

# **Photosynthesis-Irradiance-Temperature relationships of four perennial meadow-forming seagrasses in Western Australia**

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# **Photosynthesis-Irradiance-Temperature relationships of four perennial meadow-forming seagrasses in Western Australia**

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## Abstract

To assist in formulating a model of seagrass growth, the photosynthesis-irradiance (P-I) relationships of *Posidonia sinuosa*, *Posidonia australis*, *Amphibolis griffithii* and *Amphibolis antarctica* were determined by oxygen flux measurements at a range of light intensities and water temperatures. Photosynthesis and respiration rates generally increased in response to increasing temperature within the range 13-23 °C and the observed trends suggest that the optimum temperature range for photosynthesis is between 18 °C and 23 °C for *P. sinuosa* and 23 °C or greater for the other species. The geographic distributions of the seagrass species studied here are generally consistent with their respective metabolic responses to water temperature. In general, the genus *Amphibolis* has higher maximum photosynthetic rates, and these are reached at lower light intensities, than *Posidonia*. Comparisons of the metabolic rates and critical light requirements of *P. sinuosa* between summer and winter suggest that ambient environmental conditions rather than seasonal changes in physiology are primarily responsible for the seasonal differences in growth rates that occur in the field. *P. sinuosa* plants growing near their natural lower depth limit are morphologically different and their maximum photosynthetic rates are reached at lower light intensities than plants growing in shallower water, but genotypic rather than phenotypic adaptation is suggested as the cause.

# 1. Introduction

Blooms of phytoplankton and epiphytic or unattached algae associated with high anthropogenic nutrient loadings have been implicated in the decline of seagrass meadows in some West Australian coastal waters (Cambridge and McComb, 1984; Mills, 1987; Simpson and Masini, 1990). The decreased water clarity or increased shading caused by these blooms are thought to have reduced photosynthetically available radiation (PAR) to below the seagrasses' requirements for survival (eg. Cambridge *et al.* 1986; Silberstein *et al.* 1986; Shepherd *et al.* 1989).

Information on the effects of PAR and temperature on the photosynthesis, respiration and light requirements of seagrasses generated in the present study of the dominant meadow-forming seagrasses in south Western Australia have been used to develop a model of seagrass growth (Masini and van Senden, 1995). This model is a central component of a nutrient-effects ecological model being built to aid in the future management of Perth's coastal waters (Simpson *et al.* 1993).

The effects of light on the photosynthesis of some of the temperate meadow-forming seagrasses in Western Australia have been determined previously; however the effect of temperature on photosynthesis has only been determined for *Posidonia sinuosa* Cambridge & Kuo (Masini *et al.* 1995), but its metabolic rates at different times of the year and across its geographic and depth ranges have not been studied.

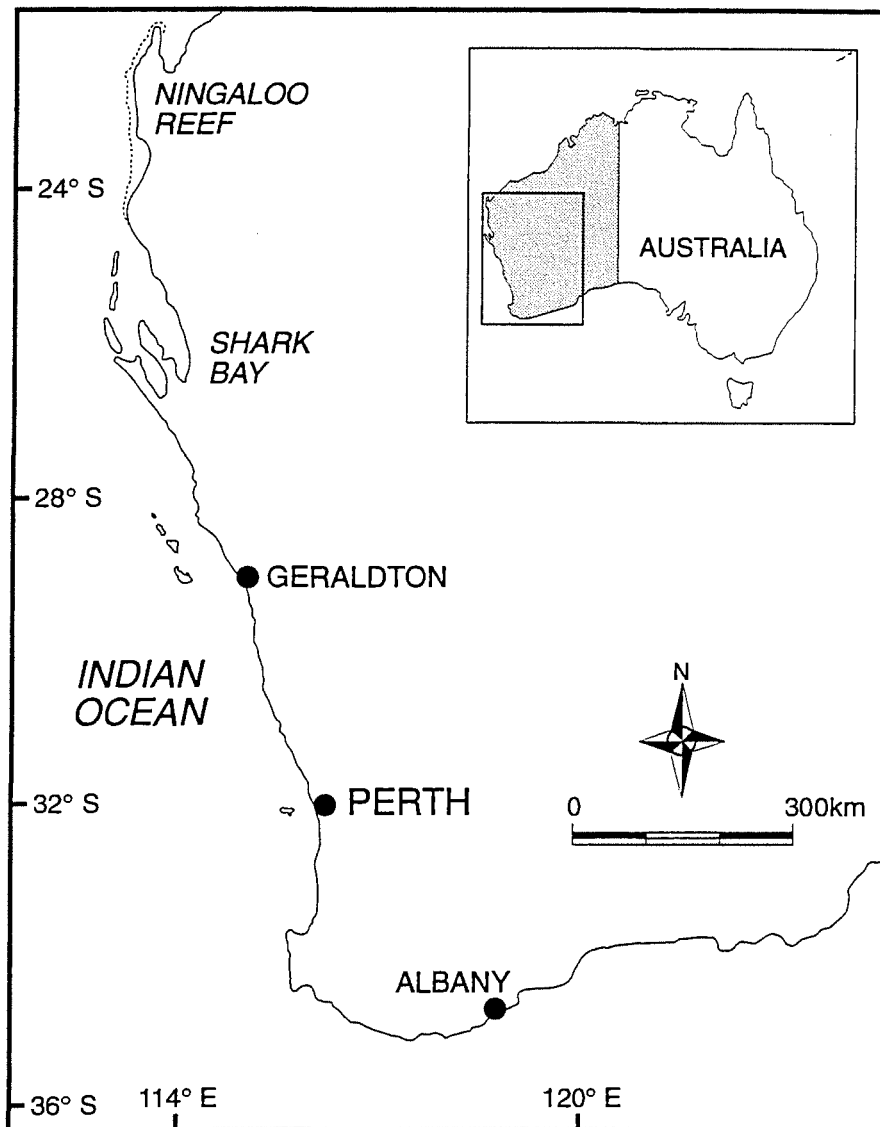
The principal aim of this study was to determine the effects of temperature on the irradiance requirements and metabolism of *Posidonia sinuosa*, *Posidonia australis* Hook.f., *Amphibolis griffithii* (Black) den Hartog and *Amphibolis antarctica* (Labill.) Sonders & Aschers. ex Aschers. A secondary aim was to compare the irradiance requirements and metabolic performance of the most common meadow-forming seagrass in south Western Australia, *Posidonia sinuosa*, during summer and winter; at Albany (~35 °S) and Perth (~32 °S), two disparate points in its geographic range; and from near the upper and lower ends of its natural depth range, under the same conditions of irradiance and temperature.

## 2. Materials and methods

### 2.1 Sampling, pre-treatment and photosynthesis — irradiance (P-I) measurement

Whole seagrass 'plants', consisting of an apical section of seagrass rhizome with leaves and roots attached, were collected from a range of water depths and locations near Perth, Western Australia (Figure 1). The plants were transported in seawater to the laboratory, transferred to an aerated bath and kept under conditions of low (approximately  $5 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) photosynthetic photon flux density (PPFD; 400-700 nm waveband), at the experimental temperature. Experiments were conducted within 4 days of collection and the photosynthetic response of replicate samples within each treatment was determined on the same day. Before determining the effects of temperature, the plants were allowed to equilibrate overnight to the experimental temperature.

Photosynthesis and dark respiration of the plants were estimated as the mean rate of change of dissolved oxygen concentration in a sealed incubation chamber (a 32 mm diameter clear acrylic tube from 510 to 640 mm long). Water was circulated within the chamber by a small submersible pump (Sicce, Italy) and a peristaltic pump (Cole-Parmer Inst. Co., Chicago Ill.) fitted with low gas-permeability Tygon (R3603) tubing. The combined flow rate was  $0.025 \text{ l s}^{-1}$ , resulting in a



**Figure 1. Locality map of south Western Australia.**

mean current of  $0.031 \text{ m s}^{-1}$  within the chamber. The peristaltic pump circulated water past a thermister (Radiospares 151-013) and a polarographic dissolved-oxygen sensor with low oxygen consumption and high-stability (model 8000, Leeds and Northrup, Millville, NJ). The sensors were connected through preamplifiers to high-resolution millivolt meters (Windrift Instruments, WA: Model 783) recording at 15 s intervals.

The light source consisted of eight 15 v 150 w quartz iodide projector lamps (Philips EFR A1/232) cooled with fans. An acrylic diffuser was placed between the lights and the chamber to provide a more uniform light field. The lamps were connected in series to a 10 amp variable voltage regulator (Voltac B-10, Yokoyama Electric Works, Ltd, Japan) which allowed PPFD to be varied from 0 to above  $2000 \mu\text{mol m}^{-2} \text{ s}^{-1}$ .

Constant temperature ( $\pm 0.25 \text{ }^\circ\text{C}$ ) was maintained by submersing the incubation chamber in a 190 litre temperature-controlled bath containing filtered ( $5 \mu\text{m}$  pore size) seawater from the sampling location.

These determinations and the calculations of critical light intensities (the compensating irradiance and point of onset of light saturation) followed the methods of Masini *et al.* (1995), to allow direct comparison with their data.



The photosynthesis versus irradiance (P-I) responses of *Posidonia sinuosa*, *P. australis*, *Amphibolis antarctica* and *A. griffithii* at a range of photosynthetic photon flux densities (PPFD, 400 to 700 nm waveband) were determined at water temperatures of 13, 18 and 23 °C. The P-I response of *P. sinuosa* plants collected from low-light environments (their local depth limits) and from shallow, high-light environments were compared to test for photoadaptation. Photosynthetic parameters and the chlorophyll *a* concentrations of leaves of *P. sinuosa* collected in different seasons and from geographically distinct areas were compared.

Photosynthetic rates were normalised to weight (g) of leaves and respiration rates to the whole plant, after drying at 70 °C for 24 h. Subsamples of each leaf were taken prior to drying, ground in 90 per cent (v/v) acetone and analysed spectrophotometrically for chlorophyll *a* content by the trichromatic method of Strickland and Parsons (1972).

## 2.2 *P. sinuosa*

The effects of season, latitude and depth of collection on the P-I relationship of *P. sinuosa* were assessed by comparing aspects of metabolic performance and critical irradiances determined over a standard range of PPFDs at 18 °C. Chlorophyll *a* concentrations of the leaves were also measured and compared, and comparisons of photosynthetic rates were made on data normalised to dry weight of leaf material and to chlorophyll *a* concentration. Respiration rates were normalised to total dry weight.

## 2.3 Statistical treatment

The effects of season, depth and latitude at which *P. sinuosa* was collected were determined by the non-parametric test of Mann-Whitney. Between-species comparisons of the measured parameters at 13, 18 and 23 °C were initially made with the non-parametric test of Kruskal-Wallis. If differences were apparent, the level of significance of the differences between species was determined by a Least Significant Difference test.

The significance of temperature on photosynthesis, respiration and critical light intensities was determined by a 1-tailed paired t-test. Data from Masini *et al.* (1995) on the effects of temperature on the P-I response of *P. sinuosa* were not significantly different to equivalent data collected in this study (see Figure 2), so were included to increase statistical power. Probabilities of less than or equal to 0.05 were taken to be significant. Unless otherwise stated, the measure of deviation of measurements about the mean is given as one standard error of the mean.

# 3. Results

## 3.1 Effects of temperature on photosynthesis

The combined P-I relationships of *P. sinuosa* collected from Albany and Perth are shown in Figure 2 for three water temperatures. The similarity of these relationships, and the curvilinear nature of the initial part of the P-I curve were apparent at all three temperatures (Figure 2a). The curves in Figure 2b highlight the general effect of temperature on the P-I response of *P. sinuosa* and in particular the more rapid onset of light saturation, but lower maximum net photosynthetic rate achieved at 13 °C compared to the higher temperatures.

While the shapes of the P-I curves of all four of the seagrass species were similar to those of *P. sinuosa* shown in Figure 2, the metabolic rates and responses to temperature of the species varied

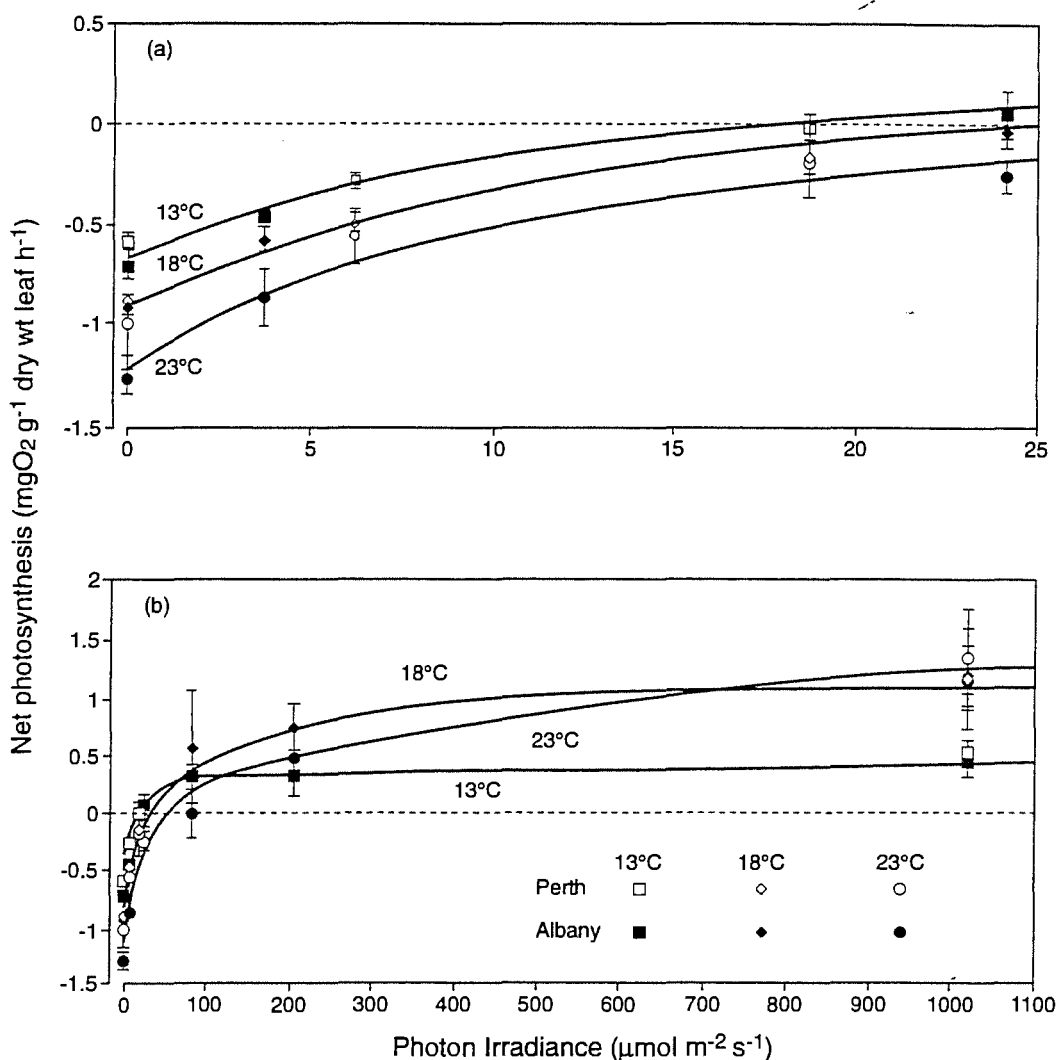


Figure 2. Net photosynthesis versus irradiance relationships at three water temperatures for *Posidonia sinuosa*, collected from Perth and Albany. (a) between 0 and 25  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , (b) between 0 and 1100  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . Error bars are  $\pm 1$  standard error of the mean, n=4. Albany data from Masini *et al.* (1995). Curves fitted by eye.

considerably. These temperature effects on photosynthesis and respiration and on the compensating and saturating irradiances of the four seagrass species are presented graphically in Figure 3. The results of statistical analyses of the effect of temperature on these parameters for each species are summarised in Table 1.

### 3.2 Compensating and saturating irradiances

There was a general tendency for the point of onset of light saturation ( $I_k$ ), and to a lesser extent for the compensating irradiance ( $I_c$ ), to increase with increasing water temperature over the range 13 °C to 23 °C (Figure 3a,b; Table 1). The  $I_c$  of *P. sinuosa* increased significantly with each 5 °C change in incubation temperature between 13 °C and 23 °C; the effect was less pronounced in the two *Amphibolis* species; and was not significant for *P. australis*. The  $I_k$  of all species except *A. antarctica* was significantly higher at 18 °C and 23 °C than at 13 °C. A significant increase in  $I_k$  between 18 °C and 23 °C was found in only the two *Amphibolis* species.

Table 1. Summary table showing results of statistical analysis (paired 1-tailed t-tests) of the effect of temperature on the compensating irradiance ( $I_c$ ), the point of onset of light saturation ( $I_k$ ), maximum gross photosynthetic rate ( $GP_{max}$ ), respiration rate (Resp.) and maximum net photosynthetic rate ( $P_{max}$ ) of four species of seagrass. Data are shown in Figure 3. 13,18 = 13 °C cf. 18 °C; 13,23= 13 °C cf. 23 °C; 18,23= 18 °C cf. 23 °C.

Species	$I_c$			$I_k$			$GP_{max}$			Resp.			$P_{max}$			n
	13,18	13,23	18,23	13,18	13,23	18,23	13,18	13,23	18,23	13,18	13,23	18,23	13,18	13,23	18,23	
<i>Posidonia sinuosa</i>	*	***	*	***	***	—	***	***	—	***	***	***	***	***	—	8
<i>P. australis</i>	—	—	—	*	*	—	***	***	***	—	*	—	*	***	*	4
<i>Amphibolis griffithii</i>	**	—	—	***	***	***	***	**	*	*	*	*	*	***	*	4
<i>A. antarctica</i>	—	—	**	—	—	*	*	*	*	*	***	**	—	—	—	4

**Key:**

- \* .01<P≤.05
- \*\* .005<P≤.01
- \*\*\* P≤.005
- not significantly different

### 3.3 Photosynthesis and respiration

The maximum gross photosynthetic rate ( $GP_{max}$ ), respiration rate (Resp.) and maximum net photosynthetic rate ( $P_{max}$ ) tended to increase with temperature over the range 13 °C to 23 °C (Figure 3,c-e;Table 1). The  $GP_{max}$  at 18 °C and at 23 °C was significantly higher than at 13 °C for all species, and similarly,  $GP_{max}$  was higher at 23 °C than at 18 °C for all species except *P. sinuosa*. The respiration rate of all species at 23 °C was almost double that at 13 °C. Respiration rates of all species except *P. australis*, increased in response to each 5 °C increase in incubation temperature. The  $P_{max}$  of *P. australis* and *A. griffithii* increased significantly over the temperature range tested but with *A. antarctica* it did not change. The  $P_{max}$  of *P. sinuosa* increased significantly between 13 °C and 18 °C, but not between 18 °C and 23 °C.

### 3.4 Between species comparisons

$I_c$  and  $I_k$ : Inter-specific variability in mean  $I_c$  was less than 9  $\mu\text{mol m}^{-2} \text{s}^{-1}$  at any of the experimental water temperatures (Figure 3a). At 13 °C the  $I_c$  of the four species did not differ significantly (Figure 3a). At 18 °C the  $I_c$  of *P. sinuosa* was significantly higher than that of the other species, whereas at 23 °C the  $I_c$  of *P. sinuosa* was higher than that of *A. griffithii* only.

The  $I_k$  of *A. griffithii* was lower than the  $I_k$  of the other species at 13 °C. The greatest range in  $I_k$  of the four species occurred at 18 °C (Figure 3b), at which temperature the  $I_k$  of *P. sinuosa* was higher than the  $I_k$  of the other species. In addition, the  $I_k$  of *P. australis* was higher than the  $I_k$ 's of the two *Amphibolis* species, which were not significantly different from each other. There were no significant differences in the  $I_k$  of the four species at 23 °C.

When the  $I_c$  data were pooled at the genus level, there was no significant difference between genera at any temperature. In contrast, the  $I_k$ 's ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) of *Posidonia* at 13 °C (36.1, se=1.5, n=12) and at 18 °C (51.1, se=2.2, n=12) were higher than those for *Amphibolis* at 13 °C (28.4, se=1.9, n=8) and at 18 °C (33.3, se=0.8, n=8) respectively.

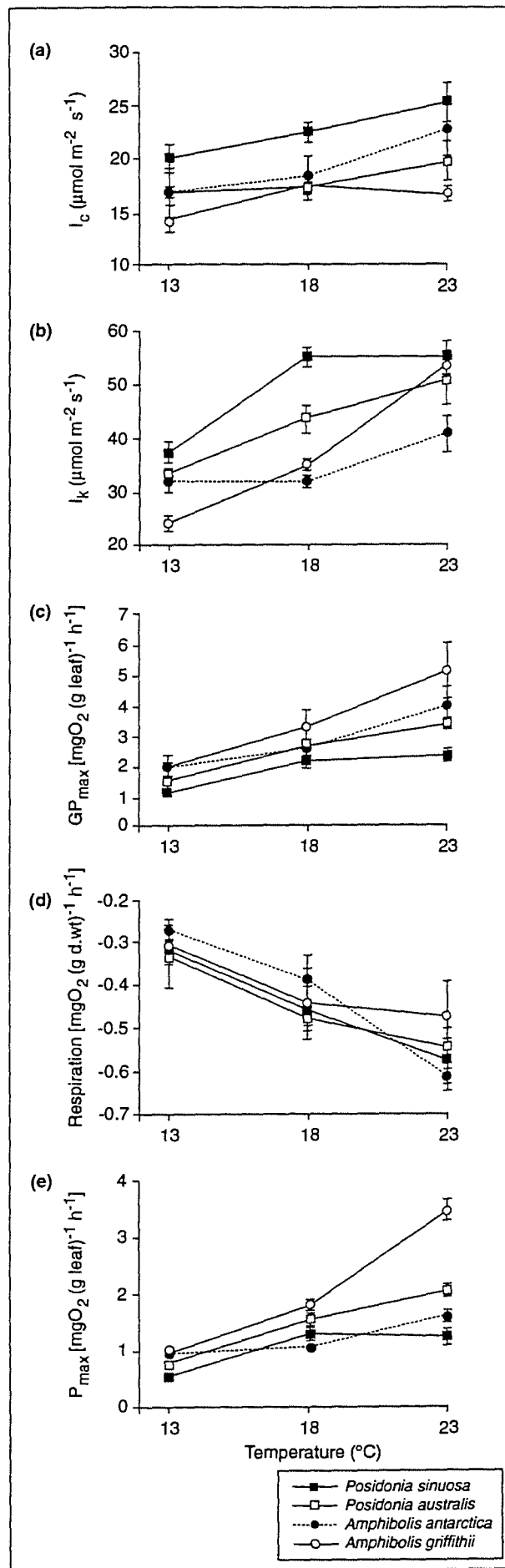


Figure 3. The effects of temperature on aspects of the photosynthesis and metabolism of *Posidonia sinuosa*, *Posidonia australis*, *Amphibolis antarctica* and *Amphibolis griffithii*. (a) compensating light intensity,  $I_c$  (b) onset of light saturation,  $I_k$  (c) maximum gross photosynthetic rate,  $GP_{max}$  (d) respiration rate, and (e) maximum net photosynthetic rate,  $P_{max}$ .

Photosynthesis and respiration: The  $GP_{max}$  of the *Amphibolis* species at 13 °C and at 23 °C were higher than those of *P. sinuosa* at the same temperatures (Figure 3c). At 13 °C the  $P_{max}$  of *A. griffithii* was higher than that of *P. sinuosa* only (Figure 3e), while at 23 °C the  $P_{max}$  of *A. griffithii* was higher than the  $P_{max}$  of the other species. There were no significant differences between species in Resp. at any of the water temperatures used in these experiments (Figure 3d).

When the data were pooled at the genus level, the  $GP_{max}$  ( $mgO_2 g leaf^{-1} h^{-1}$ ) of the two genera were not different at 13 °C, but at 18 °C the  $GP_{max}$  of *Amphibolis* (2.98,  $se=0.29$ ,  $n=8$ ) was significantly greater than that of *Posidonia* (2.39,  $se=0.16$ ,  $n=12$ ). At 23 °C the  $GP_{max}$  of *Amphibolis* (4.81,  $se=0.51$ ,  $n=8$ ) was approximately 1.7 times higher than that of *Posidonia* (2.79,  $se=0.20$ ,  $n=12$ ). There were no significant differences in the respiration rates of the two genera over the temperature range examined. The  $P_{max}$  ( $mgO_2 g leaf^{-1} h^{-1}$ ) of *Amphibolis* at 13 °C (0.96,  $se=0.10$ ,  $n=8$ ) and at 23 °C (2.78,  $se=0.47$ ,  $n=8$ ) was higher than that of *Posidonia* at 13 °C (0.64,  $se=0.08$ ,  $n=12$ ) and 23 °C (1.58,  $se=0.16$ ,  $n=12$ ).

alpha ( $\alpha$ ): The value  $\alpha$  (the slope of the initial part of the P-I curve) of *Amphibolis* was significantly higher (more than double) than the  $\alpha$  value for *Posidonia* at each temperature (Table 2). The value  $\alpha$  was significantly higher at 23 °C than at 13 °C in both genera and was also higher at 18 °C than at 13 °C for *Amphibolis*.

**Table 2. Initial slope ( $\alpha$ ) of the photosynthesis versus irradiance curve for two seagrass genera at three water temperatures. Mean and standard error (in parentheses) are shown.**

Genus	$\alpha$ ( $\mu gO_2 \mu g chl a^{-1} h^{-1}$ ) ( $\mu mol m^{-2} s^{-1}$ ) <sup>-1</sup>			n
	13 °C	18 °C	23 °C	
<i>Posidonia</i> *	0.015(.002)	0.022(.005)	0.024(.004)	12
<i>Amphibolis</i>	0.039(.006)	0.050(.007)	0.054(.005)	8

\* includes data from Masini *et al.* (1995).

### 3.5 *P. sinuosa*

Season: The effect of season on the P-I response of *P. sinuosa* was assessed by comparing the P-I response of plants collected during summer and winter from one site at Perth. Photosynthesis, respiration and critical light intensities tended to be higher in winter than in summer, but these differences were only significant for  $GP_{max}$  expressed on a leaf dry weight basis (Table 3). The chlorophyll *a* concentration of leaves was higher in winter than in summer, but there were no differences in photosynthesis and respiration rates between seasons when the data were normalised for chlorophyll *a* concentration.

Latitude: The P-I responses of *P. sinuosa* from geographically isolated populations were assessed by comparing data from Albany, which is close to its southern geographical limit in Western Australia (~35 °S; Masini *et al.* 1995), with data from Perth (~32 °S; this study), which is at about the midpoint of its geographical range (Larkum and den Hartog, 1989). Only data from plants collected during summer were used for this comparison. All parameters except Resp. and chlorophyll *a* concentration of the leaves were higher in plants collected from Albany than from Perth (Table 3). The trends in  $GP_{max}$  and  $P_{max}$  were consistent when data were normalised to leaf area and to chlorophyll *a* content.

**Depth adaptation:** The extent of depth adaptation in *P. sinuosa* was assessed by comparing the P-I response of plants from near the bottom of their natural depth range at Perth (12 and 15 m) with plants from shallow water (4 m), where lack of light would not be a limiting factor. Only data from plants collected from Perth during winter were used in this comparison. Plants collected from near their depth limits had a significantly lower  $I_k$  (Table 3) and higher  $\alpha$  ( $0.020 \pm 0.003$  ( $\mu\text{gO}_2 \mu\text{g chl } a^{-1} \text{ h}^{-1}$ )( $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ) $^{-1}$ ) than plants growing in shallow water ( $0.009 \pm 0.001$ ). The average leaf width (mm) of *P. sinuosa* from deep water ( $5.8 \pm 0.23$ ,  $n=8$ ) was less than from shallow water ( $6.7 \pm 0.20$ ,  $n=7$ ), and in addition, the specific leaf area (SLA,  $\text{cm}^2 \text{ mg leaf biomass}^{-1}$ ) of the deep-water plants ( $0.47 \pm 0.02$ ) was significantly greater than the SLA of the shallow-water plants ( $0.31 \pm 0.02$ ). However, when  $\text{GP}_{\text{max}}$  was normalised to leaf area ( $\text{mgO}_2 \text{ cm}^{-2} \text{ h}^{-1}$ ), the  $\text{GP}_{\text{max}}$  of the shallow-water plants ( $6.44 \pm 0.54$ ) was not significantly different to that of the deep-water plants ( $5.81 \pm 0.64$ ). On the other hand,  $P_{\text{max}}$  was significantly higher in the shallow-water plants when normalised to leaf area. There were no significant effects of depth of collection on  $\text{GP}_{\text{max}}$  or  $P_{\text{max}}$  when normalised to dry weight of leaves (Table 3). Although there were no significant differences in chlorophyll *a* concentrations of the leaves of deep- and shallow-water plants (Table 3), the chlorophyll *a* normalised  $\text{GP}_{\text{max}}$  ( $\mu\text{g O}_2 \mu\text{g chl } a^{-1} \text{ h}^{-1}$ ) of the deep-water plants ( $0.71 \pm 0.08$ ) was significantly higher than that of the shallow-water plants ( $0.46 \pm 0.08$ ).

**Table 3. Compensating irradiance ( $I_c$ ), onset of light saturation ( $I_k$ ), the maximum gross photosynthetic rate ( $\text{GP}_{\text{max}}$ ), the net photosynthetic rate ( $P_{\text{max}}$ ) and respiration rate (Resp.) of *Posidonia sinuosa* at 18 °C, collected from Perth and Albany. Dry weight of the component parts, leaf area and chlorophyll *a* concentrations, and details of depth and season of collection are provided. Mean and standard error (in parentheses) and results of statistical analysis (Mann-Whitney) are also shown.**

Sample category	$I_c$	$I_k$	$\text{GP}_{\text{max}}$	$P_{\text{max}}$	Respiration	Dry weight (g)		Leaf area <sup>^</sup>	Leaf chlorophyll <i>a</i> conc.	Season	Depth	n
	( $\mu\text{mol m}^{-2} \text{ s}^{-1}$ )		( $\text{mgO}_2 \text{ g leaf}^{-1} \text{ h}^{-1}$ )		( $\text{mgO}_2 \text{ g}^{-1} \text{ h}^{-1}$ )	leaves	rhizome & roots	( $\text{cm}^2$ )	( $\text{mg g}^{-1}$ )		(m)	
summer (Perth)	17.4 (0.6)	40.7 (2.4)	1.20 (0.10)	0.60 (0.11)	-0.36 (0.04)	0.61 (0.06)	0.26 (0.04)	203.8 (19.5)	3.32 (0.26)	summer	4	4
winter (shallow)	22.3 (2.0)	50.4 (4.4)	2.01* (0.26)	1.12 (0.21)	-0.49 (0.06)	0.41 (0.08)	0.32 (0.05)	137.3 (33.0)	4.56* (0.23)	winter	4	7
deep	19.0 (0.5)	39.1* (2.7)	2.74 (0.35)	1.28 (0.09)	-0.57 (0.06)	0.20 (0.04)	0.23 (0.03)	92.0 (19.2)	3.88 (0.23)	winter	12,15	8
Albany <sup>#</sup>	22.8* (1.2)	58.4* (4.7)	2.09** (0.13)	1.26** (0.08)	-0.35 (0.04)	0.62 (0.02)	0.86 (0.07)	182.1 (8.3)	2.37*** (0.04)	summer	2	8

**Key:**

- \* .01 < P ≤ .05
- \*\* .005 < P ≤ .01
- \*\*\* P ≤ .005
- <sup>^</sup> both sides of leaf
- <sup>#</sup> data from Masini *et al.* (1995)

## 4. Discussion

Photosynthesis and respiration rates and the light requirements as measured by the photo-metabolic parameters  $I_c$  and  $I_k$  generally increased over the temperature range 13 °C to 23 °C. Temperature optima for photosynthesis of *P. australis*, *A. griffithii* and *A. antarctica* were at 23 °C or above, and between 18 and 23 °C for *P. sinuosa*. The lowest  $P_{\text{max}}$  tended to occur at 13 °C, but

water temperatures are rarely this low on the west coast of Western Australia, and in the Perth region mean temperatures are generally between 16 and 23 °C (Simpson *et al.* 1993).

Water temperature has been invoked as a major influence on the biogeographic distributions of seagrasses (Setchell, 1935), although this hypothesis is largely unproved for the Australian continent (Kirkman and Walker, 1989). Any temperature controls on the geographic distribution of seagrasses are presumably related to the effect of temperature on some aspect of their eco-physiology. The northern geographic limit for temperate seagrass species in Western Australia is probably related to the maximum, rather than the minimum, prevailing water temperatures. The alongshore gradient of seawater surface temperatures on the Western Australian coast is about 0.5 °C per degree of latitude (Pearce, 1986) and the four species of seagrass examined have different, but overlapping, geographic distributions along this coastline (Larkum and den Hartog, 1989).

*Amphibolis antarctica* has the most northerly distribution; it is found as far north as Ningaloo Reef (22 °S; Walker and Prince, 1987), where mean maximum water temperatures in summer can exceed 28 °C (Simpson *et al.* 1993). This species tended to have the lowest  $I_k$  at 23 °C of all species examined, a  $GP_{max}$  temperature optimum of 23 °C or above, and a  $P_{max}$  that is largely independent of temperature. *P. australis* also had a  $GP_{max}$  temperature optimum of 23 °C or above but is found only as far north as Shark Bay (26 °S; Walker, 1989), where mean maximum temperatures are about 26 °C (Logan and Cebulski, 1970). *A. griffithii* also had a  $GP_{max}$  temperature optimum of 23 °C or above, but its  $I_k$  was strongly influenced by water temperature; it more than doubled between 13 °C and 23 °C. This indicates that *A. griffithii* requires higher light intensities to saturate photosynthesis as water temperatures increase. This species is not found as far north as Shark Bay (Walker, 1989), but is found at Geraldton (29 °S; Larkum and den Hartog, 1989), where mean maximum temperatures rarely exceed 24.5 °C (A. Pearce, CSIRO Division of Oceanography, Perth, Western Australia, pers. comm.). *P. sinuosa* had the lowest  $GP_{max}$  temperature optimum of the species examined (18-23 °C). It has a similar northern geographical limit to that of *A. griffithii*. However, in contrast to *A. griffithii*, the  $I_k$  of *P. sinuosa* was no different at 23 °C than at 18 °C.

From a review of the results of culture work and *in situ* studies, Hillman *et al.* (1989) suggest that the optimum temperature for growth of seagrasses may be lower than for photosynthesis. The relatively high temperature optima of the essentially temperate seagrass species we studied tend to support this suggestion, but the inter-species comparisons of photometabolic parameters and geographic distributions suggest that the effect of temperature on photosynthesis is a component of the overall biogeographic control mechanism.

The results discussed above were generated with plants that were kept at the experimental temperature for about 24 hours before the experiments began. Temperature acclimation of photosynthetic apparatus has been reported in a few species of algae, but only after they had been acclimated for several days or weeks at the chosen temperature (Davison, 1991). A thorough investigation of temperature-mediated physiological controls on the geographic distribution of seagrasses would require longer acclimation of experimental plants to selected water temperatures than was possible in our study.

The higher photosynthetic rates and lower  $I_k$ 's of the genus *Amphibolis* than of *Posidonia* over the experimental temperature range result from higher  $\alpha$  values, but similar respiration rates expressed on the basis of either a whole plant or chlorophyll *a*. Specific growth rates, based on either metabolic or field studies, are useful for comparing the primary productivity of different plant groups. To compare the specific growth rates (SGR) of above-ground material (% d<sup>-1</sup>) for the two genera, 'maximum' potential SGR's were calculated from mean metabolic rates at 23 °C,

by assuming  $P_{\max}$  occurs for 14 hours (approximate photoperiod during summer at 32 °S) and converting  $O_2$  flux to dry weight by applying a metabolic quotient of 1 and a dry weight:carbon conversion of 0.36 (Hillman *et al.* 1989). The SGR calculated in this way was 1.2 for *Posidonia* and 1.9 for *Amphibolis*. The metabolically derived 'maximum' potential SGR's of the two genera are 70 to 80 per cent of the maximum SGR of *Posidonia* (1.5) and *Amphibolis* (2.7) reported by Hillman *et al.* (1989) in their review of SGR data for Australian seagrasses, which they measured by *in situ* leaf-marking techniques. In addition, the relationship between the SGR of *Amphibolis* and *Posidonia* derived from metabolic measurements (1.6) was similar to the relationship derived from *in situ* leaf-marking techniques (1.8). The higher photosynthetic efficiency and lower  $I_k$  of *Amphibolis* would result in comparatively higher net photosynthetic rates at low PPFD, which may explain why this genus has a higher maximum *in situ* SGR than *Posidonia*.

The data in Table 2 indicate that  $\alpha$  increased with temperature in both genera. While this finding appears to conflict with the commonly held view that  $\alpha$  is related solely to the light 'reaction' of photosynthesis and is therefore temperature-independent (e.g. Platt and Jassby, 1976; Bulthuis, 1987), other workers (Penhale, 1977; Perez-Llorens and Niell, 1993; Olesen and Sand-Jensen, 1993) have reported results similar as found in this study.

Our results could be, in part, an artefact related more to a combination of the method of calculation of  $\alpha$  and the temperature dependence of respiration, than to a direct response to water temperature *per se*. For example, the value  $\alpha$  is expressed in terms of oxygen flux per unit chlorophyll *a* per unit light and is approximated here as the slope of a linear line of best fit through the first three points of the P-I curve (0 to ~ 24  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), using a 'least squares' method to pass the line through the respiration value (Masini *et al.*, 1995). Respiration is strongly temperature-dependent, but  $I_c$  was found to be largely temperature-independent and, because the line of best fit was forced through the respiration value,  $\alpha$  was seen to increase in response to temperature.

In addition, the curvilinear rather than linear response of photosynthesis across the irradiance levels used in the calculation of  $\alpha$  (e.g. Figure 2a) may be a result of using whole 'plants' in the metabolic chamber and the consequent inability to ensure uniform illumination of all leaf surfaces. A more uniform illumination is easier to achieve with chloroplast suspensions or leaf fragments but whole 'plants' are more representative of the primary ecological unit in a meadow, and therefore could be considered to provide information that is more relevant to environmental management.

The annual growth of *P. sinuosa* is unimodal; rates are highest in summer and lowest in winter (Hillman *et al.*, 1991). The photosynthetic responses of plants collected in summer and winter from the same meadow were similar when measured under identical conditions of light and temperature in the laboratory. These findings suggest that this seasonal growth pattern is related directly to the prevailing environmental conditions, such as water temperature, light intensity and daylength, and is not linked to an internal rhythm such as that documented for *Posidonia oceanica* (L.) Delile (Ott, 1979) and *Cymodocea nodosa* (Ucria) Aschers. (Perez and Romero, 1992).

*Posidonia sinuosa* plants collected from near their natural maximum depth limits in Perth displayed some morphological evidence of depth adaptation; their leaves were shorter and narrower and they had a higher SLA than plants growing in shallow water. Increases in SLA of aquatic angiosperms with depth (Spence *et al.*, 1973) and in response to reduced light (Olesen and Sand-Jensen, 1993) have been reported, but a reduction in leaf area is generally not considered to be an adaptation to shade (Kirk, 1983) and conflicts with the documented increases in leaf area of other seagrass species with increasing depth (Lipkin, 1979; Bulthuis and Woelkerling, 1983;



Hillman et al., 1989). However, imposed shading of *P. sinuosa* in Albany caused a reduction in leaf length after only 42 days, but had no effect on leaf width after 104 days (Gordon et al., 1994). Similar reductions in leaf length,—but not leaf width—in response to low light have been reported in other studies of *P. sinuosa* (Neverauskas, 1988) and *P. australis* (West, 1990).

The metabolic data presented here provide further evidence of depth adaptation in *P. sinuosa*. The deep-water plants had a higher photosynthetic efficiency ( $\alpha$ ) and a lower light requirement to saturate photosynthesis than the shallow-water plants. The relationship between  $GP_{max}$  of deep- and shallow-water plants varies depending on how it is expressed. When normalised to chlorophyll *a* content,  $GP_{max}$  was higher in the deep-water plants; when normalised to leaf dry weight, it tended to be higher than that of the shallow-water plants, but the difference was not significant. These trends run against the generally accepted view that shade-adapted plants have a lower photosynthetic capacity than sun-tolerant plants (Kirk, 1983). Pirc (1986) reports a lowered photosynthetic capacity for *P. oceanica* at depth; however his data were normalised to leaf area. When the data from our study are expressed on a leaf area basis a similar trend of a lower  $GP_{max}$  with depth is apparent, but the differences are not statistically significant.

When the photosynthetic rates of *P. sinuosa* collected from a eutrophication imposed depth limit were compared with plants from shallower water, Masini *et al.* (1995) found no evidence of photoadaptation. The deep edge of the meadow in their study area had receded as a result of shading by abnormally high epiphyte loads, so plants at the new depth limit would have been in the midrange of their former depth distribution. There is some evidence that seagrass meadows have been in these areas for up to 6000 years and during that time have accumulated carbonate sands and formed sub-tidal banks over 10 m thick (Davies, 1970; Semeniuk and Searle, 1986). The difference between our findings and those of Masini *et al.* (1995) suggests that *P. sinuosa* does not respond quickly (within months) to imposed low light; the timescales for 'photoadaptation' are longer and may reflect natural selection processes operating during the development of these meadows.

Morphological differences in *Halophila stipulacea* (Forskål) Aschers. along a depth gradient are thought to be genotypic rather than phenotypic, with true ecotypes of this species within short distances of each other (Lipkin, 1979). Similarly, depth-related differences in photosynthesis of *P. oceanica* appear to be genetically fixed (Pirc, 1986). The genus *Posidonia* includes 9 species, which is an unusually high number for a seagrass, and all except one occur in south Western Australia (Larkum and den Hartog, 1989). *P. australis* in the Perth region has a high level of genetic variation, with at least 15 genotypes occurring within an area of 320 m<sup>2</sup> (Waycott, 1994). It would appear that many of the attributes displayed by the deep-water *P. sinuosa* plants studied here may be genotypically derived, and are not the phenotypic responses to low light that have been documented for other genera (e.g. Drew, 1979; Dennison and Alberte, 1986; Jimenez *et al.* 1987).

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