

Spatial and temporal variation of photosynthesis in intertidal *Mazzaella laminarioides* (Bory) Fredericq (Rhodophyta, Gigartinales)

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Abstract The red alga *Mazzaella laminarioides* is an economically important species with an extended latitudinal distribution along the Chilean coast. Its populations form mid-intertidal stands, several meters wide, and therefore are differentially exposed to environmental variables that result in temporal and spatial variability in productivity. We evaluated the effect of latitude and intertidal height on productivity by *in situ* measurement of photosynthetic performance. Daily and seasonal variations of O₂-evolution rate and maximal quantum yield (F_v/F_m) were determined in plants from the upper and lower intertidal zone at two localities 1500 km apart. Results suggest that plant responses were mainly affected by irradiation, temperature and desiccation. At local level, upper intertidal plants showed a reduced photosynthetic rate and

quantum efficiency as compared to those displayed by plants from the lower intertidal, indicating their higher level of excitation energy acclimation. Stronger acclimation differences between upper and lower intertidal plants were observed in spring and summer. Differences in photosynthetic parameters between reproductive phases were recorded in autumn and winter, regardless of the position of the individuals in the intertidal zone. The effects of tidal elevation on seasonal patterns of photosynthesis were also influenced by latitude. Seasonal variation in photosynthetic efficiency was observed in plants from the northern population at both intertidal elevations, but only at the upper intertidal level in the southern population. This study shows that production variability in *M. laminarioides* results from differences in the intensity of environmental factors observed seasonally at local (intertidal) and latitudinal scales.

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Introduction

The intertidal zone of temperate rocky shores provides for macroalgae an environmental gradient characterised by significant differences of various physical factors, including irradiance, temperature, nutrient availability, salinity and desiccation (Lüning, 1990;

Lobban & Harrison, 1994; Davison & Pearson, 1996). In this context, numerous studies have demonstrated that differences between intertidal macroalgae from distinct tidal positions are related to photosynthetic physiology; i.e. net photosynthetic rate, resistance to photoinhibition and photosynthetic recovery after desiccation (Harbert & Waaland, 1988; Beer & Kautsky, 1992; Matta & Chapman, 1995; Bruhn & Gerard, 1996; Davison & Pearson, 1996; Skene, 2004). Thus, characterization of variables that regulate photosynthetic performance has been considered a crucial criterion for cultivation (Ganzon-Fortes, 1997) and optimization of management strategies (Duarte & Ferreira, 1995).

In situ photosynthetic performance, reported by quantifying both O₂-evolution and chlorophyll fluorescence (Henley et al., 1991, 1992; Hanelt et al., 1992, 1993; Magnusson, 1997; Silva et al., 1998; Ensminger et al., 2000; Häder et al., 2001; Longstaff et al., 2002), have described the occurrence of a photoinhibitory mechanism associated with the noon depression of photosynthetic efficiency followed by an afternoon recovery (Henley et al., 1991; Ensminger et al., 2001; Gévaert et al., 2003), suggesting in some case that daily photoinhibition is the result of UV radiation (Bischof et al., 1998; Häder et al., 2001). However, the extension of photosynthetic depression at noon and the photosynthetic yield (as F_v/F_m and electron transport rate) have shown to experience seasonal changes (Ensminger et al., 2001), with lower values during summer. Additionally, some studies including the analysis of both temporal and spatial variability of photosynthetic activity have demonstrated that photoinhibition susceptibility during a diurnal cycle, and photosynthesis light requirements, vary among macroalgae living at different depths (Henley et al., 1991; Hanelt et al., 1993; Beach & Smith, 1996a,b; Hanelt, 1998; Ensminger et al., 2000, 2001; Gómez et al., 2004; Skene, 2004). Similar results were observed in a single species distributed along the tidal gradient, indicating a significant degree of photosynthetic plasticity in response to temporal (daily and seasonal) and spatial (tidal) variation of environmental variables, particularly desiccation and light intensity (Beach & Smith, 1996a,b; Ensminger et al., 2000, 2001). Additionally, although physiological differences are usually considered the result of acclimation capacities of species facing different environments, they could also be explained by different genetic make up of the individuals (Zuccarello et al., 2001) that, in turn, may result in different levels of

productivity. Thus, since plant productivity is directly related to photosynthetic rate, and the latter has a complex relationship with environmental variation (Duarte & Ferreira, 1993; Magnusson, 1997), a field approach taking into account the distribution of a given species for eco-physiological studies would allow to shed light on the mechanisms evolved to successfully colonize a physically variable habitat (Ensminger et al., 2000, 2001), and also to unravel the productivity variations within a population. However, eco-physiological studies considering this approach and using economically important intertidal algal resources are scarce.

Mazzaella laminarioides (Bory) Fredericq (Gigartinales, Rhodophyta) is an ecologically and economically important alga, characterized by an alternation of isomorphic generations, distributed along the Chilean coast from 30°S to 55°S (Fig. 1). This species, together with other carreegenophytes, is one of the most exploited algal resources in Chile, with landing values of ca. 25,000 wet tons per annum, exclusively from wild stocks (Buschmann et al., 2001). The extensive populations of *M. laminarioides* form a mid-intertidal strip several meters wide, below the barnacle and mussel stands (Hannach & Santelices, 1985; Hannach & Waaland, 1986; Santelices, 1989; Hoffmann & Santelices, 1998). It grows abundantly on wave-exposed rocky platforms and individuals may vary from greenish-yellowish to darker brownish-reddish depending on their location along the tidal gradient. This differential pattern of pigmentation is particularly evident during spring and summer (Buschmann & Pizarro, 1986; Santelices, 1989) and suggests a contrasting photosynthetic behaviour within a single population. Thalli segregation related to their position along the tidal gradient has been also reported for the life history phases of *M. laminarioides* in central Chile, where gametophytic plants become dominant towards the upper limit, whereas sporophytic thalli become more abundant towards the lower intertidal (Hannach & Waaland, 1986; Luxoro & Santelices, 1989). In agreement with this contrasting pattern of distribution in the field, laboratory experiments revealed differences in growth and survival between gametophytic and sporophytic juveniles when plants were exposed to gradients of light regime, temperature and desiccation (Hannach & Santelices, 1985; Luxoro & Santelices, 1989).

Considering the above information, we used *M. laminarioides* as a model to assess the effect

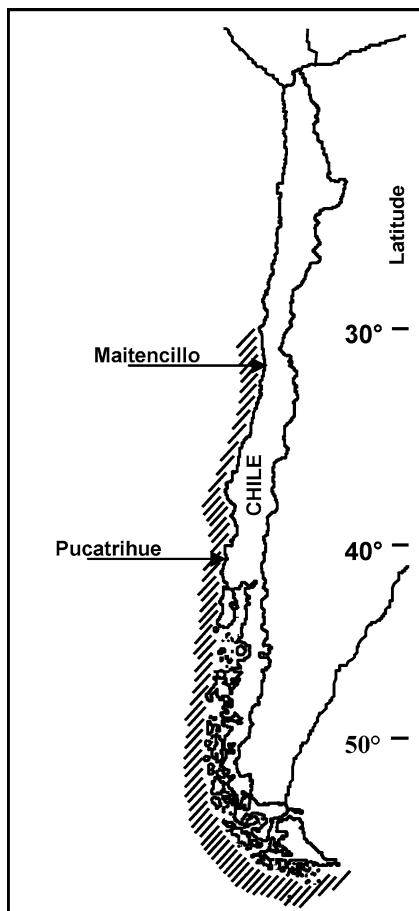


Fig. 1 Latitudinal distribution of *M. laminarioides* along the Chilean coast with indication of the study sites

environmental variability determined by season, latitude, and position of the plants along the tidal gradient, on photosynthetic performance of both gametophytic and sporophytic plants. This eco-physiological information will help the understanding of local and regional patterns of abundance of the species.

Materials and methods

Study sites and samples

Mazzaella laminarioides individuals were collected in Maitencillo (32° 38'S; 71° 40'W) and Pucatrihue (40° 28'S; 73° 44'W), both localities from the wave exposed area of the Chilean coast. Maitencillo hosts a population close to the northern distribution limit for the species (Fig. 1), characterized by 1.5–3.5 m wide stands at the middle of the intertidal zone. The upper

limit is at 2.3–2.5 m above low tide, whereas the lower limit is 1 m above the lower tide level. In Pucatrihue, located at the center of the latitudinal distribution of the species (Fig. 1), we selected a set of rocks where *M. laminarioides* conforms a stand 1–2.5 m wide, with an upper limit at 1.8–3.4 m from the lower tide level and a lower limit at 1.0–1.3 m from the lower tidal mark.

In order to evaluate photosynthetic performance, *M. laminarioides* plants were collected at each of the two localities and from a 20–30 cm strip located at the upper and lower extremes of the tidal gradient. Photosynthetic behaviour (i.e. O₂-evolution and fluorescence emission rates) during daytime was evaluated only in Maitencillo. Meanwhile its seasonal behaviour was assessed in plants from both end of intertidal zone and reproductive phase in Maitencillo and Pucatrihue.

Daily photosynthetic rate variation

Photosynthetic rate was evaluated by measuring both photosynthetic O₂ evolution and fluorescence emission rates. Diurnal evolution of photosynthetic O₂ was only measured in Maitencillo during spring 2000. Fronds without epiphytes, endophytes and reproductive structures were brushed and rinsed with filtered seawater (0.20 μm) before excising discs 1 cm in diameter which were left overnight at environment temperature in 25 mL glass bottles with 20 mL of filtered seawater. Two discs per plant ($n = 6-10$) from each tidal level were then transferred to new bottles at dawn. An additional set of bottles without discs was used as controls ($n = 3$). All bottles were transferred to 8 cm deep plastic trays placed in the field at 5–10 m from where plants were originally collected. Water in the trays was renewed at 10–15 min intervals in order to maintain the experimental temperature (15 ± 2 °C) within the range of the surrounding water. Oxygen evolution was monitored at 2 h intervals from 9:00 AM to 7:00 PM by quantifying in each bottle the concentration of dissolved O₂ (WTW Oxi-196, WTW Wissenschaftlich-Technische Werkstätten GmbH, Germany) at the beginning and end of 30–40 min of experimental trials. The rate of photosynthesis was estimated through the difference in O₂ concentration and standardized by disc weight (wet weight, ww).

Fluorescence emission rates were evaluated *in situ* using a portable fluorometer (Plant Efficiency Analyser PEA, Hansatech Instruments Ltd., UK) during April and November 2000 and January 2001, in

Maitencillo. In order to estimate the diurnal variation of photosynthetic activity, measurements were done before, during and after low tide. In each occasion, 10 vegetative fronds from plants located at low and high intertidal heights were collected. Discs of approximately 1 cm in diameter were immediately excised from the distal zone of the fronds, avoiding areas of tissue with epiphytes and reproductive structures. In order to keep the moisture of the fronds during collection, each sample was maintained in individual small plastic bags (10×5 cm) in the dark for ~ 30 min at $9 \pm 2^\circ\text{C}$.

The effect of frond desiccation on maximal photosynthetic yield or efficiency (F_v/F_m) was assessed in plants from the higher intertidal level in Maitencillo, during summer 2001. Frond discs were obtained as previously described and placed in plastic bags to maintain moisture, whereas another set of discs was placed in bags with filtered seawater to re-hydrate the tissue of those discs from plants already affected by desiccation. Moisture level was estimated by recording humidity percentage at the frond surface with a protimeter (GE Protimeter Plc, UK). Values of 70–75% correspond to fronds completely hydrated, whereas values of 30–35% indicate tissue water losses of 70–75%. Within this range, these values show a linear function with water content in the frond under laboratory conditions ($y = 0.46x + 91.9$; $r^2 = 0.94$). In addition, others parameters measured were: air humidity, recorded with a hygrometer; photon flux density, with a photometer (Li-Cor, model Li-189, USA); and temperature obtained with a thermometer ($\pm 0.1^\circ\text{C}$) under the *M. laminarioides* canopy.

Seasonal variability

Oxygen evolution rates were measured in plants from the two localities during winter 1999, and summer and autumn 2000. Material included plants from higher and lower intertidal heights and also of the two reproductive phases. Measurements were done at selected times of the day avoiding radiations higher than $1500 \mu\text{moles photons m}^{-2} \text{s}^{-1}$ that could cause photoinhibition. Fronds were selected and treated as indicated above.

Fluorescence emission was evaluated in the same plants used to measure O_2 -evolution, although an additional observation in spring. Fluorescence was measured 24 h after collection and under laboratory conditions to avoid a superimposed and confounding dial effect on seasonal variability. Samples were transported

in a cooler ($8 \pm 2^\circ\text{C}$) in individual plastic bags with filtered seawater and maintained in the laboratory under dim light and $12 \pm 2^\circ\text{C}$ until fluorescence recordings. Prior to the recordings, plants were kept in complete darkness for 30–40 min.

Statistical analyses included multivariate analysis of variance with repeated measures (Statistica, StatSoft, Inc. 1998) to assess time-dependent effect on photosynthetic efficiency. Differences in both O_2 -evolution and photosynthetic efficiency between plants were evaluated at each locality and time of observation through a multifactorial analysis of variance (Statistica StatSoft, Inc. 1998), considering reproductive phase and intertidal position as fixed variables. *A posteriori* differences were evaluated by a Tukey HSD test.

Results

Daily patterns of photosynthetic performance

Daily photosynthetic O_2 -evolution rate measured during summer in Maitencillo plants showed a continuous increase in the morning which reached a maximum of ca. $25 \mu\text{moles O}_2 \text{ h}^{-1} \text{ g}^{-1}$ at midday (Fig. 2a). This high rate, which remained relatively constant for up to 5 h, even though irradiance varied around $2000 \mu\text{moles photons m}^{-2} \text{s}^{-1}$ during the same period, declined towards late afternoon as irradiance also diminished. Comparisons of photosynthetic rates between plants from different tidal heights showed, at least in part, significant differences when comparing daytime measurements. Photosynthesis rate in lower intertidal plants was significantly higher than in upper intertidal plants ($F_{1,12} = 11.42$; $p = 0.005$) during the first hours of the day, and progressively increased until reached maximum values in late afternoon, whereas plants from the upper intertidal reach their maximum around noon (Fig. 2b).

Plants from the lower and upper intertidal zone of Maitencillo also showed differences in maximum photosynthetic efficiency (F_v/F_m) at daily and seasonal time scales (Fig. 3). In autumn (April, Fig. 3), values of F_v/F_m were high for plants from both tidal heights and mean differences were not significant ($F_{1,8} = 2.5$; $p = 0.16$). These plants exhibited lower F_v/F_m values at noon, but experienced a significant ($F_{2,16} = 18.1$; $p < 0.001$) increase towards the afternoon. In spring (November, Fig. 3) differences between plants from

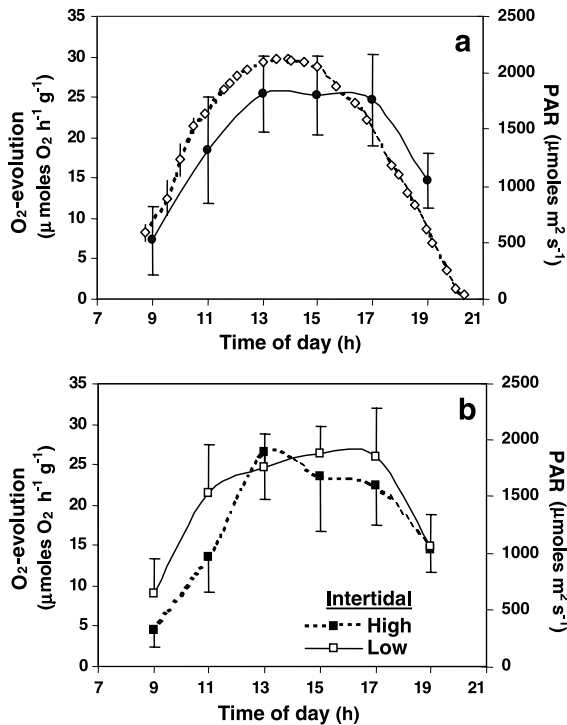


Fig. 2 (a) Mean oxygen evolution rate in *M. laminarioides* measured in Maitencillo during spring for all experimental plants (closed circles; $n = 12-20$) and photon irradiance variation along the day (open rhombi) at which the oxygen evolution was measured, and (b) plants from low and high intertidal ($n = 6-10$). Each point: mean \pm SD

the lower and upper tidal heights were significant ($F_{1,4} = 20.2$; $p = 0.01$), with lower shore plants maintaining high F_v/F_m values. Although the within plant group F_v/F_m was minimum at mid afternoon, no significant differences were found throughout the day ($F_{2,8} = 1.3$; $p = 0.33$). In summer (January, Fig. 3), plants from the two intertidal zones showed reduced F_v/F_m values, although their differences were still significant ($F_{1,7} = 135.5$; $p < 0.001$). Plants from the lower intertidal showed significantly lower F_v/F_m values during the afternoon ($F_{3,21} = 4.5$; $p = 0.014$), and increasing to the initial levels towards the end of afternoon. In contrast, plants from the upper intertidal showed a progressive reduction of F_v/F_m values to a minimum late in the afternoon.

The relation between environmental variables and F_v/F_m responses in plants from Maitencillo during summer varied according to the intertidal position of individuals (Fig. 4). In plants from the upper intertidal F_v/F_m progressively declined towards noon, coinciding with increased levels of desiccation (Fig. 4c).

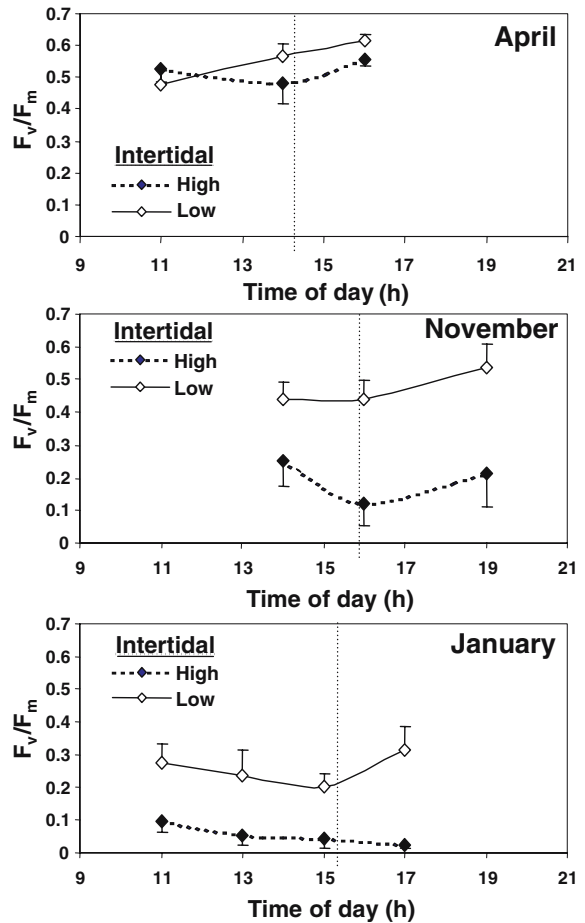
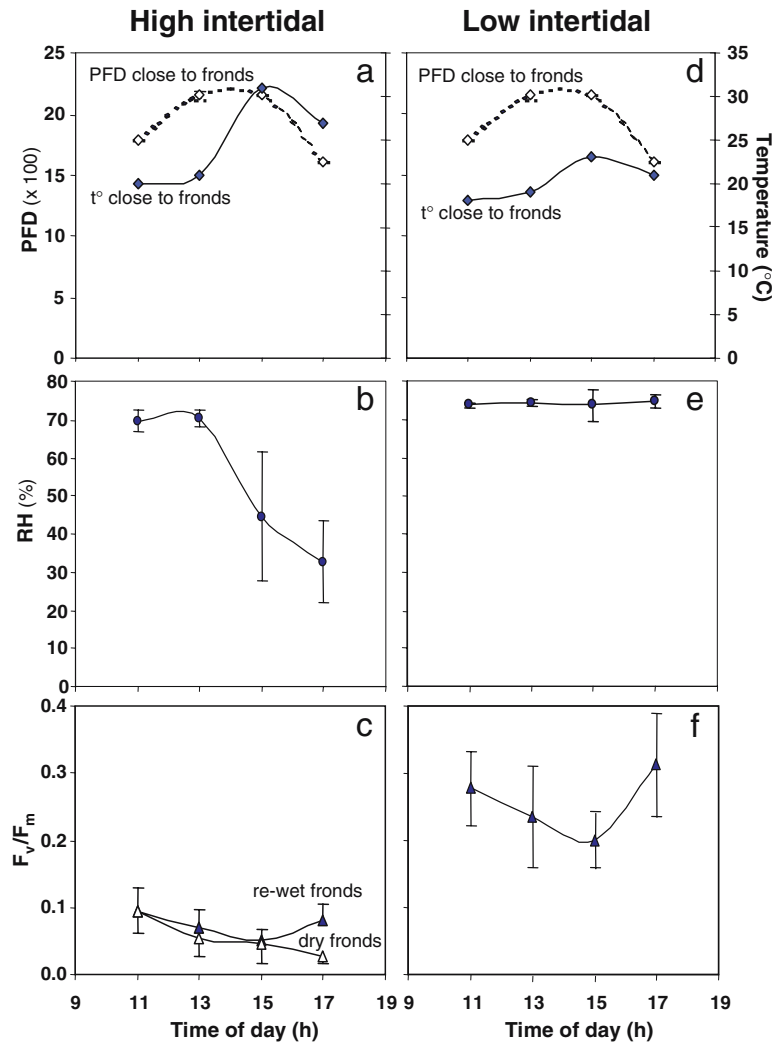


Fig. 3 Maximal photochemical efficiency (F_v/F_m) of *M. laminarioides* in April, November and January at Maitencillo measured at both tidal heights. Vertical line indicates time of low tide where the lower plants may shortly be exposed to the air. Each point: mean \pm SD, $n = 5-15$

Maximum plant desiccation was recorded late in the afternoon, when relative humidity of fronds was close to 30% (Fig. 4b); i.e. tissue water losses ca.70%. Rehydrated plants also showed reduced F_v/F_m towards noon and minimum values during mid-afternoon, although they recovered towards late afternoon (Fig. 4c). The behaviour of the F_v/F_m responses of the upper shore plants showed inverse, but not significant, relationships with irradiance ($r^2 = -0.74$; $p > 0.05$) and temperature ($r^2 = -0.73$; $p > 0.05$), with an increase towards noon and up to mid-afternoon, to then decline towards late in the afternoon (Fig. 4a). On the other hand, plants from the lower intertidal were not affected by desiccation (Fig. 4e), although F_v/F_m values declined progressively from noon to reach a minimum during mid afternoon; recovery took place in late

Fig. 4 Maximal photochemical efficiency (F_v/F_m) of *M. laminarioides* from both tidal heights (lower on the left and upper on the right) in relation to (a, b) relative humidity (RH), (c, d) photon flux density (PFD) and (e, f) temperature measured close to plants in summer. Each point: mean \pm SD, $n = 10-15$



afternoon (Fig. 4f). Variation of F_v/F_m through the day was inversely and significantly correlated to irradiance ($r^2 = -0.96$; $p < 0.05$), but not significantly with temperature ($r^2 = -0.40$; $p > 0.05$) (Fig. 4d). At both shore heights, however, the temperature effect on F_v/F_m could be influenced by incubation conditions previous to measurement (dark for ~ 30 min at $9 \pm 2^\circ\text{C}$).

Seasonal patterns of photosynthetic performance

The seasonal analysis of both photosynthetic O_2 -evolution rate and F_v/F_m carried out in the stands of Maitencillo and Pucatrihue revealed differences in plants of different tidal origin and reproductive phase, although both measures showed different patterns. In

Maitencillo, gametophytic plants showed a reduced photosynthesis rate when compared to sporophytic plants (Table 1, Fig. 5). In addition, photosynthetic O_2 -evolution rate of plants from different tidal origin also exhibited significant differences in summer and autumn, when upper tidal plants had lower photosynthetic rates than lower shore plants (Table 1, Fig. 5). On the other hand, comparisons of F_v/F_m between plants from different reproductive phases showed no significant differences. However, as before significant differences were observed between plants from different intertidal heights, with upper shore plants showing smaller F_v/F_m values (Fig. 5; Table 1). In Pucatrihue, O_2 -evolution rates were also significantly different between plants from different reproductive phases (Fig. 5; Table 1), which resulted in contrasting temporal

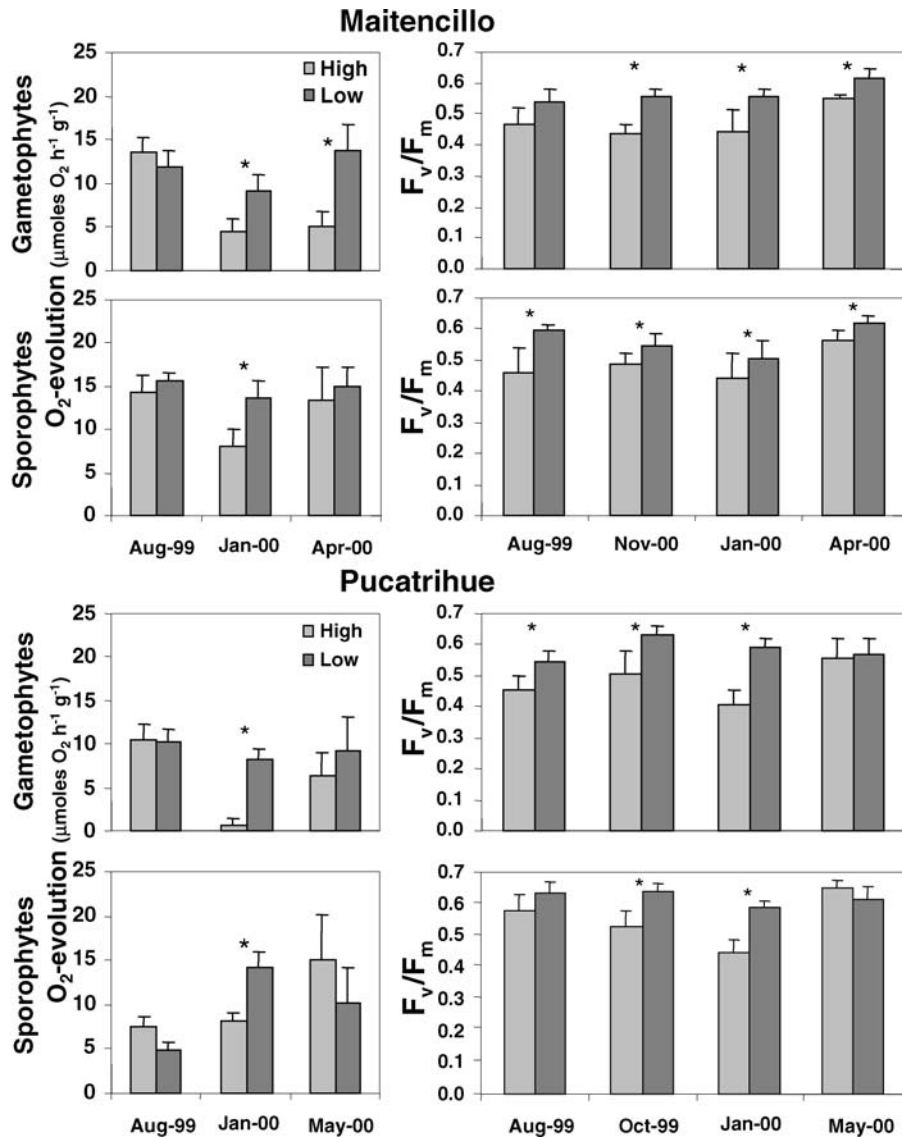


Fig. 5 Seasonal oxygen evolution rates and maximal photochemical efficiency (F_v/F_m) measured in plants from high and low tidal levels and separated by reproductive phases. Each point: mean \pm SD, $n = 6-10$. Asterisks indicate significant differences ($p < 0.05$)

patterns. In winter gametophytes had significantly higher photosynthetic rates than sporophytes, whereas in summer and autumn the rate was significantly higher in sporophytic plants (Table 1). When comparing plants from different tidal levels, O₂-evolution rates showed significant differences only in summer, where individuals from the upper tidal zone displayed the lowest rates (Fig. 5; Table 1). On the other hand, significant differences in F_v/F_m between phases were observed in August and May (Table 1; Fig. 5), whereas significantly higher values were observed in upper tidal plants in August, November and January (Fig. 5; Table 1).

The seasonal pattern of F_v/F_m differed significantly when Maitencillo and Pucatrihue were compared (Fig. 6; Table 2). Although *M. laminarioides* from both localities exhibited the lowest F_v/F_m values during spring and summer, the highest values were observed during autumn in Maitencillo and winter in Pucatrihue (Fig. 6). Furthermore, inter-annual variations were also apparent, as F_v/F_m of the two phases were significantly different during the winter of 1999 in Maitencillo, in Pucatrihue were during the winters of 1999 and 2000 (see $F \times T$ interaction in Table 2; Fig. 7a, c). Responses of F_v/F_m in plants from different tidal

Table 1 Summary of the two-way ANOVA for O₂-evolution rates ($\mu\text{moles O}_2 \text{ h}^{-1} \text{ g}^{-1}$) and maximal photosynthetic efficiency (F_v/F_m) measured at different times of the year in Maitencillo and Pucatrihue

	O ₂ -evolution rate			Maximal photosynthetic efficiency			
	August'99	January'00	April/May'00	August'99	Nov./Oct.'99	January'00	April/May'00
Maitencillo	<i>F</i>	<i>F</i>	<i>F</i>	<i>F</i>	<i>F</i>	<i>F</i>	<i>F</i>
Phase (P)	7.2*	20.1***	12.1**	0.4	0.8	1.4	0.3
Level (L)	0.1	31.4***	14.4**	9.4**	24.7***	5.0*	18.0***
P × L	2.7	0.2	6.7*	0.8	3.8	1.4	0.1
Pucatrihue							
Phase (P)	22.3***	78.5***	5.9*	20.4***	0.2	1.0	9.1**
Level (L)	2.8	72.4***	0.2	12.8***	20.8***	83.9***	0.3
P × L	6.6*	1.6	3.8	0.1	0.1	1.3	0.9

Note. Main factors were reproductive phases (P) and tidal level (L)

* $p < 0.5$

** $p < 0.01$

*** $p < 0.001$

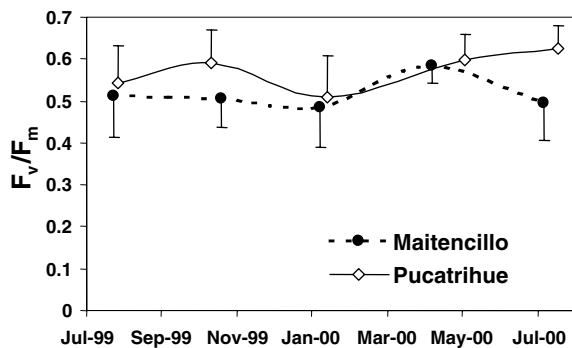


Fig. 6 Seasonal maximal photochemical efficiency (F_v/F_m) measured in Maitencillo and Pucatrihue, considering upper and lower shore plants together. Each point: mean \pm SD, $n = 20-40$

heights were also significantly different between localities (Table 2). Plants from high and low tidal heights at Maitencillo exhibited seasonal F_v/F_m changes, with upper shore plants always showing the lowest values (Fig. 7b). In contrast, lower intertidal plants from Pucatrihue showed no seasonal changes but exhibited high and relatively constant F_v/F_m ratios throughout the year. On the other hand, upper shore plants showed only seasonally high F_v/F_m ratios, just as lower shore plants (Fig. 7d).

Discussion

This ecophysiological study on *Mazzaella laminarioides* have demonstrated that daily photosynthetic variation in this species is determined by daily fluctuations

Table 2 Summary of the ANOVA maximal photosynthetic efficiency (F_v/F_m) measured at different times of the year in Maitencillo and Pucatrihue

Factors	Maximal photosynthetic efficiency	
	Maitencillo <i>F</i>	Pucatrihue <i>F</i>
Time (T)	9.9***	8.0**
Phases (P)	0.0	3.7
Level (L)	20.1*	375.6**
T × P	3.5*	4.5*
T × L	0.5	4.3*
P × L	0.6	0.0
T × P × L	1.0	1.2

Note. Main factors were time of the year (T), phases (P) and tidal level (L) where the plants came from

* $p < 0.5$

** $p < 0.01$

*** $p < 0.001$

of physical factors coupled with the position of the plants along the tidal gradient. However, their daily photosynthetic performance is also modified by season and latitude. Superimposed on the above is the reproductive phase of the plants, which also introduces an additional and significant effect on photosynthesis performance.

Tidal level effects on photosynthetic performance

Diel photosynthetic O₂-evolution rates showed a direct relationship with morning and late afternoon

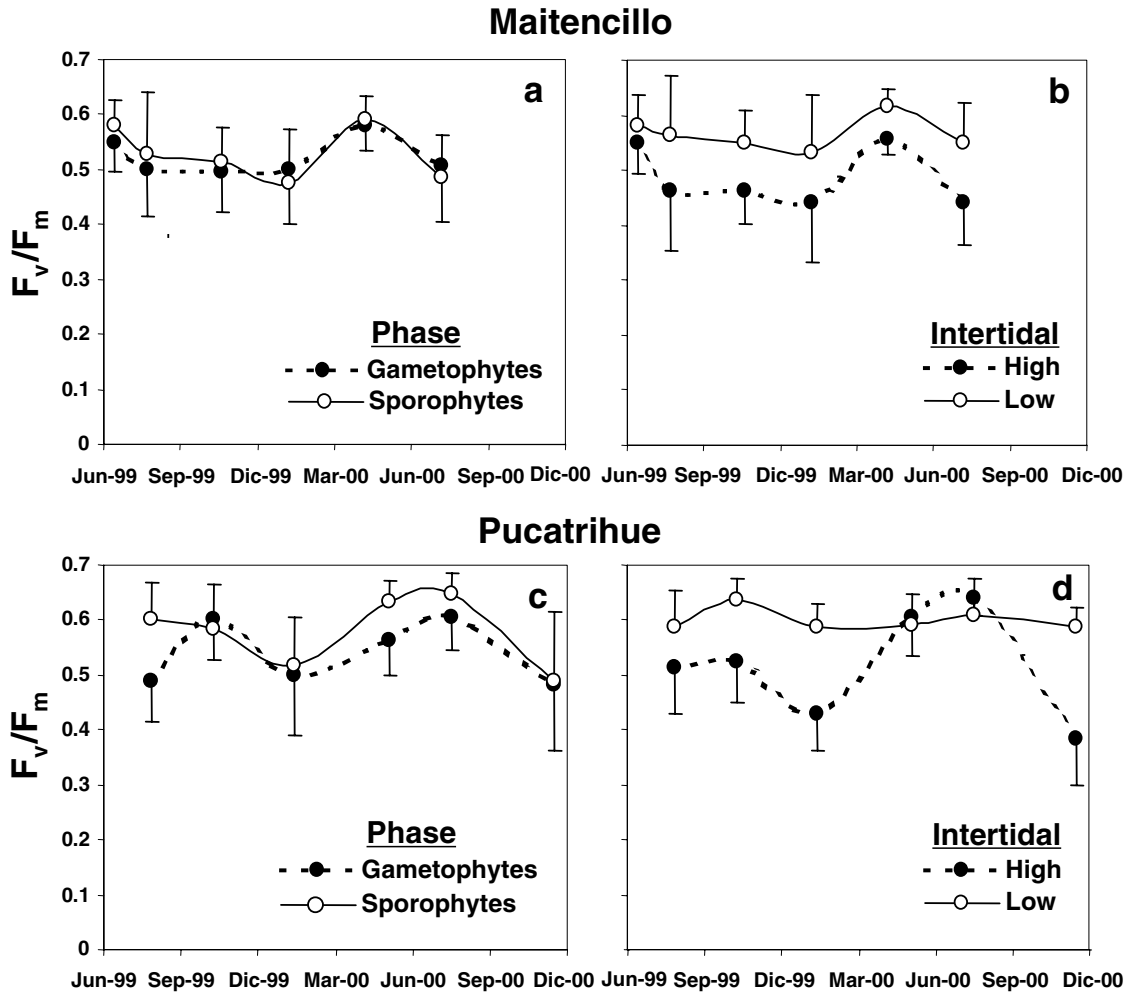


Fig. 7 Seasonal maximal photochemical efficiency (F_v/F_m) measured in plants from both tidal heights and both reproductive phases regardless their shore position in Maitencillo and Pucatrihue. Each point: mean \pm SD, $n = 10-20$

irradiance, whereas photosynthetic rates in early afternoon were constantly high despite increasing irradiance. This pattern resembles the photosynthesis-irradiance (P-I) curve. From this perspective *M. laminarioides* should show a P_{max} close to $2000 \mu\text{moles photons m}^{-2} \text{s}^{-1}$, which is comparatively high and causes photo-inhibition in many intertidal seaweeds (Herbert & Waaland, 1988; Hanelt et al., 1993; Gantt, 1990). However, some species such as *Porphyra yezoensis*, *Porphyridium pupureum* and *Sargassum vulgare*, show no significant inhibition of light-saturated photosynthesis at high solar irradiance, i.e. $1600-2300 \mu\text{moles photons m}^{-2} \text{s}^{-1}$ (Gantt, 1990).

Differences in photosynthetic O_2 -evolution rates between plants from contrasting tidal levels suggest spa-

tial differences in acclimation responses. Upper shore plants presented reduced maximum quantum efficiency (F_v/F_m) which is an indication of lower photosynthetic efficiency than lower shore plants. Maximal quantum efficiency has been used widely to assess the effects of light stress on photosynthesis (Lazár, 1999) and it may reflect the activity of protective mechanisms that regulate photosynthetic energy conversion. Plants growing at high irradiance may protect their photosynthetic apparatus from excessive excitation and potential damage through different mechanisms (Franklin & Forster, 1997) resulting in changes of photosynthesis efficiency even at unsaturated irradiance (Henley, 1993). Thus, reduced efficiency in irradiance utilisation indicates that plants from the higher intertidal are

acclimated to higher irradiance than lower shore plants (Lobban & Harrison, 1994; Falkowski & Raven, 1997). Physiological differences between plants exposed to different irradiance levels have been described as 'sun' and 'shade' acclimation responses (Öquist et al., 1992). Several studies have described acclimation differences between algal species growing at different tidal levels (Harker et al., 1999; Bischof et al., 1998; Hanelt, 1998; Almenara et al., 2000), whereas other studies have studied the variability of a single species living within a distinct depth or microhabitat (Henley et al., 1991; Sagert et al., 1997; Ensminger et al., 2000, 2001; Gévaert et al., 2002). This study is one of the few that show the importance of acclimation differences in a single species within a range of temporal and spatial scales (Beach & Smith, 1996; Stengel & Dring, 1998; Ensminger et al., 2000, 2001).

Seasonal effects at Maitencillo

Acclimation observed in plants from contrasting tidal levels also showed seasonal variation. During spring and summer upper shore plants showed lower photosynthetic efficiency, whereas in autumn all plants within the intertidal showed equally high F_v/F_m ratios. Few studies on seasonal variation in seaweed acclimation have shown different degrees of photosynthetic performance according to season, suggesting a differential photosynthetic susceptibility to environmental conditions (Duarte & Ferreira, 1995; Ensminger et al., 2000; Gévaert et al., 2002). Thus, daily and seasonal variation of photosynthetic efficiency observed at both tidal heights depends on the plant acclimation and the environmental factors affecting photosynthesis (Ensminger et al., 2000; Gévaert et al., 2002). Gomez et al. (2004) indicated that *M. laminarioides* showed a reduction of photosynthetic efficiency around midday in response to extreme summer conditions that indicated a photoinhibitory up- and down-regulation of photosynthesis. Our study shows that this response varies along the tidal distribution and time of the year. Whereas lower shore plants respond mainly to daily irradiation variation, upper shore plants must respond, in addition, to desiccation and to higher environmental temperature differences. Studies have indicated that thermal acclimation involves an increased photosynthetic efficiency (Davison, 1991; Falkowski & Raven, 1997). However, our results from upper shore plants suggest that the episodic increase

of temperature could temporally reduce photosynthetic efficiency.

Latitudinal effects on photosynthesis performance

Seasonal acclimation of *M. laminarioides* was clearly influenced by the latitude of study sites. In Maitencillo, seasonal variation of the acclimation status was observed in plants from both tidal heights, whereas in the southern site, Pucatrihue, seasonal responses were observed only in plants located at the upper intertidal. This difference could be attributed to latitude-dependent variability of environmental variables that are known to affect photosynthetic efficiency, such as irradiance dynamics, which in turn is affected by tidal amplitude, cloudy days, sun angle etc. Latitudinal effects on physiological responses of seaweeds include changes in survival and growth patterns (Peters & Breeman, 1993; Orfanidis & Breeman, 1999), development and life histories (Cunningham et al., 1993; Molenaar & Breeman, 1997), although few studies include quantification of photosynthetic parameters (Gerard, 1990). Species with an extended latitudinal distribution are exposed to high environmental variability that may promote phenotypic plasticity and/or ecotype differentiation as an adaptive response to temporal and spatial variation (Lynch & Gabriel, 1987).

Reproductive phase effects on photosynthetic performance

Differences in photosynthetic performance were further observed between reproductive phases of *M. laminarioides*. Sporophytes show higher photosynthetic rates than gametophytes. Results suggest that physiological differences between phases were similar to the effect observed in plants from both tidal heights, although the effect may be seasonally masked when the differences among plants from both tidal heights are present. These reproductive phase differences are an additional evidence of distinctive ecological characterisation for this species (Hannach & Santelices, 1985; Luxoro & Santelices, 1989). Thus, this study is the first in describing physiological differences between reproductive phases of isomorphic species.

The study of photosynthetic performance allows better understanding of the abilities of *M. laminarioides* to adapt to a changing environment by acclimation and also shows how productivity could vary along spatial and temporal scale in this species. Although both O₂-evolution and chlorophyll fluorescence have demonstrated spatial and temporal physiological differences among plants, they did not give exactly the same results. This difference could be related to the discrepancy between methods for measuring photosynthesis mainly at high irradiance (Longstaff et al., 2002). In spite of this F_v/F_m has been assumed to be proportional to the maximal quantum photosynthetic yield for O₂ evolution or CO₂ uptake (Magnusson, 1997), and thus this ratio could be also used to compare the photosystem (PSII) light utilisation efficiency. In this context, Maitencillo seems to provide a light regime less photoinhibitory and probably lower in winter, whereas very high and stressful in summer, regardless the position of *M. laminarioides* in the intertidal zone. During spring in Maitencillo, the lower tidal plants should be more efficient to use light for photosynthetic production than the upper tidal plants under similar light conditions. At this time environmental conditions should be closer to optimal for photosynthetic production. This is agreement with biomass production described for *M. laminarioides* in central Chile (Hannach & Santelices, 1985), which increases from the end of winter and declines from the middle of summer. In Pucatrihue the light regime seems to be less stressful, affecting mainly to upper intertidal plant in summer. Thus, the optimal period for photosynthesis production should be longer in this locality and the lower intertidal plants more efficient and productive than those in the upper shore during summer. Therefore, field physiological analysis indicates that management strategies for this species must consider not only temporal variation of the biological responses, as suggested elsewhere (Norambuena & Santelices, 1987; Westermeier et al., 1987), but also the spatial scales at which they occur.

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