

## Impact of light limitation on seagrasses

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### Abstract

Seagrass distribution is controlled by light availability, especially at the deepest edge of the meadow. Light attenuation due to both natural and anthropogenically-driven processes leads to reduced photosynthesis. Adaptation allows seagrasses to exist under these sub-optimal conditions. Understanding the minimum quantum requirements for growth (MQR) is revealed when light conditions are insufficient to maintain a positive carbon balance, leading to a decline in seagrass growth and distribution. Respiratory demands of photosynthetic and non-photosynthetic tissues strongly influence the carbon balance, as do resource allocations between above- and below-ground biomass. Seagrass light acclimation occurs on varying temporal scales, as well as across spatial scales, from the position along a single leaf blade to within the canopy and finally across the meadow. Leaf absorptance is regulated by factors such as pigment content, morphology and physical properties. Chlorophyll content and morphological characteristics of leaves such as leaf thickness change at the deepest edge. We present a series of conceptual models describing the factors driving the light climate and seagrass responses under current and future conditions, with special attention on the deepest edge of the meadow.

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*Keywords:* Light attenuation; Photosynthesis; Seagrass

*Abbreviations:*  $1/\Phi_{\max}$ , minimum quantum requirements for photosynthesis;  $\alpha$ , photosynthetic efficiency;  $A$ , absorptance;  $C_i$ , inorganic carbon;  $D$ , absorbance;  $\Delta F/Fm'$ , effective quantum yield of PSII;  $E_c$ , compensation irradiance;  $E_k$ , minimum saturating irradiance;  $E_s$ , surface irradiance;  $H_{\text{sat}}$ , daily period of saturating irradiance;  $K_d$ , attenuation coefficient; LAI, leaf area index; PAR, photosynthetically active radiation;  $R$ , reflectance;  $rETR_{\max}$ , maximum relative electron transport rate; SLA, specific leaf area.

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### 1. Introduction

Seagrass habitats occupy vast tracts of shallow temperate and tropical coastal waters and provide ecosystem services in excess of US\$3.8 trillion annually (Costanza et al., 1997). Over the past century, human activity has had a profound negative impact on seagrass habitats. Continued pressure from coastal development

is dramatically reducing the distribution and condition of seagrasses and altering the composition of seagrass meadows globally (Orth et al., 2006). Seagrass loss has been attributed to a suite of environmental and anthropogenic factors but still little is known about the mechanistic causes of this global decline. Seagrasses are particularly sensitive to reductions in light availability, where small decreases can cause significant declines in growth and distribution. Some of the best documented losses of seagrass due to light limitation have occurred in Australia (Bulthuis, 1983; Walker and McComb, 1992; Dennison et al., 1993; Short and Wyllie-Echeverria, 1996; Ralph et al., 2006).

Light drives photosynthesis, leading to the production of oxygen and carbohydrates that allow plants to grow. For photosynthesis to occur in seagrasses, light must penetrate the water column, enter the canopy of leaf blades, pass through a layer of epiphytes on the surface of the leaf and finally enter the leaf epidermis to reach the photosynthetic apparatus (Dalla Via et al., 1998). Light is attenuated at each of these steps. The degree of light attenuation at the depth of the seagrass meadow is controlled by external factors such as: (1) physical properties of the water (depth, dissolved organic matter content, sediment accretion and re-suspension), (2) human activities (increased sediment run-off, increased nutrient load leading to eutrophication and algal blooms, fishing, aquaculture and dredging) as well as (3) regional weather patterns (e.g. extreme storms and altered rainfall patterns). These processes are graphically presented in Fig. 1a and b.

The sensitivity of seagrasses to reductions in light availability is attributed to their high minimum light requirements (Dennison et al., 1993). Minimum light requirements for species or populations have been derived from empirical determinations of the percentage of surface irradiance at the maximum colonization depth (Chambers and Kalff, 1985; Duarte, 1991; Dennison et al., 1993). The minimum values result from simultaneous measurements of the maximum growth depth and the light attenuation coefficient of the water column ( $K_d$ ). The values also determine the water depth at which a species or population can grow and survive, depending on the inherent optical properties of the water column (i.e., absorption and scattering coefficients) and, thus, on the light availability at the top of the seagrass canopy. Due to the empirical nature of these determinations, they provide an important understanding about the minimum light requirements for seagrass growth, but little information about the mechanistic-physiological association between plant survival and light availability. Theoretical minimum light requirements for growth of

seagrasses have been estimated at 11% of surface irradiance,  $E_s$  (Duarte, 1991). Empirical determinations have however reported values between 5% to 25% of  $E_s$  (Kenworthy and Haunert, 1991; Dennison et al., 1993). The large quantum requirements of seagrasses contrast with the 1% of  $E_s$  estimated for phytoplankton communities (Strickland, 1958).

An alternate but not mutually exclusive hypothesis to explain the sensitivity of seagrasses to low light is that they often colonise hypoxic-to-anoxic, sulphide-rich subtidal sediments. Sulphide toxicity results in reduced photosynthesis, increased respiration, and decreased seagrass production and meristematic cell division (Goodman et al., 1995; Holmer and Bondgaard, 2001; Holmer et al., 2005). Under these extreme reducing-sediment conditions, seagrasses must provide sufficient oxygen to maintain metabolic processes for a large biomass of non-photosynthetic tissues (rhizomes and roots). To maintain the respiratory demands of the heterotrophic biomass under reducing conditions through photosynthetic activity, seagrasses have amongst the highest light requirements of flowering plants (Orth et al., 2006). As the quantity (and quality) of light reaching seagrass leaves limits plant growth, any reduction in light penetration or change in optical properties of the water will compromise seagrass survival, especially at the deepest edge of the meadow.

Seagrasses have adapted to the variable physical properties of estuaries and near-shore environments for over 100 million years of evolutionary history (Orth et al., 2006). However, human activities (including human-induced climate change) are responsible for most of the reduction in water transparency in coastal regions over the past hundred years, which may be too fast to allow seagrasses to adapt. Poor land management practices result in increased surface run-off, leading to increased sediment loads within estuaries. Similarly, dredging operations can re-suspend sediments, attenuating light for extended periods of time, leading to seagrass decline (Fig. 1b). Altered river flows (changes in current velocities and direction) as a result of coastal urbanization and engineering, together with other human activities such as marine and land farming can also affect light penetration, playing a role in seagrass loss. Increased nutrient loads into estuaries have both direct and indirect effects on the benthic macrophyte community. Eutrophication increases the likelihood of pelagic phytoplankton blooms that reduce light penetration (Nixon, 1995; Smith et al., 1999). Eutrophication also causes increased growth of epiphytic organisms attached to seagrass leaves, further attenuating light. Changes in climate associated with human-induced

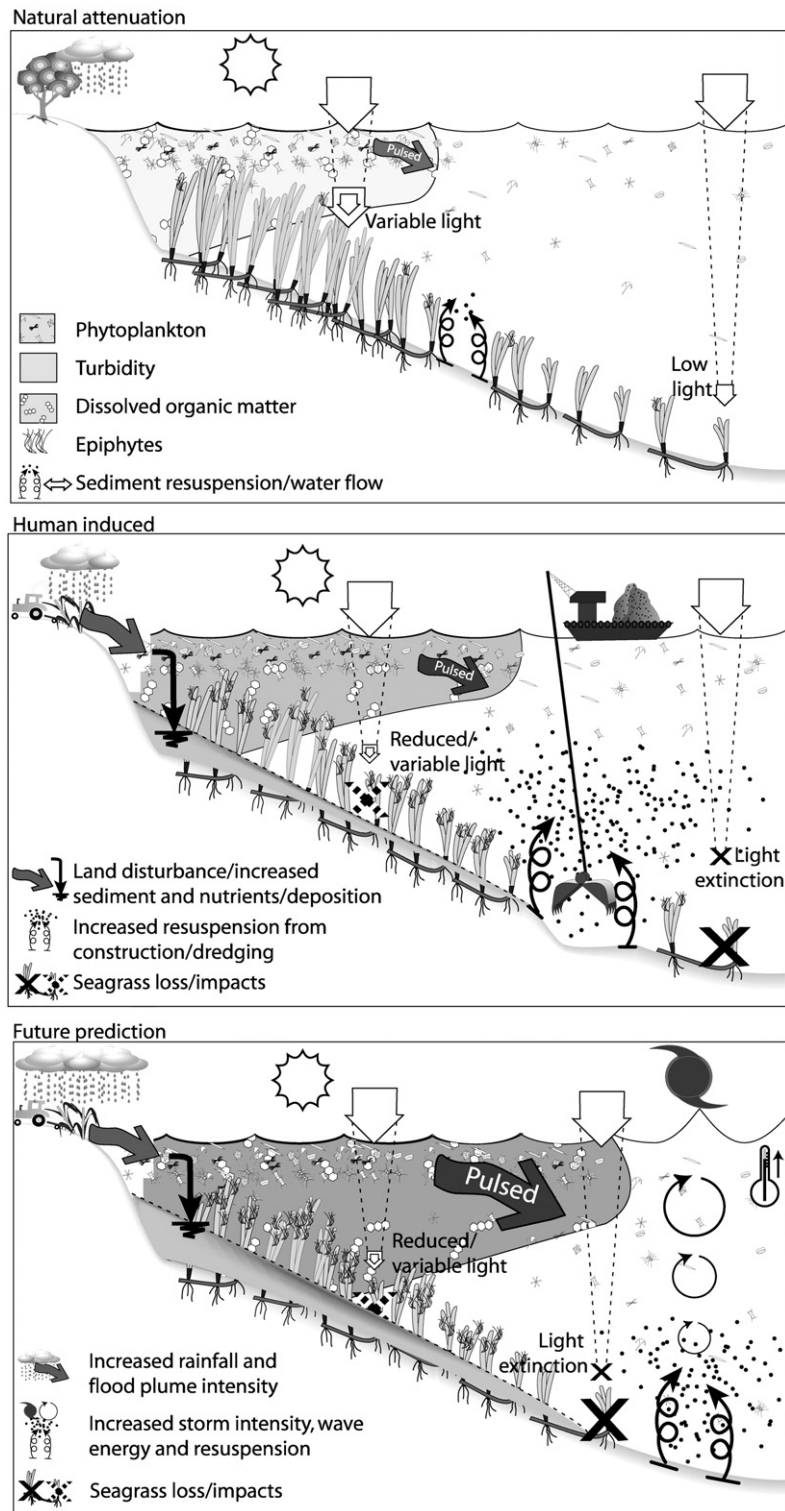


Fig. 1. Conceptual model of light reduction and impact on seagrass with the following as the legend — (A) Growth of seagrasses is strongly influenced by the optical quality of the water, including suspended sediments, dissolved organic matter and phytoplankton, which vary strongly according to run-off, as well as growth of microalgae on the leaves. (B) Human activities, both on the land and in-water have led to changes in water quality that are reducing the light available to seagrasses. (C) Future predictions are for a changing climate with increased sea surface temperature, more sporadic and intense run-off events and storms that will lead to periods of more sediment and nutrient loading and re-suspension.

increases in the concentration of atmospheric greenhouse gases are expected to impact the light regime of seagrasses (Short and Neckles, 1999). For example, the increased frequency of extreme weather will increase land run-off and sediment re-suspension (Fig. 1c), while altered rainfall patterns will encourage movement of the saline wedge within the estuaries (Short and Neckles, 1999). Furthermore, increased sea surface temperatures will increase respiration demands, which, in combination with reduced photosynthetic rates from light reduction, will alter the carbon balance (Short and Neckles, 1999). These direct and indirect effects of light on seagrass growth and survival are summarised in the conceptual model shown in Fig. 1a–c.

In this review, we consider the morphological, ecological and physiological responses of seagrasses to light limitation, highlighting knowledge gaps and developing a new conceptual model for these responses.

## 2. Importance of maintaining a positive plant carbon balance

The carbon balance of a seagrass depends upon the rate of photosynthesis, inorganic carbon ( $C_i$ ) availability, respiration rate of the leaves and respiration rate of non-photosynthetic tissues (stem and below-ground roots and rhizomes). Understanding the capacity of seagrasses to tolerate low light conditions is dependent upon knowledge about the carbon balance, which is in turn controlled by the minimum quantum requirements for photosynthesis ( $1/\Phi_{\max}$ ). Processes downstream of photosynthesis as well as processes related to resource allocation determine the minimum quantum requirements for growth (MQR). The MQR corresponds to a net carbon balance where total leaf productivity equals the respiratory demands of the whole plant. MQR is derived from mechanistic-physiological knowledge of the balance between photosynthetic carbon inputs and respiratory losses. Physiological determination of seagrass MQR, allows prediction of species and population abilities to survive under reduced light conditions.

### 2.1. Minimum quantum requirements for photosynthesis in seagrasses ( $1/\Phi_{\max}$ )

After many years of scientific debate, a consensus has been reached that for an ideal plant to synthesise one molecule of oxygen, it requires at least 8 photons (4 for each photosystem; cf. Govindjee, 1999). Therefore, the theoretical minimum quantum requirement for photosynthesis is 8. Differences in the efficiency of light absorption among tissues (i.e., effective absorption

cross-section, see Falkowki and Raven, 1997), or in the efficiency of light to carbon conversion, are both large sources of variability in the photosynthetic efficiency within and among species.

Experimental determination of the minimum quantum requirements for photosynthesis ( $1/\Phi_{\max}$ ) requires an accurate determination of photosynthetic efficiency ( $\alpha$ ) in the linear sub-saturating region of the photosynthesis-irradiance curve ( $P$  vs  $E$ ). Experimental determination also requires (1) homogeneous tissue illumination and (2) an accurate measurement of the light absorption capacity of the photosynthetic structure examined (i.e., absorbance or the fraction of incident light absorbed by a surface) and spectral correction for the experimental light source (see Björkman and Demming, 1987; Dubinsky et al., 1984, 1990). To our knowledge, there are only two estimates of the minimum quantum requirement ( $1/\Phi_{\max}$ ) of seagrasses. The first was reported for the temperate species, *Zostera marina* (Frost-Christensen and Sand-Jensen, 1992) and in a recent publication Cayabyab and Enríquez (in press) have provided  $1/\Phi_{\max}$  values for the tropical species *Thalassia testudinum*. Frost-Christensen and Sand-Jensen (1992) reported values between 14 and 20 photons required to evolve one oxygen molecule (between 0.070 and 0.050 mol  $O_2$  mol quanta absorbed<sup>-1</sup>) from this temperate species. This is more than double the number of photons established as the theoretical minimum for photosynthesis (Govindjee, 1999) and similar to the empirical average value determined for C4 plants (Björkman and Demming, 1987). Surprisingly, Cayabyab and Enríquez (in press) reported values between 8 and 12 mol quanta mol<sup>-1</sup>  $O_2$  evolved for the leaves of the tropical seagrass *T. testudinum*. This finding reveals that the leaves of *T. testudinum* maintain a more efficient use of the light absorbed than the leaves of the temperate species *Z. marina*, even in the clear, shallow tropical waters of the Caribbean. The estimated  $1/\Phi_{\max}$  values for *T. testudinum* leaves were very close to the theoretical minimum of 8 proposed by the linear photosynthesis model. If we also consider the substantial respiratory demands of the whole plant, it is probable that the minimum quantum requirements of both species are actually much higher and probably larger for the species or population with the highest respiratory demands (i.e., lowest above to below-ground biomass ratio).

Those estimates were not performed with plants growing at the deepest edge of the meadows, indicating a clear gap in our knowledge of seagrass photosynthesis. To enhance photosynthetic rates at low light depends on the ability to increase  $\alpha$ , which is regulated by (i) the capacity to reduce the leaf minimum quantum

requirements for photosynthesis ( $1/\Phi_{\max}$ ) to approach the theoretical minimum of 8; and (ii) the ability to enhance leaf absorbance.

## 2.2. Light absorption properties of seagrass leaves

Leaf absorbance is regulated by factors such as pigment content, morphology and physical properties of the area. In *Zostera capricorni* (now *Z. muelleri*), light reduction caused a decrease in chloroplast density, increase in chlorophyll content, decrease in the chlorophyll *a* to *b* ratio and a decrease in UV blocking pigments (Abal et al., 1994). Similarly, an 87–90% decrease in surface irradiance caused *Halophila wrightii* to have higher chlorophyll concentrations than controls, but pigment content was constant in *T. testudinum* (Czerny and Dunton, 1995). In another experiment, Longstaff et al. (1999) found strong differences in chlorophyll *a+b* concentrations of *Halophila ovalis* leaves: concentrations decreased in total darkness, increased at 0.5% of surface irradiance but remained constant at 0.1% surface irradiance.

Interestingly, large variations in chlorophyll content of seagrass leaves result in relatively small variations in leaf absorbance (Enríquez et al., 1992, 1994; Cummings and Zimmerman, 2003; Enríquez, 2005). This phenomenon has been ascribed to the package effect, whereby the relationship between light harvesting efficiency and chlorophyll content is non-linear due to pigment self-shading among thylakoid membranes, chloroplasts and cell layers (Kirk, 1994). A comparison between the capacity for absorbing light between seagrass leaves and a typical bifacial terrestrial leaf (amphibious plant *Mentha aquatica*) showed that chlorophyll *a* absorbs light, on average, 38% less efficiently within the leaves of the tropical seagrass *T. testudinum* than within *M. aquatica* leaves (Enríquez, 2005). However, this finding does not seem to be a general pattern as temperate seagrasses with similar leaf anatomy to *T. testudinum*, showed 1.4 higher values than *M. aquatica* (Enríquez, 2005), but highlights possible differences among seagrass species in the light absorption efficiency of their leaves.

The particularly strong package effect observed in seagrasses is largely attributed to restriction of chloroplasts to the leaf epidermis. Seagrass leaves do not have specialized tubular palisade cells that facilitate penetration of light in the leaf (Vogelmann and Martin, 1993), nor do they have a spongy mesophyll that increases the optical path length due to scattering at the interfaces between the air spaces and cells such as in terrestrial leaves (Terashima and Saeki, 1983). Despite these constraints, seagrass

leaves exhibit efficient and relatively uniform light harvesting capabilities across varying depths and water quality (Cummings and Zimmerman, 2003; Olesen et al., 2002) and significant differences in some others (Olesen et al., 2002; Enríquez, 2005; Cayabyab and Enríquez, in press). Multiple scattering within the leaf may allow it to intensify light absorption and to counterbalance pigment self-shading. Leaf morphology (i.e., leaf thickness or specific leaf area; SLA) may also contribute to the regulation of light absorption efficiency through changing the optical light path (Enríquez, 2005).

There is no evidence of a link between leaf thickness or SLA and light absorption for seagrass leaves, similar to the findings for phytoplankton (Morel and Bricaud, 1981; Agustí, 1991a,b), some macroalgal species (Ramus, 1978, 1990) and marine macrophytes (Enríquez et al., 1994). However, leaf morphology is also associated with other important functional properties such as gas and solute exchange rates. Photosynthesis in aquatic environments is strongly limited by carbon availability ( $\text{CO}_2$  and  $\text{HCO}_3^-$  diffusion rates are 4 to 5 orders of magnitude lower in water than in air, Raven, 1984). The thickness of the boundary layer surrounding the leaf is not only dependent on external hydrodynamics but on leaf morphology and, specifically on its size and shape (Nowell and Jumars, 1984). Although some studies have examined the effect of water flow on seagrass photosynthesis (Koch, 1994; Enríquez and Rodríguez-Román, 2006), little is known about the possible association between leaf morphology and seagrass photosynthesis, through its effect on the stability of the boundary layer and, consequently, on carbon limitation. The occurrence of several carbon concentration mechanisms in seagrasses (see review of Touchette and Burkholder, 2000; Invers et al., 2001; Uku et al., 2005; Enríquez and Rodríguez-Román, 2006) will counterbalance carbon limitation, but compromise photosynthetic efficiency of carbon fixation and, thus, the minimum quantum requirements. In summary, the importance of leaf morphology in the photoacclimatory response of seagrasses and in their ability to reduce the minimum quantum requirements of the leaves still remains to be tested.

Light absorption can be measured with an integrating sphere (Cummings and Zimmerman, 2003; Drake et al., 2003; Runcie and Durako, 2004; Thorhaug et al., 2006; Zimmerman, 2006; Durako, in press) or using Shibata's (1959) spectroscopic determination of leaf absorbance (Enríquez et al., 1992, 1994; Enríquez and Sand-Jensen, 2003; Enríquez, 2005). Both approaches require special attention to their methodological procedures. Correct determination of leaf absorbance should account for light that is transmitted, reflected and scattered and for

light absorption by non-photosynthetic tissue. The integrating sphere provides a direct determination of the fraction of incident light transmitted ( $T$ ) and reflected ( $R$ ). Subtracting these values from 1, it provides an estimate of the fraction of light absorbed [ $A=(1-T)-R$ ]. By multiple reflection, a diffuse light field is set up within the sphere from all light that enters it, permitting accurate measurement of the scattered radiant flux (Kirk, 1994; Zimmerman, 2006).

Alternatively, the transmission mode of the spectrophotometer provides absorbance values,  $D$ , which are related to absorbance,  $A$ , according to the equation:  $A=1-10^{-D}$ . This equation assumes that reflectance ( $R$ ) tends to zero. Accounting for scattered light can be more problematic when transmittance is estimated using spectrophotometers because of their narrow collection angles. Use of a scattering material such as opal-glass ensures minimal light losses and that both the blank and sample light beams are highly scattered, giving rise to an approximately correct value of absorbance (Shibata, 1959). Non-photosynthetic tissue absorbance should be taken into account by using a white structure, such as a bleached (peroxide or organic solvent) or etiolated leaf having a similar cross section to the leaf examined as a base-line (see Enríquez, 2005) and subtraction of absorbance at wavelengths beyond PAR (usually 720–750 nm; Cummings and Zimmerman, 2003; Drake et al., 2003; Runcie and Durako, 2004; Enríquez, 2005; Durako, in press). Shibata's (1959) opal-glass methodology is not appropriate if surface reflectance is significant and proportionally larger than the sensitivity of the photomultiplier or both. It therefore requires further correction by subtracting leaf reflectance ( $R$ ) to the former absorbance values:  $A=(1-10^{-D})-R$ . Several studies have provided reflectance values for sea grass leaves ranging between 3.5% to 9.3% of photosynthetically active radiation (PAR) with most values between 5–7% (Runcie and Durako, 2004; Enríquez, 2005; Thorhaug et al., 2006; Durako, in press). These values do not appear to vary much amongst species, but this needs confirmation before assuming that seagrass reflectance is relatively constant. Nevertheless, the subtraction of a constant 5% value to the absorbance determinations on 12 seagrasses provided by Enríquez et al. (1992) makes these values closer to the experimental determinations so far reported. In this regard, Enríquez et al. (1994) measured light absorption properties of 13 seagrasses across PAR and reported that although the species examined ranged widely in chlorophyll  $a$  density, and light absorption properties, they absorbed, on average, 59% of the incident light (average PAR absorption). This is very similar to the

overall mean  $A_L(\text{PAR})$  of  $57\pm 6\%$  reported for nine seagrasses from the east and west coasts of Australia (Durako, in press). Thus, despite structural restrictions and a strong package effect, seagrass leaves are relatively uniform and efficient light-capturing organs.

### 2.3. Minimum quantum requirements for growth

Seagrasses have minimum quantum requirements of photosynthesis ( $1/\Phi_{\text{max}}$ ) that do not correspond to the minimum quantum requirements for growth (Fourqurean and Zieman, 1991; Dunton and Tomasko, 1994). Duarte and Chiscano (1999) have shown a large variability among seagrass species in the above- to below-ground biomass ratios, which may lead to a large variability among seagrasses in their minimum quantum requirements for growth (MQR). Differences among species in their morphological plasticity, storage products, life-form (defined by Raunkier, 1934 as the ecologically important structural and phenological grouping of genotypes) and timing of response (growth rate) may explain differences in their tolerance to shading. In addition, the contribution of whole plant respiratory demands, together with the contribution of plant reserves to sustain growth under sub-optimal carbon balance, may provide the complete picture for understanding the association between seagrass morphology and the regulation of minimum quantum requirements for growth, and the tolerance or sensitivity of certain species or morphotypes to increments in light attenuation.

The theoretical and empirical estimates of minimum light for seagrass growth (Duarte, 1991; Kenworthy and Hauernt, 1991; Dennison et al., 1993) question the general assumption that seagrasses are shade-adapted plants (Dennison and Alberte, 1985; Schwarz and Hellblom, 2002; Durako et al., 2003; Larkum et al., 2006). This understanding is derived from the widespread observations that: (1) seagrass leaves usually show low  $E_c$  (compensation irradiance) and  $E_k$  (saturation irradiance) and high photosynthetic efficiency,  $\alpha$  (Olesen et al., 2002; Schwarz and Hellblom, 2002; Durako et al., 2003; Silva and Santos, 2003; Larkum et al., 2006); (2) their leaves usually show high levels of light-harvesting proteins (Larkum et al., 2006); and (3) for some species there is no increment in photosystem density nor in the unit size of PSII under low light (Major and Dunton, 2002). In contrast, increased maximum relative electron transport rates ( $r\text{ETR}_{\text{max}}$ ), minimal mid-day reduction in the effective photochemical efficiency ( $\Delta F/Fm'$  with full, late-afternoon recovery) and the presence of UV-absorbing pigments represent several sun-adapted characteristics that are present in species of *Halophila* that grow

intertidally (Durako et al., 2003; Beer et al., 2006). However, even for intertidal *Halophila stipulacea*, high levels of PAR and UV inhibit seed germination and germling growth (Malm, 2006). All these observations are indirect indicators of light-adaptation status. A recent study has provided for the first time solid evidence of the low plasticity and efficiency of the photoacclimatory responses of the leaves of the tropical seagrass *T. testudinum* (Cayabyab and Enríquez, in press). However, although the authors concluded *T. testudinum* leaves have a very efficient photosynthetic light use at low irradiances but limited photoacclimatory plasticity to enhance  $P_{\max}$  and  $E_k$  under high light (a clear shade-adapted response), they also indicate the success of this species in the oligotrophic and shallow waters of the Caribbean may rely on other levels of plant complexity such as the morphological response of the whole-plant (Cayabyab and Enríquez, in press). Clearly, further research is needed to determine the plasticity of the photosynthetic apparatus of seagrasses, as well as the full repertoire of photo-acclimatative responses at different levels of plant organization and among seagrass species.

### 3. Importance of carbon storage in below-ground tissues

Seagrasses fix less carbon under low-light conditions, thus survival under these sub-optimal conditions requires adjustments to the carbon-budget to maintain a positive balance. This involves balancing photosynthetic carbon fixation (Dennison and Alberte, 1985) with resource allocation processes and patterns of storage, as well as reducing respiratory demands (Pirc, 1989; Burke et al., 1996; Alcoverro et al., 2001). Under reduced light conditions, seagrasses mobilize stored carbohydrates to maintain metabolic processes (Alcoverro et al., 2001).

Seagrasses with larger below-ground biomass are able to move and use stored carbohydrates to optimize carbon balance (Dennison and Alberte, 1985; Ralph et al., 1992; Alcoverro et al., 1999). Changes to the above: below-ground biomass ratio occur as leaves are lost, however the rhizome takes longer to senesce (Longstaff et al., 1999; Collier, 2006), although some species show responses to light reduction that occur at the whole plant scale (Abal et al., 1994; Grice et al., 1996). Rhizomes play an important role in supplying carbohydrates in the early phase of shading, but with time, can become a respiratory burden if their biomass remains higher than the above ground biomass (Fourqurean and Zieman, 1991; Romero et al., 1994). The quantity and quality of stored carbohydrates varies among species. Respiratory demand of leaves is generally higher than that of

rhizomes per gram dry weight, but because of the dominance of below-ground biomass, rhizomes can be a huge respiratory burden (Fourqurean and Zieman, 1991; Romero et al., 1994; Masini et al., 1995). Species with lower total biomass are often found in deeper waters (e.g., *Halophila* in Australia and Florida; Coles et al., 2000) largely because there is less structural material to build and maintain. Larger species such as *Posidonia* spp. have more storage capacity and can often survive severe, short-term light reduction for longer (Czerny and Dunton, 1995; Longstaff et al., 1999) such plants can be found growing at great depth. For these larger bodied seagrasses, growth is temporally decoupled from light absorption during periods of light deprivation (Hall et al., 1991; Dixon and Leverone, 1995), especially at the deepest edge of a meadow.

Stable carbon isotope values for the large-bodied seagrasses, *Posidonia oceanica* and *T. testudinum*, indicate that as light becomes limiting (at the deep edge) carbon becomes less limiting (Cooper and DeNiro, 1989; Durako and Hall, 1992). This has been attributed to a decrease in diffusion-limited carbon demand at sub-saturating photosynthetic rates, which leads to an increase in enzymatic discrimination against  $^{13}\text{C}$  at lower irradiances resulting in more negative  $\delta^{13}\text{C}$ . This observation illustrates the relationship between carbon limitation and light in seagrasses growing under low-light conditions.

Higher respiration rates are associated with elevated water temperature (Bulthuis, 1983; Masini et al., 1995) therefore, projected increases in sea temperature suggest that respiration rates will increase in the future. Photosynthesis, on the other hand, may only increase for some species within a certain temperature range (Perez and Romero, 1992; Masini et al., 1995). For species pushed to even higher temperatures (up to 35 °C) increased photorespiration and photoinhibition may occur (Bulthuis, 1987; Campbell et al., 2006). However, light availability will probably continue to decrease as sea level rises and water quality continues to decline. Photosynthesis may be unable to balance the elevated respiratory demands (photosynthesis:respiration ratio). Seagrasses growing near their depth limit therefore could be the first affected.

#### 3.1. Competitive strategies of seagrasses

Seagrasses are clonal plants and employ different physiological strategies when competing for resources. These strategies are described as either guerilla or phalanx (Lovett-Doust, 1981). As the terms implies, guerilla species exhibit fast growth to exploit resources

quickly. In these species, older shoots tend to provide support for new shoots. This allows the plant to direct resources to points of new growth, while providing little support to existing biomass. In contrast, slow growth and a reliance on new shoots to support existing biomass distinguishes the phalanx strategy. Large-bodied, stable-selected seagrasses tend to employ the phalanx strategy (e.g., *Cymodocea* and *Thalassia*; Tomasko and Dawes, 1990; Terrados et al., 1997), whereas small-bodied, opportunist species tend to employ the guerilla strategy (e.g., *Halophila*, Dean and Durako, in press). Under light limiting conditions, it is expected that guerilla species will come and go on rapid scales, exploiting periods of elevated light availability and disappearing during low light. In contrast, phalanx species will acclimate to the low light conditions using storage reserves and morphological/physiological mechanisms; in the longer term they will change shoot leafiness and then reduce shoot density (e.g. *Posidonia sinuosa*, Collier, 2006). At the same time, slow growing and large-bodied species tend to have longer life-spans and maintain larger biomass, which may strongly increase the minimum quantum requirements for growth (MQR), while small-bodied species may have relatively low MQR for growth which approach their MQR for photosynthesis ( $1/\Phi_{\max}$ ) (e.g. *Halophila* spp.). The importance of both strategies in the photoacclimatory response of seagrasses to low light remains to be tested.

#### 4. Fluorescence-based estimates of light limitation

Over the past 10 years, a wide range of research has employed chlorophyll *a* fluorescence to investigate aspects of seagrass physiology, specifically light dependent responses. Generally, effective and maximum quantum yields decrease from a maximum with increased irradiance (Dawson and Dennison, 1996; Ralph et al., 1998; Longstaff et al., 1999; Durako and Kunzelman, 2002; Enríquez et al., 2002; Major and Dunton, 2002; Ralph et al., 2005). Specific responses to reduced light include increased photosynthetic efficiency ( $\alpha$ ), reduced maximum electron transport rate ( $rETR_{\max}$ ), and a reduction in the saturating irradiance ( $E_k$ ) as derived from rapid light curves (Ralph, 1999; Schwarz and Hellblom, 2002; Campbell et al., 2003; Ruiz and Romero, 2003; Silva and Santos, 2003; Ralph and Gademann, 2005). However, many studies have also reported no response or a response that does not follow light gradients (Pirc, 1986; Major and Dunton, 2000; Durako et al., 2003; Olesen et al., 2002). These discrepancies are possibly due to a number of field-based environmental and scale-related considerations.

#### 5. Effect of light-limitation at various spatial scales

Seagrasses are sensitive to changes in light availability across a range of spatial scales, including individual leaf responses, shoot-scale responses and alterations to the meadow structure (Dennison, 1987; Dalla Via et al., 1998; Longstaff and Dennison, 1999; Olesen et al., 2002).

##### 5.1. Leaf scale changes

Leaf morphology changes to optimise photosynthesis according to the ambient light climate of the meadow (Ruiz and Romero, 2001). Morphological changes require structural alterations to the tissue, which are governed by growth and leaf turnover rates of the particular seagrass species. Amongst the leaf morphological characteristics which respond to reductions in light are canopy height as seen in leaf length (Abal et al., 1994; Gordon et al., 1994; Longstaff and Dennison, 1999), leaf width (West, 1990; Lee and Dunton, 1997; Dalla Via et al., 1998) and leaf area (Campbell and Miller, 2002). Under low-light conditions, the leaf size is usually decreased rather than increased (Gordon et al., 1994), which will reduce the respiratory demand of the shoot yet decrease the photosynthetic capacity of the leaves (Campbell and Miller, 2002). The opposite can also occur, where leaf length (e.g., *Halodule pinifolia*; Longstaff and Dennison, 1999) or leaf width (e.g., *P. oceanica*; Dalla Via et al., 1998) increases to increase light capture area in the early stages of shading.

Morphometric plasticity in response to reduced light is highly variable amongst seagrass taxa. For example, leaf width of *T. testudinum* declines with depth in response to light reduction (Carlson and Acker, 1985; Hall et al., 1991; Lee and Dunton, 1997; Carlson et al., 2003) whereas for the genus *Posidonia*, some species increase leaf width in response to reduced light availability (Dalla Via et al., 1998) and finally other species show no change of leaf width (Gordon et al., 1994). Narrower leaves have also been associated with other environmental stresses (Phillips and Lewis, 1983; Durako, 1994) and production of female inflorescences (Durako and Moffler, 1985). Using leaf descriptors such as the Specific Leaf Area (SLA,  $\text{cm}^2 \text{g DW}^{-1}$ ), *Cymodocea nodosa* presents a significant increment in SLA with depth but *P. oceanica* does not show any significant change (Olesen et al., 2002). Species within the *H. ovalis* 'complex' show differences in morphological characteristics within regions or populations (Waycott et al., 2004) as well as along environmental gradients, such as light availability. Whereas, *P. oceanica* has

highly variable morphological characteristics at very small spatial scales (shoots and quadrats) apparently irrespective of light availability (Balestri et al., 2003).

Seagrass responses can be predicted using a model that describes the ecophysiology and ecological interactions of seagrass genera (Walker et al., 1999). As a very general rule, genera at the smaller end of the Functional Form model usually increase leaf length in response to light reduction, while larger species adjust leaf width to both acute and chronic light reduction (Abal et al., 1994; Dalla Via et al., 1998; Lee and Dunton, 1997), though exceptions to this occur (e.g. West, 1990). Furthermore, species with rapid turnover that are structurally small, such as *Halophila* species, can replace their leaf tissues with those more suited to the new light environment. These species are well suited to dynamic habitats such as estuaries (Waycott et al., 2004), yet they decline rapidly under complete shading after approximately 40 days (Longstaff et al., 1999). Another fast growing species, *Zostera noltii*, can change the architecture of its growth pattern after just 14 days of reduced light availability (Peralta et al., 2002). Much slower growing, long-lived species have less capacity for morphological adjustment and usually rely on changes that can be made within the leaf (i.e., adjustment of the photosynthetic apparatus to different light conditions, which result in changes in the capacity and efficiency to absorb light and to use the energy absorbed in carbon fixation). For example, structurally large seagrasses such as *Posidonia* spp. can survive for more than 140 days of shading (Gordon et al., 1994; Collier, 2006). Another important source of inter-specific variability to be considered is the ability of seagrass species to reabsorb leaf resources before leaves are detached from the shoot, as the capacity to replace the leaves and photoacclimate to the new light conditions may depend on the ability to minimize carbon and nutrient losses. Given the variability in morphometric and functional responses, a better mechanistic understanding is required before resource managers apply morphological metrics as indicators of low light conditioning by seagrasses.

### 5.2. Within canopy scale changes

For many seagrasses, leaf area index (LAI,  $\text{m}^2$  leaf  $\text{m}^{-2}$  of bottom) generally decreases with depth and light limitation, primarily because of reduced shoot densities (Peres and Picard, 1975; Cambridge and McComb, 1984; Orth and Moore, 1984; Giesen et al., 1990; Hall et al., 1991; Dennison et al., 1993; Onuf, 1994; Hall et al., 1999; Enríquez and Pantoja-Reyes, 2005). Whereas, shoot size (total area per shoot;  $\text{m}^2$  leaf shoot  $\text{shoot}^{-1}$ ) has not shown a consistent association with light. Occasionally shoot

size decreases with depth (*Z. marina*, Dennison and Alberte, 1986); increases with depth or shade, as has been observed in *P. oceanica* (Dalla Via et al., 1998) and *Z. capricorni* (Abal et al., 1994); or shows no association with depth, as in *P. oceanica* and *C. nodosa* (Olesen et al., 2002). Increase in shoot size with depth has been attributed to a relaxation of intra-specific competition for light as shoot densities decline (Carlson et al., 2003; Enríquez and Pantoja-Reyes, 2005) and may reflect an increase in shoot leafiness (Tomasko and Dawes, 1988; Carlson et al., 2003) or increased leaf length (Goldborough and Kemp, 1990; Short, 1991).

A recent study reported a positive correlation between leaf biomass, LAI and shoot density, with the magnitude of leaf self-shading within the canopy of the seagrass *T. testudinum*, measured as the attenuation coefficient of down-welling irradiance inside the canopy ( $K_d$ ,  $\text{m}^{-1}$ ) (Enríquez and Pantoja-Reyes, 2005). These relationships explain why above-ground biomass, and specifically seagrass shoot density tends to decrease as light availability diminishes with depth. An increment in light attenuation within the water column may induce a morphological response leading to an “open” canopy and to reduced leaf self-shading.

Gradients of light within the seagrass canopy can be so strong that the tip and base of a single leaf blade are in light environments that differ by as much as three orders of magnitude (Masini and Manning, 1995; Enríquez et al., 2002). These changes translate to differences in photosynthetic electron transport (Ralph and Gademann, 1999; Ralph et al., 2005; Collier, 2006) however they may not alter photosynthetic rate (Enríquez et al., 2002). For example, within the *T. testudinum* canopy, pigment content, chlorophyll fluorescence, absorptance and effective and maximum quantum yields all decline from the base to the apex of the leaf (Durako and Kunzelman, 2002; Enríquez et al., 2002; Enríquez, 2005). Chlorophyll content can be greatest in the mid section of leaves where light availability is reduced, compared to the apical section (Dalla Via et al., 1998; Collier, 2006); the lower region of the leaf does not have fully developed pigment pools as the tissue is immature (Enríquez et al., 2002; Enríquez, 2005; Ralph et al., 2005). However, intra-leaf and inter-leaf variation within shoots may also be higher than the variation amongst the shoots for these parameters. In models developed for terrestrial systems, the lower part of a vertical canopy represents the light compensation point for the tissue (Anten, 2005). For *T. testudinum*, the first 5 cm of leaf blade showed a negative carbon balance, possibly due to leaf self-shading within the canopy. The light compensation point was observed at around 5 cm, and beyond it the leaf exhibited a fast

increment in productivity until a maximum was reached at 15 cm (Enríquez et al., 2002). This style of assessment could provide useful guidance on the photosynthetic limitations of the deep edge of a seagrass meadow in response to periods of lowered light due to water quality reductions.

### 5.3. Meadow scale changes

Morphological characteristics at the meadow-scale that respond to reductions in light include changes in the number of leaves per shoot (Ruiz and Romero, 2001) and total shoot mass (Dennison and Alberte, 1985). This type of plasticity can simultaneously maximise exposure of the photosynthetic apparatus to light and minimise respiratory demands, therefore optimising the carbon budget (Ruiz and Romero, 2001). As stated above, reductions in shoot density with depth are commonly reported in seagrasses (Dennison, 1987; Dennison and Alberte, 1985; Tomasko and Dawes, 1990; Krause-Jensen et al., 2000; Olesen et al., 2002; Collier et al., 2007) which can benefit neighbouring shoots and/or plants. For example, in *T. testudinum*, short shoot densities decline with light reduction, but this response may take 9 months or more following light reduction (Hall et al., 1991). Whereas, in *Posidonia* species, the loss of shoots can occur within 2–3 months of intense shading, however, the meadow can persist for up to a year, even maintaining growth (Gordon et al., 1994; Ruiz and Romero, 2001; Collier, 2006). Loss of *P. sinuosa* shoots coincided with reduced light attenuation of only 9–28%, but leaf growth rates were not different from control plants (Collier, 2006); however  $P_{\max}$  was reduced under severe shading, so leaf growth was possibly supported by carbohydrate reserves.

This self-thinning response allows greater light penetration through the canopy, reducing the effects of self-shading (Dalla Via et al., 1998; Enríquez and Pantoja-Reyes, 2005) and resulting in comparable absolute light levels in the lower region of the meadow as in the upper region (Dalla Via et al., 1998). Such changes as a response to long-term reductions in light availability are a typical feature of species that form dense canopies with slow leaf turnover rates (West, 1990; Olesen et al., 2002; Collier et al., 2007) and are likely to improve photosynthesis (Lee and Dunton, 1997; Longstaff and Dennison, 1999; Ruiz and Romero, 2001). For species with a shorter, sparser canopy which show reductions in shoot density with increasing depth, it is reasonable to assume that the benefits from reduced self-shading are probably less important than the benefits of reduced respiratory demand, if the ratio of above- to below-ground biomass increases with decreasing shoot density.

The spatial distribution of seagrasses may not always be negatively impacted by low light. Near the depth limit, seagrasses can exhibit clonal “foraging” behaviour, wherein rhizomes elongate rapidly into new substrates to assess whether the new area is suitable for growth (Marbà and Duarte, 1998). Physiological integration among seagrass shoots may therefore extend the maximum depth limit slightly deeper than would be expected, based on light levels alone, due to support from shallower ramets. At the same time, the respiration demands of the underground biomass may limit clonal growth to a depth that is shallower than expected from the leaf photoacclimatory efficiency as estimated from photosynthesis-irradiance ( $P$  vs.  $E$ ) light curves.

Meadow-scale responses to low light can also involve changes in species composition, where low light-adapted species can out-compete species less capable of tolerating periods of reduced irradiance or those with less storage capacity, or both. For example, multi-year observations of seagrass distribution and abundance in western Florida Bay indicated a change in species composition and species dominance in response to long-term light reduction (Durako, 1999; Durako et al., 2002). In 1995, Johnson Key basin was dominated by *T. testudinum*, with sparse *Halodule wrightii* as an understory and small patches of mixed *Thalassia-Halodule-Syringodium filiforme* at the southern edge (Fig. 2). Over a three-year period (1995 to 1998), Johnson Key Basin exhibited the recruitment and spread of the low-light adapted, small-bodied seagrass *Halophila engelmannii* concurrent with a basin-wide 400% increase in abundance of colonizing species *H. wrightii* and a decline in abundance of the previously-dominant large-bodied *T. testudinum*. These changes, which also resulted in an increase in species diversity (Fig. 2), suggest the conversion to a shade-adapted seagrass community within this basin in response to the chronically-turbid conditions over this period.

## 6. Evidence for transfer of resources amongst plants within a meadow

Shading or removing leaves from short shoots that are connected to surrounding, non-manipulated shoots of some large-bodied, seagrasses results in no significant change in growth from that of untreated plants (Tomasko and Dawes, 1989; Terrados et al., 1997). This suggests that resource-starved shoots may be supported by unstressed shoots (Noble and Marshall, 1983; Slade and Hutchings, 1987; Oborny et al., 2001). Shaded or defoliated short shoots with severed rhizomes exhibit slower growth when compared to treated short shoots with un-severed rhizomes. Therefore, connections

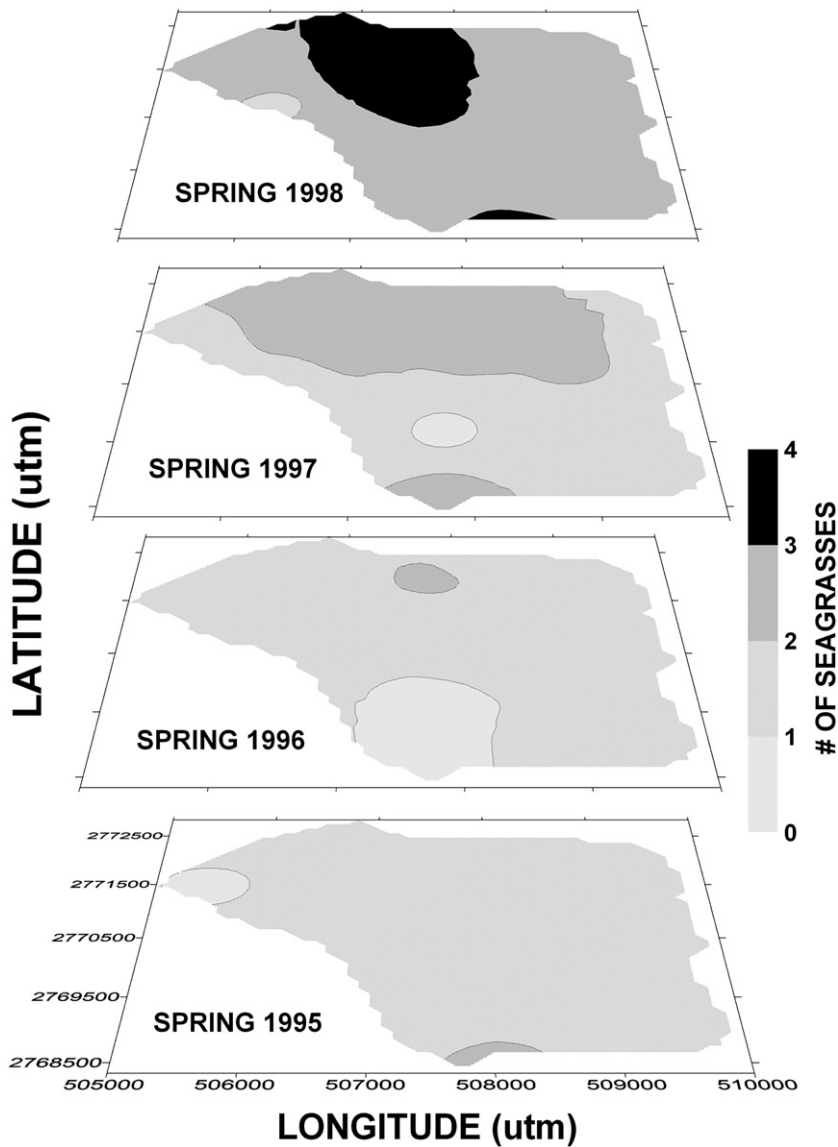


Fig. 2. Spatial distribution of seagrass species richness in Johnson Key Basin in western Florida Bay, USA from 1995–1998 (Durako, 1999).

among these long-lived short shoots may ameliorate shade stress on the plant. In contrast, small-bodied *Halophila* short shoots are short-lived and have little capacity for storage. Marbà et al. (2002) found that physiological support for *H. stipulacea* was maintained for only 1.6 days, compared to 5.4 years for the large-bodied *C. nodosa*. Unlike the larger seagrasses, carbon translocation in *H. stipulacea* exhibited little directionality. In *Halophila johnsonii*, photosynthate is allocated to ramets in proportion to their proximity to the source ramets rather than the condition of neighboring ramets (Dean and Durako, in press). It therefore appears that in species exhibiting fast turnover and short-lived leaves, no advantage is gained by selectively supporting

ramets based on condition or age. Collier (2006) found no evidence that the deep edge of the meadow is supported to any significant degree by direct translocation of newly incorporated C for two species of *Posidonia* (*P. sinuosa* and *P. australis*). This finding is in contrast to the strategies employed by the large-bodied seagrasses which exhibit slower turnover rates and show facultative and directional physiological support for light-stressed shoots (Tomasko and Dawes, 1989).

#### 6.1. Seagrass response to epiphytes

Elevated nutrients can enhance seagrass growth; however eutrophic waters are often associated with

seagrass loss, due to light limitation resulting from algal blooms in the water column or an increase in epiphytic growth (Dennison et al., 1993; Short and Wyllie-Echeverria, 1996; Ralph et al., 2006). Both algal blooms and epiphytes reduce the amount of light reaching the seagrass plants (Cambridge and McComb, 1984; Short and Wyllie-Echeverria, 1996). Epiphyte accumulation on leaves and the ensuing reduction in light availability reduces seagrass productivity (Silberstein et al., 1986) and has therefore been implicated as a causal factor for extensive seagrass loss (Cambridge et al., 1986). Epiphytic growth of flora and fauna (ranging from 3 to 99 mg cm<sup>-2</sup> normalised to leaf surface area (Brush and Nixon, 2002) or 1 to 10 g dry weight on spatial scales spanning 0.1 to 100 m (Moore and Fairweather, 2006) can attenuate light by an additional 7–67% to the seagrass leaf surface (Dixon and Leverone, 1995). For long-lived species such as *P. oceanica*, the natural epiphyte community can attenuate beyond 80% of the incident light on the oldest leaves (Cebrián et al., 1999).

The spatial distribution of epiphytes on seagrass leaves is influenced by the leaf morphology and growth rate; variations are due to leaf age, the side of the leaf, water flow over the canopy and canopy height (Dalla Via et al., 1998; Cebrián et al., 1999; Trautman and Borowitzka, 1999; Alcoverro et al., 2004). Attenuation of light by epiphytes growing on artificial leaves and intact seagrass

leaves have been measured and algorithms developed to calculate the influence of this optically dense layer on light received by the leaf surface (Brush and Nixon, 2002; Alcoverro et al., 2004). Attenuation through this layer generally follows an exponential relationship, such that a higher density of epiphytes contributes little to further light attenuation. Maximum light attenuation from epiphytes generally occurs at about 5–10 mg DW cm<sup>-2</sup> (Cebrián et al., 1999; Brush and Nixon, 2002). However, the attenuating properties of the epiphyte layer varies with algal species composition (Cebrián et al., 1999; Brush and Nixon, 2002).

The light environment of a seagrass meadow is therefore influenced via a combination of light attenuation by the water column, the canopy and the epiphytic layer. A change in the attenuation properties of any one of these could affect the others. For example, as epiphytes also require light, the epiphytic layer can also be reduced following shading (Fitzpatrick and Kirkman, 1995; Collier, 2006). Therefore, because of the inter-dependency, the attenuation of light reaching the seagrass blade is complex and dependent upon a number of factors.

### 7. Temporal responses to light-limitation

At the scale of a plant, physiological responses are usually expected to occur first, followed later by

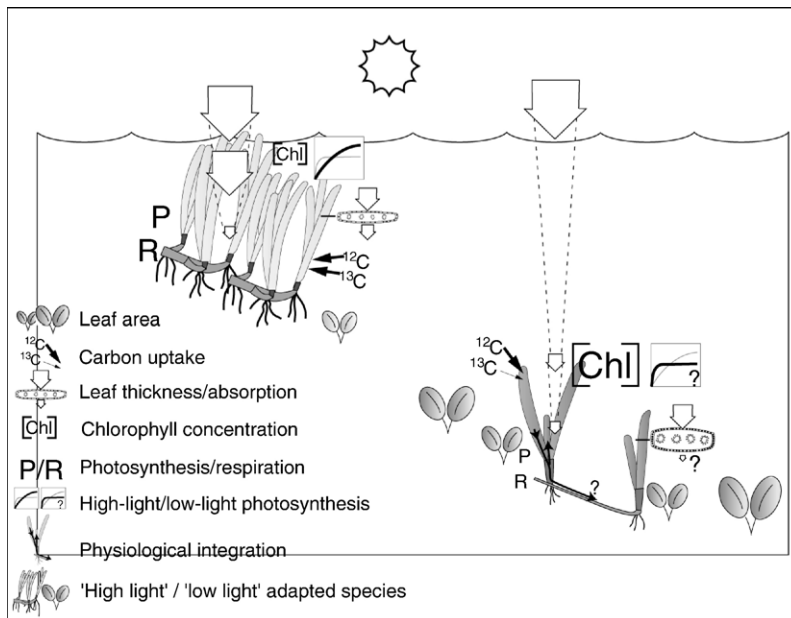


Fig. 3. Conceptual model showing a deep and shallow mixed meadow, where the differences in light attenuation result in physiological and morphological adaptation. The shallow meadow has high shoot density, with a large below-ground biomass, higher rates of photosynthesis and respiration, substantial self-shading with thinner leaves containing less chlorophyll pigments in comparison to the deeper meadow.

morphological changes if the stress persists or is acute (Longstaff and Dennison, 1999). Changes to photosynthetic characteristics can be detected within hours (Ralph and Burchett, 1995). Waycott et al. (2005) expanded on an earlier light acclimation model (Longstaff and Dennison, 1999) by speculating that after physiological, morphological and meadow-scale changes had occurred, chronic light reduction would then lead to changes in the population structure (genetics) of the seagrass meadow. Individuals that are better able to perform in a reduced light environment would start to dominate the meadow. This could be variants of an individual species, or it could be a change in species dominance (see Fig. 2).

The time-scale required to induce responses in seagrasses is highly dependant on the species. Changes to architecture and growth characteristics can be detected in as little as 9–14 days (Longstaff et al., 1999; Peralta et al., 2002). In conditions of extreme light deprivation, the ability of a seagrass to survive is likely to be influenced by its access to storage carbohydrates (Longstaff et al., 1999). Ability to survive light reduction may also be affected by the timing of light deprivation with shading in spring appearing to have the greatest effect on survival (Gordon et al., 1994; Fitzpatrick and Kirkman, 1995; Ruiz and Romero, 2001).

## 8. Models of light-limitation in seagrasses

There are a number of common models used to describe light limitation in seagrasses, we briefly describe three;

### A) Daily period of light-saturated photosynthesis:

$$H_{\text{sat}}$$

Light limitation occurs when  $H_{\text{sat}}$  (the daily period of light-saturated photosynthesis) falls below a threshold level at which photosynthesis is affected by  $H_{\text{sat}}$ . In *Z. marina* this is about 6–8 h (Dennison and Alberte, 1985). The  $H_{\text{sat}}$  model was based on summer photosynthetic rates and does not consider annual C budgets, making its application somewhat limited. What is the minimum  $H_{\text{sat}}$  required in winter or to sustain seagrasses over annual cycles, e.g. to develop carbohydrate reserves and support respiration throughout winter? In *P. sinuosa*,  $H_{\text{sat}}$  was 3-times lower (based on continuous light measurements and  $E_k$  from RLC's) in winter than in summer at the deep edge (Collier, 2006).

### B) Empirical determination of MLR

Few studies have reported the minimum light required (MLR) to sustain meadows over longer

durations. The exception is *Zostera muelleri* which requires 16 to 36% of sub-surface irradiance for survival (Longstaff, 2003) and for *P. sinuosa* it is 8 to 12% (Collier, 2006). Seagrasses globally have light requirements in the range of 4 to 36% of sub-surface irradiance (Dennison et al., 1993; Longstaff, 2003). If light availability is sustained below this level, this model predicts a complete loss of seagrass.

### C) Physiological based estimates of minimum quantum requirements for growth (MQR)

There are currently no physiological estimates of the minimum quantum requirements for whole plant growth in seagrasses. Oxygen electrode measurements of photosynthesis-irradiance curves ( $P$  vs  $E$ ) can provide an estimate of the minimum quantum requirements for photosynthesis ( $1/\Phi_{\text{max}}$ ). However, whole plant respiratory demands, together with the contribution of plant reserves to sustain growth under sub-optimal carbon balance, must be understood to determine the minimum quantum requirements for growth.

## 9. Conclusion

As described in this review, much is known about the photophysiology of seagrasses, yet much is still required for us to effectively manage this important yet diminishing resource. Understanding the mechanistic response of seagrass to light will allow better predictions of species and population abilities to survive under reduced light conditions. The complexity of this group of organisms makes this effort more difficult than for other marine taxa such as phytoplankton and macroalgae, but similar to approaches already in progress in terrestrial plant ecology. Further investigations of seagrass capacity to reduce their minimum quantum requirement for growth (MQR) as regulated by photoacclimatory efficiency of the leaves, leading to enhanced photosynthetic rates at low light availability, and by the morphological plasticity and resource allocation pattern of the whole organism to optimize plant carbon balance are therefore needed.

Other critical information not yet available is knowledge about how diverse seagrasses are with respect to the repertoire of photoacclimatory and/or photoadaptive responses. In other words, is it possible to distinguish between low-light vs. high-light “adapted” species? How plastic is the photosynthetic apparatus of seagrasses to cope with a highly variable

light environment? The existence of significant genetic variability may result in significant differences among species in their tolerance to low light conditions. Differences among species in their morphological plasticity, life-form and timing of response (growth rate) may explain differences in their tolerance to shading. In addition, the contribution of the whole plant respiratory demands, together with the contribution of plant reserves to sustain growth under sub-optimal carbon balance, may complete the whole scenario for understanding the association between seagrass morphology and the regulation of the MQR for growth, and the tolerance or sensitivity of certain species or morphotypes to increments in light attenuation (Fig. 3). In addition, differences among and within seagrass species in their photosynthetic plasticity and photoacclimation efficiency may have profound ecological implications, such as triggering trophic cascades. Despite the extensive research into seagrass ecophysiology, primary information about the photobiology of seagrasses is still missing.

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