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The effects of light and temperature on the photosynthesis of the *Asparagopsis armata* tetrasporophyte (*Falkenbergia rufolanosa*), cultivated in tanks

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Abstract

The integrated aquaculture of the tetrasporophyte of *Asparagopsis armata* Harvey (*Falkenbergia rufolanosa*) using fish farm effluents may be viable due to the species high capacity of removing nutrients and its content of halogenated organic compounds with applications on the pharmaceutical and chemical industries. In order to optimize the integrated aquaculture of *F. rufolanosa*, we followed the daily variation of the potential quantum yield (F_v/F_m) of PSII on plants cultivated at different biomass densities and different total ammonia nitrogen (TAN) fluxes to check if they are photoinhibited at any time of the day. Moreover, the photoinhibition under continuous exposure to highly saturating irradiance and its potential for subsequent recovery in the shade was assessed. The potential for year round cultivation was evaluated by measuring rates of O_2 evolution of plants acclimated at temperatures ranging from 15 to 29 °C, the temperature range of a fish farm effluent in southern Portugal where an integrated aquaculture system of *F. rufolanosa* was constructed.

Photoinhibition does not seem to be a major constrain for the integrated aquaculture of *F. rufolanosa*. Only when cultivated at a very low density of 1.5 g fresh weight (FW) l^{-1} that there was a midday decrease in maximal quantum yield (F_v/F_m). At densities higher than 4 g FW l^{-1}, no photoinhibition was observed. When exposed to full solar irradiance for 1 h, *F. rufolanosa* showed a 33% decrease in F_v/F_m, recovering to 86% of the initial value after 2 h in the shade. A midday decline of the *F. rufolanosa* F_v/F_m was also observed under the lowest TAN flux tested (~6 μM h^{-1}), suggesting that this fast and easy measurement of fluorescence may be used as a convenient diagnostic tool to detect nutrient-starved unbalance conditions of the cultures. Maximum net photosynthesis peaked at 15 °C with 9.7 mg O_2 g dry weight $(DW)^{-1}$ h^{-1} and remained high until 24 °C. At 29 °C, the net oxygen production was significantly reduced due to a dramatic increase of respiration, suggesting this to be the species' lethal temperature threshold.

Results indicate that *F. rufolanosa* has a considerable photosynthetic plasticity and confirm it as a good candidate for integrated aquaculture at temperatures up to 24° C and cultivation densities of at least 5 g FW l^{-1}. When cultivated at these densities, light does not penetrate below the first few centimetres of the surface zone. Plants circulate within the tanks, spending around 10% of the time in the first few centimetres where they are able to use efficiently the saturating light levels without damaging their photosynthetic apparatus.

Keywords: Integrated aquaculture; *Asparagopsis armata*; *Falkenbergia rufolanosa*; Fluorescence; Light; Photoinhibition; Photosynthesis; Polyculture; Temperature

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1. Introduction

There is an increasing interest in cultivating seaweed species that produce fine chemicals for the pharmaceutical and chemical industries. *Asparagopsis armata* Harvey, as most of the species of the Bonnemaisoniaceae family, is known to produce halogenated organic compounds with remarkable antibacterial and antifungal activity (McConnell and Fenical, 1977) that can be used to obtain cosmetic and/or pharmaceutical preparations. This species also produces sulphated galactans with promising therapeutic applications (Braun et al., 1983; Caporiccio et al., 1983), and new sources of anti-HIV compounds (Haslin et al., 2001). The potential economical value of the species instigated the cultivation of its tetrasporophytic phase, commonly known as *Falkenbergia rufolanosa*, to biofilter fish farm effluents (Schuenhoff et al., 2006-this issue). *F. rufolanosa* proved to be an excellent alternative to the most frequently used macroalga in polyculture, *Ulva* spp., as it showed both higher nitrogen uptake rates and biomass yields and a higher commercial value.

Both nutrient assimilation and biomass production are temperature- and light-dependent processes. In order to study the cultivation conditions that optimize the year-round production of *F. rufolanosa*, we assessed the species' photosynthetic responses to these environmental factors by O_2 evolution (*P*/*I* curves) in the laboratory and by pulse amplitude modulation (PAM) fluorescence field measurements (Schreiber et al., 1995). Short-term *P*/*I* measurements allow an estimation of temperature effects on the photosynthetic performance under saturating and sub-saturating irradiances. Such information is important for optimizing aerated tank cultivation, where the circulation pattern of plants alternately exposed them to full sunlight and darkness. At the surface, high levels of photosynthetically active radiation (PAR) may be a threat to the plant metabolism if the irradiance exceeds the demands of photosynthesis (Osmond, 1994; Aguirre-von Wobeser et al., 2000). Thus, it is important to know whether the plants are capable of photoacclimation or if they are photoinhibited at any time of the day when cultivated at different densities and nutrient fluxes. Pulse amplitude modulation (PAM) fluorescence field measurements (Schreiber et al., 1995) allow a non-intrusive assessment of the effects of stress factors such as excessive radiation.

The specific objectives of this work were (1) to test the effects of biomass density and total ammonium nitrogen (TAN) flux on photoinhibition during a daily cycle, (2) to assess photoinhibition under continuous exposure to highly saturating irradiance and the potential for subsequent recovery in the shade and (3) to assess *F. rufolanosa*'s photosynthetic light response under different temperature conditions.

2. Materials and methods

2.1. Seaweed cultivation conditions

This study was conducted in a *Falkenbergia*–biofilter system (Schuenhoff et al., 2006-this issue) on a *Sparus aurata* fish farm, Aquamarim, located in Ria Formosa lagoon, southern Portugal. *F. rufolanosa* was cultivated in 110 L (0.48 m * 0. 23 m^2) cylindrical white polyethylene aerated tanks that were supplied with particle screened (150 μm; Amiad) fishpond effluent rich in total ammonia nitrogen ($TAN = NH_4^+ + NH_3$). Irradiances inside and outside the seaweed tanks were measured with a spherical Li-193SA Underwater Quantum Sensor and a Li-190SA Quantum Sensor respectively, both connected to a Li-1000 Data Logger (Li-Cor, Lincoln, NE, USA). The light availability inside the tanks with different biomass densities was determined by measuring noontime PAR at a depth of 5, 10 and 24 cm, while stocking the tank with a stepwise increasing amount of seaweed (from 0 to 9.5 g FW l^{-1}). The pattern of exposure to light and darkness of an individual plant circulating inside the tanks was simulated by introducing a yellow neutrally buoyant plastic sponge as a thalli proxy. The period at the tank-surface and between individual surfacing events was measured 30 times.

2.2. Effects of cultivation conditions on photoinhibition

Photoinhibition was determined as the decrease of the potential quantum yield (F_v/F_m) of PSII (Hanelt, 1996; Häder et al., 1998; Jimenez et al., 1998). Chlorophyll fluorescence emission was measured with a portable pulse amplitude modulated fluorometer (Diving-PAM, Walz, Effeltrich, Germany). Samples of *F. rufolanosa* (10 replicates) were placed in the fluorometer leaf-clip holders at a distance of 7 mm from the fibre optics and dark-adapted for 10 min. Subsequently, a saturating white light pulse (approx. 4000 μmol photons m^{-2} s^{-1}; 0.4 s) was applied and F_v/F_m determined.

To assess the effects of different inoculation biomass densities on photoinhibition, tanks were incubated with the following biomass densities ($n = 2$): 1.5 (in March), 4, 5, 6, 7, 8 and 9 g FW l^{-1} (in June). Water turnover rates within the tanks were adjusted accordingly to supply *F. rufolanosa* with non-limiting TAN fluxes (~100 and 200 μM h^{-1} in March and June, respectively; see

Schuenhoff et al., 2006-this issue). TAN flux was calculated as the product of the water turnover rate within the tanks and the average TAN concentration of the fish pond effluent along the day. The effects of different TAN fluxes on photoinhibition were assessed in January using a biomass density of 5 g FW l^{-1}. Mean daily TAN fluxes of 6, 17 and 34 μM h^{-1} ($n=2$) were adjusted as at this time of the year, this range of values include limiting and non-limiting TAN fluxes (Schuenhoff et al., 2006-this issue). All culture conditions were maintained during a week before measurements. F_v/F_m was then measured along one day in 10 thalli randomly collected from each experimental tank.

The effects of an exposure to irradiance levels higher than photosynthetic saturation were determined by exposing *F. rufolanosa* to full solar irradiation (over 1600 μmol m^{-2} s^{-1}) for two periods of 1 and 3 h. F_v/F_m was measured before full light exposure, every 30 min during light exposure and during a subsequent 2-h period of recovery in the shade (50 μmol m^{-2} s^{-1}). Thalli exposed for 3 h did not recover after 2 h in the shade and were measured again after 17 h.

2.3. Temperature effects on photosynthesis

Plants were collected from the tanks and immediately transported to the laboratory in a dark and cool container. Upon arrival, they were acclimated for 3 days in a growth chamber (Fitoclima 750 E, Aralab, Lisboa, Portugal) inside 250-mL glass flasks with GF/F filtered seawater under continuous aeration, at 15, 19, 24 and 29 °C. These temperatures cover the annual range found in the fish farm effluent. The growth chamber was set at a photoperiod of 14:10 (day/night) and a light intensity of 75 μmol photons m^{-2} s^{-1} (white light, Osram Lumilux Plus L18W/21-840). To test for acclimation effects, photosynthesis measurements were also made in plants obtained directly from the farm, which were exposed at a daily mean temperature of 25 °C.

Photosynthesis was measured with a Clark type oxygen electrode (DW3 measuring chamber, Hansatech Instruments, Norfolk, UK). Samples of 3–6 mg DW were incubated in 15 ml GF/F filtered seawater while temperatures were maintained by a recirculating water bath (RayPa, Spain). Light was supplied by a slide projector (150 W halogen light bulb). Neutral density filters were used to obtain different irradiance levels. Net photosynthesis was measured as the oxygen production (mg O_2 g DW^{-1} h^{-1}) at increasing irradiance levels (6.5 to 700 μmol photons m^{-2} s^{-1}). Respiration (R_d) was measured as the consumption of oxygen in the dark before the sequence of irradiances.

The Platt et al. (1980) model was selected to analyse the photosynthesis versus irradiance (P/I) data, because it contains a parameter of photoinhibition (β) and was the model that best fitted the observations:

$$P = P_s[1-\exp(-\alpha I/P_s)]\exp(-\beta I/P_s)$$

where P stands for gross photosynthetic rate (mg O_2 g DW^{-1} h^{-1}), P_s for maximum photosynthetic rate (mg O_2 g DW^{-1} h^{-1}), I for irradiance (μmol photon m^{-2} s^{-1}), α for the ascending slope at limiting irradiance (mg O_2 g DW^{-1} h^{-1} (μmol photon m^{-2} s^{-1})$^{-1}$) and β for photosynthetic decline at saturating irradiance. The SigmaPlot software package was used to fit the curves.

2.4. Statistical analysis

One-way ANOVAs were performed to test for significant differences in the P/I photosynthetic parameters measured at different temperatures and to test for the effects of culture conditions on photoinhibition. When significant differences were found ($p \leq 0.05$), Tukey's HSD test was applied to test for significant differences in factor levels ($p \leq 0.05$).

3. Results

3.1. Cultivation conditions

The individuals of *F. rufolanosa* consist of a "pompom" of intermingled filaments. Their pattern of circulation within the tanks, characterized by a short duration at the surface (about 1 s) and a longer period below it (about 9 s) result in an alternate pattern of light/dark exposure. Light availability within the tanks rapidly decreases with depth and with biomass density (Fig. 1). When inoculated at 2 g FW l^{-1}, more than 30% of surface PAR was available at a depth of 5 cm while below 24 cm, plants were in the dark. At 5 g FW l^{-1}, only about 12% of the surface PAR was available at a depth of 5 cm and below 10 cm plants were already in the dark.

3.2. Effects of cultivation conditions on photoinhibition

Maximum values of potential quantum yield (F_v/F_m) were observed both in the morning and evening, whereas the minimum values occurred between 11:00 and 14:00 h, when irradiance was highest (Fig. 2a and b).

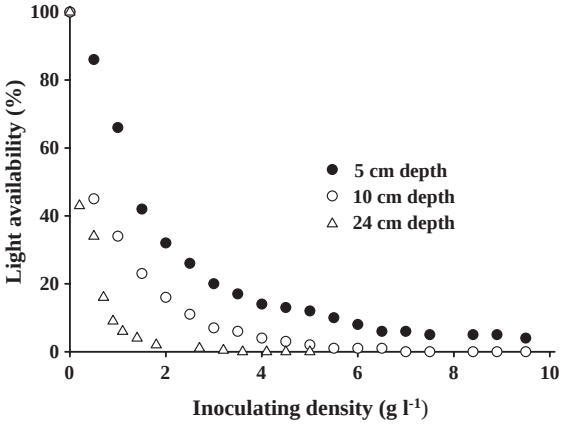

Fig. 1. Light availability at different biomass densities (g FW l^{-1}). Curves show measurements at 5 (●), 10 (○) and 24 (△) cm depth within the tanks.

With increasing density, the midday decline became less significant (Fig. 2b). F_v/F_m values were similar under all cultivation densities except at 1.5 and 4 g FW l^{-1} when they were significantly lower than the others, due to a significant midday decline. The effects of TAN flux on photoinhibition were only significant at a mean flux

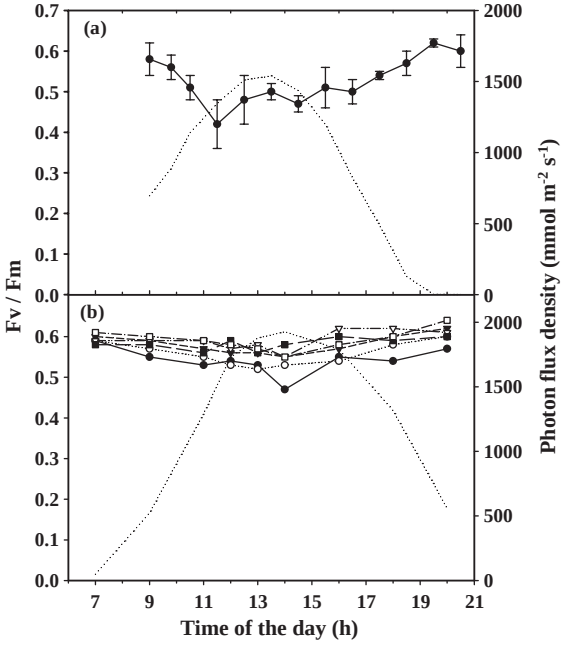

Fig. 2. Daily variation of *Falkenbergia rufolanosa* potential quantum yield (F_v/F_m) at different cultivation densities: (a) biomass density of 1.5 g FW l^{-1}, data collected in March; (b) biomass densities of 4 (●), 5 (○), 6 (▼), 7 (▽), 8 (■) and 9 g FW l^{-1} (□), data collected in June. Each data point is the average of 10 measurements. Standard deviations are only presented in panel (a). Dotted lines show the daily evolution of solar irradiance (μmol photon m^{-2} s^{-1}).

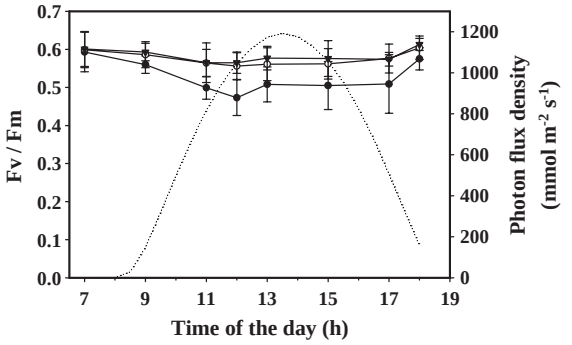

Fig. 3. Daily variation of *Falkenbergia rufolanosa* potential quantum yield (F_v/F_m) at different TAN fluxes: 6 (●), 17 (○) and 34 (▼) μM h^{-1}. Each data point is the average of 10 measurements. Bars show the standard deviations. Dotted line shows the daily evolutions of irradiance (μmol photon m^{-2} s^{-1}).

of 6 μM l^{-1} h^{-1} (Fig. 3). The maximum potential quantum yield of *F. rufolanosa* cultivated with this TAN flux experienced a significant midday decline but recovered to initial values later in the day.

Plants that were exposed to direct sunlight for 1 h showed a significant decrease in F_v/F_m, from

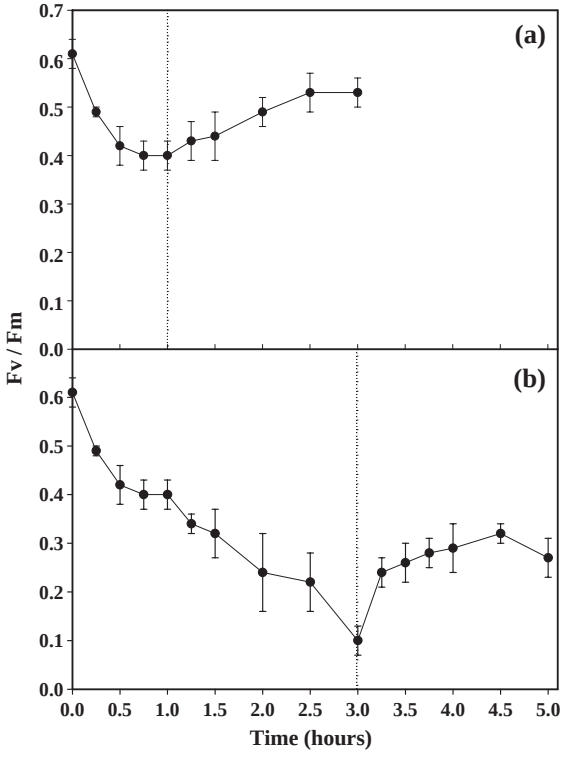

Fig. 4. Potential quantum yield (F_v/F_m) of *Falkenbergia rufolanosa* after exposure for 1 h (a) and 3 h (b) to direct sunlight (over 1600 μmol m^{-2} s^{-1}). The subsequent recovery in the shade (50 μmol m^{-2} s^{-1}) is represented on the right side of doted line.

0.61±0.03 to 0.4±0.03 (Fig. 4a). After a 2-h period in the shade, F_v/F_m recovered to 86% of the initial quantum yield value. The longer exposure time of 3 h led to a 39% decrease of the initial F_v/F_m values (Fig. 4b). In this case, F_v/F_m recovery was only up to 47% of the initial value. Even after a period of 17 h in the shade, no further recovery was observed in these plants (data not shown).

3.3. Temperature effects on photosynthesis

The adjustment of the Platt et al. (1980) model to the *P*/*I* data was better ($R^2=0.80$) in the acclimated samples (Fig. 5; 15 °C, 19 °C, 24 °C and 29 °C), than in non-acclimated plants (Fig. 5; 25 °C), where it only explained 59% of the data variance. A general decline in the photosynthetic rate (photoinhibition) of *F. rufolanosa* with irradiances above 150 μmol m^{-2} s^{-1} was observed at all temperatures tested (Fig. 5). Maximum gross photosynthetic rates were similar for samples acclimated at temperatures between 15 and 24 °C (~11 mg O_2 g DW^{-1} h^{-1}) while they increased dramatically to 46.6 mg O_2 g DW^{-1} h^{-1} at 29 °C. This difference is explained by the plant's respiration that was lower than 5 mg O_2 g DW^{-1} h^{-1} in all samples, except at 29 °C where there was a ten-fold increase (Fig. 6), suggesting the onset of a metabolic threshold. As well, the maximum net photosynthetic rates showed a slight but significant decrease with increasing incubation temperatures, from 9.74±0.6 mg O_2 g DW^{-1} h^{-1} at 15 °C to 6.63±0.3 mg O_2 g DW^{-1} h^{-1} at 24 °C, decreasing sharply to 0.43±0.9 mg O_2 g DW^{-1} h^{-1} at 29 °C (Fig. 6). The maximum net photosynthetic rates of non-acclimated farm samples, cultivated at a mean daily temperature of 25 °C, were not significantly different from thalli maintained in the laboratory at 24 °C (Fig. 6). On the other hand, dark respiration (R_d) of non-

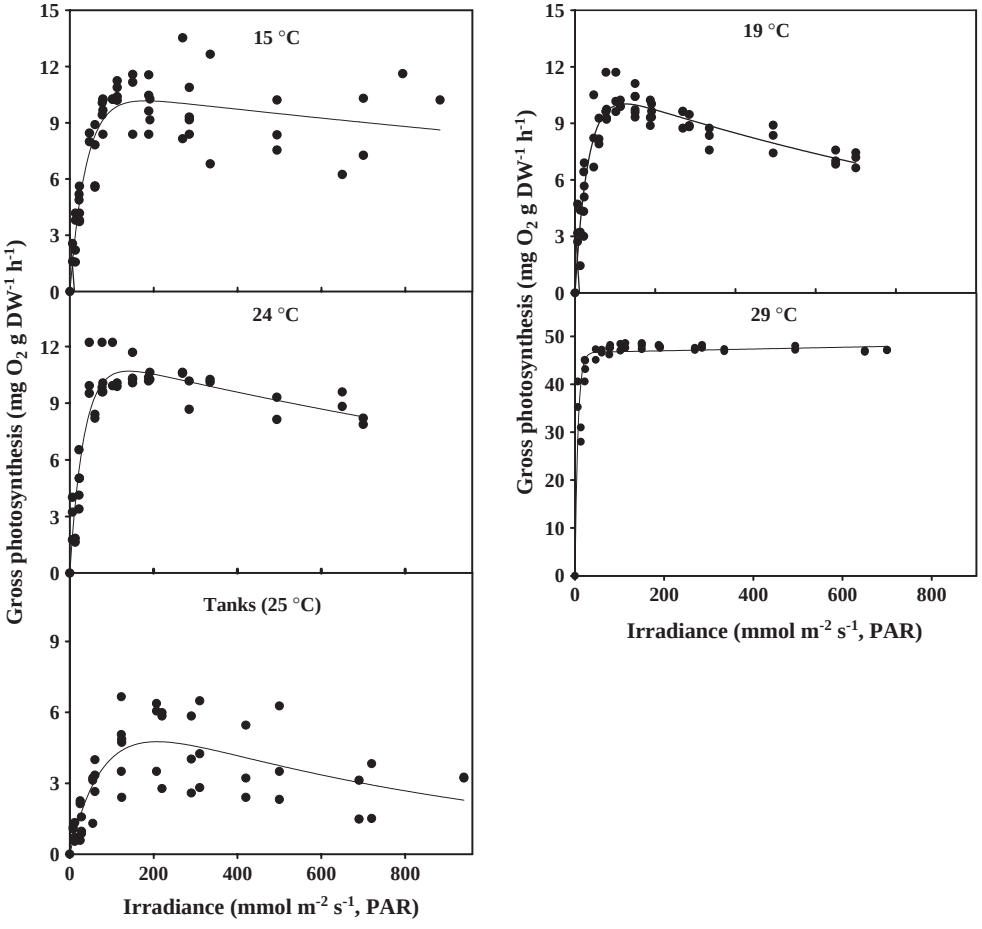

Fig. 5. Light response curves of non-acclimated (tanks) and acclimated *Falkenbergia rufolanosa* at 15, 19, 24 and 29 °C. Curves were adjusted with the Platt et al. (1980) model.

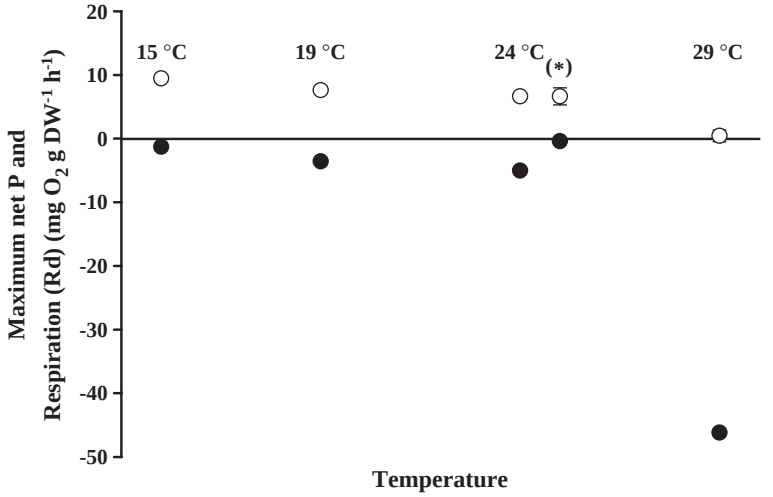

Fig. 6. Effects of temperature on the maximum net photosynthesis (○) and dark respiration (●) of both acclimated and non-acclimated *Falkenbergia rufolanosa*. Plants from the integrated aquaculture were at a temperature of 25 °C (*). Values represent means±S.E. (n=6).

acclimated thalli was lower than that of acclimated thalli.

The initial slope of the curves (α) was similar in plants acclimated to temperatures between 15 and 24 °C (~0.3 mg O_2 g DW^{-1} h^{-1} (μmol photon m^{-2} $s^{-1})^{-1}$) and higher than non-acclimated plants (0.08 mg O_2 g DW^{-1} h^{-1} (μmol photon m^{-2} $s^{-1})^{-1}$). At 29 °C, the slope increased dramatically to 6.9 mg O_2 g DW^{-1} h^{-1} (μmol photon m^{-2} $s^{-1})^{-1}$.

4. Discussion

Our results show that photoinhibition is not a major constrain for the integrated aquaculture of *F. rufolanosa*. This is a protective mechanism for the photosynthetic apparatus to dissipate the excess of absorbed energy through fluorescence and heat, which has been widely described not only in natural stands of seaweeds (Ramus and Rosenberg, 1980; Hanelt et al., 1993; Häder et al., 1996a,b, 1998; Jimenez et al., 1998) but also in both seaweed (Aguirre-von Wobeser et al., 2000; Cabello-Pasini et al., 2000) and microalgae cultivation (e.g. Vonshak et al., 2001). In this cultivation system, the midday decrease of the photochemical efficiency (F_v/F_m) of *F. rufolanosa* was only observed at inoculation densities of 1.5 g FW l^{-1}, when the illuminated zone within the tanks was up to 24 cm deep. When cultivated at high densities, the compacted filamentous "pompoms" of *F. rufolanosa* prevented light from penetrating below the first few centimetres of the surface zone. Plants spent around 10% of the time in this zone, where light levels may cause photoinhibition, but they probably had time to recover completely during the subsequent dark period. As outlined by Aguirre-von Wobeser et al. (2000), the pulse type dosage of high PAR caused by the circulation of individual plants within the tanks may reduce photoinhibition. Although cultivated *F. rufolanosa* individuals are most of the time in the shade, they do not behave strictly as shade-adapted plants as defined by Jimenez et al. (1998), because they showed a low degree of photoinhibition and a fast recovery in the shade, even when exposed to full solar irradiance during 1 h.

A midday decline of F_v/F_m was also observed in the TAN flux experiment, but only for the lowest flux tested (5.7 μM h^{-1}). Although *F. rufolanosa* was still nitrogen limited at a TAN flux of 17 μM h^{-1} (see Schuenhoff et al., 2006-this issue), F_v/F_m was already insensitive to this flux. This could be an indicator that, at the lowest flux, tested plants were under nutrient-starved conditions. Parkhill et al. (2001) provided evidence that F_v/F_m is only a sensitive indicator of nutrient-starved unbalance conditions, but when plants are acclimated to nutrient limitation, the relationship between F_v/F_m and nutrient stress fails. This fast and easy measurement of fluorescence may thus be used as a convenient diagnostic tool to detect nutrient-starved unbalance conditions of the cultures. This may be relevant to prevent plant physiological damage when, for example *F. rufolanosa* is cultivated under very low TAN fluxes in order to increase the efficiency of TAN removal from fish farm effluents (Schuenhoff et al., 2006-this issue).

Maximum net photosynthetic rates of *F. rufolanosa* peaked at 15 °C and remained high over a wide range of

temperatures, from 15 to 24 °C, a common behaviour of macroalgae (Oates and Murray, 1983; Baghdadli et al., 1990; Madsen and Maberly, 1990; Davison, 1991). The photosynthetic data is consistent with the literature results that report the lethal temperature limits of *F. rufolanosa* from the warm–temperate Mediterranean–Atlantic to be from 5 to 27 °C (Orfanidis, 1991) and the optimal temperature for growth to be from 10 °C to 21 °C (Oza, 1989; Orfanidis, 1991).

The maximum net photosynthetic rates obtained for *F. rufolanosa* acclimated to temperatures from 15° C to 24° C, varied from 9.7 to 6.6 mg O_2 g DW^{-1} h^{-1}. These rates are higher than those determined for other potentially farmable red seaweeds, such as *Gracilaria* spp. (2.6–5.2 mg O_2 g DW^{-1} h^{-1} in Rivers and Peckol, 1995; 0.77 mg O_2 g FW^{-1} h^{-1} in Lee et al., 1999) and *Hypnea musciformis* (3.1 mg O_2 g DW^{-1} h^{-1}, Rosenberg et al., 1995). The functional-form model proposed by Littler et al. (1983) in which seaweed biomass productivity is higher in sheet-like species, followed by filamentous forms and by coarsely branched ones, explains the observed differences. On the other hand, the filamentous *F. rufolanosa* showed higher net photosynthetic rates than the sheet-like species of *Porphyra* spp. (1.92–7 mg O_2 g DW^{-1} h^{-1} in Zhang et al., 1997; 7.68 mg O_2 g DW^{-1} h^{-1} in Aguilera et al., 1997). This suggests that *F. rufolanosa* is a very productive species under saturating light conditions.

Within the tanks of the integrated aquaculture the photosynthetic performance of the circulating thalli depends mostly on the light-limited portion of the *P*/*I* curve, defined by its initial slope (α), as they are only briefly exposed to saturating levels of light, being most of the time under very low light levels. The photosynthetic O_2 evolution in the light-limited zone (α) is not significantly influenced by temperature but is mainly controlled by the light reactions (Falkowski and Raven, 1997). The value of α measured in the *F. rufolanosa* plants from the integrated aquaculture suggests adaptation to light as it was lower than in the plants acclimated to the lower levels of light of the culture chambers in the laboratory. This α sensitivity to light, coupled to the ability of efficient use of saturating light levels at the water surface without damaging the photosynthetic apparatus, indicates that *F. rufolanosa* has a considerable photosynthetic plasticity. When the thalli emerge to the light zone, they are again ready to use light in an efficient manner. It has been reported that photosynthesis is more efficient per unit of light when exposed to short flashes of intense light than under continuous light (Bidwell et al., 1985).

Care must be taken when applying the laboratory observations of the temperature effects on photosynthesis to the integrated aquaculture conditions as the light and temperature regimes are very different. While in the laboratory, the plants are exposed to continuous levels of light (photoperiod) and temperature; in the aquaculture, they are exposed to varying levels along the day.

The dramatic increase of respiration observed in the laboratory acclimated plants from 24 to 29 °C suggests that a metabolic threshold was attained, in agreement with the 27 °C lethal limit observed by Orfanidis (1991) for this species. This is a strong indicator that *F. rufolanosa*-integrated aquaculture in southern Portugal in the summer, when daily maximum water temperatures within the tanks may reach 29 °C, may be difficult, in spite of putative seasonal adaptations. In fact, *F. rufolanosa* cultures were invaded by other species during the hottest summer period, due to the sharp decrease of net photosynthesis and consequently of growth rate. During the rest of the year, the species grew well and production peaked in spring with higher irradiances and photoperiod (Schuenhoff et al., 2006-this issue).

Our findings confirm *F. rufolanosa* as a good candidate for commercial tank cultivation at temperatures up to 24 °C. The species showed a high photosynthetic performance under a wide range of temperatures and irradiances. When cultivated at a biomass density of at least 5 g FW l^{-1}, there was no decrease in the photosynthetic performance due to photoinhibition.

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