Effects of light and temperature on the photosynthesis of seagrasses, epiphytes and macroalgae and implications for management of the Albany harbours

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Effects of light and temperature on the photosynthesis of seagrasses, epiphytes and macroalgae and implications for management of the Albany harbours

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Summary

A technique is described for measuring the metabolic response of 'whole plants' of seagrasses to different light intensities and water temperatures. A light regime simulating that experienced by plants in a meadow is used to more closely approximate the photosynthetic response of plants *in situ*.

The relative susceptibility to low light stress of the three species examined in this study is dependent on the source of the stress. The relative susceptibility of the three species to a reduction of light through increased turbidity in the water column would be as follows:

Posidonia australis > *Posidonia sinuosa* > *Amphibolis antarctica*

P. sinuosa is more susceptible to shading by epiphytes than the other two species as its metabolically derived growth rate is much lower (ie resulting in a low leaf turnover time) than the other species examined. As light reduction to a seagrass leaf can be related directly to epiphyte biomass it follows that each *P. sinuosa* leaf would receive less light than an equivalent leaf from the other species, thereby increasing its relative susceptibility.

The optimum temperature range for net photosynthesis in *P. sinuosa* was between 18 and 23 °C. Photoinhibition of photosynthesis was found in *P. sinuosa* under conditions of low temperature and high light intensity.

The annual cycle in energy storage and usage must be considered when determining the seasonal aspects of light stress. It appears that *P. sinuosa* depends on stored energy reserves for maintenance respiration and growth during winter. Light stress during the period when the seagrasses are storing non-structural carbohydrate would be the most detrimental for the survival of the meadow. Light reduction would have minimum impact during periods of moderate temperatures, high light intensities and long days, but only if the average incident light level is maintained above that required to saturate photosynthesis (I_{sat}).

When epiphytes are removed from *P. sinuosa*, photosynthetic responses are similar to non-epiphytised plants, suggesting that *P. sinuosa* can recover rapidly when light stress is removed. Given the importance of stored energy reserves, there is likely to be a seasonal component in the ability of the plant to recover from light stress.

Physiological adaptation to low light intensities was not found in *P. sinuosa*.

The relatively high theoretical saturating light intensity (I_k) of epiphytes and macroalgae compared to seagrasses indicates that these algae are more susceptible to low light conditions than seagrasses. Coupled with the lack of large storage organs (cf seagrass rhizomes), prolonged periods of low light are therefore likely to be more detrimental to these algae than to the seagrasses.

The potential yearly growth rates of macroalgae (based on metabolic rates) exceed that of P. sinuosa by about 25 times.

1. Introduction

Seagrass meadows are found in nearshore coastal areas throughout the world and their ecological importance as primary producers and as providers of habitat for invertebrates (Hutchings *et al.*, 1989) and juveniles of many other species is well known (Pollard, 1984; Bell and Pollard, 1989). Their growth and distribution are influenced by many environmental factors such as current regime (Fonseca and Kenworthy, 1987), nutrient resources (Bulthuis and Woelkerling, 1981; Short, 1987) and salinity (Hillman and McComb 1989; Walker and McComb, 1990). However within an existing meadow the primary factors limiting seagrass growth are light availability (eg. Drew, 1979; Dennison, 1987; Williams, 1988; Dawes and Tomasko, 1988) and water temperature (Bulthuis, 1987).

The decline of seagrass meadows in some Western Australian coastal waters and harbours has been the cause of increasing concern in recent years (Cambridge and McComb, 1984; Mills, 1987; Shepherd *et al.*, 1989; Simpson and Masini, 1990). A reduction in light reaching the meadows, either through decreased water clarity or shading by epiphytic or unattached algae is considered to be the major cause of this decline (eg. Cambridge *et al.*, 1986; Silberstein *et al.*, 1986; Shepherd *et al.*, 1989).

The effect of light and temperature on the photosynthesis of seagrasses within a meadow is not well understood. A section of seagrass meadow consisting of a leaf-bearing shoot with an attached portion of rhizome and roots could be considered to be the primary ecological unit of a seagrass meadow. For convenience, this unit is refered to in this study as a 'whole plant'. Most studies on the relationship between photosynthesis and light and/or temperature have been carried out on cut segments of seagrass leaves (Dawes and Tomasko, 1988; Bulthuis, 1983), or whole leaves (Dawes *et al.*, 1987). These procedures were used to minimise the effect of lacunal storage of gases on the measured metabolic rate, a factor which was assumed to be significant and cited as the major drawback to studying seagrass metabolism using metabolic techniques (Hartman and Brown, 1967; Nixon and Oviatt, 1972). More recently, the photosynthetic rate measured as changes in dissolved oxygen in water surrounding the plant have been shown to be of the order of 82-89% of the total photosynthetic rate (Roberts and Moriarty, 1987); in the past the difficulties of using metabolic techniques may have been overemphasised (Hillman *et al.*, 1989, Larkum *et al.*, 1989).

Data on whole plants have generally been collected using *in situ* incubations (Penhale, 1977; Williams and McRoy, 1982) in which it is difficult to determine the separate effects of temperature and light on photosynthesis. Problems also occur in isolating the relative contributions to the gas flux attributable to seagrass metabolism from faunal and bacterial respiration and the chemical demands of the sediment. Data on whole plants are more appropriate for the informed management of rapidly declining seagrass meadows.

The aims of this study were to determine 1) the light requirements of the dominant seagrass species in Princess Royal Harbour near Albany, Western Australia; 2) the light requirements of the epiphytic and unattached algae that have recently been found in nuisance proportions in Princess Royal Harbour; and 3) the effect of temperature on the photosynthesis-irradiance curve of the most prevalent seagrass species *Posidonia sinuosa*, over the annual temperature range experienced in Princess Royal Harbour.

2. Materials and methods

2.1 Sampling

Whole seagrass plants (Figure 1) were collected from site 1, offshore from Camp Quaranup, on the eastern side of Princess Royal Harbour (Figure 2). The standing crops of the seagrass and algae in the meadow and the general physical characteristics of the site have been described by Hillman *et al.*, (1990). An airlift operated from a SCUBA tank was used by divers to carefully uncover the rhizome mat, and shoots which appeared undamaged were removed with a section of rhizome and roots.

Non-epiphytised (ie relatively free of epiphytes) *Posidonia sinuosa* 'plants' consisting of 3 or 4 leaves (total length approximately 1.5 m) and a section of rhizome about 50 mm long with attached roots were collected from a depth of about 2.0 m. Epiphytised *Posidonia sinuosa* plants of a similar size were collected from 4.0 m.

Posidonia australis 'plants' were collected from about 1.0 m and consisted of 3 leaves (total length approximately 950 mm) and a section of rhizome about 130 mm long with attached root material. *Amphibolis antarctica*

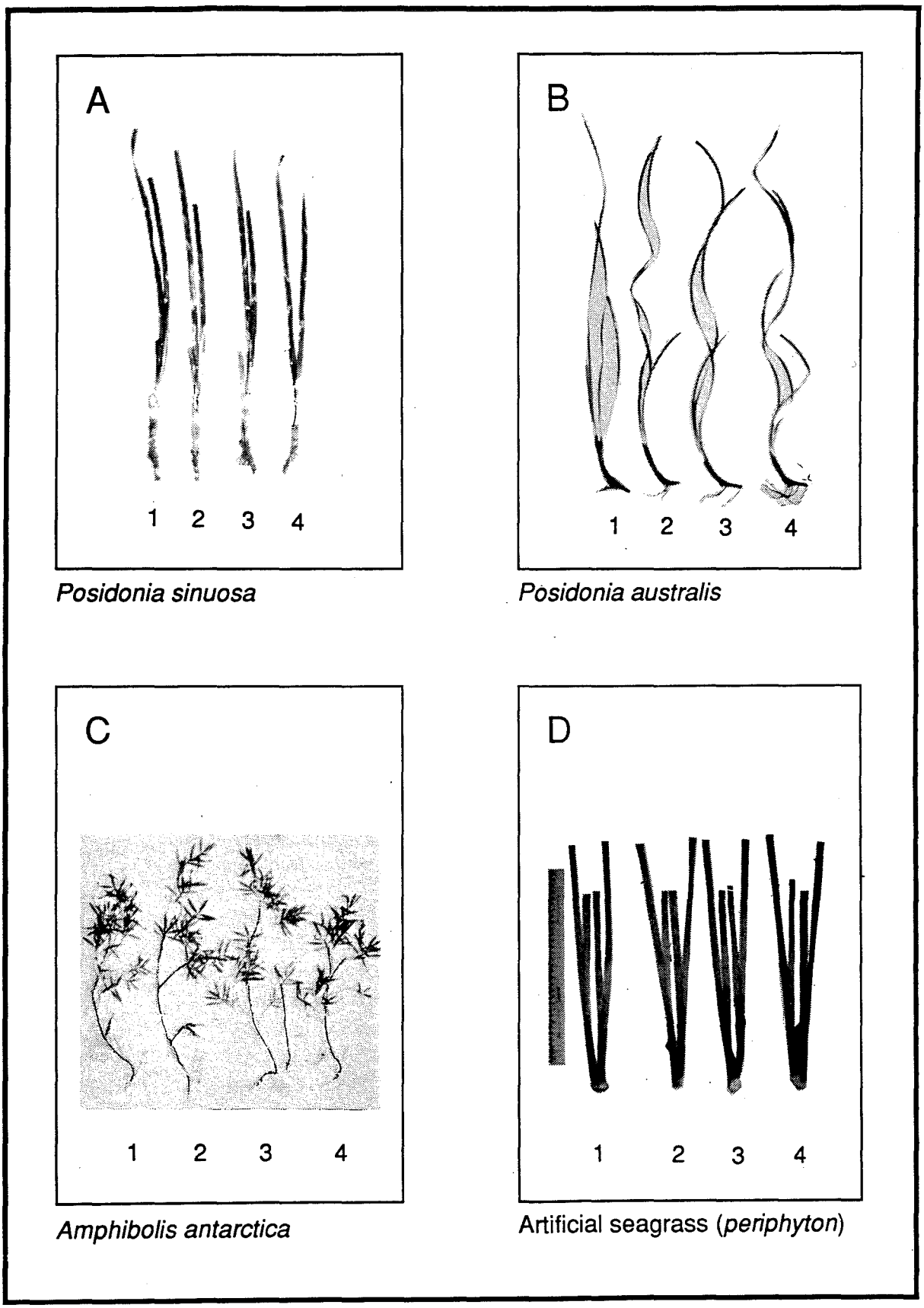

Figure 1. Typical 'whole' seagrass plants used in this study.

a) *Posidonia sinuosa*, b) *Posidonia australis*, c) *Amphibolis antarctica* and d) artificial seagrass (*periphyton*).

Figure 2. Location and bathymetry of Princess Royal Harbour, Albany.

'plants' from a depth of about 3.0 m consisted of an erect stem with approximately 100 leaflets and a 50 mm length of rhizome and root. Grab samples of unattached macroalgae (dominated by *Heterosiphonia* sp. ~75% and *Cladophora* sp. ~20%) were collected from a *P. sinuosa* meadow at a depth of about 2.0 m. Periphyton growing on artificial seagrass shoots, which consisted of 3 strips (60, 300 and 385 mm long) of 11 mm wide clear plastic attached to a wire frame in a seagrass meadow, were used to provide a sample of the epiphytic community within that meadow. The artificial seagrass was placed on the wire frame at a density of 1100 shoots m^{-2}. Two shoots, which had remained in place for 115 days at site 2 (Figure 1), were used for each determination of metabolic rate.

Samples were transported in seawater to the laboratory where they were transferred to an aerated bath containing filtered (5 µm pore size) seawater and held in dim light (approximately 5 µmol $m^{-2}s^{-1}$) at the experimental temperature. All samples were used within 4 days of collection and the photosynthetic response of replicate samples within each treatment were determined on the same day. Prior to determining the effects of temperature on photosynthetic rate, the plants were allowed to equilibrate overnight to the experimental temperature.

2.2 PAR measurements

The light climate within a seagrass meadow was characterised using a submersible 4π spherical light sensor (Licor SPQA 0266). A graduated aluminium bar was inserted vertically into the sediment to provide a reference point within the canopy. The light sensor, attached to a thin aluminium bar held parallel to the sediment surface was carefully inserted into the canopy by a diver. Photosynthetically active radiation (PAR) was measured at the top of the canopy, 0.1 m below the top of the canopy and just above the sediment surface (approx. 0.2 m below the top of the canopy). Three consecutive 10 s integrated readings of irradiance were taken at each level within the seagrass canopy and averaged to provide a mean value for each level. Thirty second integrated readings of PAR were simultaneously recorded at the top of the canopy and used to adjust the recorded levels within the canopy to percentages of incoming PAR. This procedure was repeated at 6 locations in the meadow, and the average percentage light reduction at each level was calculated.

2.3 Photosynthesis vs. irradiance (P-I) measurement

Photosynthesis was measured as rate of change of dissolved oxygen concentration per unit time in a sealed incubation chamber using a procedure adapted from Masini (1990). The chamber consisted of a 32 mm diameter clear acrylic tube ranging from 510 to 640 mm in length. Water within the tube was circulated by a small submersible pump (Sicce, Italy) and a peristaltic pump (Cole-Parmer Inst. Co., Chicago Il.) resulting in a combined flow rate of 1.5 litres per minute. The peristaltic pump circulated chamber water past a thermister (Radiospares 151-013) and high-stability, low oxygen consumption polarographic dissolved oxygen sensor (model 8000, Leeds and Northrup, Millville, NJ). The sensors were connected through preamplifiers to high-resolution millivolt meters (Windrift Instruments, WA: Model 783) and data recorded at 15 s intervals.

The light source consisted of eight 15 v 150 w quartz iodide projector lamps (Philips EFR A1/232) connected in series and attached to a 10 amp variable voltage regulator (Voltac B-10, Yokoyama Electric Works, Ltd., Japan). This enabled light intensities exceeding 2000 µmol $m^{-2}s^{-1}$ to be achieved. An acrylic diffuser was placed between the lights and the chamber to provide a more uniform light field. Light intensity inside the chamber was calculated from measurements made at a fixed position outside the chamber using a light sensor in a 2π head configuration attached to a data logger. The light meter was calibrated using a Licor Quantum/Radiometer/Photometer and 4π underwater sensor. Fans were used at all times to cool the projector lamps.

Constant temperature (±0.25 °C) was maintained by submersing the incubation chamber in a 190 litre temperature controlled bath containing filtered (5 µm pore size) seawater from the study site. The apparatus is shown in Figure 3.

The dissolved oxygen electrode was calibrated at the end of each day's experimentation. A three litre container filled with water from the incubation chamber, was held at the experimental temperature and deoxygenated by bubbling with nitrogen gas, and recirculated past the probes at the same speed as during the experiment. When the electrode output was stable the outlet tube was removed from the container and placed at the bottom of a 10 ml volumetric flask which was allowed to overflow some three times its volume. The tube was removed and the dissolved oxygen in the water sample was chemically bound using standard 'Winkler' reagents. The dissolved oxygen content was then determined using the methods of Grasshoff *et al.*, (1983). This procedure was repeated for a water sample at ambient dissolved oxygen concentration. The relationship between dissolved oxygen

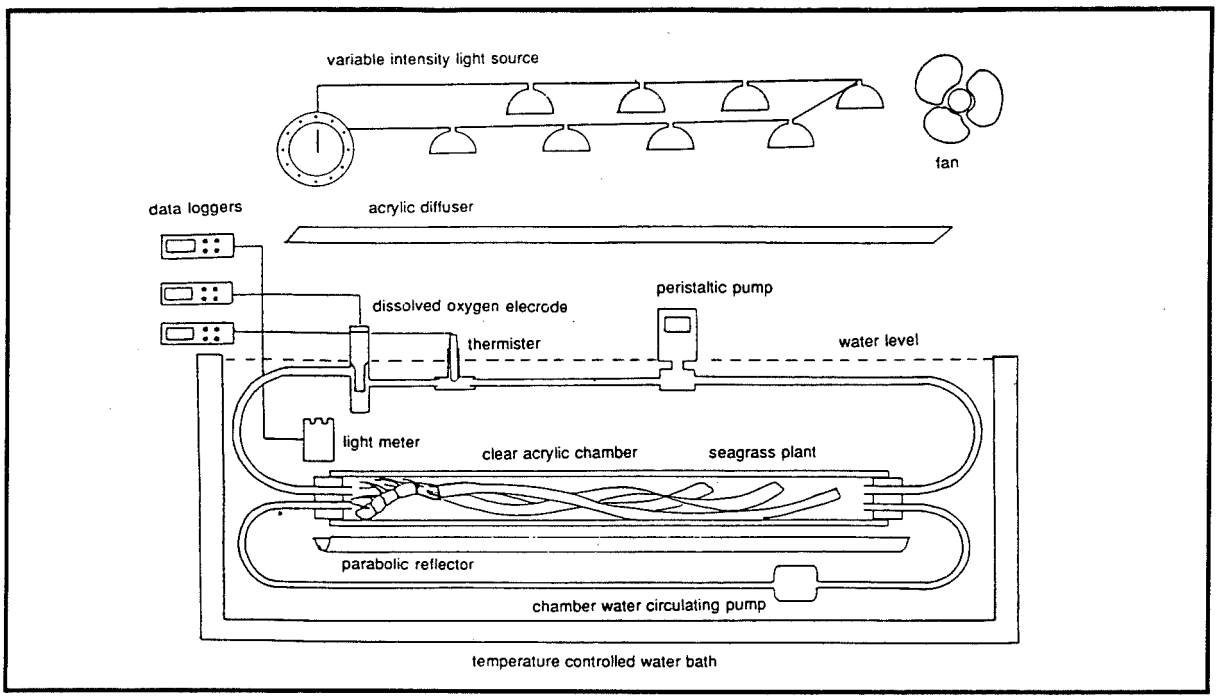

Figure 3. The experimental apparatus used to determine the effects of light and temperature on photosynthesis.

concentration and millivolt output of the sensor is linear (Masini, 1990) so the two points were used to calculate a regression equation. A precision of less than 0.0008 $mgO_2\ l^{-1}$ (2.5×10^{-2} $\mu mol\ O_2\ l^{-1}$) was obtained using the apparatus, allowing the determination of very low metabolic rates.

Initial light intensity for all experiments was zero thereafter increasing step-wise to the maximum intensity of about 2120 $\mu mol\ m^{-2}s^{-1}$. Light intensity was then returned to zero followed by the next lowest light intensity. The plant was held at each light intensity for 20 minutes but only the last 5 minutes of the run were used to calculate metabolism rate. This procedure allowed a standard time for the plant to react to a step change in light intensity and time for the dissolved oxygen electrode to respond and stabilise to the new rate.

A typical output of the last 5 minutes of a run at one light intensity is shown in Figure 4. Data were subjected to a linear regression analysis (typically n=19). The linearity of the data was determined by the coefficient of determination (r^2) which during this work was usually close to 1. The rate is determined by the slope of the regression line expressed as a change in millivolts per unit time. The millivolt change can be directly converted to $mgO_2\ l^{-1}$ per unit time using the calibration equation (see above). These data in turn can be converted to a change in carbon using a photosynthetic quotient (PQ) of 1.2 (Ryther, 1956).

On a few occasions the relative respiration rate of the rhizome and above ground segments were determined separately in a 190 mm long chamber as described for whole plants. The experiments were conducted within 30 minutes of cutting the plant.

In one experiment shade-cloth was wrapped around parts of the chamber to provide a light gradient decreasing towards the rhizome. The light gradient was constructed to simulate the rapidly-attenuated light field measured within the meadow at the study site. Within the chamber the top third of the plant received 100% of the incident light, the middle third 18.2% ± 1.03 and the bottom third 4.1% ±0.41. The effect of a horizontally-attenuated light field on a horizontally positioned plant was assumed to be equivalent to the vertically-attenuated light field experienced by vertically-aligned plants in a meadow. The P-I relationships of eight replicate *P. sinuosa* plants were determined in the uniform light field used in all other experiments and compared with the P-I relationships of a subset of these plants (n=4) in an attenuated light field.

The photosynthetic responses of 4 replicate *P. sinuosa* plants were determined at 13, 18 and 23 °C. These water temperatures span the average annual water temperature range in Princess Royal Harbour (Simpson and Masini, 1990).

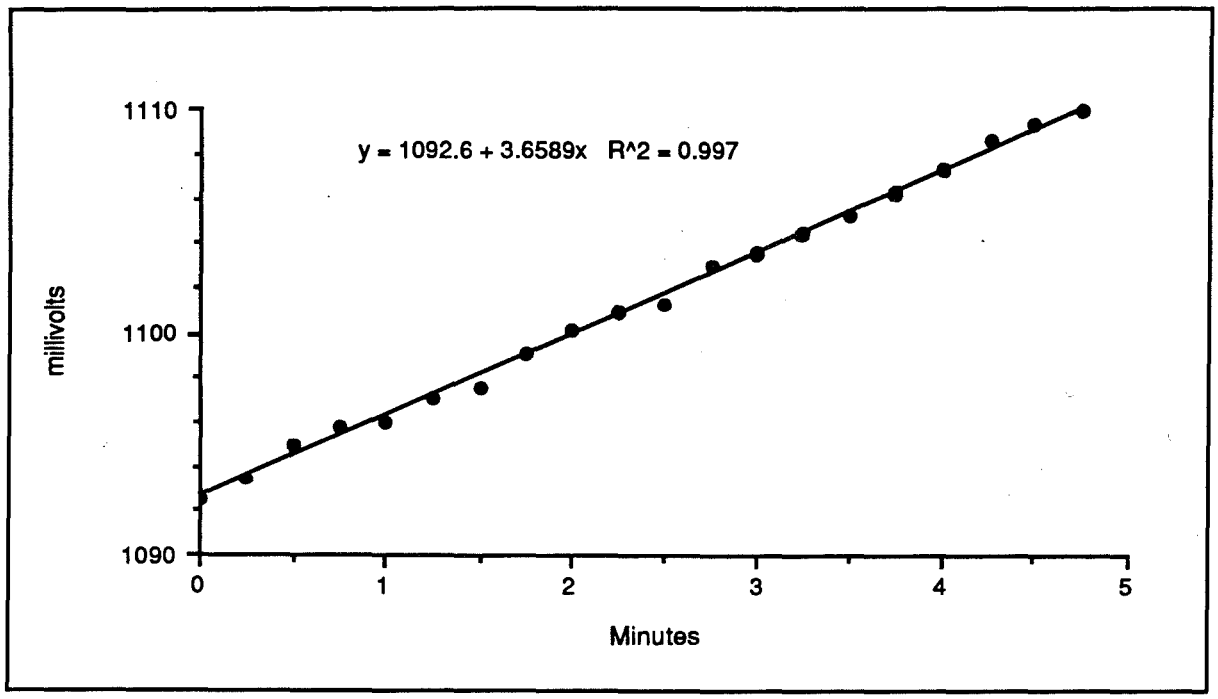

Figure 4. Plot of the dissolved oxygen electrode output (millivolts) during the last 5 minutes of a 20 minute incubation of a *Posidonia sinuosa* plant at a temperature of 23 °C and light intensity of 1020 µmol m-2s-1.

At the end of each experiment the seagrass plant was measured, divided into above- and below-ground parts and dried to constant weight at 70 °C. Subsamples of each leaf were taken prior to drying and analysed for chlorophyll *a* content according to the methods of Strickland and Parsons (1972).

2.4 Statistical treatment

The effects of different treatments and the degree of inter-species variation were analysed statistically using the non-parametric Mann-Whitney Test (U-test). The significance of temperature on metabolic rate was determined using paired t-tests. 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 the standard error (s e) of the mean.

2.5 P-I curves and their characteristics

Plots of metabolic rate versus light intensity (Figure 5) follow the classic P-I shape (Talling, 1957; Bulthuis 1983). From the P-I curve it is possible to calculate 1) the maximum net photosynthetic rate (P_{max}), 2) the respiration rate (R) which is the amount of oxygen utilised by the plant in the dark (for the purposes of this study also assumed to be the respiration rate occurring in the light), 3) the compensating light intensity (I_c) where respiration balances photosynthesis, 4) the theoretical saturating light intensity (I_k) where the initial slope (I_{slope}) plotted from the first 3 data points intersects P_{max} and 5) the actual saturating light intensity (I_{sat}).

Gross maximum primary production rates (GPP_{max}) were calculated by the following equation:

$$GPP_{max} = P_{max} + |R|$$

For comparative purposes both net and gross primary production values were normalised to leaf area (cm^2), chlorophyll *a* content ($\mu g\ g^{-1}$) and dry weight of leaves, rhizomes and whole plants (g), where appropriate.

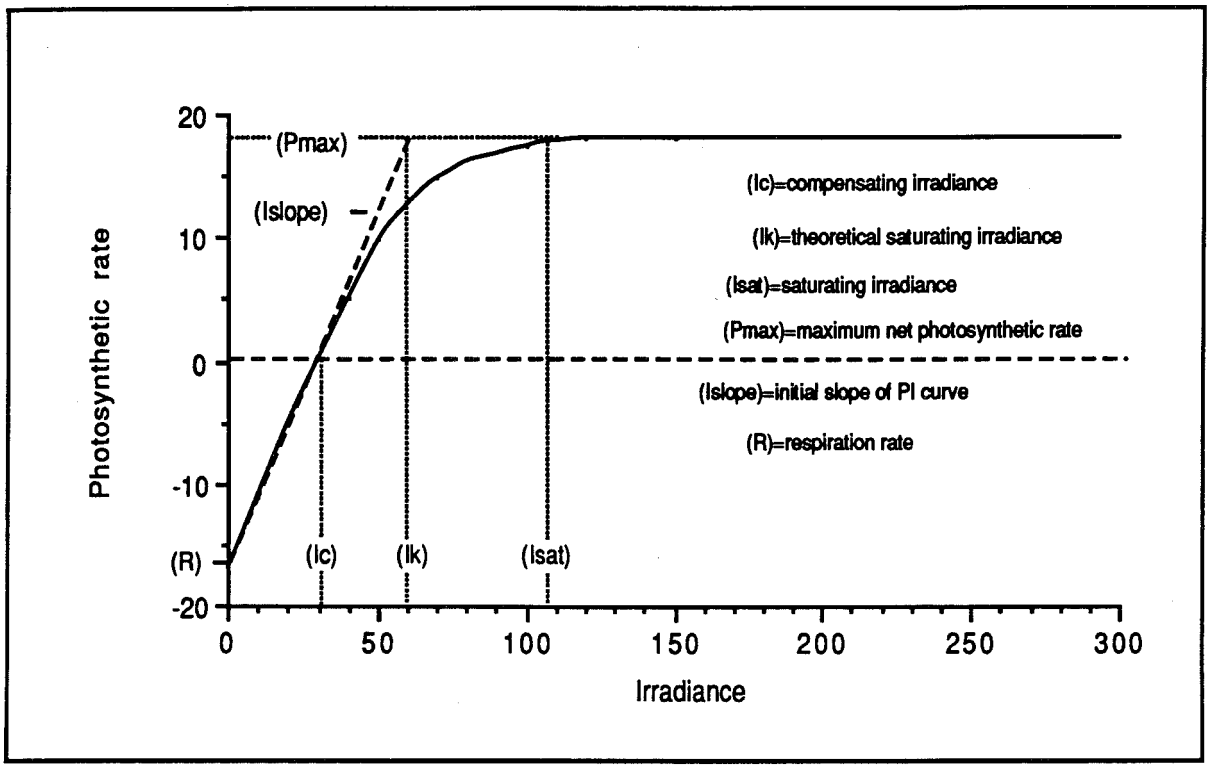

Figure 5. Typical photosynthesis versus irradiance (PI) curve showing metabolic rates and critical light intensities.

3. Results

3.1 Seagrasses

3.1.1 Compensating and saturating light intensities

Inter-specific variation: The light requirements of the dominant seagrass species found in the harbours are summarised in Table 1. The interspecific variations in average I_c and I_k were 5 and 36 μmol $m^{-2}s^{-1}$ respectively. The I_c of the three seagrass species ranged from 20 μmol $m^{-2}s^{-1}$ in *A. antarctica* to 25 μmol $m^{-2}s^{-1}$ in *P. australis*. The I_c of *P. australis* was significantly higher (U-test, $p \leq .05$) than the I_c of *A. antarctica*. No other significant interspecific difference in I_c were identified. In contrast, greater variation occurred in the I_k value for the three seagrasses. The I_k of *P. australis* was significantly higher (U-test, $p \leq .05$) than the I_k of *A. antarctica* and the I_k of *P. sinuosa*. The I_k of *A. antarctica* lay midway between that of the other species and was significantly higher (U-test, $p \leq .05$) than the I_k of *P. sinuosa* collected from depths of about 2.0 m, and also 4.0 m with the epiphytes removed.

Depth adaptation: The mean I_k and I_c of *P. sinuosa* collected from a depth of 2.0 m were not significantly different from those measured for plants collected from a depth of 4.0 m, with epiphytes removed.

3.1.2 Photosynthetic efficiency

The maximum gross primary productivity (GPP_{max}) of the three seagrass species normalised to leaf area, leaf weight and chlorophyll *a* content are shown in Table 2.

Oxygen production per unit area of leaf was significantly different (U-test, $p \leq .05$) between all species. The GPP_{max} of *A. antarctica* was about 1.6 times and 2.7 times greater than the GPP_{max} of *P. australis* and *P. sinuosa* respectively. Normalised for leaf dry weight, the GPP_{max} of *P. australis* and *A. antarctica* were not significantly different, but the GPP_{max} of *P. sinuosa* was about 0.6 of the GPP_{max} of *P. australis* (U-test, $p \leq .05$) and 0.7 that of *A. antarctica* (U-test, $p \leq .05$). The relative efficiency of chlorophyll *a* in *A. antarctica* was

about 2.8 times greater than in *P. australis* (U-test, p≤.05) and twice that of *P. sinuosa* (U-test, p≤.05). The relative photosynthetic efficiencies of *P. sinuosa* and *P. australis* were not significantly different when normalised for chlorophyll *a*.

Table 1. Compensating irradiance (I_c), theoretical saturating irradiance (I_k) and the initial slope of the photosynthesis versus irradiance curve (I_{slope}) at 18 °C for three species of seagrass, the suite of unattached macroalgae and epiphytes from Princess Royal Harbour during February, 1989. Mean and standard error (in brackets) are shown (n=4). n.d. = not determined.

Species	Collection depth (m)	I_c (μmol $m^{-2}s^{-1}$)	I_k	I_{slope} (μgO_2 μgchl $a^{-1}hr^{-1}$ μmol $m^{-2}s^{-1}$)
Posidonia australis	1.5	25 (1.3)	92 (4.0)	0.009 (.001)
Amphibolis antarctica	3.0	20 (0.9)	73 (2.1)	0.032 (.001)
Posidonia sinuosa	2.0	23 (1.6)	56 (3.2)	0.014 (.001)
P. sinuosa -epiphytes	4.0	24 (2.2)	56 (5.4)	0.020 (.005)
P. sinuosa +epiphytes	4.0	26 (0.7)	97 (1.7)	n.d.
unattached macroalgae	2.0	22 (1.7)	122 (10.1)	0.055(.005)
periphyton on artificial seagrass	2.0	27 (0.7)	112 (4.5)	0.074 (.007)
epiphytes on *P. sinuosa*	4.0	24 (4.1)	179 (11.5)	n.d.

Table 2. Gross maximum primary production (GPP max) of *Posidonia sinuosa*, *Posidonia australis* and *Amphibolis antarctica* at 18 °C. Mean and standard errors are shown. n=4.

Species	GPP max. μgO_2 cm^{-2} leaf hr^{-1}		mgO_2 g^{-1} leaf hr^{-1}		μgO_2 μgchl a^{-1} hr^{-1}	
	x	s.e.	x	s.e.	x	s.e.
P. sinuosa	6.9	(.69)	2.1	(.27)	1.20	(.36)
P. australis	11.8	(.75)	3.4	(.20)	0.84	(.07)
A. antarctica	18.5	(.81)	3.1	(.13)	2.37	(.18)

3.1.3 Partitioning of respiration rates

Preliminary experiments using two *P. australis* plants indicated that the sum of the separately determined respiration rates of the leaves and of the rhizome plus roots accounted for 103% and 108% of the respiration rates determined for the intact plants. The relative contribution of the plant parts to the total respiration of intact plants of *P. sinuosa* and *P. australis* were very similar (Table 3). The rhizome contributed about 30% and the leaves contributed about 70% of the total respiratory demand in both species. Considerably higher dry weight-adjusted respiration rates were obtained for leaf material than for the rhizome/roots component in both species.

Table 3. Relative percentage contributions of the rhizome and leaf segments to the respiration rate of intact plants of *P. australis* and *P. sinuosa*. Biomass adjusted respiration rates of the plant parts and the whole plant are also shown.

Segment	units	*P. australis* mean±s.e.	*P. sinuosa* mean±s.e.
leaves	% of intact plant	71.1±3.2, n=2	70.1±7.4, n=4
rhizome	% of intact plant	31.0±1.8, n=4	32.2, n=1
leaves	mgO_2 g d.wt^{-1}hr^{-1}	-0.80±.078, n=2	-0.74±.067, n=4
rhizome	mgO_2 g d.wt^{-1}hr^{-1}	-0.16±.021, n=4	-0.34, n=1
whole plant	mgO_2 g d.wt^{-1}hr^{-1}	-0.33±.050, n=4	-0.49±.08, n=4

3.1.4 Light climate within the seagrass meadow

Incident sun-light was rapidly attenuated by the seagrass canopy. Light intensities reaching the surface of the canopy were reduced by approximately 85% and 95% at distances of 100 mm and 200 mm into the canopy respectively. The mean biomass of the canopy was about 480 g d.wt m^{-2} (Gordon *et al.*, in prep.)

3.1.5 Photosynthesis in attenuated and uniform PAR fields

The mean I_c and I_k of *P. sinuosa* plants in a horizontally-attenuated light field were 41% higher and 57% higher respectively (U-test, $p \leq .05$), than for plants in a uniform light field (Table 4). The initial slope of the P-I curve (I_{slope}) was not significantly different between treatments.

Gross primary production was significantly higher (U-test, $p \leq .05$) in the horizontally attenuated light field (7.43±.607 μgO_2 cm^{-2}h^{-1}) compared to in the uniform light field (6.17±.392 μgO_2 cm^{-2}h^{-1}). Mean respiration rates were not significantly different between treatments.

Table 4. Mean compensating irradiance (I_c), theoretical saturating irradiance (I_k) and initial slope of the photosynthesis versus irradiance curve (I_{slope}) at 18 °C for *Posidonia sinuosa* in a uniform light field and a horizontally-attenuated light field simulating the light regime *in situ*. Mean and standard error (in brackets) are shown. n= number of determinations; nsd=not significantly different.

Treatment	I_c	I_k	I_{slope}	(n)
	μmol m^{-2}s^{-1}			
uniform light field	22 (1.2)	60 (5.1)	.014(.001)	8
attenuated light field	31 (3.7)	94 (7.5)	.011 (.001)	4
% increase in attenuated light field	41	57	nsd	

3.1.6 The effect of temperature on the photosynthesis and metabolism of *Posidonia sinuosa*

The effects of temperature on metabolic parameters of four replicate *P. sinuosa* plants are shown in Figure 6a-f. Paired t-tests were used to determine the significance of any differences between treatments (temperatures).

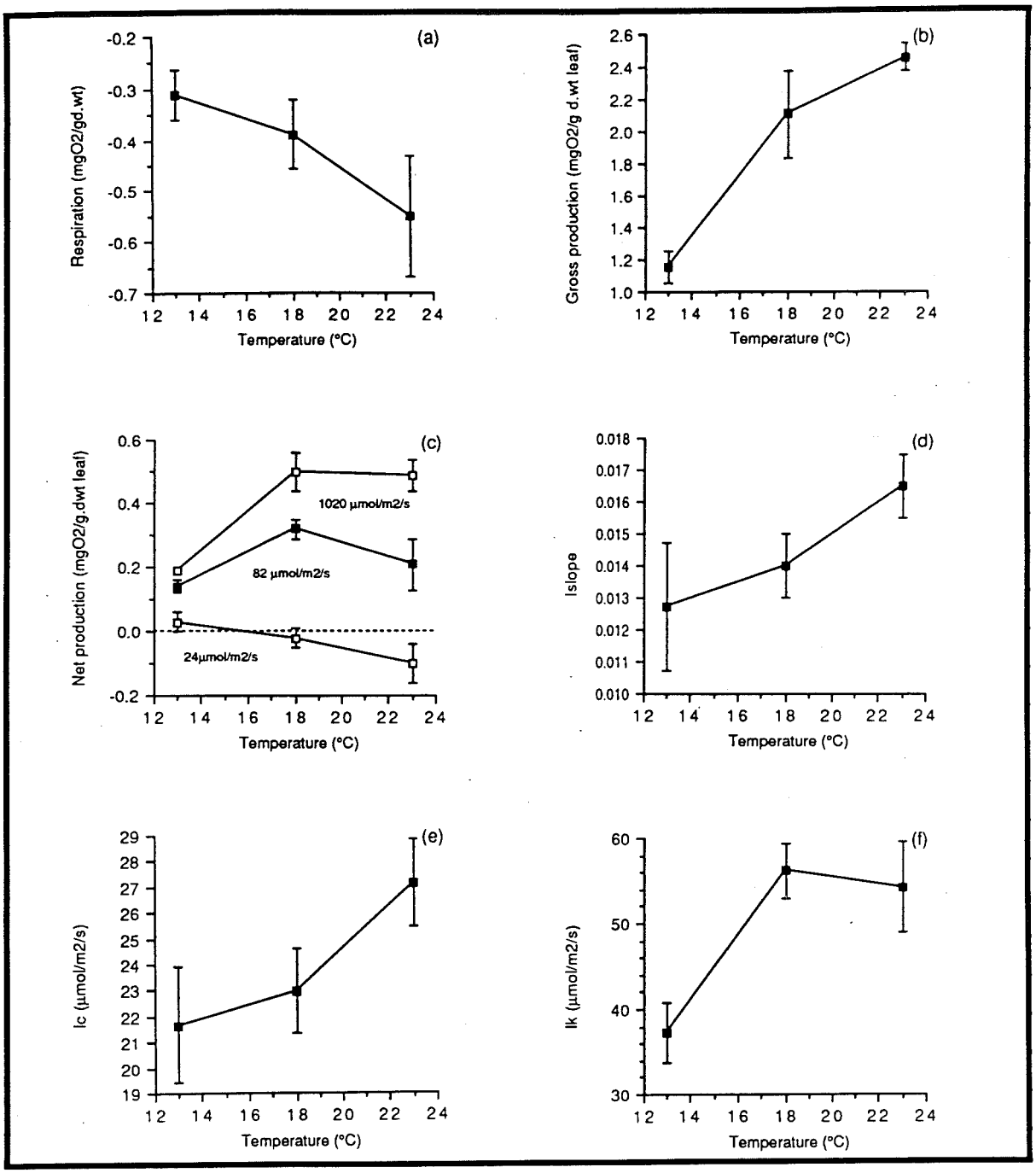

Figure 6. The effects of temperature on photosynthesis and metabolism of *Posidonia sinuosa* from Princess Royal Harbour during February, 1989. Vertical bars indicate standard errors.

a) Respiration rate; b) Gross maximum primary production; c) Net maximum primary production at 24, 82 and 1020 µmol $m^{-2}s^{-1}$; d) Initial slope of the P-I curve (I_{slope}); Compensating light intensity (I_c); theoretical saturating light intensity (I_k); Initial slope of the P-I curve (I_{slope}).

Respiration: Respiration rate tended to increase with temperature (r=.982, n=3) and was about 77% higher at 23 °C than at 13 °C (t=3.531, p≤.025) when expressed on a dry weight basis (Figure 6a). Significant differences in respiration rate were also found between 13 and 18 °C (t=2.975, p≤.025) but not between 18 and 23 °C.

Maximum gross primary production: GPP_{max} normalised for leaf weight, approximately doubled (t=-21.077, p≤.0005) between 13 and 23 °C (Figure 6b). GPP_{max} increased significantly between 13 and 18 °C

(t=5.403, p≤.01) but not between 18 and 23 °C. Similar trends were evident when GPP_{max} was normalised for leaf area and total plant weight.

Net production: P_{max} occurred at 1020 µmol $m^{-2}s^{-1}$ and increased significantly by a factor of about 2.5 between 13 and 18 °C (t=-5.755, p≤.005) and between 13 and 23 °C (t=-6.032, p≤-6.032), but did not alter significantly between 18 and 23 °C (Figure 6c). At low light intensity (24 µmol $m^{-2}s^{-1}$), net production decreased significantly between 13 and 23 °C (t=-3.454, p≤.025). At a light intensity of 82 µmol $m^{-2}s^{-1}$, net production approximately doubled when the temperature was increased from 13 to 18 °C (t=5.308, p≤.01). Net production rates increased significantly as light increased from 24 to 1020 µmol $m^{-2}s^{-1}$ at each experimental temperature.

I_{slope}: The I_{slope} (µg O_2 µgchl*a* h^{-1} µmol $m^{-2}s^{-1}$), which may be considered as an index of photosynthetic efficiency, was significantly greater (t=2.852, p≤.05) at 23 °C (0.16±.001) than at 13 °C (0.13±.002) (Figure 6d).

I_c and I_k: Compensating irradiances increased linearly (r=.996, n=3) as temperature increased between 13 and 23 °C (Figure 6e). The theoretical saturating irradiance increased significantly between 13 and 18 °C (t=4.83, p≤.01) and between 13 and 23 °C (t=3.614, p≤.025), but not between 18 and 23 °C (Figure 6 f).

Photoinhibition: Net photosynthetic rate at 13 °C at 2020 µmol $m^{-2}s^{-1}$ (0.28±.048 mgO_2 g d.wt $leaf^{-1}h^{-1}$) was significantly lower (t=-2.913,p≤.05) than at 1020 µmol $m^{-2}s^{-1}$ (0.44±.021). Photoinhibition was not significant at the two higher temperatures.

3.2 Epiphytes and unattached macroalgae

3.2.1 Compensating and saturating light intensities

The I_c and I_k of epiphytes and macroalgae are shown in Table 1. The data for epiphytes on *P. sinuosa* were obtained by subtraction of the gross photosynthetic rate after epiphyte removal from the gross photosynthetic rate of the plants prior to epiphyte removal. The mean I_c of all algae (macroalgae, epiphytes and periphyton) was approx. 24 µmol $m^{-2}s^{-1}$ and not significantly different to the mean I_c of the three seagrasses (23 µmol $m^{-2}s^{-1}$). In contrast, the mean I_k of the algae (138 µmol $m^{-2}s^{-1}$) was significantly higher (U-test, p≤.05) than the mean I_k of seagrasses (69 µmol $m^{-2}s^{-1}$). The I_k values of epiphytes on seagrass leaves were significantly higher than periphyton ('epiphytes' on artificial leaves) (U-test, p≤.05). In contrast, the I_c values of epiphytes and periphyton were not significantly different.

3.2.2 Photosynthetic efficiency

The light-harvesting efficiency of periphyton expressed as GPP_{max} per unit chlorophyll *a* (Table 5) was more than 5 times higher than the efficiency of epiphytes on seagrass leaves (U-test, p≤.05). This large difference was due in part to the low chlorophyll *a* concentration of the periphyton (0.27 mg chl *a* g $d.wt^{-1}$) compared to the epiphytes (0.89 mg chl *a* g $d.wt^{-1}$). When the GPP_{max} is adjusted for biomass the periphyton were also photosynthetically more efficient than the epiphytes (U-test, p≤.05) but expressed on an area basis this trend was reversed.

The GPP_{max} of the macroalgae normalised for chlorophyll *a* content was significantly lower than that of periphyton (U-test, p≤.05) but not significantly different from the GPP_{max} of epiphytes on *P. sinuosa*. Normalised for dry weight, the photosynthetic efficiency of the macroalgae was significantly higher than the efficiency of epiphytes on *P. sinuosa* (U-test, p≤.05) but no different from the efficiency of periphyton.

3.2.3 Photoinhibition

The photosynthetic rates of all types of algae (macroalgae, epiphytes and periphyton) were inhibited significantly between 1020 and 2020 µmol $m^{-2}s^{-1}$. Macroalgal photosynthesis was inhibited by about 11% (paired-t=-9.786, p≤.005) and periphyton photosynthesis on artificial seagrass by 27% (paired-t=-12.89,p≤.0005). The photosynthetic rates of epiphytes on *P. sinuosa* decreased by about 17% (paired-t=-5.832, p≤.005) over the same range of light intensity.

Table 5. Gross maximum primary production (GPP_{max}) of unattached macroalgae, periphyton and epiphytes on *P. sinuosa*, at 18 °C. Mean and standard errors are shown. n=4, n.d.= not determined.

Algal type	GPP max.					
	μgO_2 cm-2 leaf hr-1		mgO_2 g-1 leaf hr-1		μgO_2 µg chl *a*-1.hr-1	
	x	s.e.	x	s.e.	x	s.e.
unattached macroalgae*	n.d.	(-.--)	7.6	(1.00)	7.0	(0.96)
periphyton	7.7	(0.50)	8.2	(0.38)	30.9	(1.42)
epiphytes	10.0	(0.85)	5.2	(0.66)	5.8	(0.74)

* comprised of ~75% *Polysiphonia* sp and ~20% *Cladophora* sp.

3.3 Simple photosynthesis model

The relationships between metabolic rates of *P. sinuosa* at different temperatures and light intensities may be used to approximate seasonal changes in production rates for a given set of conditions. Such a simple model assumes a lack of seasonality in the effect of light and temperature on photosynthesis, and that light and temperature account for all the observed changes in photosynthetic rate. The respiration rate in the light is assumed to equal the respiration rate in the dark.

Monthly averages of mean daily total global radiation over 18-20 yrs (Western Australian Bureau of Meteorology) and mean daylength for each month were used to calculate a mean daily PAR for each month. Attenuation coefficients for Princess Royal Harbour collected bimonthly in 1988-89 (Hillman pers. comm.) and averaged for 3 month periods were used in conjunction with mean daily PAR to calculate the average amount of light penetrating to various depths in Princess Royal Harbour (see Table 7). The average light level during daylight hours at depths of less than 4 m were above I_{sat} for *P. sinuosa* throughout the year. Maximum gross photosynthesis rates in a uniform light field, plus 20% to account for the increased production in an attenuated light field (considered to approximate more closely the conditions in a seagrass meadow, see section 3.1.5), were used for all calculations.

Seasonal water temperature data have been recorded intermittently by the Department of Marine and Harbours from a depth of 8 m at the Albany town wharf between 1984 and 1988 and these data were used to estimate mean monthly water temperatures (Table 6). The relationship between temperature (T) and 1) respiration rate (R) and 2) GPP_{max} were described by the following equations:

1) $R=-0.0153 + 0.024T$, $r^2=0.96$
2) $GPP_{max}=-1.9124 + 0.2576T - 0.0056T^2$, $r^2=1$

Average hourly respiration and production rates (normalised for total plant dry weight) were calculated for each month. The daily respiration rate was obtained by multiplying the hourly rate by 24. Average daily GPP_{max} was calculated by multiplying the average daylight hours during each month by the hourly GPP_{max} rate. Net daily maximum production was obtained by subtracting the average daily respiratory cost from the average daily GPP_{max}. To account for the low angle of the sun immediately after sunrise and before sunset the procedure was repeated using 'daylight hours-1' and 'daylight hours-2' to calculate daily GPP max. The model assumed that compensation (ie net production = 0) occurred during the 1 or 2 hour period subtracted from the actual daylength and that GPP_{max} + 20% occurred during the remaining daylight hours.

Results are presented in Table 6 and Figure 7. The sum of monthly net production for the seagrasses at P_{max} for the total daylight hours was 36.3 mgO_2 g d.wt-1d-1 resulting in a daily average of 3.03 mgO_2 g $d.wt^{-1}d^{-1}$. If the plants are assumed to be at compensation for 1 daylight hour per day the average daily production per year is 1.94 mgO_2 g $d.wt^{-1}d^{-1}$. It decreases to 0.84 mgO_2 g $d.wt^{-1}d^{-1}$ respectively when 2 daylight hours per day are used. When a period of compensation of 1 hour a day is assumed, the plants appear to be in a negative carbon balance during June and July. Given 2 hours of compensating irradiance each day the period of negative carbon balance extends to between April and August inclusive.

A similar procedure was carried out to estimate the seasonal changes in growth of the unattached macroalgae, except that temperature was assumed to remain constant throughout the year and daylight hours were taken to be daylength -1hr. Oxygen flux was converted to carbon using a PQ of 1.2 and carbon was converted to dry weight

Table 6. Simulated average daily net photosynthetic rates for P.sinuosa in Princess Royal Harbour. Respiration and production data are expressed as mgO_2 g d wt^{-1} d^{-1}.

T=water temperature (°C)

Respiration (mgO_2 g d wt^{-1} hr^{-1})=-0.0153 + 0.024T

GPP_{max} (mgO_2 g d wt^{-1} hr^{-1}) =-1.9124 + 0.2576T - 0.0056T^2

Net Production 1 assumes GPP_{max} + 20% occurs for all daylight hours.

Net production 2 assumes GPP_{max} + 20% occurs for daylight hours - 1, and compensation occurs for 1 hour.

Net production 3 assumes GPP_{max} +20% occurs for daylight hours - 2, and compensation occurs for 2 hours.

	Month											
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Daylight hours	14.23	13.33	12.32	11.18	10.28	9.82	10.03	10.82	11.88	12.97	13.97	14.50
Mean temperature (°C)	22.1	21.7	20.9	19.7	18.2	16.8	15.7	15.3	15.8	17.0	18.4	20.5
Respiration	-12.4	-12.1	-11.7	-11.0	-10.1	-9.3	-8.7	-8.4	-8.7	-9.4	-10.2	-11.4
Gross production	17.9	16.6	15.2	13.3	11.4	9.8	9.0	9.3	10.8	13.2	15.6	17.7
Net production 1	5.5	4.5	3.5	2.3	1.2	0.5	0.4	0.9	2.1	3.8	5.4	6.2
Net production 2	4.2	3.3	2.3	1.1	0.1	-0.5	-0.5	0.0	1.2	2.8	4.3	5.0
Net production 3	3.0	2.0	1.0	-0.1	-1.0	-1.5	-1.4	-0.8	0.3	1.7	3.1	3.8

using a multiplication factor of 2.78 (Hillman *et al.*, 1989). Dry weight increment per day was used to calculate a doubling time. The average production rate was 50.8 mgO_2 g $dwt^{-1}d^{-1}$ and was highest in December. Doubling times ranged from 12 days in December to 25 days in June.

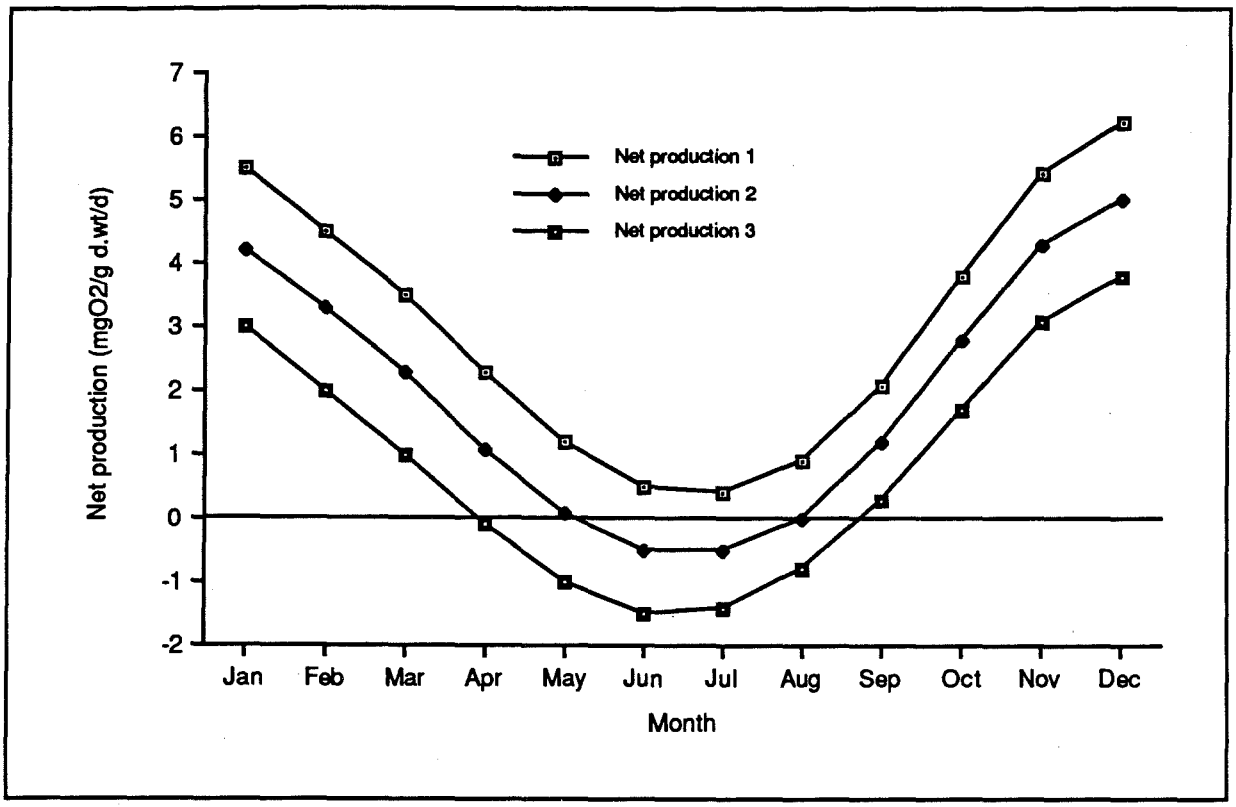

Figure 7. Simulated average daily net photosynthetic rate of *Posidonia sinuosa* from Princess Royal Harbour, Albany. Data from Table 6.

4. Discussion

4.1 I_c and I_k in relation to seagrass depth distribution

Seagrass biomass generally decreases along natural increasing depth gradients and this is mainly attributed to reduced light availability (eg Bulthuis and Woelkerling, 1981; Hillman and McComb 1990). The vertical distribution of different seagrass species is also considered to be determined by minimum light requirements (Dennison, 1987; Dawes and Tomasko, 1988), but little information is available for Australian species.

The depth distribution of the dominant seagrass species found in Princess Royal Harbour overlap considerably. *P. sinuosa* typically occurs in depths of 1.5 to 5.0 m whereas *A. antarctica* has the same lower depth limit in Princess Royal Harbour but can be found in water as shallow as 0.25 m (K Hillman, pers. comm.). *A. antarctica* has the lowest I_c of all the species examined in this study and this may account for its ability to survive at 5 m in Princess Royal Harbour. I_k and I_c were highest for *P. australis* suggesting that this species requires considerably more light than the other two species. *P. australis* is typically found in shallower water than the other species (≤1.5 m in Princess Royal Harbour). The I_k of *P. sinuosa* was lower than the I_k of *A. antarctica*, suggesting that *P. sinuosa* has a lower light requirement than *A. antarctica* and so this species should occur at greater depths than *A. antarctica*.

In contrast, all species had similar compensating irradiances, despite their different depth distributions, suggesting that compensating irradiance (I_c) does not reflect the critical light requirements of a seagrass as much as saturating light intensity (I_k). Both parameters are single points derived from the P-I curve, and both incorporate the respiration rate and initial slope, but I_k also incorporates I_c and P_{max}. The apparent importance of the I_k may be due in part to the ability of seagrass plants to store non-structural carbohydrates in the

rhizomeand translocate these reserves when PAR is low (Drew, 1979; Masini, 1982) or when stressed by other environmental factors (Zieman, 1975). The controls on depth distribution may be related to the amount of time PAR is equal to or greater than I_k, or some light intensity related to I_k, at given depths. The amount of time incident light is above this theoretical saturating light intensity may be important in the production of energy storage compounds necessary for the plant to survive during seasons where the light climate is below the maintenance requirements of the species.

From the curves of photosynthesis vs. irradiance (eg. Figure 5) it is clear that photosynthesis is not saturated at the I_k, but at some higher light intensity. The actual light intensity which saturates photosynthesis is difficult to quantify, but it is related to the I_k (a quantifiable point) and from examination of PI curves it is suggested that a closer approximation of the true saturating irradiance in a uniform light field could be obtained by the equation $I_k \times 2$.

4.2 Attenuated and uniform PAR fields

Light is rapidly attenuated through the canopy of a seagrass meadow. Only about 15% of the light reaching the top of the canopy remains at a depth of 100 mm into the canopy and less than 6% reaching the top of the canopy penetrates to 200 mm. The photosynthetic rates of *P. sinuosa* plants in light fields similar to those experienced in the meadow were considerably different to the rates of the same plants in uniform light fields. The I_c and I_k values discussed above were generated from plants in uniform light fields, and should be considered as minimal in view of the effects of using an attenuated light field. The difference in I_c and I_k found between plants in uniform and attenuated light fields suggest that a relationship of about 1.5 times the tabulated values would more closely approximate those occurring in a vertically attenuated light field, simulating that of a *P. sinuosa* meadow at the study site. The relationship between I_k measured in a uniform light field and that in a meadow may well differ between meadows as the attenuation of light through the seagrass canopy will alter with different standing crops and different species (Gerard, 1984).

4.3 Photosynthesis saturating irradiance in a meadow

The photosynthetic response of *P. sinuosa* at low light intensities is greater in a uniform light field, when compared to the attenuated light field that characterises the light climate within a meadow. If the I_k in the simulated meadow is assumed to be about 1.5 times higher than in a uniform light field and that the actual irradiance intensity that saturates photosynthesis is approximately $2 \times I_k$, it follows that the saturating light intensity within a meadow (I_{sat}) would be 3 times the tabulated I_k values (Table 1). When I_{sat} is calculated for the seagrasses and algae and used with average daily light intensity to form depth limit contours over the four growth periods (Table 7) described in section 3.3, the minimum depths closely correlate with the depth distributions of these seagrass species in Princess Royal Harbour.

4.4 Photoinhibition

The different I_c and I_k in the attenuated and uniform light fields reflect slight differences in respiration and production rates. The 25% increase in net production rate in an attenuated light field may be partly explained by photoinhibition, although according to Hillman *et al.*, (1989) photoinhibition has yet to be satisfactorily demonstrated for any Australian seagrass species. A significant depression in photosynthetic rate of approximately 10% occurred as irradiance increased from 1020 and 2020 $\mu mol\ m^{-2}s^{-1}$ when all photosynthesis data for *P. sinuosa* in a uniform light field (excluding epiphytised plants) were pooled (paired-t=2.388, $p \leq 0.025$, n=20). This was largely a result of a 35% depression in maximum photosynthetic rate of plants at 13 °C. Although photosynthetic efficiency was not determined for segments of the leaf blade in *P. sinuosa*, a lack of photoinhibition and a higher P_{max} in the attenuated light field (ie irradiance decreasing towards the base) compared to the uniform light field, suggest that the inhibition may be occurring in the young or basal sections of the leaves which are normally well shaded by the canopy and relatively free of epiphytes.

If photoinhibition in the basal segments of the leaf is evoked as the probable cause of the difference in net production of *P. sinuosa* in horizontally attenuated and uniform light fields, it is likely to be of ecological significance in a number of ways. For instance, the upper depth limit of 1.5 m for *P. sinuosa* may be related to photoinhibition. In shallow areas, photoinhibition of leaf bases may also help explain why seagrass meadow expansion is very slow (Williams, 1988) and revegetation of patches of bare sediments in meadows is rare (Lewis, 1987; Kirkman, 1989). Colonising plants and plants on the edge of a meadow would be exposed to similar light levels found at the top of the canopy. As a result photosynthesis of the newly-formed basal

Table 7. Average daily PAR intensities at depths of 1-5 m in Princess Royal Harbour for three monthly periods calculated from average attenuation coefficient, daylength and global radiation. The contour lines represent the maximum depth interval where photosynthesis of the seagrasses or algae would saturate (I_{sat}*) for each 3 month period. *$I_{sat}=I_k$ X 3.

Depth	PAR (μmol $m^{-2}s^{-1}$)			
(m)	Jan-Mar (23 °C)	Apr-Jun (18 °C)	Jul-Sep (13 °C)	Oct-Dec (18 °C)
1	641	372	403	653
2	444	264	272	462
3	307	187	184	327
4	212	132	124	232
5	147	94	84	164

.... macroalgae (~75% *Polysiphonia sp* and 20% *Cladophora sp*)
—— epiphytes on artificial seagrass
▪▪▪ *Posidonia australis*
-— *Amphibolis antarctica*
▪ ▪ *Posidonia sinuosa*

segments may be inhibited, reducing the plants ability to lay down the carbohydrate reserves necessary for long-term survival. Without adequate reserves the shoot may be vulnerable in times of extreme light/temperature stress to such an extent that net growth is unattainable. In addition to substrate instability, the low rate of establishment of seedlings on bare sand areas (Zieman, 1975) may also be related to reduced vigour as a result of photoinhibition in shallow water.

Future studies of seagrass and light interactions should examine the relationship between light and photosynthesis along the length of the leaf blade in *P. sinuosa* and other dominant seagrasses on the Western Australian coast.

4.5 Depth adaptation

No evidence of physiological adaptation to low light was found in *P. sinuosa* over the depth range used in this study. The mean I_c and I_k of *P. sinuosa* plants (scraped free of epiphytes) collected from the lower end of their depth distribution in Princess Royal Harbour (4.0 m) were virtually identical to those obtained from non-epiphytised plants collected from shallow water (2.0 m). This also indicates that the apparent lack of 'vigour' associated with epiphytised plants is largely a result of reduced photosynthetic activity due to epiphyte shading of the seagrass leaves, and not some other factor such as competition for nutrients. Upon removal of the light stress (ie. epiphytes) the critical light values (ie. I_c and I_k) were identical to those of non-epiphytised plants. Some seagrasses such as *Halophila stipulacea* can adjust to light stress by chloroplast reorientation in a matter of hours (Drew, 1979). Assuming that the *P. sinuosa* plants growing in about 4.0 m are light-stressed and plants in about 2.0 m are not light stressed, the results suggest that unlike *H. stipulacea*, the light capturing efficiency and therefore the I_k of *P. sinuosa* is not a plastic feature that can respond to changing light regime caused by shading by epiphytes or growth in deeper water. Further investigations incorporating a seasonal component and quantified light stress are required to resolve this question more fully.

4.6 Partitioning of respiration rates

The respiration rate of the leaves of a *Posidonia* plant are about 3 to 5 times higher than the rhizome and roots. This suggests that if a plant experiences prolonged energy stress, the most energy efficient response would be a reduction in the amount of leaf material in preference to rhizome material. Reduction of above ground biomass has been observed in seagrass meadows subjected to chronic light reduction (Gordon *et al.* in prep). The interspecific ratios of leaf respiration to the rhizome and root respiration of what were termed 'whole plants' in this study are remarkably similar. This similarity supports the assumption that 'whole plants', as arbitrarily defined by us in these experiments, are in fact the primary ecological unit within a seagrass meadow. As such their use as analogues to investigate the behaviour of the meadow is more valid than using cut segments of plants.

4.7 Macroalgae and epiphytes

The compensating light requirements of the algae were very similar to the seagrasses but the algae required considerably more light (about twice) for photosynthetic saturation. Differences in photosynthetic efficiency were evident between these two types of aquatic plants. The photosynthetic efficiency of the algae per unit chlorophyll *a* was approximately 10 times that of the seagrasses, but when normalised for dry weight of photosynthetic tissue this difference was reduced to about 2.5 times. The metabolically derived growth rate of the epiphytic algae compared to the seagrasses on a per unit leaf area basis were about 0.6 for *P. australis* and *A. antarctica* and about 1.3 for *P. sinuosa*. Assuming that seagrass above-ground growth is about 70% of the total growth of the plant, it is likely that the rapid leaf production and leaf shedding of *P. australis* and *A. antarctica* would help keep epiphyte accumulation in check. *P. sinuosa* however would be expected to have a higher standing crop of epiphytes per unit area of leaf than the other 2 species.

4.8 Seagrass, macroalgae, epiphytes and light

The photosynthesis-irradiance data for seagrass were derived from experiments using plants that were largely free from epiphytes. Epiphytes are an integral component of all seagrass meadows but their biomass is generally elevated in eutrophic environments. The epiphytic coating on seagrass leaves absorb light, effectively shading the plant. Silberstein *et al.*, (1986) derived a relationship where epiphyte biomass (expressed as chlorophyll *a* cm^{-2}) could be used to estimate the degree of light reduction. Although epiphyte cover is low on new sections of leaves the average epiphyte biomass of *P. sinuosa* plants collected from about 4.0 m was 1.62 µg chl *a* cm^{-2}, which equates to a light reduction of approximately 55%. Increased epiphyte loading of seagrass meadows near the lower end of their depth distribution could reduce available PAR to below the minimum required for survival. The I_c of the epiphytised seagrass plants would theoretically increase from non-epiphytised value of 24 to about 50 µmol $m^{-2}s^{-1}$. Similarly the I_k would increase from 56 to about 120 µmol $m^{-2}s^{-1}$, which equates to an I_{sat} of about 360 µmol $m^{-2}s^{-1}$.

Macroalgae are also associated with seagrass meadows in eutrophic ecosystems, sometimes accumulating in banks over 1 m thick (Authors' pers. obs.). Gordon (1981) recorded no measurable light at a depth of 10 mm into a bed of *Cladophora* sp. Other work on the light reduction through banks of *Chaetomorpha* and *Ulva* has resulted in attenuation coefficients of 0.1 and 0.084 mm^{-1} respectively (Lavery, 1989). The percent light reduction for each 10 mm of a macroalgal bed with an attenuation coefficient of 0.1 mm^{-1} would be about 90%. Under these conditions, a seagrass plant below 10 mm of algae would require an incident light intensity of about 240 µmol $m^{-2}s^{-1}$ to achieve compensation and 560 µmol $m^{-2}s^{-1}$ to reach I_k. In a meadow the incident light intensity required to reach I_{sat} would be nearly 1700 µmol $m^{-2}s^{-1}$.

These data indicate that macroalgal coverage of seagrass meadows or epiphytic cover of seagrass leaves can markedly reduce light reaching the leaf surface causing a significant reduction in the photosynthetic capacity of individual plants within a meadow.

4.9 Effects of temperature on photosynthesis

The most pronounced effect of temperature on photosynthesis in *P. sinuosa* occurred between 13 and 18 °C. Although significant differences attributable to temperature were not found in all of the parameters measured (ie. I_k, I_c etc), the trend in most cases was for an increase in the parameter value with an increase in temperature. With the exception of I_{slope} these trends are similar to those found by Bulthuis (1983) who tested the effect of temperature on photosynthesis in *Heterozostera tasmanica*. The I_c of *P. sinuosa* tended to increase with

temperature, but at a lower rate (0.55T) than that of *H. tasmanica* (0.89T, r^2=.98, n=6). This indicates that *P. sinuosa* requires more light to maintain a positive carbon balance during the summer months when water temperatures are highest. I_{slope} is used in the calculation of I_c and I_k and is a measure of the initial rate of increase of photosynthetic rate with increasing irradiance. I_{slope} is reported to remain constant with changing temperature (Bulthuis, 1983; 1987) as it is related to the light reactions of photosynthesis, which are largely temperature independent. In contrast, I_{slope} tended to increase with temperature in this study (I_{slope}=0.000375T+0.008, r^2=0.964, n=3), and was significantly higher at 23 °C than at 13 °C. Penhale (1977) examined the effect of 3 temperatures (15, 22 and 29 °C) on photosynthesis in *Zostera marina* and found 22 °C to be optimal, with a higher P_{max} and steeper initial slope than at the other temperatures.

The temperature optimum for net photosynthetic production at saturating light intensity was between 18 and 23 °C for *P. sinuosa*. At low light intensities (24 µmol $m^{-2}s^{-1}$) the temperature optima declined to 13 °C. Bulthuis (1983) found a similar trend in *H. tasmanica* with a temperature optima of 5 °C or less at 37 µmol $m^{-2}s^{-1}$. As suggested by Bulthuis (1987) for *H. tasmanica*, it appears that photosynthetic rates of *P. sinuosa* at low light intensities will be highest during winter when water temperatures are low. These generalisations hold true for instantaneous measurements of photosynthesis but seasonal changes in daylength need to be considered when relating these findings to seagrass growth in the field.

Ratios of net production and respiration exceeded 1 and were highest at 18 °C, slightly above 1 at 23 °C and less than 1 at 13 °C. In a 12h day/12h night cycle P_{max}/R values >1 indicate net organic carbon production while values <1 indicate a net organic carbon loss. Daylength in winter is below 12h and it appears that even under conditions of saturating PAR, *P. sinuosa* is in carbon debt at low water temperatures. The results of the simple photosynthetic model show this in more detail. This model, although only a first approximation, indicates that *P. sinuosa* is likely to be 'stressed' (ie. consuming energy reserves) during the June-July period when daylength is short. Conversely *P. sinuosa* appears to be most productive between November and January when daylength is longest. When actual irradiance levels are greater than I_{sat}, daylength becomes the most important factor. Daily photoperiod was found to be the principal control of the depth distribution of *Zostera marina* (Dennison and Alberte, 1985).

A positive annual carbon balance is essential for seagrass viability. Survival during periods of negative carbon balance where daily organic carbon consumption is greater than organic carbon production requires an alternate source of energy. This energy must come from stored reserves, which are predominantly in the rhizome. These reserves must accumulate during periods when organic carbon production is in excess of the requirements for leaf extension, root and rhizome growth, and reproduction. Discrepancies between simulated net organic carbon production and measured net organic carbon production (eg *in situ* leaf extension) may indicate the time of year when seagrasses are most likely to be storing non-structural carbohydrate. In *H.ovalis* this occurs in late summer/autumn when water temperatures are beginning to fall and daylengths shorten but fine and calm conditions often prevail (Masini, 1982). Similar patterns of carbohydrate storage have been reported for *Posidonia oceanica* in the Mediterranean (Pirc, 1985), and this is likely to be the same for most seagrasses in temperate regions.

The predictive ability of the model would increase substantially if temporal changes in the response of seagrass photosynthesis to temperature (if they occur) were known.

5. Conclusions and implications for management

5.1 Relative susceptibility to low light stress

The relative susceptibility of the three species examined in this study to a reduction of light through increased turbidity in the water column would be as follows:

Posidonia australis > *Posidonia sinuosa* > *Amphibolis antarctica*

If a reduction in light was due primarily to epiphyte shading compared to increased turbidity, the relative susceptibility of *Posidonia sinuosa* would increase. The relatively low growth rate of *P. sinuosa*, and hence longer leaf turnover times would allow a greater accumulation of epiphytes on the leaf blade compared to the faster growing species such as *Posidonia australis*. Light reduction to a seagrass leaf can be related directly to epiphyte biomass (Silberstein *et al.*,1986) so each *P. sinuosa* leaf would receive less light than an equivalent leaf from the other species, thereby increasing its relative susceptibility. If the light reduction was due to macroalgal

smothering of seagrass beds as is occurring in Princess Royal Harbour, the susceptibility of *Amphibolis antarctica* would increase relative to the other species. This increased susceptibility is a result of the different morphology of *Amphibolis* compared to that of the genus *Posidonia*. The dense cluster of leaves on the thin erect stem of *Amphibolis* species easily entangles macroalgae and break off as water movement redistributes the macroalgae during periods of strong current or wave action. In contrast the long blades of *Posidonia* would allow relatively free movement of macroalgae across them with minimal entanglement.

5.2 Seasonal aspects of light stress

The annual cycle in energy storage and usage must be considered when determining the season in which reduced light levels might most severely affect seagrass survival. From the photosynthesis simulation model it appears that *P. sinuosa* depends on stored energy reserves for maintenance respiration and growth during winter and that this is balanced by a positive energy budget during spring and early summer. There appears to be little excess energy remaining after a complete annual cycle. It would seem that light stress during the period when the seagrasses are storing non-structural carbohydrate would be the most detrimental for meadow survival. Thus the effect of moderate light stress during summer may not become apparent until the following winter.

Conversely, light reduction would have minimum impact during periods of moderate temperatures, high light intensities and long days, but only if average incident light levels are maintained above I_{sat}. Given these conditions, there are unlikely to be any disruptions to the energy storage processes.

5.3 Recovery from light stress

When epiphytes are removed from *P. sinuosa*, photosynthetic behaviour is similar to non-epiphytised plants, suggesting that *P. sinuosa* can rapidly recover from light stress. However it was not possible to assess how long the epiphytised seagrass plants had been light stressed (ie how long they had high epiphyte biomass) before the experiments. Given the importance of stored energy reserves, there is likely to be a seasonal component in the ability of the plant to recover from light stress.

5.4 Adaptation of *Posidonia sinuosa* to low light

No evidence of adaptation to low light intensities were seen in *P. sinuosa*. During the experiments reported here, the low light conditions were brought about by epiphyte shading. Experiments on plants from the extremes of their depth range in unperturbed areas are needed to understand the physiological ability of plant adaption to low light conditions.

5.5 Competitive ability of seagrasses and epiphytes

The relatively high I_k of epiphytes compared to seagrasses indicates that epiphytes are more susceptible to low light conditions than seagrasses. Coupled with the lack of large storage organs (ie like the rhizome of seagrasses) in epiphytes, prolonged periods of low light may significantly reduce epiphyte loadings. Growth rates of *P. sinuosa* are lower than those of epiphytes, and so this species may be disadvantaged in areas with high epiphyte growth (see section 5.1).

5.6 Competitive ability of seagrasses and macroalgae

The annual growth rate of macroalgae (based on metabolic rates) exceeds that of *P. sinuosa* by about 25 times. Doubling times of macroalgal biomass in ideal conditions may be as low as 12 days in summer. This has important implications if mechanical harvesting is used as a management tool. Given equivalent conditions a comparative doubling time for *P. sinuosa* is about 1.6 years, highlighting the very slow net growth of the large seagrasses. The high I_k of the unattached macroalgal population suggests that, as with epiphytes, it may be possible to control biomass by reducing light availability. The greater relative cell size of macroalgae compared to epiphytes, suggests a greater capacity for energy storage and therefore macroalgae may take a longer time to succumb to a particular light stress than epiphytes.

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