

# PHOTOSYNTHETIC LIGHT-RESPONSE CURVES IN MARINE BENTHIC PLANTS FROM THE THAU LAGOON

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## Introduction

Photosynthetic light-response curves (so-called P-I curves) are widely used in studies and models of algal productivity and to characterize photoacclimation as adaptative responses to environmental conditions. A few fundamental parameters are commonly used to define the P-I function: rate of respiration in darkness ( $R_d$ ), light saturated photosynthetic rate ( $P_m$ ), ascending slope at limiting irradiance ( $\alpha$ ), compensation point ( $P_c$ ), saturation point ( $P_s$ ). However, light saturation parameter  $I_k$  (1) is the most often used because it is independent of the units used for expressing photosynthesis.  $I_k$  is often a better indicator of  $P_m$  than  $\alpha$  in comparing individuals acclimated to different irradiances as reported for phytoplankton (2) and confirmed for macroalgae (3) and therefore only the  $I_k$  data are presented in this paper. To the west of Montpellier, in the Thau Lagoon ( $43^{\circ}24'$  N and  $3^{\circ}32'$  E) of above 7000 ha in area and the mean and maximum depth of above 4 and 10 m, respectively, cultures of oysters and mussels have been carried out. Beside their great economic importance, the oyster cultures play also a significant role in functioning of lagoon ecosystem. By filtering organic matter they affect phytoplankton development and accelerate biodeposition processes in the sediments. The increased amount of organic matter in the sediments promotes oxygen deficiency in the bottom water layers and the risk of anoxia is the greatest from June till October when water temperature exceeds  $20^{\circ}$  C. The abundant macrophyte assemblages developing on the bottom of the lagoon as well as on the ropes with mussel cultures have an essential effect on oxygen conditions. In the lagoon over 80 taxa of benthic plants have been found (4). The study reported here was done to obtain knowledge of photosynthetic rate, oxygen evolution and light requirements in different species.

## Material and methods

The measurements of gas exchange intensities in 33 species belonging to green (10 species), brown (3) and red (18) algae and vascular plants (2) were performed in October 1993 and September 1994. The plants were collected from the same stations (zones A and B) (4) from the ropes with oyster cultures and also from the bottom of the lagoon. The majority of species was taken from the depth of 0-1 m, part from 4-5 m and 11 species from the both depths. Beside irradiance, the shape of P-I curve is strongly influenced by temperature,  $CO_2$  concentration and physiological state of algae. Therefore the experiments were carried out: 1. at the same temperature as in natural environment ( $18^{\circ}$ C in October 1993 and  $21^{\circ}$ C in September 1994), 2. at constant and relatively high  $CO_2$  level (0.03% in the gas phase of measuring chambers maintained by Warburg no. 10 carbonate buffer), 3. to characterize the physiological state of thalli, P-I measurements

should begin as soon as possible after collecting from the field (5) and therefore plants were analysed during two days at the longest, 4. to avoid self-shading the measurements were carried out using small pieces of thallus. The results obtained enable to compare light requirements and gas exchange rates of plants belonging to different classes with different morphology and adaptations but growing at similar conditions.

The gas exchange rates were determined by the microvolumetric method described elsewhere (6). The measurements were carried out in the laboratory at least in 4 replicates. Photosynthetic available radiation (PAR) was measured using quanta-meter with a cosine collector and expressed in  $\mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ . According to the review of (5), unfortunately many P-I data sets contain too few or noisy data in the light-limited region, so that slope estimates are unreliable. Indeed, some published P-I curves have most of their data near the light-saturated region because of poor selection of irradiance. PAR was increased by small increments with at least five values below  $I_k$  to provide robust estimates of the P-I parameters. In macroalgae photosynthetic rates are usually normalized to some biomass parameter, typically fresh weight (fw), dry weight (dw) or surface area (7). In this paper photosynthesis and respiration were expressed in  $\text{mm}^3 \text{O}_2\cdot\text{h}^{-1}\cdot\text{mg}^{-1}$  fw and the coefficients for counting over the data on dry weight were given.

### Results

The values of selected parameters for macrophytes taken at a depth of 0-1 m, from the ropes and the bottom of the lagoon were presented in Tab. I and II, respectively.  $P_m$  changed from 6.1 to  $0.15 \text{ mm}^3 \text{O}_2\cdot\text{h}^{-1}\cdot\text{mg}^{-1}$  fw, i.e. 40x and appeared to be the most variable parameter. Its greatest values were found in *A. plumula* and *D. hutchinsiae* (red algae) and *C. pygmaea*, *E. linza* and *B. plumosa* (green algae) and the lowest in *C. fragile*, *G. bursa-pastoris*, *G. verrucosa* and *L. pinnatifida*.  $R_d$  values changed from -0.67 to  $-0.07 \text{ mm}^3 \text{O}_2\cdot\text{h}^{-1}\cdot\text{mg}^{-1}$  fw, i.e. only about 10x. Both the greatest and the lowest  $R_d$  rates were noted in the same species as in the case of  $P_m$ . Light requirements of the plants, determined by  $P_c$ ,  $I_k$  and  $P_s$ , changed in relatively narrow range, about 3x.  $P_c$  values were from 3 to 10 and 2.5 to  $9.5 \mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  in bottom plants and algae from the ropes, respectively. The greatest values were observed in *Chondrus* sp., *L. hakodatensis*, *P. mottei*, *G. verrucosa* and *G. doryphora* and the lowest in *D. hutchinsiae*, *B. plumosa* and *U. rigida*. In the algae from the ropes  $I_k$  changed from 30 to 70 and in plants growing on the bottom from 15 to  $55 \mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ . The greatest values were found in *B. plumosa*, *C. pygmaea*, *L. hakodatensis* and the lowest in *C. fragile*, *G. doryphora*, *N. punctatum* and both *Zostera* species. Photosynthesis saturation was at 60-140 and 40-100  $\mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  in the algae from the ropes and bottom plants, respectively. The greatest and lowest  $P_s$  values were noted in the same species as in the case of  $I_k$ . At the highest PAR intensities used (500-600  $\mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) a decrease in  $P_m$  usually was not observed or it was very slight. P-I curves were compared in 11 species (7 from the ropes and 4 from the bottom) collected at 0-1 and 4-5 m depths. It was found that in 10 species  $P_m$  was considerably higher in algae taken at 4-5 m depth (by about 10-20%) with the exception of *C. linum* showing similar  $P_m$  values. Also the majority of thalli from 4-5 m was characterized by lower  $R_d$  and  $P_c$  values than thalli from the upper layer.

### Discussion

Studies of P-I curves in a large number of benthic algal species from the same region are not numerous. Such investigations were carried out in the Baltic (8, 9) but there is a lack of similar data from the Mediterranean. It was found that the species with high or low  $P_m$  values also show respectively high or low  $R_d$  rates. Species belonging to various taxonomical groups but with thin thalli formed by one or two layers of cells or with strongly branched thalli and branches formed by a series of single cells show high gas exchange rate per fw. These are usually annual species. On the other hand, perennial species with thick thalli formed by many cell layers are characterized by low  $P_m$  and  $R_d$

values. Also  $P_c$  is usually low in species with delicate thalli and high in species with thick ones. These data indicate that beside other factors (10) the morphology of the thallus has an essential effect on light efficiency and  $CO_2$  utilization. The light intensity required to

Table I. Commonly used parameters to define the P-I function in algae growing on the ropes at 0-1 m depth. October 1993, temp. 18°C.

Plant class	Species	$P_m$	$R_d$	$P_c$	$I_k$	$P_s$	dw/fw	Symbols
Green	<i>Bryopsis plumosa</i>	4.79	-0.22	2.5	70	140	0.196	D
algae	<i>Cladophora pygmaea</i>	5.97	-0.61	4.5	55	80	0.478	I
	<i>Cladophora</i> sp.	2.06	-0.25	4.0	50	80	0.263	I
	<i>Codium fragile</i>	0.17	-0.09	7.0	30	90	0.089	D
	<i>Enteromorpha linza</i>	4.93	-0.52	5.5	45	100	0.296	I
	<i>Ulva rigida</i>	1.52	-0.24	5	40	65	0.273	I, A
Brown	<i>Dictyota linearis</i>	3.14	-0.34	4.0	40	80	0.371	I
algae	<i>Sargassum muticum</i>	0.48	-0.14	6.5	40	80	0.174	D, P
Red	<i>Antithamnion plumula</i>	6.14	-0.67	3.0	35	70	0.412	A, B, T
algae	<i>Ceramium diaphanum</i>	1.54	-0.24	6.0	45	110	0.189	A, B, T
	<i>Chylocladia verticillata</i>	0.46	-0.10	5.0	35	70	0.098	A, B
	<i>Dasya hutchinsiae</i>	4.48	-0.29	2.5	40	90	0.404	A, B, T
	<i>Gracilaria verrucosa</i>	0.29	-0.07	8.5	40	80	0.160	P, B
	<i>Grateloupia doryphora</i>	0.62	-0.36	8	30	70	0.179	A, B
	<i>Laurencia pinnatifida</i>	0.42	-0.13	7.5	35	90	0.120	P, B, S
	<i>Lomentaria hakodatensis</i>	0.96	-0.16	4.5	35	80	0.169	P, B, T
	<i>Nitophyllum punctatum</i>	1.81	-0.28	4.0	30	60	0.232	A, B
	<i>Polysiphonia elongata</i>	1.64	-0.45	6.5	35	70	0.310	P, B, T
	<i>Polysiphonia mottei</i>	1.63	-0.41	9.5	50	90	0.194	P, G

Table II. Algae growing on the bottom at 0-1 m depth. September 1994, temp. 21°C.

Green	<i>Bryopsis plumosa</i>	2.98	-0.27	3	40	90	0.143	D
algae	<i>Chaetomorpha linum</i>	0.63	-0.11	4	45	80	0.229	I
	<i>Cladophora</i> sp.	1.22	-0.45	7	30	60	0.314	I
	<i>Codium fragile</i>	0.23	-0.09	5.5	30	80	0.143	D
	<i>Enteromorpha flexuosa</i>	2.37	-0.24	5	50	90	0.287	I
	<i>Ulva rigida</i>	1.5	-0.34	3.5	35	60	0.343	I, A
Brown	<i>Dictyota linearis</i>	1.43	-0.27	5	45	90	0.233	I
algae	<i>Dilophus</i> sp.	1.63	-0.23	4	40	80	0.099	
	<i>Sargassum muticum</i>	0.38	-0.13	7	30	80	0.147	D, P
Red	<i>Alsidium corallinum</i>	0.7	-0.11	4	45	60	0.236	F
algae	<i>Centroceras clavulatum</i>	2.0	-0.44	4	35	90	0.294	S
	<i>Chondrus</i> sp.	0.32	-0.11	10	40	70	0.352	A, B
	<i>Dasya hutchinsiae</i>	3.83	-0.73	6	45	90	0.376	A, B
	<i>Gracilaria bursa-pastoris</i>	0.15	-0.05	3.5	25	70	0.107	P, B, T
	<i>Hypnea musciformis</i>	0.57	-0.12	4	35	80	0.137	S
	<i>Lomentaria hakodatensis</i>	0.85	-0.22	8.5	55	100	0.199	P, B
	<i>Prionitis</i> sp.	0.53	-0.18	7.5	40	90	0.193	
Vascular	<i>Zostera marina</i>	0.26	-0.17	4.5	15	40	0.228	
plants	<i>Zostera noltii</i>	0.53	-0.37	6	25	80	0.250	

Symbols of species: A -annual, P -perennial, I -isomorphic, D -diplont, B -diplobiont

Symbols of thallus: T -tetrasporophyte, S -sterile thalli, F -fertile thalli, G -gametophyte with cystocarp

saturate photosynthesis varies markedly from one species to another (10). This is partly because of the inherent difficulty in identifying saturation irradiance in a P-I curve.  $P_s$  values reported in the literature (7, 10) are often much higher than those noted in the present study. It could be additionally due to the fact that the measurements in the field are usually carried out on whole thalli resulting in self-shading effect. In the present work  $I_k$  and  $P_s$  were in the range of 30-45 and 60-90  $\mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , respectively. It means that photosynthesis saturation in algae was at irradiance 2 times higher than  $I_k$ . These values are consistent with the data obtained for phytoplankton (11).

Photosynthesis rates in thalli taken at 4-5 m depth were significantly higher than in thalli from 0-1 m. Similar observations in some species from harbour water at Woods Hole were made (12), however, contrary relationships could also be found. Tab. III presents comparison of the results from the present work with the data obtained by the same method but for algae from other geographic regions (9, 13). The measurements performed on plant material collected from 0-5 m depth were carried out in different months and temperatures but in the period of abounding development of macrophyte assemblages. In arctic algae  $P_m$  and  $R_d$  are distinctly low, 2-3 times lower as compared to algae from temperate regions. Light requirements of these algae, characterized by  $P_c$ ,  $I_k$  and  $P_s$ , are also very low. Contrary to the algae from temperate region, arctic algae show a decrease in photosynthetic rate at higher PAR values. In arctic algae  $P_m$  was reduced by low temperature so it may predispose algae to photoinhibition. In spite of many similarities, e.g. ranges of  $R_d$  and  $P_c$ , the algae from cold- and warm-temperate regions also show some differences.  $P_m$  range is 2 times higher in the algae from warm-temperate region and  $P_s$  values are also considerably higher.

Table III

Parameter	Arctic region Spitsbergen August 3°C	Cold-temperate region Baltic Sea July 18°C	Warm-temperate region Mediterranean Sea September-October 18-21°C
$P_m$	0.045-0.62	0.14-3.23	0.15-6.14
$R_d$	-0.035-0.305	-0.05-0.81	-0.05-0.73
$P_c$	1.8-5.5	2.7-14.5	2.5-10
$I_k$	7-18	15-70	25-70
$P_s$	18-36	25-120	60-140

#### References

- 1 Talling, J.F. (1957) *New Phytol.* 56, 29-50
- 2 Beardall, J. and Morris, I. (1976) *Mar. Biol. (Berl.)* 37, 377-387
- 3 Henley, W.J. (1992) *J. Phycol.* 28, 625-634
- 4 Gerbal, M. (1994) These Docteur de l'Universite d'Aix-Marseille II pp. 240
- 5 Henley, W.J. (1993) *J. Phycol.* 29, 729-739
- 6 Zurzycki, J and Starzecki, W. (1971) in *Plant Photosynthetic* (Šesták, Z., Čatský, J. and Jarvis, P.G., eds) pp. 257-275, Dr W. Junk N.V. Publishers, The Hague
- 7 King, R.J. and Schramm, W. (1976) *Mar. Biol. (Berl.)* 37, 209-213
- 8 King, R.J. and Schramm, W. (1976) *Mar. Biol. (Berl.)* 37, 215-222
- 9 Latała, A. (1991) *Acta Ichthol. et Pisc.* 21, 85-100
- 10 Kirk, J.T.O. (1983) pp. 401, Cambridge University Press, Cambridge
- 11 Harris, G.P. (1980) in *The Physiological Ecology of Phytoplankton* (Morris I, ed.) pp 129-187, Blackwell Scientific Publications, Oxford
- 12 Ramus, J, Beale S. and Mauzerall D. (1976) *Mar. Biol.* 37, 231-238
- 13 Latała, A. (1990) *Polar Research* 8, 303-307

**Acknowledgments** The author is grateful to Dr J-M Deslous-Paoli from IFREMER Station in Sète for providing laboratory facilities and Dr M. Lauret and Dr M. Verlaque for verification of macrophyte designation.

This work was partly supported by ATP E01 and BW UG.