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*Ericaria crinita* population from Minorca. Photography taken by Enric Ballesteros in June 2021.

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# Homogeneity of photosynthetic features in canopy-forming macroalgae of the order Fucales from shallow and sheltered environments

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## ABSTRACT

Photosynthetic features of different canopy-forming macroalgae of the order Fucales (Phaeophyceae) living in shallow and sheltered environments show a high homogeneity when compared with other morphologically similar species living across a depth gradient. Photosynthesis at saturation (situated around  $5 \text{ mg O}_2 \text{ gAFDM}^{-1} \text{ h}^{-1}$ ) and photosynthetic efficiency [around  $0.4 \text{ mg O}_2 \cdot \text{m}^2 \text{ s}^{-1}$  ( $\mu\text{mol photon} \cdot \text{gAFDM} \cdot \text{h}^{-1}$ )] are relatively low, while dark respiration (around  $1 \text{ mg O}_2 \text{ gAFDM}^{-1} \text{ h}^{-1}$ ) and light at compensation (around  $24 \mu\text{mol photon} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ ) are relatively high, as it corresponds to the characteristics of “sun” plants. C:N and C:P ratios suggest a strong nutrient limitation for growth and photosynthesis, in agreement with the low dissolved nutrient levels usually found in shallow Mediterranean waters. Homogeneity in photosynthetic features points to a good local adaptation of the different species to the prevailing light conditions but opens the question of which are the factors allowing the coexistence of different species of Fucales in sheltered and shallow Mediterranean environments.

## KEY WORDS

Macroalgae,  
Fucales,  
marine forest,  
shallow infralittoral,  
photosynthesis,  
light.

## RÉSUMÉ

*Homogénéité des caractéristiques photosynthétiques des macroalgues de l'ordre des Fucales formant une canopée dans les environnements peu profonds et protégés.*

Les caractéristiques photosynthétiques de différentes algues de l'ordre Fucales (Phaeophyceae) qui croissent dans des environnements peu profonds et protégés montrent une grande homogénéité si on les compare avec d'autres espèces de morphologie similaire présentes dans d'autres environnements le long du gradient bathymétrique. La photosynthèse en saturation (située aux environs de  $5 \text{ mg O}_2 \text{ g}$  masse sèche sans cendres<sup>1</sup> h<sup>-1</sup>) et l'efficacité photosynthétique [environ  $0.4 \text{ mg O}_2 \cdot \text{m}^2 \text{ s}^{-1}$  ( $\mu\text{mol photon} \cdot \text{g}$  masse sèche sans cendres<sup>1</sup> · h<sup>-1</sup>)] sont relativement basses, alors que la respiration sombre (environ  $1 \text{ mg O}_2 \text{ g}$  poids sec sans cendres<sup>1</sup> h<sup>-1</sup>) et la lumière à compensation (environ  $24 \mu\text{mol photon} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ ) sont relativement élevées, comme c'est le cas avec les caractéristiques des plantes « de soleil ». Les rapports C:N et C:P suggèrent une forte limitation par N et P, ce qui est congruent avec les niveaux de nutriments très bas qu'on observe régulièrement dans les eaux peu profondes méditerranéennes. L'homogénéité des caractéristiques photosynthétiques indique une adaptation locale des différentes espèces aux conditions de lumière présentes mais pose la question des facteurs permettant la coexistence des différentes espèces de Fucales dans les environnements méditerranéens peu profonds et protégés.

## MOTS CLÉS

Macroalgues,  
Fucales,  
forêt marine,  
infralittoral peu profond,  
photosynthèse,  
lumière.

## INTRODUCTION

Marine forests are the ocean equivalent of terrestrial forests, where canopy-forming macroalgae play some of the same roles trees have in a forest (Wernberg & Filbee-Dexter 2019). The main canopy-forming algae belong to the orders Laminariales, Tilopteridales and Fucales (Phaeophyceae, Stramenopiles) and they are commonly observed in rocky shores and shallow subtidal habitats, from arctic to tropical seas. Marine forests play a pivotal role in coastal environments by providing food, habitat and shelter for other organisms and by decreasing wave impact on the shore, which in turn decreases coastal erosion (Dayton 1985; Steneck *et al.* 2002; Smale *et al.* 2013; Piazzini *et al.* 2018; Pinna *et al.* 2020). Marine forests are threatened by a wide array of human-driven pressures such as direct destruction, pollution, overgrazing, climate change and coastal development (e.g. Steneck *et al.* 2002; Arévalo *et al.* 2007; Mangialajo *et al.* 2008; Sales & Ballesteros 2009; Coleman & Wernberg 2017; Smale 2020). Despite these evidences, marine forests regression is not happening everywhere (i.e., Friedlander *et al.* 2020), with local stressors being very important in the regional final outcome (Krumhansl *et al.* 2016; Wernberg *et al.* 2019).

Although kelp forests are not an important element of Mediterranean ecosystems, members of the order Fucales replace them as the main habitat-forming species in shallow waters (Rodríguez-Prieto *et al.* 2013). The Mediterranean Sea is heavily impacted by human activities and the regression of the populations of Fucales in several areas has been thoroughly described (Cormaci & Furnari 1999; Boudouresque 2003; Thibaut *et al.* 2005, 2015, 2016; Bianchi *et al.* 2014; Mancuso *et al.* 2018; Mariani *et al.* 2019). We are currently witnessing efforts to recover lost populations (Verdura *et al.* 2018; De la Fuente *et al.* 2019; Gianni *et al.* 2020; Medrano *et al.* 2020; Orlando-Bonaca *et al.* 2021), but we still do not have enough ecophysiological studies that address the photosynthetic and growth responses of each species to different relevant environmental parameters that can be critical for the success of restoration actions.

One of the main factors explaining the distribution of aquatic macrophytes is light (Kirk 1994; Rodríguez-Prieto *et al.* 2013), which is critical when predicting their depth distribution ranges (Giaccone & Bruni 1973; Sant & Ballesteros 2020). In fact, the depth distribution patterns of members of the order Fucales in the Mediterranean is related to the photosynthetic features at the species level (Sant & Ballesteros 2021a), with deep water species showing high photosynthetic activity at light saturation levels and high photosynthetic efficiencies at low light levels. However, the trend of increasing maximum photosynthetic rates and efficiency with depth shown by Sant & Ballesteros (2021a) involved one (or two) species per depth range, questioning the validity of the observed pattern. The same authors (Sant & Ballesteros 2021b) showed that the intraspecific variability in the photosynthetic features with depth agreed with the results observed in the depth-related trends in different species, adding consistency to the previous results.

Given the results obtained by Sant & Ballesteros (2021a, b) it may be expected that species of Fucales growing together in the same light environment should display similar photosynthetic features that allow their coexistence in the absence of differences in other critical factors such as hydrodynamism (Giaccone 1973; Ballesteros 1992), temperature (Tremblin *et al.* 1986; Verdura *et al.* 2021), nutrients (Delgado *et al.* 1994; Celis-Plá *et al.* 2014), desiccation (Delgado *et al.* 1995), salinity (Tremblin *et al.* 1986; Celis-Plá *et al.* 2016) or grazing intensity (Vergés *et al.* 2009). Thus, our hypothesis is that canopy-forming algae of the order Fucales living in the same environment should show similar photosynthetic features. In particular, we want to assess if Mediterranean species coexisting in sheltered shallow waters display similar photosynthetic efficiencies and maximum photosynthetic rates. We also compare these values with data obtained with other Mediterranean Fucales inhabiting different environments (Sant & Ballesteros 2021a). We finally look at the content of carbon, nitrogen and phosphorus in tissue samples and the ratios between them, since nutrients have been claimed as a limiting factor for photosynthesis and growth in Mediterranean macroalgae (Ballesteros 1992; Delgado *et al.* 1994).

## MATERIAL AND METHODS

We follow the recent nomenclatural changes proposed by Molinari-Novoa & Guiry (2020), which divide the Mediterranean members of the ancient genus *Cystoseira* in three genetically (Draisma *et al.* 2010) and also morphologically (Orellana *et al.* 2019) different clades belonging to the genera *Gongolaria* Boehmer, *Cystoseira* C. Agardh and *Ericaria* Stackhouse. The selected species are *Gongolaria barbata* (Stackhouse) Kuntze [syn. *Cystoseira barbata* (Stackhouse) C. Agardh], *Cystoseira compressa* (Esper) Gerloff & Nizamuddin subsp. *pustulata* Ercegović ex Verlaque, *Cystoseira foeniculacea* (Linnaeus) Greville f. *tenuiramosa* (Ercegović) Gómez-Garreta *et al.*, and *Ericaria crinita* (Duby) Molinari-Novoa & Guiry (syn. *Cystoseira crinita* Duby). We follow the morphological criteria established by Verlaque (1988) and Verlaque in Thibaut *et al.* (2015) concerning the distinction between *Cystoseira compressa* subsp. *pustulata* and *Cystoseira humilis* Schousboe ex Kützing.

The four species studied here are distributed across the Mediterranean Sea although *G. barbata* also extends its geographical distribution to the Black Sea and adjacent Atlantic shores (Ercegović 1952; Ribera *et al.* 1992; Sales *et al.* 2012; Rodríguez-Prieto *et al.* 2013; Thibaut *et al.* 2015). They are regarded as threatened by the Barcelona Convention (Verlaque *et al.* 2019). These species are considered to be perennial although *C. compressa* subsp. *pustulata* and *C. foeniculacea* f. *tenuiramosa* can accomplish their life cycle in one year (Ballesteros pers. obs.). Only *E. crinita* is strictly epilithic since the other three species can grow also attached to seagrass rhizomes (Sales & Ballesteros 2009) and in the case of *C. compressa* subsp. *pustulata* epiphytizing other algae (Thibaut *et al.* 2015). All the species mainly grow in shallow and sheltered environments

(Feldmann 1937; Giaccone & Bruni 1973; Rodríguez-Prieto *et al.* 2013; Thibaut *et al.* 2015; Blanfuné *et al.* 2016) and make abundant populations in bays and coves at the island of Minorca (Balearic islands, western Mediterranean) (Sales & Ballesteros 2009).

Sampling area was located in the Marine Protected Area (MPA) situated at the northern side of the island of Minorca. Samples were collected at two different sites: inside the bay of Fornells (*G. barbata*, *C. compressa* subsp. *pustulata* and *C. foeniculacea* f. *tenuiramosa*) and inside the bay of Tirant (*E. crinita*). The sampling site in Fornells (40°1'53.368"N, 4°7'29.798"E) was located in a sheltered seagrass meadow of *Cymodocea nodosa* (Ucria) Ascherson. The three species were attached to the rhizomes of the seagrass or grew over small cobbles, between 0.4 and 0.8 m depth. Green algae were amongst the most abundant accompanying species: *Halimeda tuna* (Ellis & Solander) Lamouroux, *Caulerpa prolifera* (Forsskal) Lamouroux, *Dasycladus vermicularis* (Scopoli) Krasser and *Acetabularia acetabulum* (Linnaeus) Silva. The sampling site in Tirant (40°3'10.055"N, 4°6'3.474"E) was located in the rocky bottoms situated around several small islets, between 0.3 and 0.8 m depth. Other common species were the encrusting coralline *Neogoniolithon brassica-florida* (Harvey) Setchell and Mason at the basal layer, *D. vermicularis* at the turf layer and *Haliptilon virgatum* (Zanardini) Garbary & Johansen growing as an epiphyte.

Methods mostly follow those described in Sant & Ballesteros (2021a). Sampling was performed between late April and mid May, when the Mediterranean members of shallow water Fucales show their maximum development and growth (Sauvageau 1912; Feldmann 1937; Ballesteros 1992; Sales & Ballesteros 2012). Collection of specimens was performed by snorkelling. Specimens of the selected species were collected during late afternoon, every day, and maintained overnight submerged at sea inside mesh bags protected from direct light until next morning. Specimens were sorted and prepared for photosynthesis and respiration assays in the early morning just before the experiments began (Sant & Ballesteros 2020). Material selection, manipulation and assays were performed according to the recommendations made by Littler (1979), Littler & Arnold (1980) and Littler & Littler (1985). Photosynthesis assays were performed in 270 mL Winkler glass bottles. Apical branches with a length of 2-3 cm were selected among the collected material, cleaned of epiphytes and introduced in the glass bottles containing seawater and a glass marble hanging inside the bottle and subjected with a nylon line. The bottles with the algal specimens were tightly closed and hung in a structure hanging from a buoy and placed in the sea at Fornells Bay, at 0.5 m depth. Waves moved the structure and the glass marbles shook the water inside the bottle, breaking diffusion gradients. Different photon flux densities (PFDs) were obtained by covering the structure with a different number of neutral filters, using a black filter to measure dark respiration. Four replicates per species and four empty bottles (to account for variation not due to macroalgae) were assayed every day at a different PFD mak-

ing a total of 20 assays per day. Nine different PFDs were assayed. Ambient light in each assay was measured using a spherical sensor Li-1000 SPQA deployed at the same site and depth of the hanging structure. PFD attenuation inside the hanging structure with increasing number of filters was also measured ( $y = 100e^{-0.52x}$ ,  $R^2 = 0.99$ ,  $x =$  number of neutral filters,  $y =$  % ambient PFD). Light intensities ranged between 0 and 2126  $\mu\text{mol photon m}^{-2} \text{s}^{-1}$ . Incubation times ranged between three and four hours and assays were always performed between 10:00 am and 2:00 pm local time. Each specimen was used only once, which made every assay independent from the others. Oxygen was measured after the assay with an Oxygen Analyzer Orbisphere 2607 with an accuracy of 0.01  $\text{mg O}_2 \text{l}^{-1}$ . Oxygen production/dark consumption was measured as the difference between the oxygen from each bottle containing a specimen and the average of the four empty bottles. Specimens used in the assays were dried at 60°C for 48 hours to obtain their dry mass (DM) (Boudouresque 1971; Romero 1981; Ballesteros 1986). The specimens were then burned in an oven for four hours at 500°C to obtain the ash free dry mass (AFDM; Brinkhuis 1985).

The data obtained in the assays was pooled together for every species to obtain the photosynthesis/PFD curves. We did not adjust any function to the curves due to the existence of different models (see Jones *et al.* 2014 for a discussion). Alternatively, we have obtained the different photosynthetic parameters directly based on photosynthesis at saturation levels ( $P_{\text{max}}$ ) and variation of photosynthesis at low light levels (photosynthetic efficiency,  $\alpha$ ) (Arenas *et al.* 1995; Gómez *et al.* 1996; Gómez & Wiencke 1997), which allows comparisons within our data (Sant & Ballesteros 2020). The photosynthetic parameters finally obtained were dark respiration ( $R_d$  in  $\text{mg O}_2\text{-gAFDM}^{-1}\text{-h}^{-1}$ ), light compensation point ( $I_c$  in  $\mu\text{mol photon}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ), photosynthetic efficiency [ $\alpha$  in  $\text{mg O}_2 \text{m}^2 \text{s}^{-1} (\mu\text{mol photon}\cdot\text{gAFDM}\cdot\text{h})^{-1}$ ], light at saturation levels ( $I_k$  in  $\mu\text{mol photon}\cdot\text{m}^{-2} \text{s}^{-1}$ ), and photosynthesis at saturation levels ( $P_{\text{max}}$  in  $\text{mg O}_2\text{-gAFDM}^{-1}\text{-h}^{-1}$ ) (Fig. 2).

Nutrient content in tissues for each species was measured from specimens collected at the same depths as the specimens used for the photosynthetic assays. The samples were frozen after collection and on arrival in the laboratory, they were defrosted, dried and triturated. Carbon and nitrogen were measured with a Carlo-Erba Autoanalyzer (Serveis Científico-Tècnics, University of Barcelona) and phosphorus was analysed with an inductively coupled plasma mass spectrometer (ICP) after acid digestion of the samples, following Mateo & Sabaté (1993).

Differences between  $P_{\text{max}}$  and  $R_d$  between species were tested with a one-way ANOVA followed by a Tukey test. To compare the lineal part of the photosynthesis/PFD curves ( $\alpha$ ) a two-way (species and light) ANOVA followed by a Tukey test was used. Data was log-transformed in order to accomplish the assumptions of ANOVA. Relationships between parameters were estimated using Pearson lineal correlations. All statistical analyses were performed using SYSTAT® (SPSS Inc.).

TABLE 1. — Photosynthetic parameters:  $P_{max}$ , photosynthesis at saturation, in mg O<sub>2</sub>·g AFDM<sup>-1</sup>·h<sup>-1</sup>; **sd**, standard deviation;  $I_k$ , light at saturation, in μmol photon·m<sup>-2</sup>·s<sup>-1</sup>;  $I_c$ , light at compensation, in μmol photon·m<sup>-2</sup>·s<sup>-1</sup>;  $R_d$ , dark respiration, in mg O<sub>2</sub>·g AFDM<sup>-1</sup>·h<sup>-1</sup>; % $R_d/P_{max}$ , ratio between  $R_d$  and  $P_{max}$  (in percentage).

Species	$P_{max}$	± sd	$I_k$	$I_c$	$R_d$	± sd	% $R_d/P_{max}$
<i>Gongolaria barbata</i> (Stackhouse) Kuntze	6.49	1.08	147.2	25.7	1.36	0.17	21.0
<i>Cystoseira compressa</i> subsp. <i>pustulata</i> Ercegovic ex Verlaque	5.50	1.72	123.4	23.9	1.21	0.20	22.0
<i>Cystoseira foeniculacea</i> f. <i>tenuiramosa</i> (Ercegovic) A.Gómez Garreta, M.C.Barceló, M.A.Ribera & J.Rull Lluch	4.53	0.64	128.3	26.1	0.98	0.18	21.6
<i>Ericaria crinita</i> (Duby) Molinari & Guiry	4.27	0.48	198.1	21.7	0.58	0.06	13.6

TABLE 2. — Results of the one-way ANOVA (species) variables  $P_{max}$  and  $R_d$ , the Tukey test for the variable  $P_{max}$ , and results of the two-way ANOVA (species and light) and the Tukey test between species for the linear part of the Photosynthesis/PFD curves ( $\alpha$ ). Abbreviations: **df**, degrees of freedom; **MS**, mean squares; %**var.**, percentage of explained variance; **F**, F value; **p**, signification level; **ns**, non significant; \*, p<0.05; \*\*, p<0.01; \*\*\*, p<0.001; **barb.**, *Gongolaria barbata*; **comp.**, *Cystoseira compressa* subsp. *pustulata*; **crin.**, *Ericaria crinita*; **foen.**, *Cystoseira foeniculacea* f. *tenuiramosa*.

Variable	factor	df	MS	%var.	F	p	species	barb.	comp.	crin.
$P_{max}$	species	3	9.64	30.2	6.2	***	comp.	ns	–	–
	error	43	1.55	69.8	–	–	crin.	**	ns	–
	–	–	–	–	–	–	foen.	*	ns	ns
$\alpha$	light	4	40.08	86.6	251.6	***	–	–	–	–
	species	3	0.49	0.8	3.1	*	comp.	ns	–	–
	interaction	12	1.17	7.6	7.3	***	crin.	ns	*	–
	error	58	0.16	5	–	–	foen.	ns	ns	ns
$R_d$	species	3	0.47	81.5	17.6	***	–	–	–	–
	error	12	0.03	18.5	–	–	comp.	ns	–	–
	–	–	–	–	–	–	crin.	***	***	–
	–	–	–	–	–	–	foen.	*	ns	*

TABLE 3. — Lineal fitting of the initial part of every Photosynthesis/PFD curve (0 to 90 μmol photon·m<sup>-2</sup>·s<sup>-1</sup>) where  $\alpha$  is the slope of the fitted line (= photosynthetic efficiency). Abbreviations: **se**, standard error; **interc.**, intercept; **R<sup>2</sup>**, R-squared value; **n**, number of assays; \*\*\*, p<0.001.

Species	$\alpha$	± se	interc.	± se	R <sup>2</sup>	n	F	p
<i>Gongolaria barbata</i> (Stackhouse) Kuntze	0.053	0.003	-1.37	0.16	0.94	20	281.0	***
<i>Cystoseira compressa</i> subsp. <i>pustulata</i> Ercegovic ex Verlaque	0.055	0.003	-1.32	0.15	0.94	18	273.2	***
<i>Cystoseira foeniculacea</i> f. <i>tenuiramosa</i> (Ercegovic) A.Gómez Garreta, M.C.Barceló, M.A.Ribera & J.Rull Lluch	0.044	0.003	-1.15	0.17	0.90	20	166.4	***
<i>Ericaria crinita</i> (Duby) Molinari & Guiry	0.024	0.001	-0.52	0.06	0.96	20	386.0	***

TABLE 4. — Carbon (%C), nitrogen (%N) and phosphorus (%P) contents in algal tissues (mean ± sd).

Species	%C	± sd	%N	± sd	%P	± sd
<i>Gongolaria barbata</i> (Stackhouse) Kuntze	30.82	0.20	0.43	0.01	0.036	0.004
<i>Cystoseira compressa</i> subsp. <i>pustulata</i> Ercegovic ex Verlaque	34.09	0.10	0.46	0.02	0.042	0.000
<i>Cystoseira foeniculacea</i> f. <i>tenuiramosa</i> (Ercegovic) A.Gómez Garreta, M.C.Barceló, M.A.Ribera & J.Rull Lluch	29.08	0.50	0.38	0.11	0.031	0.003
<i>Ericaria crinita</i> (Duby) Molinari & Guiry	30.02	0.26	0.40	0.05	0.035	0.001

## RESULTS

Interspecific differences in the Photosynthesis/PFD curves (Fig. 1A) were low, with  $P_{max}$  values very similar (Table 1), being slightly higher in *G. barbata* when compared to *E. crinita* and *C. foeniculacea* f. *tenuiramosa* (Table 2). The lineal part of the Photosynthesis/PFD curves (Fig. 1B) was also similar, with relatively higher photosynthetic efficiencies ( $\alpha$ ) for *C. compressa* subsp. *pustulata* and *G. barbata* than for *E. crinita* (Table 3) being only different between *E. crinita* and *C. compressa* subsp. *pustulata* (Table 2). Light at compensation ( $I_c$ ) ranged between 21.7 (*E. crinita*) and 26.1 μmol photon m<sup>2</sup> s<sup>-1</sup> (*C. foeniculacea* f. *tenuiramosa*), while light at saturation ( $I_k$ ) roughly ranged

between 120 and 200 μmol photon m<sup>2</sup> s<sup>-1</sup>, with the highest value for *E. crinita*. Dark respiration ( $R_d$ ) ranged between 0.58 (*E. crinita*) and 1.36 (*G. barbata*) mg O<sub>2</sub>·gAFDM<sup>-1</sup>·h<sup>-1</sup> (Table 1), showing differences between *E. crinita* and all the other species and between *G. barbata* and *C. foeniculacea* f. *tenuiramosa* (Table 2).

Carbon content in branches ranged between 29% (*C. foeniculacea* f. *tenuiramosa*) and 34% (*C. compressa* subsp. *pustulata*) (Table 4). *C. compressa* subsp. *pustulata* also showed the highest values of nitrogen and phosphorous (with N = 0.46% and P = 0.042%), followed by *G. barbata* (N = 0.43% and P = 0.036%), while the lowest values corresponded to *C. foeniculacea* f. *tenuiramosa*, with N = 0.38% and P = 0.031% (Table 4).

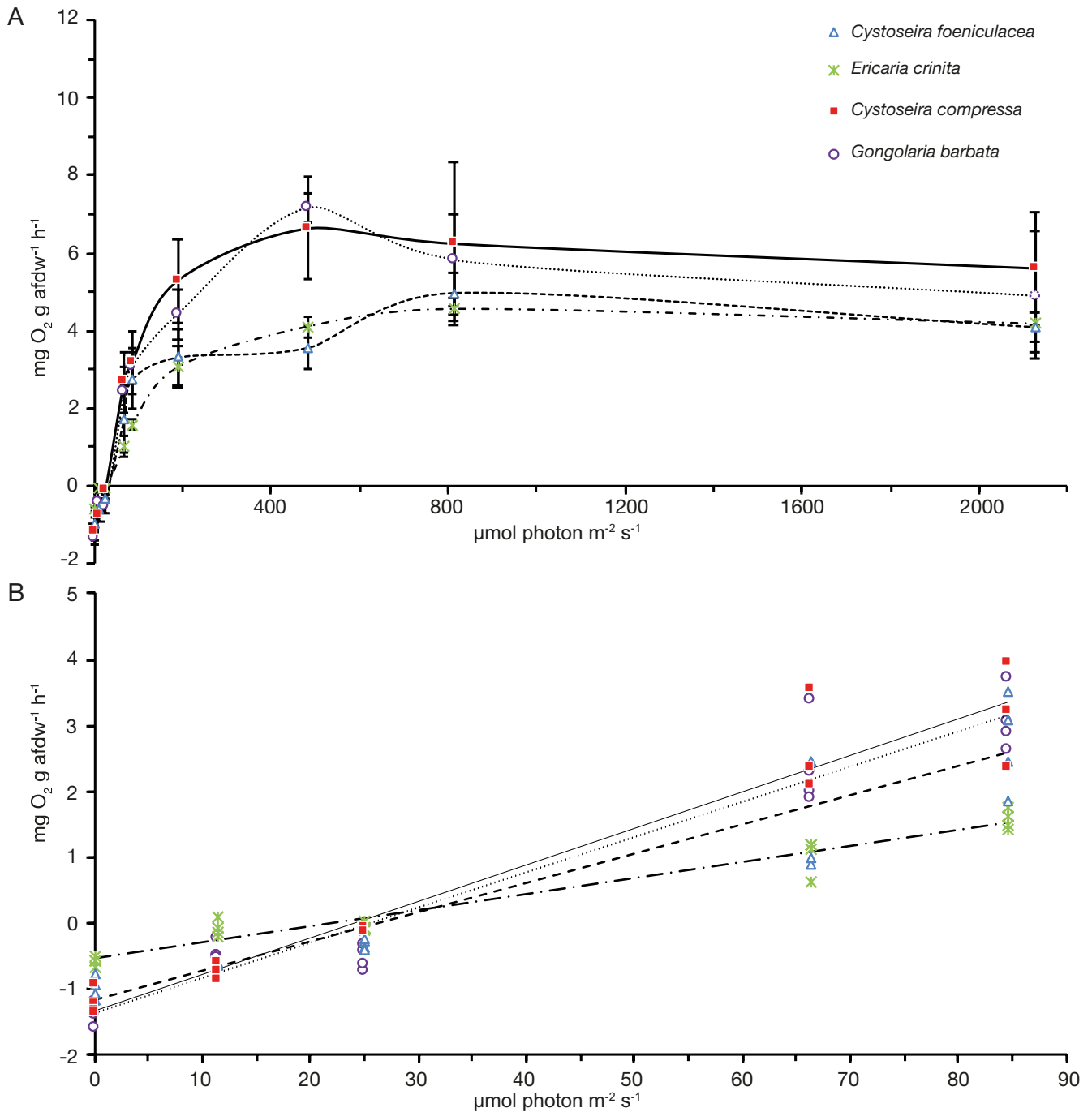


FIG. 1. — **A**, photosynthesis/PFD curves for the tested algae, error bars refer to SE; **B**, lineal fitting of the Photosynthesis/PFD data for the tested algae at the lineal part of the curve. *Cystoseira compressa* stands for *Cystoseira compressa* subsp. *pustulata* (Ercegovic) Verlaque and *Cystoseira foeniculacea* for *Cystoseira foeniculacea* f. *tenuiramosa* (Ercegovic) A.Gómez Garreta, M.C.Barceló, M.A.Ribera & J.Rull Lluch.

Atomic ratios C:N, C:P and N:P (Fig. 2) were very similar. C:N is always higher than 82 and C:P always exceeds 2000.

## DISCUSSION

There is a relative homogeneity of photosynthetic parameters of the species tested in this study. Regarding  $P_{max}$ , even if *G. barbata* showed a slightly significant higher values than

*E. crinita* and *C. foeniculacea* f. *tenuiramosa*, it ranged between 4.3 and 6.5 mg O<sub>2</sub> gAFDM<sup>-1</sup> h<sup>-1</sup>, which falls into the same range of values obtained for *Ericaria amentacea* (C. Agardh) Molinari-Novoa & Guiry (5.4 mg O<sub>2</sub> gAFDM<sup>-1</sup> h<sup>-1</sup>) collected at 0 m and for *Ericaria brachycarpa* (J. Agardh) Molinari-Novoa & Guiry (6.3 mg O<sub>2</sub> gAFDM<sup>-1</sup> h<sup>-1</sup>) collected at 10 m depth (Sant & Ballesteros 2021a). It is also similar to the values obtained for *E. brachycarpa* from 3 m (6.2 mg O<sub>2</sub> gAFDM<sup>-1</sup> h<sup>-1</sup>) and 10 m (6.0 mg O<sub>2</sub> gAFDM<sup>-1</sup> h<sup>-1</sup>) in another study

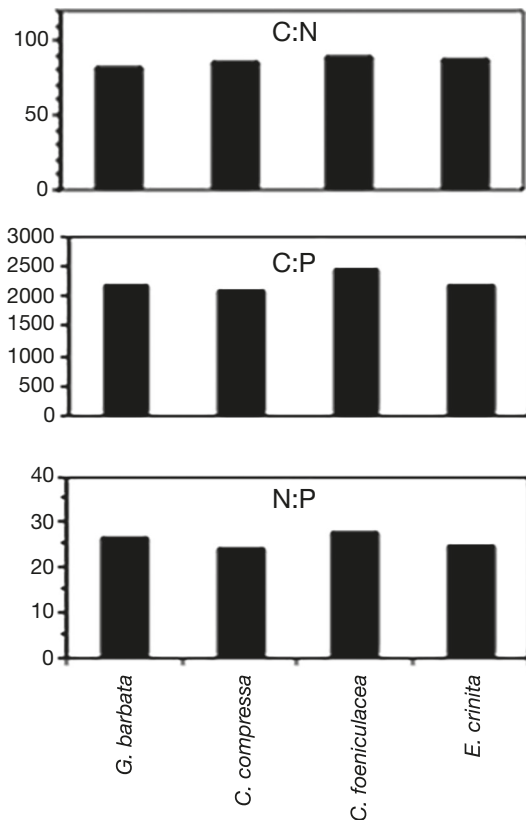


Fig. 2. — C:N, C:P, N:P ratios in tissues for each of the studied species. Names are abbreviations from those in Figure 1.

by Sant & Ballesteros (2021b). This contrasts with  $P_{max}$  from deep water *Ericaria* and *Gongolaria* species, which range between 9.2 and 15.3 mg O<sub>2</sub> gAFDM<sup>-1</sup> h<sup>-1</sup> (Sant & Ballesteros 2021a) and with data obtained for *E. brachycarpa* collected at 20 m depth (7.6 mg O<sub>2</sub> gAFDM<sup>-1</sup> h<sup>-1</sup>) (Sant & Ballesteros 2021b). Therefore, it seems that depth is a very good predictor of  $P_{max}$  in Mediterranean Fucales, although it is also species and season-dependent, as it happens in *Gongolaria montagnei* (C. Agardh) Kuntze and *Ericaria zosteroides* (C. Agardh) Molinari-Novoa & Guiry (Sant 2003). A similar pattern is observed with photosynthetic efficiency ( $\alpha$ ), with shallow water species showing values ranging from 0.024 to 0.057 mg O<sub>2</sub>·m<sup>2</sup> s (μmol photon·gAFDW·h)<sup>-1</sup> (Sant & Ballesteros 2021a, b; this study) and deep water species or specimens ranging between 0.065 and 0.121 mg O<sub>2</sub>·m<sup>2</sup> s (μmol photon·gAFDW·h)<sup>-1</sup>. No differences are observed for PFD at saturation but PFD at compensation is much higher in species studied in this work than in species studied by Sant & Ballesteros (2021a, b). The higher  $I_c$  can be easily explained because our specimens come from very shallow and sheltered waters, with a much greater light availability than for species living much deeper. Even *C. amentacea* has a lower  $I_c$ , which could be explained by the rough environment where this species thrives, that decreases light availability.

All these data add support to the importance of photosynthetic features in driving the already well-known depth and light-related distribution of the species of the order Fucales

in the Mediterranean (Giaccone 1973; Giaccone & Bruni 1973). Shallow water Fucales studied here perform like “sun plants” (Boardman 1977) with low photosynthesis at saturation and photosynthetic efficiency and high dark respiration rates and PFD at compensation, adding evidences to the morphology-independent patterns of adaptation to low light intensity previously suggested by Sant & Ballesteros (2021a, c): the four species show contrasting differences in thallus structure (monopodial versus sympodial), branching density and growth form (Gómez-Garreta *et al.* 2001; Cormaci *et al.* 2012; Rodríguez-Prieto *et al.* 2013) and, still, they show similar photosynthetic parameters.

All the species studied here showed similar nutrient content in tissues and similar ratios, which agrees with their similar photosynthetic features. The amount of N and P was two to three fold lower than values obtained for deep water species reported in Sant & Ballesteros (2020, 2021a), which should be related to the lowest nutrient concentrations found in surface waters when compared to deep waters (Ballesteros 1992; Ballesteros & Zabala 1993). This is reflected by the huge differences in the C:N and N:P ratios between shallow and deep water species, which in shallow water species exceeded by far the median C:N:P atomic ratio (550:30:1) for benthic marine macroalgae (Atkinson & Smith 1983), suggesting a strong nutrient limitation for growth. In fact, Ballesteros (1989) already grouped shallow *Cystoseira* (including *Ericaria* and *Gongolaria*) species from sheltered environments in the Mediterranean macroalgae group whose production is nutrient-dependent.

Regarding the similar photosynthetic parameters shown by the species studied here, their similar nutrient contents in tissues and their similar palatability to herbivory by fish *Sarpa salpa* (Linnaeus, 1758) (at least between *E. crinita* and *C. compressa* subsp. *pustulata*) (Vergés *et al.* 2009), there must be other features that explain the possibility of these species to coexist in the same environment without one outcompeting the other. Thus, fine scale ecological and ecophysiological studies are needed in order to understand the diversity of the order Fucales in shallow and sheltered Mediterranean habitats.

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