrient availability. Essential nutrients for seagrass growth may be derived from decomposition of organic matter in water column and sediments (Opsahl and Benner, 1993; Ziegler and Benner, 1999; Holmer and Olsen, 2002; Kilminster et al., 2006). Seagrass litter is likely the main organic source for regenerated nutrients in seagrass beds (Mateo and Romero, 1997; Opsahl and Benner, 1993; Holmer and Olsen, 2002), and nutrient recycling within these beds can be accomplished through rapid *in situ* decomposition of organic matter (Opsahl and Benner, 1993; Holmer and Olsen, 2002). In tropical areas, bacterial N fixation also provides

Table 8
Seagrass production and nutrient concentrations in the water column and sediment pore water

Species	Location	Latitude	Water column (µM)			Sediment pore water (µM)			Production (g dw m^{-2} d^{-1})	Source
			NH_4^+	$NO_3^-+NO_2^-$	PO_4^{3-}	NH_4^+	$NO_3^-+NO_2^-$	PO_4^{3-}		
Temperate										
Posidonia oceanica	Levante Bay, Spain (inner Harbor)	37°N		0.07–2.21	0.001–0.01				1–6[a]	Ruiz and Romero (2003)
	Levante Bay, Spain (intermediate harbor)	37°N		0.18–2.05	0.001–0.005				2.8–3.0[a]	Ruiz and Romero (2003)
	Levante Bay, Spain (outer harbor)	37°N		0.27–0.64	0.001–0.01				3.8–9.4[a]	Ruiz and Romero (2003)
	Levante Bay, Spain (reference)	37°N		0.05–0.54	0.001–0.006				3–9[a]	Ruiz and Romero (2003)
Zostera capensis	Kromme Estuary, South Africa (lower site)	34°S		0.63±0.47	0.71±0.55				0.93	Hanekom and Baird (1988)
	Kromme Estuary, South Africa (upper site)	34°S		0.63±0.47	0.71±0.55				1.98	Hanekom and Baird (1988)
Zostera capricorni	Wanga Wallen banks, Australia	27°25′S				7.4		4.7	3.7	Udy and Dennison (1997)
	Wanga Wallen banks, Australia	27°25′S				7.4		4.7	2.6[e]	Udy and Dennison (1997)
	Moreton Bay, Australia (10% of Incident light)	27°S				14–25			0.69±0.11	Hansen et al. (2000)
	Moreton Bay, Australia (50% of Incident light)	27°S				18–25			1.70±0.11	Hansen et al. (2000)
Zostera japonica	Dadae Bay, Korea	34°43′N	0.1–6.0	0.5–84	0.03–2.3				1.7±0.2	Lee et al. (2006)
	Yaquina Bay, USA	44°N	2–27 (DIN)		0.5–2	600–2400 (DIN)		5–45	0.69	Kaldy (2006)
Zostera marina	Koje Bay, Korea	34°N	0.2–9.0	0.3–16.2	0.2–1.8	58.3–650.1	0.3–17.4	0.8–6.5	0.24–3.74	Lee et al. (2005)
	Kosung Bay, Korea	34°N	0.0–21.3	0.2–90.0	0.1–2.9	57.2–473.9	0.1–3.7	0.7–18.9	0.04–2.79	Lee et al. (2005)
	Dadae Bay, Korea	34°43′N	0.1–6.0	0.5–84	0.03–2.3				2.6±0.2	Lee et al. (2006)
	York River, USA (transplant, Y11 site)	37°N	3–18 (DIN)		0.5–1.0				0.06–2.05[a]	Moore et al. (1996)
	York River, USA (transplant, Y26 site)	37°N	3–20 (DIN)		0.7–1.6				0.07–0.65[a]	Moore et al. (1996)
	Great Harbor, USA (shallow, controlled, Nov.)	40°31.5′N				380			0.02	Dennison et al. (1987)
	Great Harbor, USA (shallow, in situ, Jun.)	40°31.5′N				270			2.4	Dennison et al. (1987)
	Great Harbor, USA (shallow, controlled, Mar.)	40°31.5′N				185			0.6	Dennison et al. (1987)
	Great Harbor, USA (shallow, in situ, Aug.)	40°31.5′N				835			7.0	Dennison et al. (1987)
	Great Harbor, USA (deep, controlled)	40°31.5′N				497.5			0.3	Dennison et al. (1987)

	Great Harbor, USA (deep, in situ)	40°31.5′N				1032.5			1.3	Dennison et al. (1987)
	New Hampshire, USA (mud tank)	43°N				22.1±12.3		20.8±3.7	8.4±3.1[a]	Short (1987)
	New Hampshire, USA (sand tank)	43°N				42.3±13.1		2.9±1.8	4.1±0.5[a]	Short (1987)
	New Hampshire, USA (control, mesocosm)	43°N	3.21–8.26		0.50–0.74				1–11	Short et al. (1995)
	Padilla Bay, USA (control)	48°N	1.9						2.92[b]	Williams and Ruckelshaus (1993)
	Friday Harbor, USA	48°32′11″N	0.05–1.69	24.3	0.37–2.46				1.5–9.8	Nelson and Waaland (1997)
	Øresund, Denmark	55°N	1–5	1.5–6.0		240–1300			1.5–24[d]	Pedersen and Borum (1993)
	Åland Islands, Finland (site 1, shallow)	60°N	0–0.12		0–0.022	5.0		0.5	0.075±0.006	Bostrőm et al. (2004)
	Åland Islands, Finland (site 1, intermediate)	60°N	0–0.12		0–0.022	6.1		0.7	0.083±0.008	Bostrőm et al. (2004)
	Åland Islands, Finland (site 1, deep)	60°N	0–0.12		0–0.022	7.8		0.9	0.131±0.014	Bostrőm et al. (2004)
	Åland Islands, Finland (site 2, shallow)	60°N	0–0.19		0–0.036	5.6		1.8	0.367±0.050	Bostrőm et al. (2004)
	Åland Islands, Finland (site 2, intermediate)	60°N	0–0.19		0–0.036	2.8		0.3	0.252±0.039	Bostrőm et al. (2004)
	Åland Islands, Finland (site 2, deep)	60°N	0–0.19		0–0.036	5.6		0.4	0.286±0.046	Bostrőm et al. (2004)
Tropical/subtropical										
Cymodocea rotundata	Vipingo, Kenya	3°45′S	1.98	2.4	0.68	291.1	32.8	51.8	1.95	Uku and Bjőrk (2005)
	Nyali Beach, Kenya	4°03′S	1.55	7.6	0.78	409.4	50.3	52.1	2.2	Uku and Bjőrk (2005)
Cymodocea serrulata	Wanga Wallen banks, Australia	27°25′S				7.4		4.7	1.2	Udy and Dennison (1997)
	Wanga Wallen banks, Australia	27°25′S				7.4		4.7	1.3[e]	Udy and Dennison (1997)
Enhalus acoroides	Barang Lompo, Indonesia	5°S	2.2±1.9	0.9±0.6	0.8±0.4	49.7±16.8	3.4±1.6	10.9±3.9	0.09–0.57	Erftemeijer and Herman (1994)
	Gusung Tallang, Indonesia	5°S	3.2±2.8	1.4±1.3	1.4±0.6	68.7±13.3	2.6±2.0	5.5±1.0	0.24–0.35	Erftemeijer and Herman (1994)
	Santa Barbara, The Philippines	16°20.60′N				150	4	2	75[a]	Terrados et al. (1999a)
	Pislatan, The Philippines	16°22.12′N				150	9	7	60[a]	Terrados et al. (1999a)
	Binabalian loob, The Philippines	16°23.09′N				100	4	0.5	45[a]	Terrados et al. (1999a)
	Silaqui, The Philippines	16°26.35′N				45	0.9	1.1	52[a]	Terrados et al. (1999a)

(continued on next page)

Table 8 (*continued*)

Species	Location	Latitude	Water column (μM)			Sediment pore water (μM)			Production (g dw m^{-2} d^{-1})	Source
			NH_4^+	$NO_3^-+NO_2^-$	PO_4^{3-}	NH_4^+	$NO_3^-+NO_2^-$	PO_4^{3-}		
Halodule uninervis	Green Island, Australia	16°45′S				6.2		1.1	2.0	Udy et al. (1999)
	Green Island, Australia	16°45′S				6.2		1.1	1.29[e]	Udy et al. (1999)
	Wanga Wallen banks, Australia	27°25′S				7.4		4.7	1.2	Udy and Dennison (1997)
	Wanga Wallen banks, Australia	27°25′S				7.4		4.7	1.7 [e]	Udy and Dennison (1997)
Halodule wrightii	Florida Bay, USA	24°–25°N	6.8–80.7			190.8±59.5		0.1–3.0	0.013±0.013	Powell et al. (1989)
Syringodium filiforme	Green Island, Australia	16°45′S				6.2		1.1	0.3	Udy et al. (1999)
Thalassia hemprichii	Vipingo, Kenya	3°45′S	1.98	2.4	0.68	370.5	28.6	40.3	2.85	Uku and Bjőrk (2005)
	Nyali Beach, Kenya	4°03′S	1.55	7.6	0.78	166.8	59.3	24.2	5.4	Uku and Bjőrk (2005)
	Barang Lompo, Indonesia	5°S	2.2±1.9	0.9±0.6	0.8±0.4	49.7±16.8	3.4±1.6	10.9±3.9	1.02–5.08	Erftemeijer and Herman (1994)
	Barang Lompo, Indonesia (blank)	5°05′S							4.27±0.50[c]	Erftemeijer et al. (1994)
Thalassia testudinum	Carrie Bow Cay, Belize (0.5 m depth)	16°N	0.28	0.09					0.665	Tomasko and Lapointe (1991)
	Carrie Bow Cay, Belize (2.0 m depth)	16°N	0.28	0.09					0.498	Tomasko and Lapointe (1991)
	Twin Cays, Belize (0.5 m depth)	16°N	1.05	0.05					1.327	Tomasko and Lapointe (1991)
	Twin Cays, Belize (2.0 m depth)	16°N	1.05	0.05					0.901	Tomasko and Lapointe (1991)
	Big Pine Key, USA (0.5 m depth)	24°N	1.64	2.32					0.306	Tomasko and Lapointe (1991)
	Big Pine Key, USA (2.0 m depth)	24°N	1.64	2.32					1.083	Tomasko and Lapointe (1991)
	Cutoe Key, USA (0.5 m depth)	24°N	0.15	0.35					0.768	Tomasko and Lapointe (1991)
	Cutoe Key, USA (2.0 m depth)	24°N	0.15	0.35					1.372	Tomasko and Lapointe (1991)
	Key West, USA (eutrophic site)	24°33′20.3″N	26.33		0.49				3.87[a]	Lapointe et al. (1994)
	Key West, USA (mesotrophic site)	24°33′14.0″N	19.57		0.41				3.50[a]	Lapointe et al. (1994)
	Key West, USA (oligotrophic site)	24°27′50.5″N	10.77		0.16				4.17[a]	Lapointe et al. (1994)
	Big Pine, USA (mesotrophic site)	24°38′59.8″N	23.15		0.43				5.59[a]	Lapointe et al. (1994)

	Big Pine, USA (oligotrophic site)	24°32′56.4″N	11.64		0.21				8.23[a]	Lapointe et al. (1994)
	Big Pine, USA (hypereutrophic site)	24°41′44.8″N	53.07		1.27				1.45[a]	Lapointe et al. (1994)
	Big Pine, USA (eutrophic site)	24°40′32.1″N	28.79		0.54				3.53[a]	Lapointe et al. (1994)
	Long Key, USA (eutrophic site)	24°50′30.5″N	18.45		0.32				3.69[a]	Lapointe et al. (1994)
	Long Key, USA (mesotrophic site)	24°50′45.2″N	21.53		0.19				4.33[a]	Lapointe et al. (1994)
	Long Key, USA (oligotrophic site)	24°51′04.1″N	14.64		0.21				5.12[a]	Lapointe et al. (1994)
	Florida Bay, USA (control)	24°–25°N	6.8–80.7			190.8±59.5			1.84±0.43	Powell et al. (1989)
	Lower Laguna Madre, USA (1.7 m depth)	26°N	0.7–2.9	0–3.0					0.5–2.0	Kaldy and Dunton (2000)
	Lower Laguna Madre, USA (1.3 m depth)	26°N	0–3.1	0–2.5					0.4–3.5	Kaldy and Dunton (2000)
	Lower Laguna Madre, USA (1.7 m depth)	26°N	0.7–2.9	0–3.0					0.1–0.8[e]	Kaldy and Dunton (2000)
	Lower Laguna Madre, USA (1.3 m depth)	26°N	0–3.1	0–2.5					0.1–1.7[e]	Kaldy and Dunton (2000)
	Lower Laguna Madre, USA (control)	26°09′N				15.1–45.2			1.37[a]	Lee and Dunton (1999a)
	Lower Laguna Madre USA (control)	26°09′N	1.22±0.08	0.84±0.06		30	3.07±0.23	15.08±2.25	2.5	Lee and Dunton (2000)
	Corpus Christi Bay, USA	27°49′N		0.1–1.0					0.07–5.9	Lee and Dunton (1996)
	Corpus Christi Bay, USA	27°49′N				37.4–109.3			4.34[a]	Lee and Dunton (1999a)
	Corpus Christi Bay, USA	27°49′N	1.16±0.06	0.84±0.05		100	3.42±0.38	23.80±3.71	4.86–9.37	Lee and Dunton (2000)
	St. Joseph Bay, USA (-N, - Pinfish)	29.8°N	0.25–1.80	0.02–0.50	0–0.29				1.8–5.9[a]	Heck et al. (2000)
Thalassodendron ciliatum	Vipingo, Kenya	3°45′S	1.98	2.4	0.68	217.5	47.8	52.5	2.35	Uku and Bjőrk (2005)
	MM, Gazi Bay, Kenya	4°S	0.4	0.45	0.45				4.92±0.08	Hemminga et al. (1995)
	MS, Gazi Bay, Kenya	4°S	0.8	0.3	0.4				9.47±0.13	Hemminga et al. (1995)
	CS, Gazi Bay, Kenya	4°S	0.8		0.3				7.48±0.07	Hemminga et al. (1995)
	Nyali Beach, Kenya	4°03′S	1.55	7.6	0.78	233.7	49.2	21.5	3.4	Uku and Bjőrk (2005)

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a. mg dw shoot^{-1} d^{-1}; b. cm shoot^{-1} d^{-1}; c. g AFDW m^{-2} d^{-1}; d. Whole plant; e. Below-ground.

substantial inputs of N to seagrasses (Capone and Taylor, 1980; O'Donohue et al., 1991; Moriarty and O'Donohue, 1993; Blackburn et al., 1994). Nutrient pools in seagrass beds can have rapid turnover rates ranging from 0.3 to 6 d (Capone, 1982; Moriarty et al., 1985; Boon et al., 1986; Lee and Dunton, 1999b). In *T. testudinum* beds, for example, DIN turnover time in both water column and sediment pore water was less than 2 d (Lee and Dunton, 1999b). These rapid turnover rates indicate the importance of nutrient regeneration in supporting seagrass production (Moriarty et al., 1985; Boon et al., 1986).

4.4. Inorganic carbon limitation

Because of the high DIC concentrations in seawater, little attention has been paid to C limitation in seagrass growth. However, since carbon accounts for 30 to 40% of seagrass tissue dry weight (Duarte, 1990; Fourqurean et al., 1997; Lee and Dunton, 1999b), seagrasses need to assimilate large amounts of inorganic carbon. In contrast to terrestrial system, CO_2 supply for photosynthesis in seawater can be restricted due to low solubility and diffusion rates (Björk et al., 1997). Thus, many seagrasses have adapted to utilize bicarbonate (HCO_3^-), which is the most abundant form of DIC in seawater, for C fixation (Beer, 1989; Durako, 1993; Larkum and James, 1996; Beer and Rehnberg, 1997; Invers et al., 2001). Uncharged CO_2 may permeate cells by passive diffusion, whereas HCO_3^- acquisition usually involves extracellular carbonic anhydrase (CA) for HCO_3^- dehydration to CO_2 prior to uptake (James and Larkum, 1996; Beer and Rehnberg, 1997; Björk et al., 1997; Invers et al., 1999). Thus, the affinity for CO_2 may be higher than that of HCO_3^-. However, utilization of HCO_3^- is important in seagrasses if they are to sustain relatively high photosynthetic rates. Beer and Rehnberg (1997) concluded that *Z. marina* can utilize HCO_3^-, as a major source of inorganic C, from seawater for photosynthesis at close-to-ambient conditions.

Although seagrasses can utilize HCO_3^- for their photosynthetic needs, it would appear that seagrasses are less efficient in HCO_3^- use than marine macroalgae (Beer, 1994; Beer and Rehnberg, 1997; Björk et al., 1997). Consequently, seagrass photosynthesis may not be saturated with DIC at natural seawater concentrations (Beer and Koch, 1996; Beer and Rehnberg, 1997; Zimmerman et al., 1997). Thus, C limitation for seagrass photosynthesis has been suggested for both temperate and tropical species (Björk et al., 1997; Invers et al., 2001). Carbon limitation of photosynthesis appears to be a common physiological feature for seagrasses, and may become intensified in stagnant waters due to boundary layer resistance of CO_2 diffusion (Barko et al., 1986).

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References

Abal, E.G., 1996. Light, nutrient and water quality interactions with the seagrass, *Zostera capricorni* Aschers. PhD Thesis, Department of Botany, The University of Queensland, Brisbane, Australia.

Abal, E.G., Loneragan, N., Bowen, P., Perry, C.J., Udy, J.W., Dennison, W.C., 1994. Physiological and morphological responses of the seagrass *Zostera carpricorni* Aschers. to light intensity. J. Exp. Mar. Biol. Ecol. 178, 113–129.

Addicott, F.T., Lyon, J.L., 1973. Physiological ecology of abscission. In: Kozlowski, T.T. (Ed.), Shedding of Plant Part. Academic Press, New York, pp. 85–124.

Agawin, N.S.R., Duarte, C.M., Fortes, M.D., 1996. Nutrient limitation of Philippine seagrasses (Cape Bolinao, NW Philippines): in situ experimental evidence. Mar. Ecol. Prog. Ser. 138, 233–243.

Agawin, N.S.R., Duarte, C.M., Fortes, M.D., Uri, J.S., Vermaat, J.E., 2001. Temporal changes in the abundance, leaf growth and photosynthesis of three co-occurring Philippine seagrasses. J. Exp. Mar. Biol. Ecol. 260, 217–239.

Agostini, S., Pergent, G., Marchand, B., 2003. Growth and primary production of *Cymodocea nodosa* in a coastal lagoon. Aquat. Bot. 76, 185–193.

Alcoverro, T., Romero, J., Duarte, C.M., López, N.I., 1997. Spatial and temporal variations in nutrient limitation of seagrass *Posidonia oceanica* growth in the NW Mediterranean. Mar. Ecol. Prog. Ser. 146, 155–161.

Alcoverro, T., Manzanera, M., Romero, J., 1998. Seasonal and age-dependent variability of *Posidonia oceanica* (L.) Delile photosynthetic parameters. J. Exp. Mar. Biol. Ecol. 230, 1–13.

Backman, T.W., Barilotti, D.C., 1976. Irradiance reduction: effects on standing crops of the eelgrass *Zostera marina* in a coastal lagoon. Mar. Biol. 34, 33–40.

Barber, B.J., Behrens, P.J., 1985. Effects of elevated temperature on seasonal in situ leaf productivity of *Thalassia testudinum* Banks ex König and *Syringodium filiforme* Kützing. Aquat. Bot. 22, 61–69.

Barko, J.W., Adams, M.S., Clesceri, N.L., 1986. Environmental factors and their consideration in the management of submersed aquatic vegetation: a review. J. Aquat. Plant Manage. 24, 1–10.

Bay, D., 1984. A field study of the growth dynamics and productivity of *Posidonia oceanica* (L.) Delile in Calvi Bay, Corsica. Aquat. Bot. 20, 43–64.

Beer, S., 1989. Photosynthesis and photorespiration of marine angiosperms. Aquat. Bot. 34, 153–166.

Beer, S., 1994. Mechanisms of inorganic carbon acquisition in marine macroalgae (with special reference to Chlorophyta). Prog. Phycol. Res. 10, 179–207.

Beer, S., Koch, E., 1996. Photosynthesis of marine macroalgae and seagrasses in globally changing CO_2 environments. Mar. Ecol. Prog. Ser. 141, 199–204.

Beer, S., Rehnberg, J., 1997. The acquisition of inorganic carbon by the seagrass *Zostera marina*. Aquat. Bot. 56, 277–283.

Beer, S., Waisel, Y., 1982. Effects of light and pressure on photosynthesis in two seagrasses. Aquat. Bot. 13, 331–337.

Biebl, R., McRoy, C.P., 1971. Plasmatic resistance and rate of respiration and photosynthesis of *Zostera marina* at different salinities and temperatures. Mar. Biol. 8, 48–56.

Björk, M., Weil, A., Semesi, S., Beer, S., 1997. Photosynthetic utilisation of inorganic carbon by seagrasses from Zanzibar, East Africa. Mar. Biol. 129, 363–366.

Blackburn, T.H., Nedwell, D.B., Wiebe, W.J., 1994. Active mineral cycling in a Jamaican seagrass sediment. Mar. Ecol. Prog. Ser. 110, 233–239.

Boon, P.I., Moriarty, D.J.W., Saffigna, P.G., 1986. Rates of ammonium turnover and the role of amino-acid deamination in seagrass (*Zostera capricorni*) beds of Moreton Bay, Australia. Mar. Biol. 91, 259–268.

Borum, J., 1985. Development of epiphytic communities on eelgrass (*Zostera marina*) along a nutrient gradient in a Danish estuary. Mar. Biol. 87, 211–218.

Boström, C., Roos, C., Rönnberg, O., 2004. Shoot morphometry and production dynamics of eelgrass in the northern Baltic Sea. Aquat. Bot. 79, 145–161.

Bulthuis, D.A., 1983a. Effects of in situ light reduction on density and growth of the seagrass *Heterozostera tasmanica* (Martens ex Aschers.) den Hartog in Western Port, Victoria, Australia. J. Exp. Mar. Biol. Ecol. 67, 91–103.

Bulthuis, D.A., 1983b. Effects of temperature on the photosynthesis–irradiance curve of the Australian seagrass, *Heterozostera tasmanica*. Mar. Biol. Lett. 4, 47–57.

Bulthuis, D.A., 1987. Effects of temperature on photosynthesis and growth of seagrasses. Aquat. Bot. 27, 27–40.

Bulthuis, D.A., Woelkerling, W.J., 1981. Effects of in situ nitrogen and phosphorus enrichment of the sediments on the seagrass *Heterozostera tasmanica* (Martens ex Aschers.) den Hartog in Western Port, Victoria, Australia. J. Exp. Mar. Biol. Ecol. 53, 193–207.

Bulthuis, D.A., Axelrad, D.M., Mickelson, M.J., 1992. Growth of the seagrass *Heterozostera tasmanica* limited by nitrogen in Port Phillip Bay, Australia. Mar. Ecol. Prog. Ser. 89, 269–275.

Burd, A.B., Dunton, K.H., 2001. Field verification of a light-driven model of biomass changes in the seagrass *Halodule wrightii*. Mar. Ecol. Prog. Ser. 209, 85–98.

Burkholder, J.M., Mason, K.M., Glasgow Jr., H.B., 1992. Water-column nitrate enrichment promotes decline of eelgrass *Zostera marina*: evidence from seasonal mesocosm experiments. Mar. Ecol. Prog. Ser. 81, 163–178.

Burkholder, J.M., Glasgow Jr., H.B., Cooke, J.E., 1994. Comparative effects of water-column nitrate enrichment on eelgrass *Zostera marina*, shoalgrass *Halodule wrightii*, and widgeongrass *Ruppia maritima*. Mar. Ecol. Prog. Ser. 105, 121–138.

Cabello-Pasini, A., Lara-Turrent, C., Zimmerman, R.C., 2002. Effect of storms on photosynthesis, carbohydrate content and survival of eelgrass populations from a coastal lagoon and the adjacent open ocean. Aquat. Bot. 74, 149–164.

Cabello-Pasini, A., Muñiz-Salazar, R., Ward, D.H., 2003. Annual variations of biomass and photosynthesis in *Zostera marina* at its southern end of distribution in the North Pacific. Aquat. Bot. 76, 31–47.

Caffrey, J.M., Kemp, W.M., 1991. Seasonal and spatial patterns of oxygen production, respiration and root-rhizome release in *Potamogeton perfoliatus* L. and *Zostera marina* L. Aquat. Bot. 40, 109–128.

Cambridge, M.L., McComb, A.J., 1984. The loss of seagrasses in Cockburn Sound, Western Australia. I. The time course and magnitude of seagrass decline in relation to industrial development. Aquat. Bot. 20, 229–243.

Cambridge, M.L., Chiffings, A.W., Brittan, C., Moore, L., McComb, A.J., 1986. The loss of seagrass in Cockburn Sound, Western Australia. II. Possible causes of seagrass decline. Aquat. Bot. 24, 269–285.

Campbell, S.J., McKenzie, L.J., Kerville, S.P., 2006. Photosynthetic responses of seven tropical seagrasses to elevated seawater temperature. J. Exp. Mar. Biol. Ecol. 330, 455–468.

Capone, D.G., 1982. Nitrogen fixation (acetylene reduction) by rhizosphere sediments of the eelgrass *Zostera marina*. Mar. Ecol. Prog. Ser. 10, 67–75.

Capone, D.G., Taylor, B.F., 1980. N_2 fixation in the rhizosphere of *Thalassia testudinum*. Can. J. Microbiol. 26, 998–1005.

Carruthers, T.J.B., Walker, D.I., 1997. Light climate and energy flow in the seagrass canopy of *Amphibolis griffithii* (J.M. Black) den Hartog. Oecologia 109, 335–341.

Carruthers, T.J.B., Walker, D.I., 1999. Sensitivity of transects across a depth gradient for measuring changes in aerial coverage and abundance of *Ruppia megacarpa* Mason. Aquat. Bot. 65, 281–292.

Coleman, V.L., Burkholder, J.M., 1994. Community structure and productivity of epiphytic microalgae on eelgrass (*Zostera marina* L.) under water-column nitrate enrichment. J. Exp. Mar. Biol. Ecol. 179, 29–48.

Connell, E.L., Colmer, T.D., Walker, D.I., 1999. Radial oxygen loss from intact roots of *Halophila ovalis* as a function of distance behind the root tip and shoot illumination. Aquat. Bot. 63, 219–228.

Czerny, A.B., Dunton, K.H., 1995. The effects of in situ light reduction on the growth of two subtropical seagrasses, *Thalassia testudinum* and *Halodule wrightii*. Estuaries 18, 418–427.

Dawes, C.J., Lawrence, J.M., 1980. Seasonal changes in the proximate constituents of the seagrasses *Thalassia testudinum*, *Halodule wrightii*, and *Syringodium filiforme*. Aquat. Bot. 8, 371–380.

Dawes, C.J., Tomasko, D.A., 1988. Depth distribution of *Thalassia testudinum* in two meadows on the west coast of Florida; a difference in effect of light availability. PSZN I: Mar. Ecol. 9, 123–130.

Dawes, C., Chan, M., Chinn, R., Koch, E.W., Lazar, A., Tomasko, D., 1987. Proximate composition, photosynthetic and respiratory responses of the seagrass *Halophila engelmannii* from Florida. Aquat. Bot. 27, 195–201.

Dawes, C.J., Lobban, C.S., Tomasko, D.A., 1989. A comparison of the physiological ecology of the seagrasses *Halophila decipiens* Ostenfeld and *H. johnsonii* Eiseman from Florida. Aquat. Bot. 33, 149–154.

Dennison, W.C., 1987. Effects of light on seagrass photosynthesis, growth and depth distribution. Aquat. Bot. 27, 15–26.

Dennison, W.C., Alberte, R.S., 1982. Photosynthetic responses of *Zostera marina* L. (eelgrass) to in situ manipulations of light intensity. Oecologia 55, 137–144.

Dennison, W.C., Alberte, R.S., 1985. Role of daily light period in the depth distribution of *Zostera marina* (eelgrass). Mar. Ecol. Prog. Ser. 25, 51–61.

Dennison, W.C., Alberte, R.S., 1986. Photoadaptation and growth of *Zostera marina* L. (eelgrass) transplants along a depth gradient. J. Exp. Mar. Biol. Ecol. 98, 265–282.

Dennison, W.C., Aller, R.C., Alberte, R.S., 1987. Sediment ammonium availability and eelgrass (*Zostera marina*) growth. Mar. Biol. 94, 469–477.

Dennison, W.C., Orth, R.J., Moore, K.A., Stevenson, J.C., Carter, V., Kollar, S., Bergstrom, P.W., Batiuk, R.A., 1993. Assessing water quality with submersed aquatic vegetation. Bioscience 43, 86–94.

Drew, E.A., 1978. Factors affecting photosynthesis and its seasonal variation in the seagrasses *Cymodocea nodosa* (Ucria) Aschers, and *Posidonia oceanica* (L.) Delile in the Mediterranean. J. Exp. Mar. Biol. Ecol. 31, 173–194.

Drew, E.A., 1979. Physiological aspects of primary production in seagrasses. Aquat. Bot. 7, 139–150.

Drysdale, F.R., Barbour, M.G., 1975. Response of the marine angiosperm *Phyllospadix torreyi* to certain environmental variables: a preliminary study. Aquat. Bot. 1, 97–106.

Duarte, C.M., 1990. Seagrass nutrient content. Mar. Ecol. Prog. Ser. 67, 201–207.

Duarte, C.M., 1991. Seagrass depth limits. Aquat. Bot. 40, 363–377.

Duarte, C.M., Kalff, J., 1987. Latitudinal influences on the depths of maximum colonization and maximum biomass of submerged angiosperms in lakes. Can. J. Fish. Aquat. Sci. 44, 1759–1764.

Dunton, K.H., 1990. Production ecology of *Ruppia maritima* L. s.l. and *Halodule wrightii* Aschers. in two subtropical estuaries. J. Exp. Mar. Biol. Ecol. 143, 147–164.

Dunton, K.H., 1994. Seasonal growth and biomass of the subtropical seagrass *Halodule wrightii* in relation to continuous measurements of underwater irradiance. Mar. Biol. 120, 479–489.

Dunton, K.H., 1996. Photosynthetic production and biomass of the subtropical seagrass *Halodule wrightii* along an estuarine gradient. Estuaries 19, 436–447.

Dunton, K.H., Tomasko, D.A., 1994. In situ photosynthesis in the seagrass *Halodule wrightii* in a hypersaline subtropical lagoon. Mar. Ecol. Prog. Ser. 107, 281–293.

Durako, M.J., 1993. Photosynthetic utilization of $CO_{2(aq)}$ and HCO_3^- in *Thalassia testudinum* (Hydrocharitaceae). Mar. Biol. 115, 373–380.

Durako, M.J., Moffler, M.D., 1985. Spatial influences on temporal variations in leaf growth and chemical composition of *Thalassia testudinum* Banks ex König in Tampa bay, Florida. Gulf Res. Rep. 8, 43–49.

Edgecumbe, D.J., 1980. Some preliminary observations on the submerged aquatic *Zostera capensis* Setchell. J. South. Afr. Bot. 46, 53–66.

Enríquez, S., Pantoja-Reyes, N.I., 2005. Form-function analysis of the effect of canopy morphology on leaf self-shading in the seagrass *Thalassia testudinum*. Oecologia 145, 235–243.

Enríquez, S., Agustí, S., Duarte, C.M., 1994. Light absorption by marine macrophytes. Oecologia 98, 121–129.

Enríquez, S., Duarte, C.M., Sand-Jensen, K., 1995. Patterns in the photosynthetic metabolism of Mediterranean macrophytes. Mar. Ecol. Prog. Ser. 119, 243–252.

Enríquez, S., Merino, M., Iglesias-Prieto, R., 2002. Variations in the photosynthetic performance along the leaves of the tropical seagrass *Thalassia testudinum*. Mar. Biol. 140, 891–900.

Erftemeijer, P.L.A., Herman, P.M.J., 1994. Seasonal changes in environmental variables, biomass, production and nutrient contents in two contrasting tropical intertidal seagrass beds in South Sulawesi, Indonesia. Oecologia 99, 45–59.

Erftemeijer, P.L.A., Stapel, J., Smekens, M.J.E., Drossaert, W.M.E., 1994. The limited effect of in situ phosphorus and nitrogen additions to seagrass beds on carbonate and terrigenous sediments in South Sulawesi, Indonesia. J. Exp. Mar. Biol. Ecol. 182, 123–140.

Evans, A.S., Webb, K.L., Penhale, P.A., 1986. Photosynthetic temperature acclimation in two coexisting seagrasses, *Zostera marina* L. and *Ruppia maritima* L. Aquat. Bot. 24, 185–197.

Flanigan, Y.S., Critchley, C., 1996. Light response of D1 turnover and photosystem II efficiency in the seagrass *Zostera capricorni*. Planta 198, 319–323.

Fourqurean, J.W., Cai, Y., 2001. Arsenic and phosphorus in seagrass leaves from the Gulf of Mexico. Aquat. Bot. 71, 247–258.

Fourqurean, J.W., Zieman, J.C., 1991. Photosynthesis, respiration and whole plant carbon budget of the seagrass *Thalassia testudinum*. Mar. Ecol. Prog. Ser. 69, 161–170.

Fourqurean, J.W., Moore, T.O., Fry, B., Hollibaugh, J.T., 1997. Spatial and temporal variation in C:N:P ratios δ^{15}N and δ^{13}C of eelgrass *Zostera marina* as indicators of ecosystem processes, Tomales Bay, California, USA. Mar. Ecol. Prog. Ser. 157, 147–157.

Fourqurean, J.W., Zieman, J.C., Powell, G.V.N., 1992a. Phosphorus limitation of primary production in Florida bay: evidence from C:N:P ratios of the dominant seagrass *Thalassia testudinum*. Limnol. Oceanogr. 37, 162–171.

Fourqurean, J.W., Zieman, J.C., Powell, G.V.N., 1992b. Relationships between porewater nutrients and seagrasses in a subtropical carbonate environment. Mar. Biol. 114, 57–65.

Fry, B., Virnstein, R.W., 1988. Leaf production and export of the seagrass *Syringodium filiforme* Kütz. in Indian River Lagoon, Florida. Aquat. Bot. 30, 261–266.

Gallegos, C.L., Correll, D.L., Pierce, J.W., 1990. Modeling spectral diffuse attenuation, absorption, and scattering coefficients in a turbid estuary. Limnol. Oceanogr. 35, 1486–1502.

Giesen, W.B.J.T., van Katwijk, M.M., den Hartog, C., 1990. Eelgrass condition and turbidity in the Dutch Wadden Sea. Aquat. Bot. 37, 71–85.

Gilbert, S., Clark, K.B., 1981. Seasonal variation in standing crop of the seagrass *Syringodium filiforme* and associated macrophytes in the northern Indian River, Florida. Estuaries 4, 223–225.

Goodman, J.L., Moore, K.A., Dennison, W.C., 1995. Photosynthetic responses of eelgrass (*Zostera marina* L.) to light and sediment sulfide in a shallow barrier island lagoon. Aquat. Bot. 50, 37–47.

Gordon, D.M., Grey, K.A., Chase, S.C., Simpson, C.J., 1994. Changes to the structure and productivity of a *Posidonia sinuosa* meadow during and after imposed shading. Aquat. Bot. 47, 265–275.

Gras, A.F., Koch, M.S., Madden, C.J., 2003. Phosphorus uptake kinetics of a dominant tropical seagrass *Thalassia testudinum*. Aquat. Bot. 76, 299–315.

Greenway, M., 1974. The effects of cropping on the growth of *Thalassia testudinum* (König) in Jamaica. Aquaculture 4, 199–206.

Grice, A.M., Loneragan, N.R., Dennison, W.C., 1996. Light intensity and the interactions between physiology, morphology and stable isotope ratios in five species of seagrass. J. Exp. Mar. Biol. Ecol. 195, 91–110.

Hanekom, N., Baird, D., 1988. Distribution and variations in seasonal biomass of eelgrass *Zostera capensis* in the Kormme estuary, St. Francis Bay, South Africa. S. Afr. J. Mar. Sci. 7, 51–59.

Hansen, J.W., Udy, J.W., Perry, C.J., Dennison, W.C., Lomstein, B.A., 2000. Effect of the seagrass *Zostera capricorni* on sediment microbial processes. Mar. Ecol. Prog. Ser. 199, 83–96.

Harlin, M.M., Thorne-Miller, B., 1981. Nutrient enrichment of seagrass beds in a Rhode Island coastal lagoon. Mar. Biol. 65, 221–229.

Heck Jr., K.L., Westone, G.S., 1977. Habitat complexity and invertebrate species richness and abundance in tropical seagrass meadows. J. Biogeogr. 4, 135–142.

Heck Jr., K.L., Pennock, J.R., Valentine, J.F., Coen, L.D., Sklenar, S.A., 2000. Effects of nutrient enrichment and small predator density on seagrass ecosystems: an experimental assessment. Limnol. Oceanogr. 45, 1041–1057.

Hemminga, M.A., Gwada, P., Slim, F.J., de Koeyer, P., Kazungu, J., 1995. Leaf production and nutrient contents of the seagrass *Thalassodendron ciliatum* in the proximity of a mangrove forest (Gazi Bay, Kenya). Aquat. Bot. 50, 159–170.

Hena, M.K.A., Misri, K., Sidik, B.J., Hishamuddin, O., Hidir, H., 2001. Photosynthesis of seagrass *Cymodocea serrulata* (Magnoliophyta/Potamogetonales/Cymodoceaceae) in field and laboratory. Indian J. Mar. Sci. 30, 253–256.

Henley, W.J., 1993. Measurement and interpretation of photosynthetic light-response curves in algae in the context of photoinhibition and diel changes. J. Phycol. 29, 729–739.

Herzka, S.Z., Dunton, K.H., 1997. Seasonal photosynthetic patterns of the seagrass *Thalassia testudinum* in the western Gulf of Mexico. Mar. Ecol. Prog. Ser. 152, 103–117.

Herzka, S.Z., Dunton, K.H., 1998. Light and carbon balance in the seagrass *Thalassia testudinum*: evaluation of current production models. Mar. Biol. 132, 711–721.

Hillman, K., Walker, D.I., Larkum, A.W.D., McComb, A.J., 1989. Productivity and nutrient limitation. In: Larkum, A.W.D., McComb, A.J., Shepherd, S.A. (Eds.), Biology of Seagrasses: A Treatise on the Biology of Seagrasses with Special Reference to the Australian Region. Elsevier, Amsterdam, pp. 635–685.

Hillman, K., McComb, A.J., Walker, D.I., 1995. The distribution, biomass and primary production of the seagrass *Halophila ovalis* in the Swan/Canning Estuary, Western Australia. Aquat. Bot. 51, 1–54.

Hines, M.E., Lyons, W.B., 1982. Biogeochemistry of nearshore Bermuda sediments. I. Sulfate reduction rates and nutrient generation. Mar. Ecol. Prog. Ser. 8, 87–94.

Holmer, M., Bondgaard, E.J., 2001. Photosynthetic and growth response of eelgrass to low oxygen and high sulfide concentrations during hypoxic events. Aquat. Bot. 70, 29–38.

Holmer, M., Nielsen, S.L., 1997. Sediment sulfur dynamics related to biomass-density patterns in *Zostera marina* (eelgrass) beds. Mar. Ecol. Prog. Ser. 146, 163–171.

Holmer, M., Olsen, A.B., 2002. Role of decomposition of mangrove and seagrass detritus in sediment carbon and nitrogen cycling in a tropical mangrove forest. Mar. Ecol. Prog. Ser. 230, 87–101.

Huh, S.H., Kitting, C.L., 1985. Trophic relationships among concentrated populations of small fishes in seagrass meadows. J. Exp. Mar. Biol. Ecol. 92, 29–43.

Huppe, H.C., Turpin, D.H., 1994. Interaction of carbon and nitrogen metabolism in plant and algal cells. Annu. Rev. Plant Physiol. Plant Mol. Biol. 45, 577–607.

Ibarra-Obando, S.E., Huerta-Tamayo, R., 1987. Blade production of *Zostera marina* L. during the summer-autumn period on the pacific coast of Mexico. Aquat. Bot. 28, 301–315.

Iizumi, H., Hattori, A., 1982. Growth and organic production of eelgrass (*Zostera marina* L.) in temperate waters of the Pacific coast of Japan. III. The kinetics of nitrogen uptake. Aquat. Bot. 12, 245–256.

Iizumi, H., Hattori, A., McRoy, C.P., 1982. Ammonium regeneration and assimilation in eelgrass (*Zostera marina*) beds. Mar. Biol. 66, 59–65.

Invers, O., Pérez, M., Romero, J., 1999. Bicarbonate utilization in seagrass photosynthesis: role of carbonic anhydrase in *Posidonia oceanica* (L.) Delile and *Cymodocea nodosa* (Ucria) Ascherson. J. Exp. Mar. Biol. Ecol. 235, 125–133.

Invers, O., Zimmerman, R.C., Alberte, R.S., Pérez, M., Romero, J., 2001. Inorganic carbon sources for seagrass photosynthesis: an experimental evaluation of bicarbonate use in species inhabiting temperate waters. J. Exp. Mar. Biol. Ecol. 265, 203–217.

James, P.L., Larkum, A.W.D., 1996. Photosynthetic inorganic carbon acquisition of *Posidonia australis*. Aquat. Bot. 55, 149–157.

Jiménez, C., Niell, F.X., Algarra, P., 1987. Photosynthetic adaptation of *Zostera noltii* Hornem. Aquat. Bot. 29, 217–226.

Johnson, M.W., Heck Jr., K.L., Fourqurean, J.W., 2006. Nutrient content of seagrasses and epiphytes in the northern Gulf of Mexico: evidence of phosphorus and nitrogen limitation. Aquat. Bot. 85, 103–111.

Jørgensen, B.B., 1977. The sulfur cycle of a coastal marine sediment (Limfjorden, Denmark). Limnol. Oceanogr. 22, 814–832.

Jørgensen, B.B., 1982. Mineralization of organic matter in the sea bed —the role of sulphate reduction. Nature 296, 643–645.

Kaldy, J.E., 2006. Production ecology of the non-indigenous seagrass, dwarf eelgrass (*Zostera japonica* Ascher, & Graeb.), in a Pacific Northwest Estuary, USA. Hydrobiologia 553, 201–217.

Kaldy, J.E., Dunton, K.H., 1999. Ontogenetic photosynthetic changes, dispersal and survival of *Thalassia testudinum* (turtle grass) seedlings in a sub-tropical lagoon. J. Exp. Mar. Biol. Ecol. 240, 193–212.

Kaldy, J.E., Dunton, K.H., 2000. Above- and below-ground production, biomass and reproductive ecology of *Thalassia testudinum* (turtle grass) in a subtropical coastal lagoon. Mar. Ecol. Prog. Ser. 193, 271–283.

Kenworthy, W.J., Fonseca, M.S., 1996. Light requirements of seagrasses *Halodule wrightii* and *Syringodium filiforme* derived from the relationship between diffuse light attenuation and maximum depth distribution. Estuaries 19, 740–750.

Kenworthy, W.J., Haunert, D.E., 1991. The light requirements of seagrasses: proceedings of a workshop to examine the capability of water quality criteria, standards and monitoring programs to protect seagrasses. NOAA Technol. Mem. NMFS-SEFC-287, NOAA.

Kenworthy, W.J., Zieman, J.C., Thayer, G.W., 1982. Evidence for the influence of seagrasses on the benthic nitrogen cycle in a coastal plain estuary near Beaufort, North Carolina (USA). Oecologia 54, 152–158.

Kilminster, K.L., Walker, D.I., Thompson, P.A., Raven, J.A., 2006. Limited nutritional benefit to the seagrass *Halophila ovalis*, in culture, following sediment organic matter enrichment. Estuar. Coast. Shelf Sci. 68, 675–685.

Koch, E.W., 1994. Hydrodynamics, diffusion-boundary layers and photosynthesis of the seagrasses *Thalassia testudinum* and *Cymodocea nodosa*. Mar. Biol. 118, 767–776.

Koch, E.W., Beer, S., 1996. Tides, light and the distribution of *Zostera marina* in Long Island Sound, USA. Aquat. Bot. 53, 97–107.

Koch, M.S., Benz, R.E., Rudnick, D.T., 2001. Solid-phase phosphorus pools in highly organic carbonate sediments of Northeastern Florida Bay. Estuar. Coast. Shelf Sci. 52, 279–291.

Kuo, J., den Hartog, C., 2006. Seagrass morphology, anatomy, and ultrastructure. In: Larkum, A.W.D., Orth, R.J., Duarte, C.M. (Eds.), Seagrasses: Biology, Ecology and Conservation. Springer, pp. 51–87.

Lara, C., Romero, J.M., Guerrero, M.G., 1987. Regulated nitrate transport in the cyanobacterium *Anacystis nidulans*. J. Bacteriol. 169, 4376–4378.

Lapointe, B.E., Tomasko, D.A., Matzie, W.R., 1994. Eutrophication and trophic state classification of seagrass communities in the Florida Keys. Bull. Mar. Sci. 54, 696–717.

Larkum, A.W.D., James, P.L., 1996. Towards a model for inorganic carbon uptake in seagrasses involving carbonic anhydrase. In: Kuo, J., Phillips, R.C., Walker, D.I., Kirkman, H. (Eds.), Seagrass Biology. The University of Western Australia, Nedlands, Australia, pp. 191–196.

Lee, K.-S., Dunton, K.H., 1996. Production and carbon reserve dynamics of the seagrass *Thalassia testudinum* in Corpus Christi Bay, Texas, USA. Mar. Ecol. Prog. Ser. 143, 201–210.

Lee, K.-S., Dunton, K.H., 1997. Effects of in situ light reduction on the maintenance, growth and partitioning of carbon resources in *Thalassia testudinum* Banks ex König. J. Exp. Mar. Biol. Ecol. 210, 53–73.

Lee, K.-S., Dunton, K.H., 1999a. Influence of sediment nitrogen-availability on carbon and nitrogen dynamics in the seagrass *Thalassia testudinum*. Mar. Biol. 134, 217–226.

Lee, K.-S., Dunton, K.H., 1999b. Inorganic nitrogen acquisition in the seagrass *Thalassia testudinum*: development of a whole-plant nitrogen budget. Limnol. Oceanogr. 44, 1204–1215.

Lee, K.-S., Dunton, K.H., 2000. Effects of nitrogen enrichment on biomass allocation, growth, and leaf morphology of the seagrass *Thalassia testudinum*. Mar. Ecol. Prog. Ser. 196, 39–48.

Lee, K.-S., Park, S.R., Kim, J.-B., 2005. Production dynamics of the eelgrass, *Zostera marina* in two bay systems on the south coast of the Korean peninsula. Mar. Biol. 147, 1091–1108.

Lee, S.Y., Kim, J.B., Lee, S.M., 2006. Temporal dynamics of subtidal *Zostera marina* and intertidal *Zostera japonica* on the southern coast of Korea. Mar. Ecol. 27, 133–144.

Longstaff, B.J., Dennison, W.C., 1999. Seagrass survival during pulsed turbidity events: the effects of light deprivation on the seagrasses *Halodule pinifolia* and *Halophila ovalis*. Aquat. Bot. 65, 105–121.

Longstaff, B.J., Loneragan, N.R., O, 'Donohue, M.J., Dennison, W.C., 1999. The effects of light deprivation on the survival and recovery of the seagrass *Halophila ovalis*. J. Exp. Mar. Biol. Ecol. 234, 1–27.

Luning, K., Dring, M.J., 1979. Continuous underwater light measurement in the sublittoral region. Helgol. Wiss. Meeressunters. 32, 403–424.

Macauley, J.M., Clark, J.R., Price, W.A., 1988. Seasonal changes in the standing crop and chlorophyll content of *Thalassia testudinum* Banks ex König and its epiphytes in the northern Gulf of Mexico. Aquat. Bot. 31, 277–287.

Major, K.M., Dunton, K.H., 2000. Photosynthetic performance in *Syringodium filiforme*: seasonal variation in light-harvesting characteristics. Aquat. Bot. 68, 249–264.

Markager, S., Sand-Jensen, K., 1992. Light requirements and depth zonation of marine macroalgae. Mar. Ecol. Prog. Ser. 88, 83–92.

Marsh Jr., J.A., Dennison, W.C., Alberte, R.S., 1986. Effects of temperature on photosynthesis and respiration in eelgrass (*Zostera marina* L.). J. Exp. Mar. Biol. Ecol. 101, 257–267.

Masini, R.J., Manning, C.R., 1997. The photosynthetic responses to irradiance and temperature of four meadow-forming seagrasses. Aquat. Bot. 58, 21–36.

Masini, R.J., Cary, J.L., Simpson, C.J., McComb, A.J., 1995. Effects of light and temperature on the photosynthesis of temperate meadow-forming seagrasses in Western Australia. Aquat. Bot. 49, 239–254.

Masini, R.J., Anderson, P.K., McComb, A.J., 2001. A *Halodule*-dominated community in a subtropical embayment: physical environment, productivity, biomass, and impact of dugong grazing. Aquat. Bot. 71, 179–197.

Mateo, M.A., Romero, J., 1997. Detritus dynamics in the seagrass *Posidonia oceanica*: elements for an ecosystem carbon and nutrient budget. Mar. Ecol. Prog. Ser. 151, 43–53.

Mazzella, L., Alberte, R.S., 1986. Light adaptation and the role of autotrophic epiphytes in primary production of the temperate seagrass, *Zostera marina* L. J. Exp. Mar. Biol. Ecol. 100, 165–180.

McPherson, B.F., Miller, R.L., 1987. The vertical attenuation of light in Charlotte Harbor, a shallow, subtropical estuary, south-western Florida. Estuar. Coast. Shelf Sci. 25, 721–737.

McRoy, C.P., McMillan, C., 1977. Production ecology and physiology of seagrasses. In: McRoy, C.P., Helfferich, C. (Eds.), Seagrass Ecosystems: A Scientific Perspective. Dekker, New York, pp. 53–81.

Middelboe, A.L., Markager, S., 1997. Depth limits and minimum light requirements of freshwater macrophytes. Freshw. Biol. 37, 553–568.

Moore, K.A., Neckles, H.A., Orth, R.J., 1996. *Zostera marina* (eelgrass) growth and survival along a gradient of nutrients and turbidity in the lower Chesapeake Bay. Mar. Ecol. Prog. Ser. 142, 247–259.

Moore, K.A., Wetzel, R.L., Orth, R.J., 1997. Seasonal pulses of turbidity and their relations to eelgrass (*Zostera marina* L.) survival in an estuary. J. Exp. Mar. Biol. Ecol. 215, 115–134.

Moriarty, D.J.W., O, 'Donohue, M.J., 1993. Nitrogen fixation in seagrass communities during summer in Gulf of Carpentaria, Australia. Aust. J. Mar. Freshw. Res. 44, 117–125.

Moriarty, D.J.W., Boon, P.I., Hansen, J.A., Hunt, W.G., Poiner, I.R., Pollard, P.C., Skyring, G.W., White, D.C., 1985. Microbial biomass and productivity in seagrass beds. Geomicrobiol. J. 4, 21–51.

Morris, L.J., Tomasko, D.A. (Eds.), 1993. Proceedings and Conclusions of Workshops on the Submerged Aquatic Vegetation Initiative and Photosynthetically Active Radiation. Special Publication SJ93-SP13. St. Johns River Water Management District, Palatka, FL, pp. 149–158.

Murray, L., Dennison, W.C., Kemp, W.M., 1992. Nitrogen versus phosphorus limitation for growth of an estuarine population of eelgrass (*Zostera marina* L.). Aquat. Bot. 44, 83–100.

Nelson, T.A., Waaland, J.R., 1997. Seasonality of eelgrass, epiphyte, and grazer biomass and productivity in subtidal eelgrass meadows subjected to moderate tidal amplitude. Aquat. Bot. 56, 51–74.

Neverauskas, V.P., 1988. Response of a *Posidonia* community to prolonged reduction in light. Aquat. Bot. 31, 361–366.

Nielsen, O.I., Koch, M.S., Jensen, H.S., Madden, C.J., 2006. *Thalassia testudinum* phosphate uptake kinetics at low in situ concentrations using a ^{33}P radioisotope technique. Limnol. Oceanogr. 51, 208–217.

O 'Donohue, M.J., Moriarty, D.J.W., McRae, I.C., 1991. Nitrogen fixation in sediments and the rhizosphere of the seagrass *Zostera capricorni*. Microb. Ecol. 22, 53–64.

Olesen, B., Sand-Jensen, K., 1993. Seasonal acclimatization of eelgrass *Zostera marina* growth to light. Mar. Ecol. Prog. Ser. 94, 91–99.

Olesen, B., Enríquez, S., Duarte, C.M., Sand-Jensen, K., 2002. Depth-acclimation of photosynthesis, morphology and demography of *Posidonia oceanica* and *Cymodocea nodosa* in the Spanish Mediterranean Sea. Mar. Ecol. Prog. Ser. 236, 89–97.

Onuf, C.P., 1994. Seagrasses, dredging and light in Laguna Madre, Texas, U.S.A. Estuar. Coast. Shelf Sci. 39, 75–91.

Opsahl, S., Benner, R., 1993. Decomposition of senescent blades of the seagrass *Halodule wrightii* in a subtropical lagoon. Mar. Ecol. Prog. Ser. 94, 191–205.

Orth, R.J., 1977. Effect of nutrient environment on growth of the eelgrass *Zostera marina* in the Chesapeake Bay, Virginia, USA. Mar. Biol. 44, 187–194.

Orth, R.J., Moore, K.A., 1983. Chesapeake Bay: an unprecedented decline in submerged aquatic vegetation. Science 222, 51–53.

Orth, R.J., Moore, K.A., 1986. Seasonal and year-to-year variations in the growth of *Zostera marina* L. (eelgrass) in the lower Chesapeake Bay. Aquat. Bot. 24, 335–341.

Orth, R.J., Heck Jr., K.L., van Montfrans, J., 1984. Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator-prey relationships. Estuaries 7, 339–350.

Parnik, T., Bil, K., Kolmakov, P., Titlyanov, E., 1992. Photosynthesis of the seagrass *Thalassodendron ciliatum*: leaf anatomy and carbon metabolism. Photosynthetica 26, 213–223.

Pedersen, M.F., Borum, J., 1992. Nitrogen dynamics of eelgrass *Zostera marina* during a late summer period of high growth and low nutrient availability. Mar. Ecol. Prog. Ser. 80, 65–73.

Pedersen, M.F., Borum, J., 1993. An annual nitrogen budget for a seagrass *Zostera marina* population. Mar. Ecol. Prog. Ser. 101, 169–177.

Pedersen, M.F., Paling, E.I., Walker, D.I., 1997. Nitrogen uptake and allocation in the seagrass *Amphibolis antarctica*. Aquat. Bot. 56, 105–117.

Peduzzi, P., Vukovič, A., 1990. Primary production of *Cymodocea nodosa* in the Gulf of Trieste (Northern Adriatic Sea): a comparison of methods. Mar. Ecol. Prog. Ser. 64, 197–207.

Penhale, P.A., 1977. Macrophyte-epiphyte biomass and productivity in an eelgrass (*Zostera marina* L.) community. J. Exp. Mar. Biol. Ecol. 26, 211–224.

Peralta, G., Pérez-Lloréns, J.L., Hernández, I., Vergara, J.J., 2002. Effects of light availability on growth, architecture and nutrient content of the seagrass *Zostera noltii* Hornem. J. Exp. Mar. Biol. Ecol. 269, 9–26.

Pérez, M., Romero, J., 1992. Photosynthetic response to light and temperature of the seagrass *Cymodocea nodosa* and the prediction of its seasonality. Aquat. Bot. 43, 51–62.

Pérez, M., Romero, J., Duarte, C.M., Sand-Jensen, K., 1991. Phosphorus limitation of *Cymodocea nodosa* growth. Mar. Biol. 109, 129–133.

Pérez-Lloréns, J.L., Niell, F.X., 1993. Seasonal dynamics of biomass and nutrient content in the intertidal seagrass *Zostera noltii* Hornem. from Palmones River estuary, Spain. Aquat. Bot. 46, 49–66.

Philippart, C.J.M., 1995. Effects of shading on growth, biomass and population maintenance of the intertidal seagrass *Zostera noltii* Hornem. in the Dutch Wadden Sea. J. Exp. Mar. Biol. Ecol. 188, 199–213.

Phillips, R.C., McMillan, C., Bridges, K.W., 1983. Phenology of eelgrass, *Zostera marina* L., along latitudinal gradients in North America. Aquat. Bot. 15, 145–156.

Powell, G.V.N., Kenworthy, W.J., Fourqurean, J.W., 1989. Experimental evidence for nutrient limitation of seagrass growth in a tropical estuary with restricted circulation. Bull. Mar. Sci. 44, 324–340.

Ralph, P.J., 1998. Photosynthetic response of laboratory-cultured *Halophila ovalis* to thermal stress. Mar. Ecol. Prog. Ser. 171, 123–130.

Ralph, P.J., Burchett, M.D., Pulkownik, A., 1992. Distribution of extractable carbohydrate reserves within the rhizome of the seagrass *Posidonia australis* Hook. f. Aquat. Bot. 42, 385–392.

Roesler, C.S., Perry, M.J., Carder, K.L., 1989. Modeling in situ phytoplankton absorption from total absorption spectra in productive inland marine waters. Limnol. Oceanogr. 34, 1510–1523.

Romero, J., Lee, K.-S., Pérez, M., Mateo, M.A., Alcoverro, T., 2006. Nutrients dynamics in seagrass ecosystems. In: Larkum, A.W.D., Orth, R.J., Duarte, C.M. (Eds.), Seagrasses: Biology, Ecology and Conservation. Springer, pp. 227–254.

Ruiz, J.M., Romero, J., 2001. Effects of in situ experimental shading on the Mediterranean seagrass *Posidonia oceanica*. Mar. Ecol. Prog. Ser. 215, 107–120.

Ruiz, J.M., Romero, J., 2003. Effects of disturbances caused by coastal constructions on spatial structure, growth dynamics and photosynthesis of the seagrass *Posidonia oceanica*. Mar. Pollut. Bull. 46, 1523–1533.

Ruiz, J.M., Pérez, M., Romero, J., 2001. Effects of fish farm loadings on seagrass (*Posidonia oceanica*) distribution, growth and photosynthesis. Mar. Pollut. Bull. 42, 749–760.

Sand-Jensen, K., 1975. Biomass, net production and growth dynamics in an eelgrass (*Zostera marina* L.) population in Vellerup Vig, Denmark. Ophelia 14, 185–201.

Sand-Jensen, K., 1988. Minimum light requirements for growth in *Ulva lactuca*. Mar. Ecol. Prog. Ser. 50, 187–193.

Sand-Jensen, K., Borum, J., 1983. Regulation of growth of eelgrass (*Zostera marina* L.) in Danish coastal waters. Mar. Technol. Soc. J. 17, 15–21.

Schwarz, A.-M., 2004. Contribution of photosynthetic gains during tidal emersion to production of *Zostera capricorni* in a North Island, New Zealand estuary. N. Z. J. Mar. Freshw. Res. 38, 809–818.

Seddon, S., Cheshire, A.C., 2001. Photosynthetic response of *Amphibolis antarctica* and *Posidonia australis* to temperature and desiccation using chlorophyll fluorescence. Mar. Ecol. Prog. Ser. 220, 119–130.

Setchell, W.A., 1929. Morphological and phenological notes on *Zostera marina* L. Univ. Calif. Publ. Bot. 14, 389–452.

Sfriso, A., Ghetti, P.F., 1998. Seasonal variation in biomass, morphometric parameters and production of seagrasses in the lagoon of Venice. Aquat. Bot. 61, 207–223.

Sheldon, R.B., Boylen, C.W., 1977. Maximum depth inhabited by aquatic vascular plants. Am. Midl. Nat. 97, 248–254.

Short, F.T., 1983. The seagrass, *Zostera marina* L.: plant morphology and bed structure in relation to sediment ammonium in Izembek Lagoon, Alaska. Aquat. Bot. 16, 149–161.

Short, F.T., 1987. Effects of sediment nutrients on seagrasses: literature review and mesocosm experiment. Aquat. Bot. 27, 41–57.

Short, F.T., McRoy, C.P., 1984. Nitrogen uptake by leaves and roots of the seagrass *Zostera marina* L. Bot. Mar. 27, 547–555.

Short, F.T., Davis, M.W., Gibson, R.A., Zimmermann, C.F., 1985. Evidence for phosphorus limitation in carbonate sediments of the seagrass *Syringodium filiforme*. Estuar. Coast. Shelf Sci. 20, 419–430.

Short, F.T., Dennison, W.C., Capone, D.G., 1990. Phosphorus-limited growth of the tropical seagrass *Syringodium filiforme* in carbonate sediments. Mar. Ecol. Prog. Ser. 62, 169–174.

Short, F.T., Burdick, D.M., Kaldy, J.E., 1995. Mesocosm experiments quantify the effects of eutrophication on eelgrass, *Zostera marina*. Limnol. Oceanogr. 40, 740–749.

Short, F.T., Wyllie-Echeverria, S., 1996. Natural and human-induced disturbance of seagrasses. Environ. Conserv. 23, 17–27.

Silberstein, K., Chiffings, A.W., McComb, A.J., 1986. The loss of seagrass in Cockburn Sound, Western Australia. III. The effect of epiphytes on productivity of *Posidonia australis* Hook. F. Aquat. Bot. 24, 355–371.

Silva, J., Santos, R., 2004. Can chlorophyll fluorescence be used to estimate photosynthetic production in the seagrass *Zostera noltii*? J. Exp. Mar. Biol. Ecol. 307, 207–216.

Smith, R.D., Dennison, W.C., Alberte, R.S., 1984. Role of seagrass photosynthesis in root aerobic processes. Plant Physiol. 74, 1055–1058.

Stapel, J., Aarts, T.L., van Duynhoven, B.H.M., de Groot, J.D., van den Hoogen, P.H.W., Hemminga, M.A., 1996. Nutrient uptake by leaves and roots of the seagrass *Thalassia hemprichii* in the Spermonde Archipelago, Indonesia. Mar. Ecol. Prog. Ser. 134, 195–206.

Steward, J.S., Virnstein, R.W., Morris, L.J., Lowe, E.F., 2005. Setting seagrass depth, coverage, and light targets for the Indian River Lagoon System, Florida. Estuaries 28, 923–935.

Strickland, J.D.H., 1958. Solar radiation penetrating the ocean. A review of requirements, data and methods of measurement, with particular reference to photosynthetic productivity. J. Fish. Res. Board Can. 15, 453–493.

Summerson, H.C., Peterson, C.H., 1984. Role of predation in organizing benthic communities of a temperate-zone seagrass bed. Mar. Ecol. Prog. Ser. 15, 63–77.

Terrados, J., Ros, J.D., 1995. Temperature effects on photosynthesis and depth distribution of the seagrass *Cymodocea nodosa* (Ucria) Ascherson in a Mediterranean coastal lagoon: the Mar Menor (SE Spain). Mar. Ecol. 16, 133–144.

Terrados, J., Williams, S.L., 1997. Leaf versus root nitrogen uptake by the surfgrass *Phyllospadix torreyi*. Mar. Ecol. Prog. Ser. 149, 267–277.

Terrados, J., Agawin, N.S.R., Duarte, C.M., Fortes, M.D., Kamp-Nielsen, L., Borum, J., 1999a. Nutrient limitation of the tropical seagrass *Enhalus acoroides* (L.) Royle in Cape Bolinao, NW Philippines. Aquat. Bot. 65, 123–139.

Terrados, J., Borum, J., Duarte, C.M., Fortes, M.D., Kamp-Nielsen, L., Agawin, N.S.R., Kenworthy, W.J., 1999b. Nutrient and mass allocation of South-east Asian seagrasses. Aquat. Bot. 63, 203–217.

Thacker, A., Syrett, P.J., 1972. The assimilation of nitrate and ammonium by *Chlamydomonas reinhardi*. New Phytol. 71, 423–433.

Thom, R.M., 1990. Spatial and temporal patterns in plant standing stock and primary production in a temperate seagrass system. Bot. Mar. 33, 497–510.

Thursby, G.B., Harlin, M.M., 1982. Leaf–root interaction in the uptake of ammonia by *Zostera marina*. Mar. Biol. 72, 109–112.

Thursby, G.B., Harlin, M.M., 1984. Interaction of leaves and roots of *Ruppia maritima* in the uptake of phosphate, ammonia and nitrate. Mar. Biol. 83, 61–67.

Tomasko, D.A., Dawes, C.J., 1989. Evidence for physiological integration between shaded and unshaded short shoots of *Thalassia testudinum*. Mar. Ecol. Prog. Ser. 54, 299–305.

Tomasko, D.A., Hall, M.O., 1999. Productivity and biomass of the seagrass *Thalassia testudinum* along a gradient of freshwater influence in Charlotte Harbor, Florida. Estuaries 22, 592–602.

Tomasko, D.A., Lapointe, B.E., 1991. Productivity and biomass of *Thalassia testudinum* as related to water column nutrient availability and epiphyte levels: field observations and experimental studies. Mar. Ecol. Prog. Ser. 75, 9–17.

Torquemada, Y.F., Durako, M.J., Lizaso, J.L.S., 2005. Effects of salinity and possible interactions with temperature and pH on growth and photosynthesis of *Halophila johnsonii* Eiseman. Mar. Biol. 148, 251–260.

Touchette, B.W., 1999. Physiological and developmental responses of eelgrass (*Zostera marina* L.) to increases in water-column nitrate and temperature. Ph.D. Dissertation, North Carolina State University, Raleigh, NC.

Touchette, B.W., Burkholder, J.M., 2000. Review of nitrogen and phosphorus metabolism in seagrasses. J. Exp. Mar. Biol. Ecol. 250, 133–167.

Turpin, D.H., 1991. Effects of inorganic N availability on algal photosynthesis and carbon metabolism. J. Phycol. 27, 14–20.

Turpin, D.H., Botha, F.C., Smith, R.G., Feil, R., Horsey, A.K., Vanlerberghe, G.C., 1990. Regulation of carbon partitioning to respiration during dark ammonium assimilation by the green alga *Selenastrum minutum*. Plant Physiol. 93, 166–175.

Tutin, T.G., 1942. *Zostera*. J. Ecol. 30, 217–266.

Udy, J.W., Dennison, W.C., 1997. Growth and physiological responses of three seagrass species to elevated sediment nutrients in Moreton Bay, Australia. J. Exp. Mar. Biol. Ecol. 217, 253–277.

Udy, J.W., Dennison, W.C., Lee Long, W.J., McKenzie, L.J., 1999. Responses of seagrass to nutrients in the Great Barrier Reef, Australia. Mar. Ecol. Prog. Ser. 185, 257–271.

Uku, J., Björk, M., 2005. Productivity aspects of three tropical seagrass species in areas of different nutrient levels in Kenya. Estuar. Coast. Shelf Sci. 63, 407–420.

Van Lent, F., Verchuure, J.M., van Veghel, L.J., 1995. Comparative study on populations of *Zostera marina* L. (eelgrass): in situ nitrogen enrichment and light manipulation. J. Exp. Mar. Biol. Ecol. 185, 55–76.

Van Montfrans, J., Wetzel, R.G., Orth, R.J., 1984. Epiphyte–grazer relationships in seagrass meadows: consequences for seagrass growth and production. Estuaries 7, 289–309.

Van Tussenbroek, B.I., 1995. *Thalassia testudinum* leaf dynamics in a Mexican Caribbean coral reef lagoon. Mar. Biol. 122, 33–40.

Vermaat, J.E., Verhagen, F.C.A., 1996. Seasonal variation in the intertidal seagrass *Zostera noltii* Hornem.: coupling demographic and physiological patterns. Aquat. Bot. 52, 259–281.

Vermaat, J.E., Hootsmans, M.J.M., Nienhuis, P.H., 1987. Seasonal dynamics and leaf growth of *Zostera noltii* Hornem., a perennial intertidal seagrass. Aquat. Bot. 28, 287–299.

Walker, D.I., McComb, A.J., 1988. Seasonal variation in the production, biomass and nutrient status of *Amphibolis antarctica* (Labill.) Sonder ex Aschers. and *Posidonia australis* Hook.f. in Shark Bay, Western Australia. Aquat. Bot. 31, 259–275.

Watanabe, M., Nakaoka, M., Mukai, H., 2005. Seasonal variation in vegetative growth and production of the endemic Japanese seagrass *Zostera asiatica*: a comparison with sympatric *Zostera marina*. Bot. Mar. 48, 266–273.

Wear, D.J., Sullivan, M.J., Moore, A.D., Millie, D.F., 1999. Effects of water-column enrichment on the production dynamics of three seagrass species and their epiphytic algae. Mar. Ecol. Prog. Ser. 179, 201–213.

Weidemann, A.D., Bannister, T.T., 1986. Absorption and scattering coefficients in Irondequoit Bay. Limnol. Oceanogr. 31, 567–583.

West, R.J., 1990. Depth-related structural and morphological variations in an Australian *Posidonia* seagrass bed. Aquat. Bot. 36, 153–166.

Wetzel, R.L., Penhale, P.A., 1983. Production ecology of seagrass communities in the lower Chesapeake Bay. Mar. Technol. Soc. J. 17, 22–31.

Wiginton, J.R., McMillan, C., 1979. Chlorophyll composition under controlled light conditions as related to the distribution of seagrasses in Texas and the U.S. Virgin Islands. Aquat. Bot. 6, 171–184.

Williams, S.L., Ruckelshaus, M.H., 1993. Effects of nitrogen availability and herbivory on eelgrass (*Zostera marina*) and epiphytes. Ecology 74, 904–918.

Ziegler, S., Benner, R., 1999. Nutrient cycling in the water column of a subtropical seagrass meadow. Mar. Ecol. Prog. Ser. 188, 51–62.

Zieman, J.C., 1975. Seasonal variation of turtle grass, *Thalassia testudinum* König, with reference to temperature and salinity effects. Aquat. Bot. 1, 107–123.

Zieman, J.C., Wetzel, R.G., 1980. Productivity in seagrasses: methods and rates. In: Phillips, R.C., McRoy, C.P. (Eds.), Handbook of Seagrass Biology: An Ecosystem Perspective. Garland STPM Press, New York, pp. 87–116.

Zimmerman, R.C., Smith, R.D., Alberte, R.S., 1987. Is growth of eelgrass nitrogen limited? A numerical simulation of the effects of light and nitrogen on the growth dynamics of *Zostera marina*. Mar. Ecol. Prog. Ser. 41, 167–176.

Zimmerman, R.C., Cabello-Pasini, A., Alberte, R.S., 1994. Modeling daily production of aquatic macrophytes from irradiance measurements: a comparative analysis. Mar. Ecol. Prog. Ser. 114, 185–196.

Zimmerman, R.C., Reguzzoni, J.L., Alberte, R.S., 1995. Eelgrass (*Zostera marina* L.) transplants in San Francisco Bay: role of light availability on metabolism, growth and survival. Aquat. Bot. 51, 67–86.

Zimmerman, R.C., Kohrs, D.G., Steller, D.L., Alberte, R.S., 1997. Impacts of CO_2 enrichment on productivity and light requirements of eelgrass. Plant Physiol. 115, 599–607.