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Daily variation patterns in seagrass photosynthesis along a vertical gradient

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ABSTRACT: The relationship between the available photosynthetic active radiation (PAR) and the photosynthetic yield of Photosystem II (PSII), measured by chlorophyll *a* fluorescence, was assessed in the intertidal seagrasses of Ria Formosa, a coastal lagoon in southern Portugal. Most of the lagoon's intertidal is occupied by a monospecific population of *Zostera noltii* (Hornemann), which occupies a vertical gradient of about 2 m. The upper distribution limit of this species comprises the edge of a *Spartina maritima* (Curtis) Fernald saltmarsh and the lower limit the transition to the subtidal, dominated by *Cymodocea nodosa* (Ucria) Ascherson. Diurnal changes in the pattern of rapid-light curves (RLCs) was investigated with pulse amplitude-modulated (PAM) fluorometry in *Z. noltii* and in *C. nodosa* in the upper and lower intertidal. The light reactions of photosynthesis were assessed by fitting photosynthesis-irradiance (*P-I*) models to the RLCs. The photosynthetic parameters of *Z. noltii* revealed that this plant species exhibits sun- and shade-type responses in its upper and lower vertical distribution limits, respectively. At the lower distribution limit in low light, the initial slopes of all RLCs were significantly higher than at the upper site, but decreased with increasing irradiances, while at the upper distribution limit, although lower, the slopes were unaffected by increasing irradiance. *C. nodosa* presented a typical shade-type response, as evidenced by the daily variation and light dependence of both photosynthetic efficiency and optimal quantum yield. The relationship between the maximum electron-transport rate and irradiance suggests that this species is strongly light-limited. We suggest that attempts to characterize the photosynthetic behaviour of an intertidal meadow should consider both diurnal fluctuations in the plants' photosynthetic activity as well as its vertical distribution frequency.

KEY WORDS: Daily variation · Seagrasses · Intertidal · Photosynthesis · Pulse amplitude-modulated fluorescence · PAM · *Zostera noltii* · *Cymodocea nodosa*

INTRODUCTION

Intertidal seagrasses colonise one of the harshest marine habitats, in which conditions change very rapidly and in a very significant manner. Stress factors are imposed and relaxed in accordance with the combined rhythms of tides and diurnal irradiance. Plants are forced to maintain a permanent and very dynamic trade-off between photosynthetic efficiency and photoprotection.

Like their terrestrial relatives, seagrasses perform real-time adjustments in their photosynthetic activity in response to diurnal changes in the available photosynthetic active radiation (PAR) (Ralph et al. 1998). Although photosynthesis usually parallels daily irradiance, a midday depression in photosynthetic activity may occur under high irradiance. This depression is common among marine plants, together with a real-time photoacclimation capacity expressed by rapid adjustments in pigment contents and ratios (Dennison & Alberte 1986, Abal et al. 1994).

Light availability is considered to be the most important factor regulating the depth distribution of seagrass beds, and has been widely used in predicting the lower vertical limits of a number of species (Duarte 1991, Dennison et al. 1993, Kenworthy & Fonseca 1996, Bach et al. 1998). The interaction between high nutrient loads, the concentration of phytoplankton and turbid-

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ity determines the light attenuation in the water column (Abal & Dennison 1996, Koch 2001). These parameters may undergo considerable variations, either on long-term (e.g. seasonal) or short-term (e.g. daily, tidal) scales, particularly in meadows with an important intertidal component, where physical, chemical and biological parameters tend to vary more dramatically than in the subtidal environment.

Intertidal meadows are regularly exposed to oversaturating irradiances that induce light stress and aggravate conditions of thermal and desiccation stress. However, through morphological traits, intertidal plants usually cope well with desiccation (Leuschner et al. 1998, Björk et al. 1999). In this specific type of environment, the ability to cope with irradiances that can exceed saturation values by as much as 7 to 8 times appears to be the major prerequisite for plant survival.

Plants have the capacity to adapt to their light environment in a number of ways, from the morphological down to the biochemical level (Falkowski & LaRoche 1991, Evans & Poorter 2001). Physiologically, plants are able to regulate photosynthesis in a highly dynamic way in response to several external factors. When the factor is high irradiance, the response is usually photoprotection, involving non-photosynthetic thermal dissipation of energy through a process often called 'non-photochemical quenching' (Krause & Weis 1991, Demmig-Adams 1998, Ort 2001). This response enables maintenance of the crucial balance between energy absorption and photosynthetic light utilization by carbon fixation, thus preventing photo-oxidative damages in Photosystem II (PS II; Ensminger et al. 2001).

Chlorophyll fluorescence measurements have proved to be very useful in the assessment of photosynthetic light responses, as the amount of energy dissipated in this way is inversely correlated to photosynthetic efficiency (Krause & Weis 1991). The description of a linear relationship between the chlorophyll *a* fluorescence parameter $(F_m' - F_s)/F_m'$ (where F_s is fluorescence in the light when only part of the reaction centres are closed, and F_m' is maximal fluorescence of a light-adapted leaf immediately after closure of all reaction centres by a saturating pulse) and the quantum yield of photosynthesis by Genty et al. (1989) opened the way for photosynthetic measurements using fluorometry-based instruments (Seaton & Walker 1990). Subsequently, the pulse amplitude-modulated (PAM) fluorescence method has been widely used and improved (Schreiber et al. 1995). *In situ* measurements of chlorophyll fluorescence in seagrasses were made possible after the development of a submersible PAM fluorometer (Beer et al. 1998, Ralph et al. 1998, Björk et al. 1999, Beer & Björk 2000, Schwarz et al. 2000, Seddon & Cheshire 2001, Durako & Kunzelman 2002). PAM fluorescence has been used for the evaluation of seagrass responses to specific environmental stresses such as desiccation, elevated temperatures or high irradiances. In parallel, it has also provided valuable insights into the dynamic behaviour of the photosynthetic apparatus of seagrass species under fluctuating field conditions. Chlorophyll fluorescence has proved to be particularly useful in the assessment of several aspects of the diurnal pattern of photosynthetic activity in seagrasses (Ralph et al. 1998, Enríquez et al. 2002, Figueroa et al. 2002), as it allows a considerable number of measures throughout the day under field conditions.

The existence of considerable alterations in photosynthetic performance during a diurnal cycle is widely recognised and must be taken into account when long-term measures or estimates of photosynthesis are required. On the other hand, in SW Europe, where tides are semi-diurnal, with daily changes in amplitude and time, the daily light regime in intertidal seagrass meadows fluctuates as a function of both time of day and tide schedule. When a third factor, the vertical distribution of plants within a meadow, is introduced, it becomes impossible to predict global photosynthetic performance without taking into consideration that a number of distinct light regimes occur simultaneously at different levels of a same meadow.

The aim of the present work was to assess how the vertical position of seagrasses in the intertidal determines their diurnal photosynthetic performance. The relationship between diurnal changes in available PAR and the photosynthetic yield of PSII, measured by chlorophyll *a* fluorescence, was investigated in the intertidal zone of Ria Formosa, southern Portugal, which is dominated by monospecific meadows of the seagrass *Zostera noltii*. The transition to the subtidal is colonised by a band of the seagrass *Cymodocea nodosa*.

MATERIALS AND METHODS

Study site and plant distribution. Ria Formosa is a shallow mesotidal lagoon on the south coast of Portugal. Its tidal amplitude varies between 3.50 m on spring tides and 1.30 m on neap tides. *Zostera noltii* (Hornemann) meadows occupy a vertical gradient of ca. 2 m. Their upper distribution limit comprises the edge of the *Spartina maritima* (Curtis) Fernald saltmarsh and their lower distribution limit the transition to the subtidal, which is dominated by *Cymodocea nodosa* (Ucria) Ascherson. This transition zone emerges only at the lowest water level of spring tides, while the upper limit of the *Z. noltii* meadows has an average emersion period of 6 to 8 h per tidal cycle (12 h). Environmental conditions, particularly light, vary greatly throughout the intertidal seagrass habitat. In the winter, the lower edge of the meadows receives an average daily PAR dose of 4 mol photons m^{-2}, whereas the upper edge receives around 15 mol photons m^{-2}. The range of pH variations is also higher at the upper site (7.4 pH at low tide, up to 8.8 pH at high tide) than at the lower site (7.9 to 8.3 pH).

In southern Portugal (37° N, 8° W), where tides are semidiurnal (2 low and 2 high tides every 24 h), low tide occurs in the early morning and late afternoon during spring tides and at midday during neap tides (Fig. 1). The combination of this tidal rhythm with daily changes in solar radiation leads to strong differences in the light environment at the upper and lower edges of the seagrass meadows.

This experiment was conducted under the neap-tide conditions shown in Fig. 1b. Low tide was coincident with solar noon, allowing lower plants to receive the maximum possible PAR.

Sampling strategy. Rapid-light curves (RLCs) were obtained by PAM fluorometry (Diving-PAM, Walz) every 2 to 3 h from pre-dawn until sunset, for *Cymodocea nodosa* (transition to subtidal) and for 2 *Zostera noltii* sites (1 at its lowest and 1 at its highest intertidal edge). All measurements were performed *in situ* at ambient temperature (16 to 18°C). RLCs were obtained from 5 replicates for each site.

An underwater planar PAR measuring device (Li-192SA underwater quantum sensor connected to a Li-1000 data logger; Li-Cor) mounted on a telescopic tower was installed in the transition between *Zostera noltii* and *Cymodocea nodosa*, at the exact location where samples of both species were collected. PAR radiation at the upper site of *Z. noltii* was measured with an identical set of instruments. Both devices were calibrated against each other.

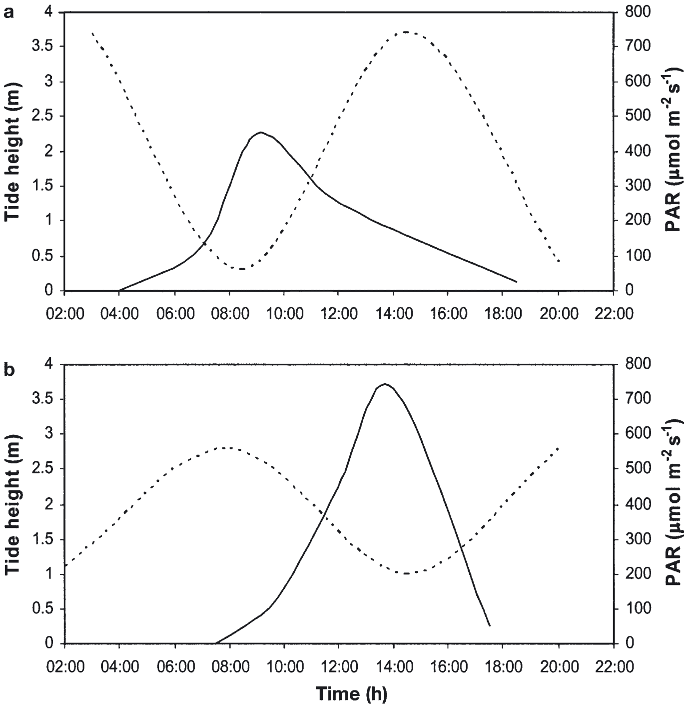

Fig. 1. *Zostera noltii*. Typical patterns of tidal cycle (······) and available photosynthetically active radiation, PAR (—), at lower end of a meadow during (a) spring and (b) neap tides

Absorption factor (AF). The absorption factor (AF), which represents the fraction of incident PAR that is absorbed by the leaves, was determined according to Beer et al. (2000) by placing seagrass leaves on top of the fluorometer PAR quantum sensor and irradiating them perpendicularly at a fixed distance with the instrument's own optic fibre. Irradiance reaching the sensor with and without leaves was recorded underwater in 10 replicates of each species, and AF was calculated as the percentage of light absorbed by the leaves. The use of this specific absorption factor instead of the instrument's pre-defined and commonly used value of 0.84 allowed the calculation of absolute (µmol e$^-$ m^{-2} s^{-1}) instead of relative electron-transport rates.

Fluorescence measurements. Seagrass leaves (2nd to 3rd youngest for *Zostera noltii* and 3rd youngest for *Cymodocea nodosa*) were placed in the fluorometer leaf-distance clip and shaded from ambient light for the duration of the measurement of each curve to prevent superimposition of ambient light on the light supplied by the instrument's optic fibre. Samples were irradiated with a series of 8 increasing pre-set irradiance steps supplied by the fluorometer's halogen lamp. At the end of each irradiance step (15 s periods), a 0.6 s saturating-light pulse (ca. 4000 µmol photons m^{-2} s^{-1}) was applied for maximum fluorescence (F_m') determination. Effective quantum yield of PS II [$Y = (F_m' - F_s)/F_m' = \Delta F/F_m'$] (Genty et al. 1989) was computed and the electron-transport rate [ETR = $Y \times$ irradiance (I) $\times$ AF $\times$ 0.5] (Schreiber et al. 1995) was calculated for each irradiance step.

The light reactions of photosynthesis were assessed by the parameters obtained directly through PAM fluorometry and by the parameters derived from the equation model fitted to the RLCs. The curves (ETR-I) were fitted with the adapted hyperbolic tangent model equation of Jassby & Platt (1976): $\text{ETR} = \text{ETR}_m \times \tanh(\alpha \times I/\text{ETR}_m)$, where I is irradiance, α is the ascending slope at limiting irradiances, and ETR_m is the maximum electron-transport rate. The half-saturation irradiance, I_k, was calculated as the ratio between ETR_m and α.

Parallel to the rapid-light curves, potential quantum yield ($F_m - F_o/F_m = F_v/F_m$) (where F_o is fluorescence in the dark when all reaction centres are open) was also assessed for both *Zostera noltii* types and for *Cymodocea nodosa* throughout the day. For this purpose, dark leaf-clips were used to dark-adapt portions of attached functional leaves. Leaves were left for 15 min (previously determined as being sufficient time for full oxidation of reaction centres) in the dark, after which a saturating-light pulse, identical to that used in the RLCs, was applied for determination of the potential quantum yield, expressed as F_v/F_m.

All results are presented as means ± SE. We used 1- or 2-way ANOVAs to test for the significant differences among variables ($\alpha = 0.05$) (Sokal & Rohlf 1981). Tukey's HSD test was used to establish significant differences between individual means.

RESULTS

The absorption factor (AF) determined for *Zostera noltii* (0.79 ± 0.02) was lower than the standard value pre-introduced in the PAM (0.84), whereas the AF of *Cymodocea nodosa* (0.88 ± 0.01) was higher. These values differed from each other and from the standard value and were therefore used to calculate the absolute electron-transport rates of the respective species. AF values for *Z. noltii* were identical along its vertical distribution in the intertidal.

The ambient photosynthetic active radiation reaching the 2 sampling sites followed a similar trend throughout the day, but with very different absolute values (Fig. 2). At the lower site, where both *Zostera noltii* and *Cymodocea nodosa* were sampled (Fig. 2b,c) PAR peaked at ca. 800 µmol m^{-2} s^{-1}, while at the upper site (Fig. 2a) it reached 1400 µmol m^{-2} s^{-1}. Considering the fact that low tide was around solar noon, the PAR measured at the lower site reached its highest possible value, which was almost half the irradiance measured at the upper site.

During the day, *Cymodocea nodosa* attained its highest maximum electron-transport rate, ETR$_m$ (69.9 ± 9.2 µmol e$^-$ m^{-2} s^{-1}), at solar noon (14:00 h) (Fig. 2c). At the same time, the upper-site *Zostera noltii* attained a similar value (68.9 ± 11.3 µmol e$^-$ m^{-2} s^{-1}; Fig. 2a). The ETR$_m$ of *Z. noltii* at the lower site was significantly lower (55.4 ± 11.6 µmol e$^-$ m^{-2} s^{-1}, Fig. 2b), and was attained earlier, at 10:30 h. No significant changes in ETR$_m$ were observed until solar noon.

The half-saturation irradiances (I_k) were always significantly higher for the upper site *Zostera noltii* than for plants from the lower site, more particularly from 12:00 to 16:00 h, the period of higher irradiance (Fig. 2). The I_k of *Cymodocea nodosa* remained below those of the 2 *Z. noltii* sites, except at 13:00 h, when it was significantly higher (278 µmol m^{-2} s^{-1}). From solar noon to the end of the day, I_k values for all plants decreased in parallel.

The initial slopes of *Zostera noltii* RLCs (α, Fig. 3) were always significantly higher at the lower site than at the upper site. In *Z. noltii* plants from both sites, α remained fairly constant throughout the day (Fig. 3a,b), in contrast to *Cymodocea nodosa*, the α of which showed a very strong oscillatory tendency: it peaked in the early morning, with significantly higher values than *Z. noltii*, and decreased markedly at solar noon (Fig. 3c).

There were no significant changes in lower *Zostera noltii* F_v/F_m throughout the day (Fig. 3b). At the upper site, 2 depressions were observed, 1 in the early morn-

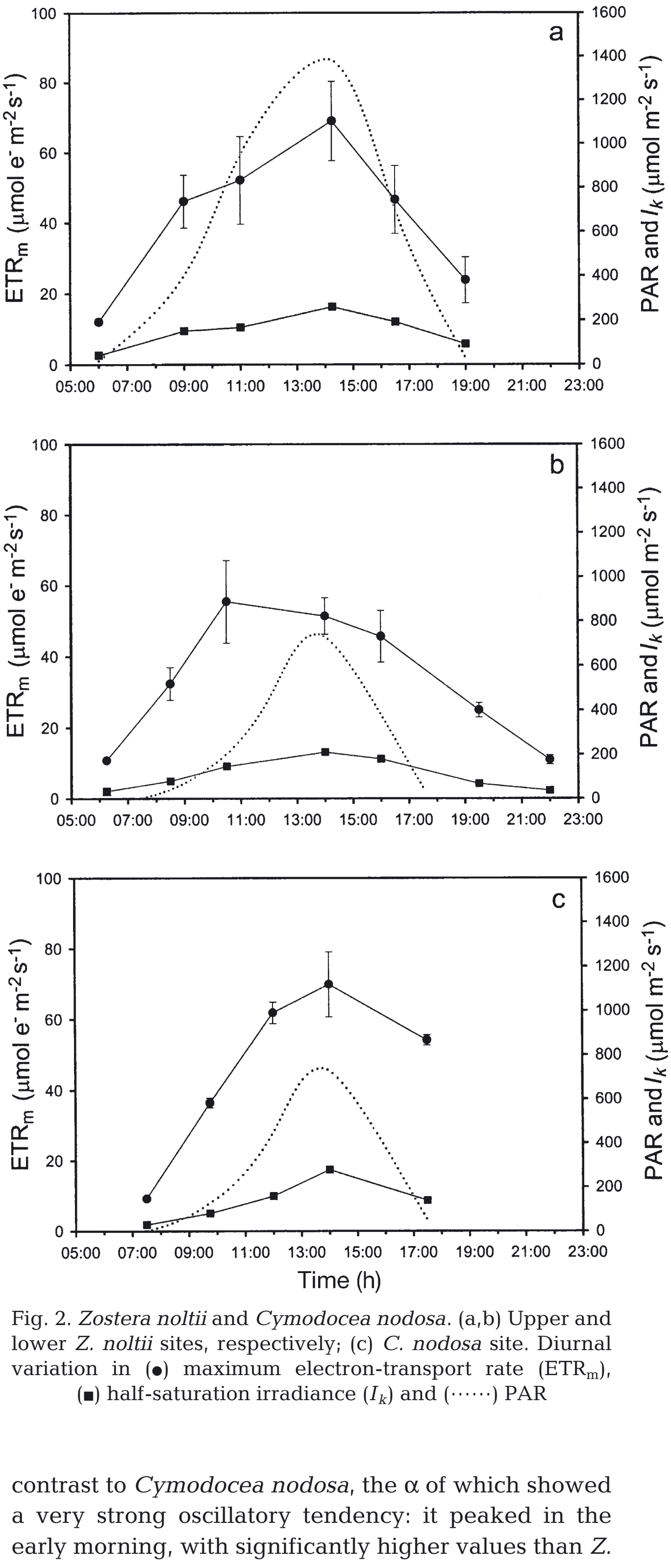

Fig. 2. *Zostera noltii* and *Cymodocea nodosa*. (a,b) Upper and lower *Z. noltii* sites, respectively; (c) *C. nodosa* site. Diurnal variation in (●) maximum electron-transport rate (ETR$_m$), (■) half-saturation irradiance (I_k) and (······) PAR

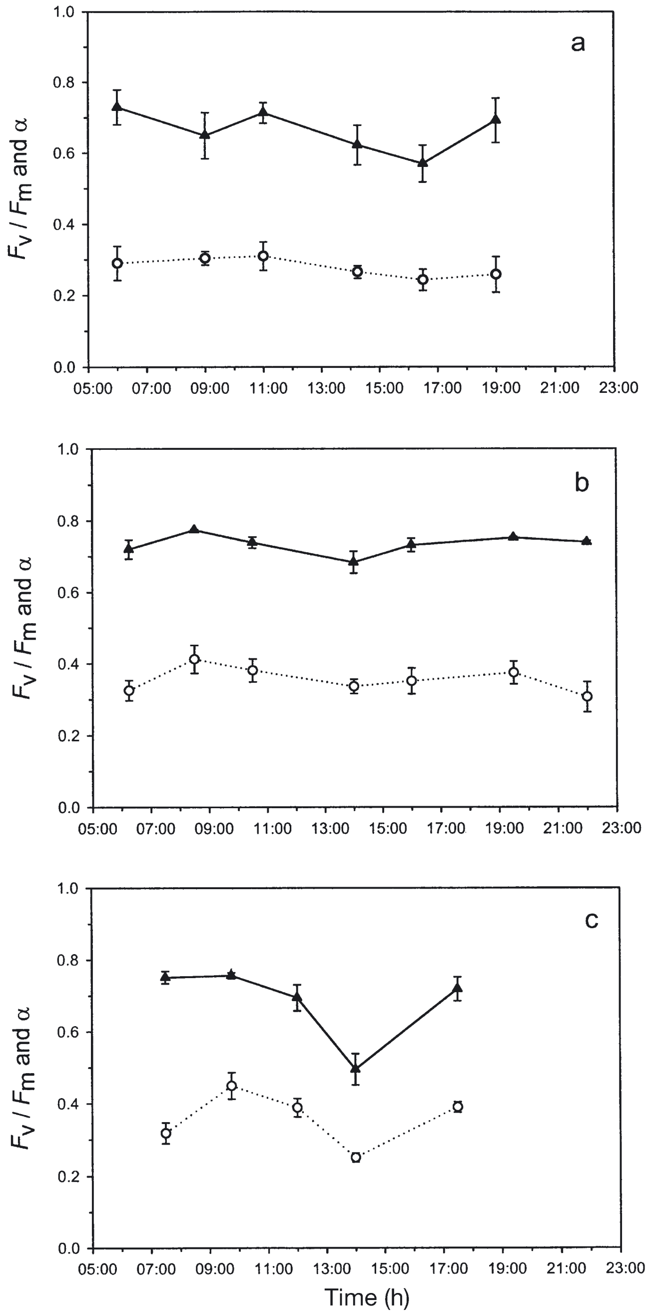

Fig. 3. *Zostera noltii* and *Cymodocea nodosa*. (a,b) Upper and lower *Z. noltii* sites, respectively; (c) *C. nodosa* site. Diurnal variation in (▲) optimum quantum yield (F_v/F_m) and (○) initial slope of rapid light curves (α)

ing and 1 in the early afternoon (Fig. 3a). In *Cymodocea nodosa*, F_v/F_m followed the same pattern as α, with a marked midday depression and full recovery towards the afternoon (Fig. 3c).

For identical PAR values, the electron-transport rates of *Cymodocea nodosa* were always significantly higher than those of both *Zostera noltii* samples (Fig. 4). Neither *Z. noltii* from the upper site nor *C. nodosa* showed any saturation tendency of ETR_m; on the contrary, there was a clear tendency of increasing ETR_m with increasing irradiance. The ETR_m of the lower *Z. noltii* appears to have saturated at a medium irradiance of about 500 µmol m^{-2} s^{-1}, decreasing thereafter (Fig. 4b).

The upper *Zostera noltii* plants were less efficient at low light than both the lower *Z. noltii* and *Cymodocea nodosa*, but α remained constant with increasing PAR (Fig. 4). Both the lower *Z. noltii* and *C. nodosa* were significantly more efficient in the use of low light. For these plants, the initial slope of the RLCs, α, peaked before 200 µmol m^{-2} s^{-1}, and decreased with increasing irradiance thereafter. At higher irradiances (750 µmol m^{-2} s^{-1}), the photosynthetic efficiency of the upper *Z. noltii* was about the same as that of both the lower *Z. noltii* and of *C. nodosa*.

DISCUSSION

The amount of light that can be absorbed by a leaf depends mostly on its pigment content (Beer et al. 2000). This implies that all environmental factors capable of influencing the pigment content of a plant are also responsible for changes in the absorption factor values. Such factors include geographical location, time of year, depth, leaf age and nutrient status. AF values in seagrasses are therefore expected to vary considerably, either interspecifically or even intraspecifically. One example of such variation is the difference between the AF value determined by Beer et al. (1998) for *Cymodocea nodosa* collected in the eastern Mediterranean (Israel) (0.72 ± 0.11) and the AF value measured in the present study (0.88 ± 0.01) for plants of the same species collected in south Portugal, which was higher than any published value for a seagrass species. In Ria Formosa, *C. nodosa* leaves are large, extremely thick, and highly pigmented (data not shown); this could explain its high optical density. The absorption factor determined for *Zostera noltii* (0.79 ± 0.02), although lower than the standard value, was identical to the highest published values for seagrasses, namely *Thalassia testudinum* (Durako & Kunzelman 2002).

Previously published AF values for seagrasses appear to have 2 common features: the considerable differences between them (from 0.44 in *Zostera marina* to 0.78 in *Thalassia testudinum*; Beer et al. 1998, Durako & Kunzelman 2002) and the fact that all of them are lower than the standard value of 0.84 originally reported for terrestrial plants. Determination of the leaf AF is thus essential for calculating absolute electron-transport rates, particularly when relating ETR to oxygen production. Although the latter aspect was not examined in the present work, we still believe

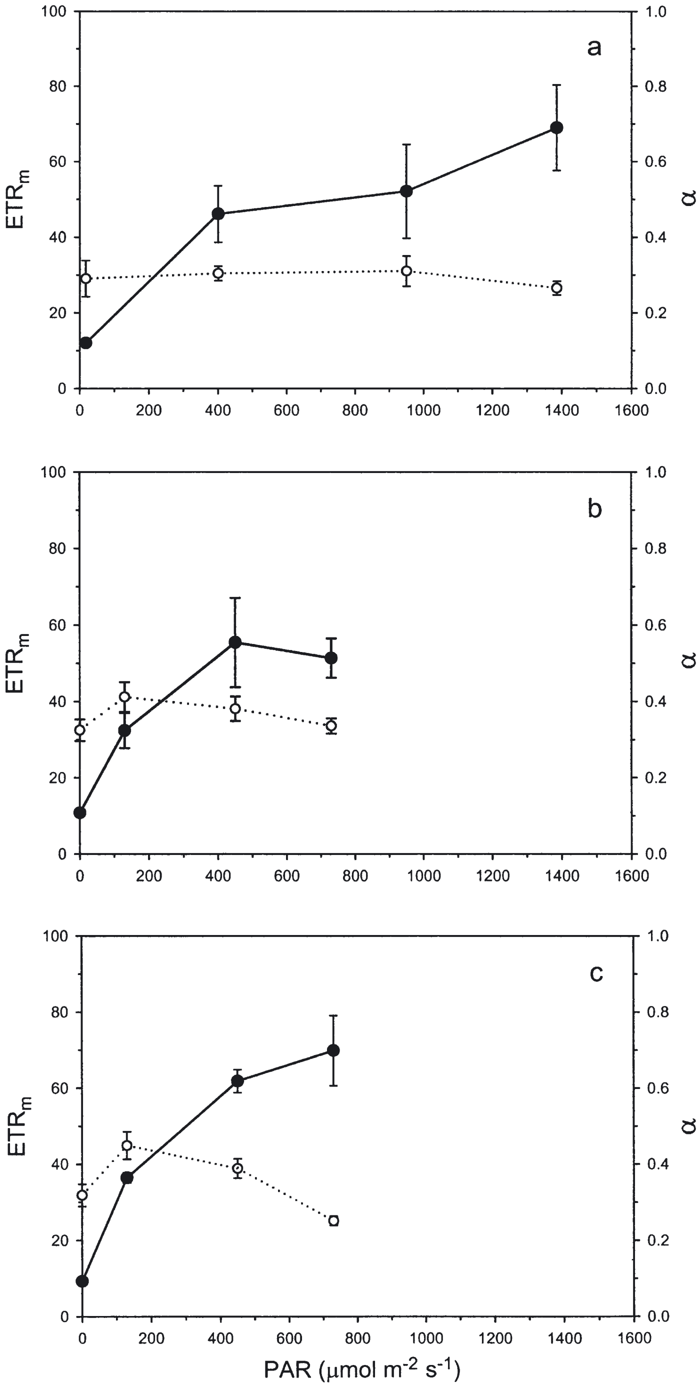

Fig. 4. *Zostera noltii* and *Cymodocea nodosa*. (a,b) Upper and lower *Z. noltii* sites, respectively; (c) *C. nodosa* site. Relationship between PAR and (●) maximum electron-transport rate (ETR_m) and (○) initial slope of rapid light curves (α)

it to be good practice to measure AF, since considerable differences are likely to be found and published values are rare.

Cymodocea nodosa presented typical shade-type plant responses, evidenced by the light-dependence of both photosynthetic efficiency and optimal quantum yield (Fig. 3c). These plants displayed a very efficient use of low light, and were very sensitive to higher irradiances. The relationship between the maximum electron-transport rate and irradiance (Fig. 4c) suggests that this species is strongly light-limited.

At the upper and lower edges of its vertical distribution, respectively, *Zostera noltii* clearly exhibited responses typical of sun- and shade-type plants during photosynthesis. Upper *Z. noltii* plants attained a significantly higher ETR_m (Fig. 2a,b), and the light-response curves saturated at higher irradiances than those of lower plants. This saturation resulted mainly from the consistently lower initial slopes of the curves, expressed by the α parameter, which in itself constitutes a useful indicator for distinguishing sun-adapted from shade-adapted plants (Henley 1993). The plot of ETR_m vs ambient PAR at different times of day in Fig. 4 represents a diurnal global light-response curve. It allowed an overall analysis of the reaction of the 2 *Z. noltii* types to increasing irradiance, and showed that the lower plants were more efficient in the use of limiting irradiance, whereas the upper plants responded better at higher PAR values. Similar intraspecific differences have been described previously for subtidal seagrass species growing at different depths (Schwarz et al. 2000) or acclimated to different irradiances (Major & Dunton 2002), but this is the first time that these differences have been described for an intertidal seagrass.

The fact that a particular *Zostera noltii* type growing in the upper intertidal displayed a sun-adapted response is not particularly interesting in itself. Interesting is the particular conditions to which *Z. noltii* adapted in Ria Formosa.

On a day in which low tide occurs at noon, plants are emersed for ca. 10 h, from 09:00 to 19:00 h, being exposed to direct sun light for the whole day. However, *Z. noltii* in the Ria Formosa intertidal never undergo severe desiccation because of the high density of their packed leaves, which retain water. In such conditions, *Z. noltii* is able to maintain some degree of photosynthetic carbon uptake through rapid diffusion of CO_2 from the air (Leuschner et al. 1998). Such carbon uptake depends on light-driven photosynthesis, which, in our study, occurred throughout the whole period near-air exposure. The photosynthetic yield of upper *Z. noltii* was significantly lower than that of low intertidal plants, indicating that despite adaptation to a high-light environment, the plants must dissipate some energy, channelling it through a non-photochemical quenching pathway, a process that appears to be common amongst seagrasses (Ralph et al. 1998). Our observations support the existence of such a process in *Z. noltii* that involves thermal dissipation of energy, and a consequent reduction in the fluorescence emission yield.

When high tide occurs at noon, plants receive the highest light intensities during the early morning hours and remain submersed for most of the day. Under these conditions, photosynthetic responses were similar to those when low tide occurred at noon (data not shown), indicating that their sun- and shade-adaptation is not related to time of the low tide, but to the vertical position of the plants.

Photosynthesis is usually measured by traditional methods such as gas-exchange techniques, but care must be taken as to the time of day at which samples are processed, as their recent light-exposure history has a significant effect on photosynthetic responses. Repeated measures of photosynthetic oxygen production are difficult to achieve over a diurnal cycle, particularly in underwater conditions. On the other hand, the chlorophyll fluorescence method provides information about light-driven reactions only, and therefore cannot be used as a stand-alone method for assessing absolute photosynthetic production, because processes such as photorespiration and changes in rates of dark respiration cannot be accounted for (Beer et al. 1998). Another important aspect is that the spectral composition of the fluorometer's halogen lamp differs from that of ambient light, and this can influence the ETR values through possible chromatic regulation, with consequent effects on charge separation at the PSII level (Kroon at al. 1993). On balance, weighting the constraints and the advantages, PAM fluorometry remains the choice method for field estimates of photosynthesis, especially in aquatic environments.

The vertical distribution of seagrasses on the intertidal is associated with a diversity of level-dependent environmental conditions that lead to pronounced differences in the plants' ecophysiology, even within the same species, as shown here for *Zostera noltii*. We propose that attempts to characterize the photosynthetic production of an intertidal meadow should consider both diurnal fluctuations in the plants' photosynthetic activity as well as their vertical distribution frequency. The need for considering diurnal changes in photosynthesis is evidenced by the fact that $\mathrm{ETR_m}$ (which in theory is directly correlated with gross photosynthesis) varies throughout the day within a range that is 3 to 4 times greater than its lowest value, which occurs at the onset of photosynthesis. In an intertidal system like Ria Formosa, for example, a productivity estimate based solely on $\mathrm{ETR_m}$ values obtained around noon would yield greatly overestimated results. Therefore, for productivity estimation purposes, daily integrals must be used to account for the dynamics of real-time adjustments in photosynthesis. A possible modelling approach would be to establish differentiated and vertically limited 'productivity bands' in intertidal meadows according to specific local conditions, and to calculate daily integrals of photosynthesis for each of those bands.

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