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Short communication

Leaf optical properties and photosynthetic leaf absorptances in several Australian seagrasses

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Abstract

This study investigated within- and among-species variability in the leaf optical properties of eight large-bodied seagrasses, *Posidonia australis*, *Posidonia sinuosa*, *Posidonia coriacea*, *Posidonia angustifolia*, *Amphibolis antarctica*, *Amphibolis griffithii*, *Zostera tasmanica*, and *Zostera capricorni* and the small-bodied *Halophila ovalis* from the east and west coasts of Australia.

Leaf spectral transmittance [$T_L(\lambda)$], reflectance [$R_L(\lambda)$], and non-photosynthetic absorptance [A_L(NP)] were measured in order to calculate leaf spectral absorptance [$A_L(\lambda)$] and photosynthetic leaf absorptance [A_L(PAR)]. Leaf spectra for the seagrasses were similar in shape, but variable in magnitude. Greatest among-species differences in leaf optical properties were present across green (500–600 nm) and near infrared (700–750 nm) wavelengths. This suggests differences in seagrass leaf optical properties are mainly due to variations in accessory pigments and leaf functional anatomy (e.g., internal structure, sclerenchyma fibers, etc.). Reflectance of photosynthetically active radiation (PAR) by leaves [$\%R_L$(PAR)] ranged from 4.6 to 9.3% with a mean of 6.1 ± 1.2%. A_L(NP) was more variable (16 ± 5%) than $\%R_L$(PAR) among species and sites. *P. coriacea*, a seagrass characteristic of high energy environments with the most structurally reinforced leaves, had the highest values of $\%R_L$(PAR) (9.3 ± 1.4%) and A_L(NP) (29 ± 8%). A_L(PAR) values ranged from 45 ± 3% for *H. ovalis* from a shallow (1 m) open coastal site in Western Australia to 68 ± 3% for *P. australis* from a deeper (3 m) protected site in New South Wales. The overall mean A_L(PAR) of 57 ± 6% for the seagrasses measured here is over 30% lower than the absorption factor of 84%, commonly used in PAM fluorometric studies of seagrasses. Because of the relatively low within-species variability in this parameter, A_L(PAR) was significantly higher for the eight large-bodied species (59 ± 6%) compared to the small-bodied *H. ovalis* (53 ± 5%). This limited survey of seagrass leaf optical characteristics indicates relatively low variability in light absorption across a wide range of leaf morphologies and environments consistent with previous suggestions of constraints on light absorption by aquatic plants.

Keywords: Seagrasses; Optical properties; Spectral absorptance; Absorption factor

1. Introduction

Recent advances in fluorescence instrumentation have allowed for rapid assessments of the photo-physiology of seagrasses (Beer et al., 2001). Pulse amplitude modulated (PAM) fluorometers provide measurements of effective- and maximal-photochemical quantum yield of photosystem II (Genty et al., 1989; Schreiber, 2004). However, calculation of absolute photosynthetic electron transport rates (ETR) from effective quantum yield ($\Delta F/F_{m'}$) requires accurate measurements of the flux of photosynthetically active radiation (PAR) at the leaf surface and the fraction of the PAR absorbed by the leaf (Beer et al., 1998, 2000, 2001; Beer and Björk, 2000; Schreiber, 2004). The fraction of incident PAR absorbed by a leaf is the photosynthetic leaf absorptance [A_L(PAR)], which depends on both the spectral transmittance and reflectance characteristics of the photosynthetic and non-photosynthetic tissue (Cummings and Zimmerman, 2003; Zimmerman, 2003; Runcie and Durako, 2004).

Until recently, measurements of seagrass photosynthesis using PAM fluorescence techniques have applied an absorption factor (AF) that is calculated based on the transmittance of PAR through leaves. This AF has no correction for non-photosynthetic tissue absorptance, nor does it account for leaf reflectance. Thus, only relative electron transport rates (rETR) can be estimated (Beer et al., 2001). Reported seagrass AF values range from 44 ± 2% S.D. for *Zostera marina* L., 50 ± 3% S.D. for *Halophila stipulacea*, 72 ± 11% S.D. for *Cymodocea nodosa* (Beer et al., 1998) to 84 ± 7% S.E. for *Thalassia testudinum* Banks ex König (Major and Dunton,

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2002); most are lower than the instrument (PAM fluorometer, Walz GmbH, Germany) default value of 84% which is a representative value of fraction of incident light absorbed by a leaf (i.e., accounts for spectral reflectance but not non-photosynthetic absorptance) for terrestrial plant leaves (Björkmann and Demmig, 1987; Knapp and Carter, 1998). Photosynthetic leaf absorptance [A_L(PAR)] has been measured in *Thalassia testudinum* (47%), *Zostera marina* (56%, Cummings and Zimmerman, 2003) and *Posidonia australis* (68 ± 3% S.D., Runcie and Durako, 2004). In the latter study, the application of A_L(PAR) instead of AF in the ETR calculations suggested that, at least in the case of *P. australis*, previous estimates of ETR were about 24% too high (assuming the PSII:PSI absorption ratio is unity).

Seagrasses photoacclimate to changing irradiance levels by varying pigment levels in their leaves (Dennison and Alberte, 1982; Abal et al., 1994; Major and Dunton, 2002). However, it has recently been shown that even with large differences in leaf chlorophyll concentrations and ambient light environments, leaf-specific photosynthetic absorptances and photosynthetic light harvesting efficiencies of *Zostera marina* and *Thalassia testudinum* were quite similar (Cummings and Zimmerman, 2003). This suggests limited variability in leaf optical characteristics within and among seagrass species due to a strong package effect, partially a result of chloroplasts being limited to the leaf epidermis in seagrasses (Cummings and Zimmerman, 2003; Enríquez, 2005). Despite their simple leaf anatomy, if non-photosynthetic tissue absorptance is included, the total leaf absorptances of *Z. marina*, *T. testudinum* and *P. australis* are very similar to the leaves of higher plants (≈84%, Cummings and Zimmerman, 2003; Runcie and Durako, 2004). The objective of this study was to further investigate within- and among-species variability of the measured leaf optical properties: spectral transmittance [$T_L(\lambda)$], reflectance [$R_L(\lambda)$], and non-photosynthetic absorptance [A_L(NP)] and the derived properties: leaf spectral absorptance [$A_L(\lambda)$] and photosynthetic leaf absorptance [A_L(PAR)] in a wider diversity of seagrasses from both the east and west coasts of Australia. Samples were collected of eight species of large-bodied seagrasses and the small-bodied *Halophila ovalis* at a variety of sites in order to gain insights into among-species and among-site optical plasticity.

2. Materials and methods

2.1. Sampling location and conditions

Seagrasses were collected from three sites in New South Wales (NSW) and six sites in Western Australia (WA), Australia between February and June 2004 (Table 1). At each site and depth, 10 separate short shoots of the large-bodied seagrasses (*P. australis*, *Posidonia sinuosa*, *Posidonia coriacea*, *Posidonia angustifolia*, *Amphibolis antarctica*, *Amphibolis griffithii*, *Zostera tasmanica*, and *Zostera capricorni*) or 10 rhizome fragments of *H. ovalis* were selected within an area of approximately 10 m radius. Individual short shoots or rhizome segments were placed in plastic bags and kept moist and in the dark until optical properties were measured (usually within 4 h). The middle of the rank 2 leaf of the large-bodied seagrasses or the middle of one of the leaves of the second leaf pair back from the rhizome apex for *H. ovalis* were sampled. Rank 2 leaves were chosen as they represent the youngest fully-developed leaves and have much lower surface fouling than higher rank leaves (Durako and Kunzelman, 2002; Drake et al., 2003).

2.2. Leaf optical properties

Leaf optical properties were measured as described by Runcie and Durako (2004). Before each measurement, epiphytes were removed by gently scraping the leaf surface with the edge of a glass slide. Leaves were gently patted with a paper towel to remove excess water before being placed in a lexan holder to keep the leaf fixed in position over the sample port of each of the integrating spheres. Leaf spectral transmittance [$T_L(\lambda)$] and reflectance [$R_L(\lambda)$] were measured from 350 to 750 nm at 2 nm resolution using a fiber-optic spectrometer (Ocean Optics USB2000) interfaced (50 μm diameter fiber) with a FOIS-1 [$T_L(\lambda)$] or ISP-REF [$R_L(\lambda)$] integrating sphere (Ocean Optics, USA).

For transmittance measurements, a collimated beam from a tungsten-halogen light source was adjusted to completely irradiate the single sample port (100% T). Leaf samples were then placed over the sample port and positioned to determine $T_L(\lambda)$. Spectral leaf reflectance [$R_L(\lambda)$] was calculated by dividing the portion of diffuse light reflected from a leaf sample by the diffuse light reflected from a >98% reflective polytetrafluoroethylene (PTFE) Lambertian reference surface (Labsphere OSRS-99-010, USA), placed consecutively over the single sample port of the ISP-REF integrating sphere. All spectra were corrected for electrical noise using dark spectra. Irradiance levels, optic-fiber diameters and spectral-integration times were optimized to attain a maximum signal of 3500 counts in scope mode. Leaf transmittance [T_L(PAR)] and reflectance [R_L(PAR)] of photosynthetically active radiation (PAR) were calculated as the spectral average of $T_L(\lambda)$ and $R_L(\lambda)$ from 400 to 700 nm.

A spectral photosynthetic absorption factor ($\mathrm{AF_{PAR}}$), which does not account for reflectance nor non-photosynthetic absorptance, was derived by converting T_L(PAR) to absorptance:

$$\mathrm{AF_{PAR}} = 1 - \left[\frac{T_L(\mathrm{PAR})}{100}\right]$$

Photosynthetic leaf absorptance [A_L(PAR)] was determined by converting transmittance to absorptance (see above), followed by corrections for leaf reflectance and non-photosynthetic absorptance at 720 or 750 nm [A_L(NP)] (Cummings and Zimmerman, 2003; Drake et al., 2003). Non-photosynthetic absorptance at 720 nm was used rather than $A_L(750)$ for the samples from NSW because the low irradiance output of the available halogen light source at $\lambda > 720$ nm resulted in a high noise-to-signal ratio.

$$A_L(\mathrm{NP}) = \left[1 - T_L\left(\frac{720}{750}\right)\right] - R_L\left(\frac{720}{750}\right)$$

$$A_L(\lambda) = [1 - T_L(\lambda)] - [R_L(\lambda)] - A_L(\mathrm{NP})$$

Table 1
Among-species variability in optical properties of seagrass leaves collected from New South Wales and Western Australia, Australia between February and June 2004

Genus	Species	Month	Site	Latitude, longitude	Depth (m)	A_L(PAR) (%)		AF$_{PAR}$ (%)		R_L(PAR) (%)		A_L(NP) (%)	
						MN	S.D.	MN	S.D.	MN	S.D.	MN	S.D.
Zostera	*capricorni*	February	Jervis Bay, NSW	35°05′S, 150°42′E	3	55	10	77	5	5.7	1.0	16	9
		February	Jervis Bay, NSW	35°05′S, 150°42′E	1	52	11	76	10	4.9	0.9	19	9
Zostera	*tasmanica*	February	Jervis Bay, NSW	35°05′S, 150°42′E	3	62	6	81	7	4.6	0.7	14	9
		April	Cottesloe, WA	31°58′S, 115°45′E	2	51	4	67	4	5.5	0.4	11	2
Posidonia	*australis*	February	Jervis Bay, NSW	35°05′S, 150°42′E	3	59	2	88	2	6.1	0.4	23	2
		February	Cresswell, NSW	35°07′S, 150°42′E	4	68	3	9	2	6.9	0.7	16	3
		April	Cockburn Sound, WA	32°11′S, 115°44′E	1.5	58	2	86	3	6.1	0.2	21	1
		April	Cockburn Sound, WA	32°11′S, 115°44′E	4	63	2	89	2	6.6	0.2	19	1
		June	Oyster Harbour, WA	35°00′S, 116°58′E	1.5	65	2	86	2	7.1	0.4	14	1
		June	Safety Harbour, WA	32°19′S, 115°42′E	1.5	67	1	91	1	7.4	0.4	16	2
		June	Shoalwater Bay, WA	32°18′S, 115°42′E	1.5	66	1	93	1	6.6	0.2	20	1
Posidonia	*sinuosa*	April	Cockburn Sound, WA	32°11′S, 115°44′E	6	54	2	80	4	8.0	1.2	18	4
		April	Cockburn Sound, WA	32°11′S, 115°44′E	10	57	3	83	3	6.7	0.4	19	3
		April	Cockburn Sound, WA	32°11′S, 115°44′E	1.5	64	4	8	3	4.6	0.8	10	4
		June	Safety Harbour, WA	32°19′S, 115°42′E	1.5	59	3	87	2	6.0	0.5	22	4
		June	Shoalwater Bay, WA	32°18′S, 115°42′E	1.5	63	3	89	2	5.8	0.6	20	2
Posidonia	*coriacea*	April	Cockburn Sound, WA	32°11′S, 115°44′E	4	54	5	92	3	9.3	1.4	29	8
Posidonia	*angustifolia*	June	Cockburn Sound, WA	32°11′S, 115°44′E	8	47	4	70	7	5.9	1.3	17	4
Amphibolis	*antarctica*	May	Cottesloe, WA	31°58′S, 115°45′E	2	49	3	75	5	5.2	1.2	21	4
		June	Safety Harbour, WA	32°19′S, 115°42′E	1.5	48	4	70	6	4.6	0.8	17	3
		June	Shoalwater Bay, WA	32°18′S, 115°42′E	1.5	53	5	72	5	3.5	1.6	15	4
Amphibolis	*griffithii*	June	Safety Harbour, WA	32°19′S, 115°42′E	1.5	57	2	82	4	5.8	0.2	20	3
		June	Shoalwater Bay, WA	32°18′S, 115°42′E	1.5	55	2	81	3	4.6	0.9	21	3
Halophila	*ovalis*	February	Jervis Bay, NSW	35°05′S, 150°42′E	4	52	3	67	4	6.8	0.7	9	3
		March	Little Manly, NSW	33°48′S, 151°17′E	1	56	3	69	4	5.6	0.9	7	4
		March	Little Manly, NSW	33°48′S, 151°17′E	3.5	62	5	71	4	5.4	0.8	6	2
		April	Swan River, WA	31°58′S, 115°49′E	0.5	51	4	76	3	6.6	1.1	18	5
		April	Cockburn Sound, WA	32°11′S, 115°44′E	1.5	55	2	74	3	6.9	0.4	12	2
		May	Cottesloe, WA	31°58′S, 115°45′E	1	45	3	64	2	6.9	0.6	11	2
		May	Cottesloe, WA	31°58′S, 115°45′E	4	50	5	69	6	7.1	0.7	12	2

Photosynthetic leaf absorptance [A_L(PAR)] was calculated as the spectral average of the corrected leaf-specific spectral absorptance values [$A_L(\lambda)$] from 400 to 700 nm.

2.3. Data analysis

The significance of variability in leaf optical properties among sites or species was determined using one-way analysis of variance. Normality was tested using the Kolmogorov–Smirnov test with Lilliefors' Correction. Homogeneity of variance was tested using the Levene Median test. Krukal–Wallis analyses of variance on ranks was used when the normality or homogeneity of variance tests failed. Significant factors were tested pairwise by Tukey's multiple comparison procedure or Dunn's multiple comparison procedure on parametric and non-parametric data, respectively. Tests were conducted using Sigma Stat (SPSS, Inc.). Significance for all tests was assessed at $p < 0.05$, and variance is expressed in terms of standard deviation (S.D.).

3. Results and discussion

Transmittance, reflectance and absorptance spectra for the seagrass leaves examined in this study were all similar in shape, but usually variable in magnitude (example spectra are shown in Figs. 1–3). Leaf spectra for the nine Australian seagrasses were typical of terrestrial vascular plants (Björkmann and Demmig, 1987; Knapp and Carter, 1998) and similar to those reported for *Zostera marina* and *Thalassia testudinum* (Cummings and Zimmerman, 2003; Enríquez, 2005). Leaf spectral absorptance [$A_L(\lambda)$] was highest [i.e., low $T_L(\lambda)$ and $R_L(\lambda)$] in the Soret Band (400–500 nm) and around the chlorophyll *a* peak of 660–680 nm. Almost 80% of incident irradiance was absorbed in these two spectral regions. The green wavelengths (500–600 nm) were the spectral region of PAR with the highest $T_L(\lambda)$ and $R_L(\lambda)$, resulting in the lowest $A_L(\lambda)$. In this region of the spectra only 20–50% of the incident irradiance is absorbed. However, green wavelengths are the region of PAR where the greatest among-species differences in leaf optical properties were present. This is particularly evident when comparing transmittance, reflectance and absorptance spectra for *P. australis* and *P. sinuosa* to those of *A. antarctica* and *A. griffithii* from Shoalwater Bay, WA (Fig. 2a and c). There is clear spectral separation, across the green wavelengths, between the two genera, with a lower degree of spectral separation between the two species within each genus. This suggests species-based differences in seagrass leaf optical

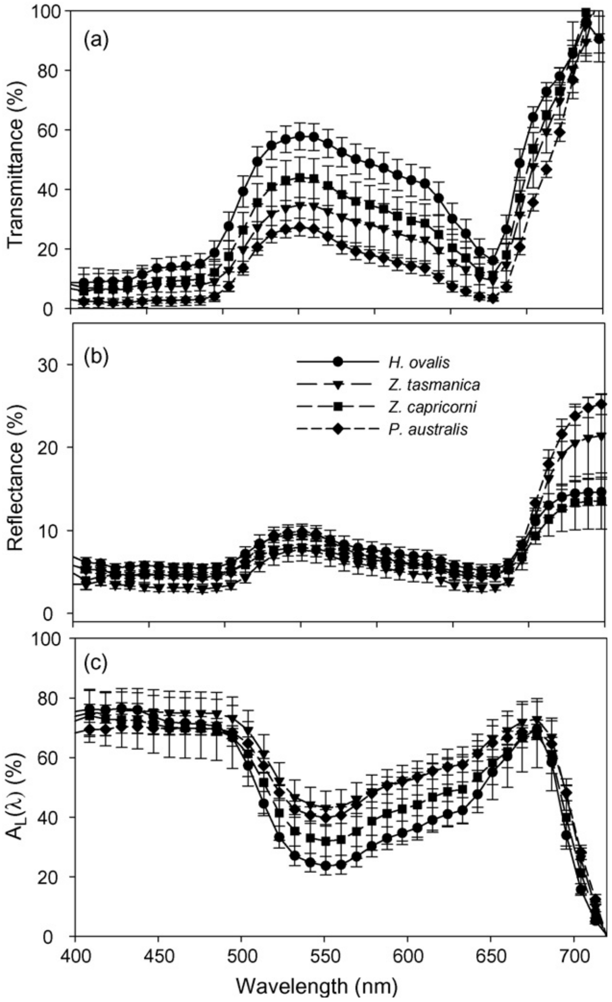

Fig. 1. Average (±standard deviation) leaf (a) spectral transmission, (b) reflectance, and (c) absorptance [$A_L(\lambda)$] for *Halophila ovalis*, *Zostera tasmanica*, *Z. capricorni*, and *Posidonia australis* collected from Jervis Bay, New South Wales, Australia.

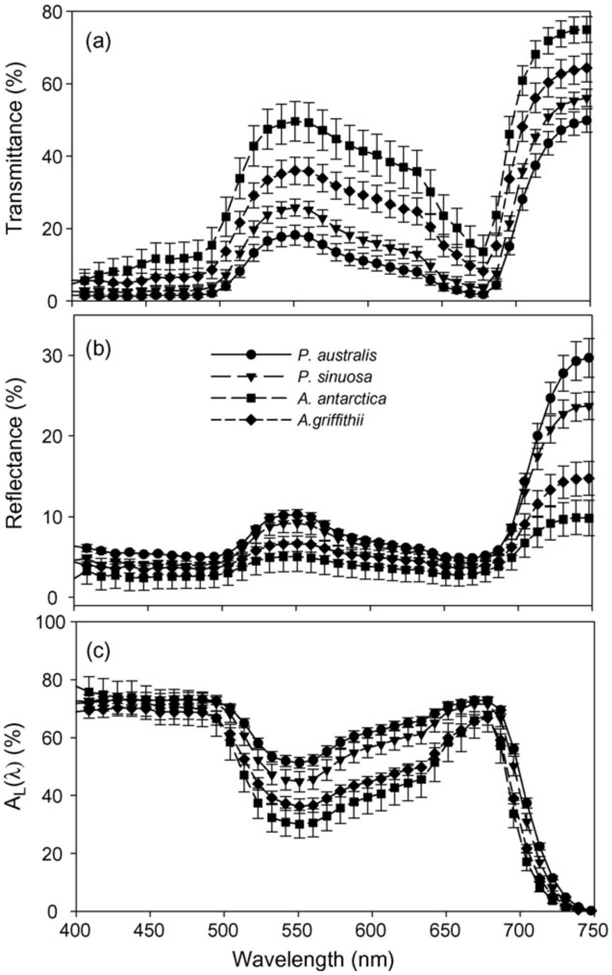

Fig. 2. Average (±standard deviation) leaf (a) spectral transmission, (b) reflectance, and (c) absorptance [$A_L(\lambda)$] for *Posidonia australis*, *P. sinuosa*, *Amphibolis antarctica*, and *A. griffithii* collected from Shoalwater Bay, Western Australia.

properties across PAR may be due to variations in accessory pigments (carotenoids, xanthophylls and anthocyanins, Fyfe, 2003; Thorhaug et al., 2006).

In contrast, large variations in chlorophyll contents in seagrass leaves result in relatively small variations in leaf absorptance (Enríquez et al., 1992, 1994; Cummings and Zimmerman, 2003; Enríquez, 2005). This phenomenon, which is evident in the convergence of leaf spectra among species and sites at 660–680 nm (Figs. 1–3), 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 thyllakoid layers (Kirk, 1994). The particularly strong package effect observed in seagrasses is largely attributed to restriction of chloroplasts to the leaf epidermis. Despite this constraint, seagrass leaves exhibit efficient and relatively uniform light-harvesting capabilities across varying depths and water quality (Cummings and Zimmerman, 2003; Enríquez, 2005). Intra-leaf variation in fluorescence characteristics and optical properties of seagrass leaves may be greater than variation due to depth and location, reflecting age-dependent changes in leaf thickness and pigment levels (Durako and Kunzelman, 2002; Enríquez, 2005). Thus, it is important to obtain absorptance measurements at the same position on the leaf as fluorescence measurements to more accurately estimate photosynthetic electron transport rates (Enríquez, 2005).

Fyfe (2003) reported the greatest differences in reflectance spectra among *Z. capricorni*, *P. australis*, and *H. ovalis* from southeastern NSW were also present across green wavelengths from 520 to 600 nm and in the near infra-red (NIR, 720–900 nm). In this regard, both transmittance and reflectance in the nine species examined here were highest and also highly variable among species at wavelengths >700 nm. As an example, *P. coriacea*, a species characteristic of high-energy environments (Cambridge, 1999), had the lowest transmittance and highest reflectance among four species of *Posidonia*, at NIR wavelengths (Fig. 3a and b). This may be an optical manifestation of having the lowest specific leaf area known for any Western Australian seagrass (7.2 $m^2\ kg^{-1}$, Cambridge and Lambers, 1998) and the presence of heavy sclerenchyma fiber reinforcement in its robust leaves (Cambridge, 1999).

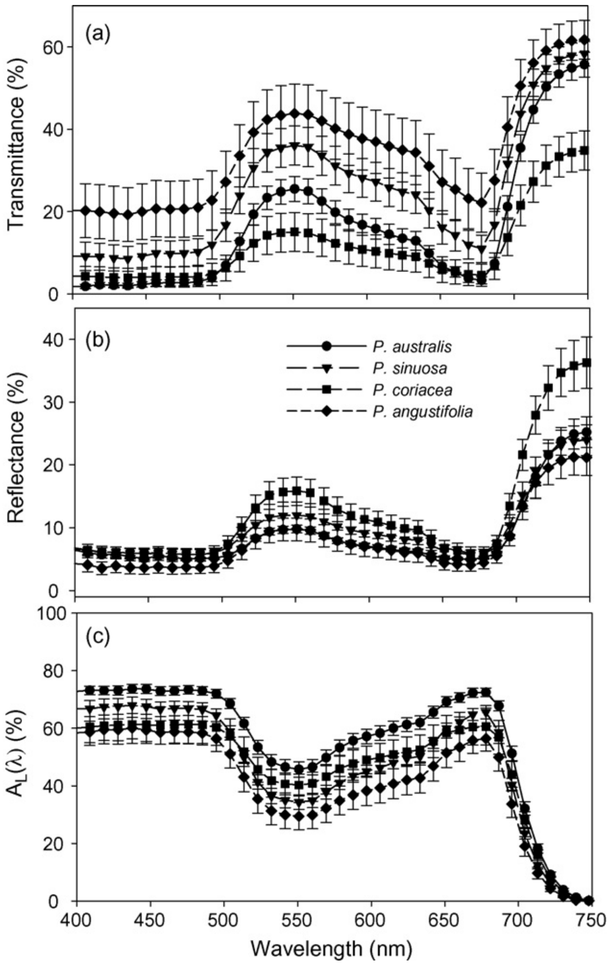

Fig. 3. Average (±standard deviation) leaf (a) spectral transmission, (b) reflectance, and (c) absorptance [$A_L(\lambda)$] for *Posidonia australis*, *P. sinuosa*, *P. coriacea*, and *P. angustifolia* collected from Cockburn Sound, Western Australia.

Several previous determinations of seagrass leaf AF have considered reflectance to be insignificant (Beer et al., 1998, 2001; Beer and Björk, 2000; Major and Dunton, 2002). For the nine species examined here reflectance of PAR by leaves [R_L(PAR)] ranged from 4.6 to 9.3%, which is almost identical to the range of 4–9% reported by Lüning and Dring (1985) for nine species of green, red and brown algae and similar to the PAR leaf reflectance of 5.5% for *Thalassia testudinum* (Enríquez, 2005). Although seagrass leaf R_L(PAR) was relatively low, with an overall mean of 6.1% (±1.2%) for the nine seagrasses, it exhibited almost twice the relative among-sample variability (±19.7%) compared to A_L(PAR) and $\mathrm{AF}_{\mathrm{PAR}}$ (Table 1). As stated above, *P. coriacea* from Cockburn Sound, WA had the highest R_L(PAR) (9.3 ± 1.4%). This is slightly higher than the R_L(PAR) value of 7.0 ± 1.0% reported for *P. australis* from a relatively protected site in Jervis Bay, NSW (Runcie and Durako, 2004). There was no other apparent species-specific pattern in R_L(PAR), with relatively low R_L(PAR) values (<5%) distributed across one or more of the sites in four of the other eight species.

Leaf non-photosynthetic absorptance [A_L(NP)] was even more variable (16 ± 5%) than R_L(PAR), exhibiting ± 31% variation among species and sites (Table 1). Not surprisingly, *P. coriacea*, the seagrass with the most structurally reinforced leaves (Cambridge, 1999), had the highest values (29 ± 8%) of A_L(NP), at the high end of the 24–29% range of non-photosynthetic absorptance recorded for the less structurally complex *Zostera marina* and *Thalassia testudinum* (Cummings and Zimmerman, 2003).

Calculated photosynthetic leaf absorptance [A_L(PAR)] values ranged from 45 ± 3% for the small-bodied *H. ovalis* from a shallow (1 m) open coastal site in Western Australia to 68 ± 3% for *P. australis* from a deeper (3 m) protected site in New South Wales (Table 1). All seagrass A_L(PAR) values were significantly lower than the Diving-PAM default ETR-factor value of 84%, representative of terrestrial plant leaves (Björkmann and Demmig, 1987). The overall mean A_L(PAR) for the seagrasses examined in this study was 57 ± 6%, indicating only ±10% variation around the mean in this parameter among nine species of seagrasses from a variety of sites along both the east and west coasts of Australia. Structural complexity did not correspond to higher absorptances as A_L(PAR) values for *P. coriacea* (54 ± 5%) were below the overall mean A_L(PAR) for the species examined here. Enríquez et al. (1994) examined light absorption by 90 species of macroalgae and 13 marine angiosperm species and reported that they absorbed an average of 59% of PAR, despite wide variations in thickness, chlorophyll *a* densities and chlorophyll-specific optical cross-sections. Cummings and Zimmerman (2003) indicated that *Zostera marina* and *Thalassia testudinum* leaves absorb 48–56% of PAR, across a wide variety of optical environments. Because of the relatively low within-species variability in this parameter, mean A_L(PAR) was significantly higher ($F_{1,215} = 39.9$, $p < 0.001$) for the eight large-bodied species (59 ± 6%) compared to the mean for the small-bodied *H. ovalis* (53 ± 5%), even though the difference was relatively small (≈10%).

There was also significant among-site variation in A_L(PAR) within most species that were collected at multiple sites. *H. ovalis* ($F_{6,64} = 17.6$, $p < 0.001$) exhibited highest values (62 ± 5%) of A_L(PAR) at the deeper (3.5 m) Little Manly Beach, NSW site and lowest values (45 ± 3%) at a shallow (1 m) Cottesloe Beach, WA site (Table 1). *Zostera tasmanica* also had higher A_L(PAR) values ($F_{1,18} = 20.2$, $p < 0.001$) at a deeper (3 m) Jervis Bay, NSW site (62 ± 6%) compared to the 2 m deep Cottesloe Beach, WA site (51 ± 4%). Likewise, A_L(PAR) for the large-bodied species *P. australis* exhibited significant among-site variation ($F_{6,61} = 22.0$, $p < 0.001$), with highest values observed at the deepest (4 m) Cresswell, NSW site (68 ± 3%) and lowest values at the shallow (1.5 m) Cockburn Sound site (58 ± 2%). Although there was again, significant among-site variation ($F_{4,44} = 16.5$, $p < 0.001$) in *P. sinuosa* A_L(PAR), highest values for this species were recorded for the relatively shallow (1.5 m) Cockburn Sound (64 ± 4%) and Shoalwater Bay, WA (63 ± 3%) sites with significantly lower A_L(PAR) values being observed for two deep (6 m, 54 ± 2% and 10 m, 57 ± 3%) Cockburn Sound sites. The A_L(PAR) values for these two deeper sites were not significantly different from each other nor to the shallow (1.5 m) Safety Harbour, WA site (59 ± 3%). *P. sinuosa* at the shallow Cockburn Sound and Shoalwater Bay sites also shared relatively low R_L(PAR) (Table 1). Neither *A. antarctica* ($F_{1,29} = 3.2$, $p = 0.56$) nor *A. griffithii* ($F_{1,18} = 1.6$, $p = 0.22$) exhibited significant among-site variation in A_L(PAR), however, A_L(PAR) was significantly different between these two species ($F_{1,48} = 21.6$, $p < 0.001$). Although *A. griffithii*, like *P. coriacea*, is also characteristic of high-energy areas, most of its structural reinforcement (and biomass) is allocated to its tough stems rather than possessing any changes to the functional anatomy (e.g., sclerenchyma fibers) of its leaves (Cambridge, 1999). Thus, no distinctive leaf optical characteristics, such as relatively high A_L(NP) were detected.

Estimates of the spectral absorption factor (AF_{PAR}), derived by simply subtracting the average leaf spectral transmittance from 400 to 700 nm from 1 (i.e., no correction for leaf reflectance or non-photosynthetic absorptance), were always higher than A_L(PAR), ranging from 64 ± 2% for *H. ovalis* from a shallow (1 m) open coastal site to 93 ± 1% for *P. australis* from a shallow (1.5 m) bay site, both in Western Australia (Table 1). These values are similar to previous AF estimates empirically derived by placing seagrass leaves over flat cosine PAR sensors (Beer and Björk, 2000; Major and Dunton, 2002), but which ignore reflectance and non-photosynthetic absorptance. The overall mean AF_{PAR} for all seagrasses examined in this study was 79 ± 8%, which is over 20% higher than A_L(PAR), but also exhibiting only ±10% variation among species and sites. As indicated by Runcie and Durako (2004), application of AF_{PAR} rather than A_L(PAR) in PAM-derived calculations of electron transport rate (ETR) will result in overestimations of 20–25%.

This limited survey of seagrass leaf optical characteristics indicates relatively low variability (±10%) in light absorption across a wide range of leaf morphologies and environments. As suggested by Cummings and Zimmerman (2003), despite structural restrictions and a strong package effect, seagrass leaves are relatively efficient light-capturing organs. Highest relative variability was observed in non-photosythetic absorptance, which averaged 10% for the small-bodied *H. ovalis* versus 18% for the eight large-bodied seagrasses. For researchers attempting to estimate photosynthetic rates using a PAM fluorometer, in vivo determinations of A_L(PAR) at the site of the fluorometer measurements will result in the most accurate determinations of ETR. However, for most practitioners application of a 6% reflectance correction and either a 10% (*Halophila*) or 18% (large-bodied seagrasses) correction for non-photosynthetic absorptance to AF measurements obtained by placing leaves over the cosine-corrected quantum sensor of the Diving-PAM will result in a significant improvement to ETR estimates versus current practices.

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References

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

Beer, S., Björk, M., 2000. Measuring rates of photosynthesis of two tropical seagrasses by pulse amplitude modulate (PAM) fluorometry. Aquat. Bot. 66, 69–76.

Beer, S., Vilenkin, B., Weil, A., Veste, M., Susel, L., Eshel, A., 1998. Measuring photosynthetic rates in seagrasses by pulse amplitude modulated (PAM) fluorometry. Mar. Ecol. Prog. Ser. 174, 293–300.

Beer, S., Larsson, C., Poryan, O., Axelsson, L., 2000. Photosynthetic rates of *Ulva* (Chlorophyta) measured by pulse amplitude modulated (PAM) fluorometry. Eur. J. Phycol. 35, 69–74.

Beer, S., Björk, M., Gademann, R., Ralph, P.J., 2001. Measurement of photosynthesis in seagrasses. In: Short, F.T., Coles, R. (Eds.), Global Seagrass Research Methods. Elsevier Publishers, The Netherlands, pp. 202–221.

Björkmann, O., Demmig, B., 1987. Photon yield of O_2-evolution and chloroplast fluorescence characteristics at 77 K among vascular plants of diverse origins. Planta 170, 489–504.

Cambridge, M.L., 1999. Growth strategies of Rottnest Island seagrasses. In: Walker, D.I., Wells, F.E. (Eds.), The Seagrass Flora and Fauna of Rottnest Island, Western Australia. Western Australian Museum, Perth, pp. 1–24.

Cambridge, M.L., Lambers, H., 1998. Specific leaf area and functional leaf anatomy in Western Australian seagrasses. In: Lambers, H., Poorter, H., Van Vuuren, M.M.I. (Eds.), Inherent Variation in Plant Growth. Physiological Mechanisms and Ecological Consequences. Backhuys Publisher, Leiden, The Netherlands, pp. 89–99.

Cummings, M.E., Zimmerman, R.C., 2003. Light harvesting and the package effect in the seagrasses *Thalassia testudinum* Bank ex König and *Zostera marina* L.: optical constraints on photoacclimation. Aquat. Bot. 75, 261–274.

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

Drake, L.A., Dobbs, F.C., Zimmerman, R.C., 2003. Effects of epiphyte load on optical properties and photosynthetic potential of the seagrasses *Thalassia testudinum* Bank ex König and *Zostera marina* L. Limnol. Oceanogr. 48 (1 part 2), 456–463.

Durako, M.J., Kunzelman, J.I., 2002. Photosynthetic characteristics of *Thalassia testudinum* Banks ex König measured *in situ* by pulse amplitude modulated (PAM) fluorometry: methodological and scale-based considerations. Aquat. Bot. 73, 173–185.

Enríquez, S., 2005. Light absorption efficiency and the package effect in the leaves of the seagrass *Thalassia testudinum*. Mar. Ecol. Prog. Ser. 289, 141–150.

Enríquez, S., Agustí, S., Duarte, C.M., 1992. Light absorption by seagrass *Posidonia oceanica* leaves. Mar. Ecol. Prog. Ser. 86, 201–204.

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

Fyfe, S.K., 2003. Spatial and temporal variation in spectral reflectance: are seagrass species spectrally distinct? Limnol. Oceanogr. 48 (1 Part 2), 464–479.

Genty, B., Briantias, J.M., Baker, N.R., 1989. The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. Biochim. Biophys. Acta 990, 87–92.

Kirk, J.T.O., 1994. Light & Photosynthesis in Aquatic Ecosystems. Cambridge University Press, Cambridge, UK.

Knapp, A.K., Carter, G.A., 1998. Variability in leaf optical properties among 26 species from a broad range of habitats. Am. J. Bot. 85 (7), 940–946.

Lüning, K., Dring, M.J., 1985. Action spectra amd spectral quantum yield of photosynthesis in marine macroalgae with thin and thick thalli. Mar. Biol. 87, 119–129.

Major, K.M., Dunton, K.H., 2002. Variations in light-harvesting characteristics of the seagrass *Thalassia testudinum*: evidence for photoacclimation. J. Exp. Mar. Biol. Ecol. 275, 173–189.

Runcie, J.W., Durako, M.J., 2004. Among-shoot variability and leaf-specific absorptance characteristics affect diel estimates of in situ electron transport of *Posidonia australis*. Aquat. Bot. 80, 200–209.

Schreiber, U., 2004. Pulse-amplitude (PAM) fluorometry and saturation pulse method. In: Papageorgiou, G., Govindjee, (Eds.), Chlorophyll Fluorescence: A Signature of Photosynthesis. Kluwer Academic Publishers, Dordrecht, pp. 279–319.

Thorhaug, A., Richardson, A.D., Berlyn, G.P., 2006. Spectral reflectance of *Thalassia testudinum* (Hydrocharitaceae) seagrass: low salinity effects. Am. J. Bot. 93 (1), 110–117.

Zimmerman, R.C., 2003. A bio-optical model of irradiance distribution and photosynthesis in seagrass canopies. Limnol. Oceanogr. 48 (1 Part 2), 568–585.