Laminaria saccharina photosynthesis measured *in situ*: photoinhibition and xanthophyll cycle during a tidal cycle

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ABSTRACT: Photosynthetic activity in thalli of *Laminaria saccharina* (Lamouroux) was followed *in situ* in the upper subtidal zone of a Northern Brittany rocky shore (Roscoff, France), using a submersible pulse amplitude modulated (PAM) fluorometer. Two fluorescence parameters, the effective quantum yield of photosystem II (Φ_{PSII}) and the relative electron transport rate (rETR), were estimated at various stages of a tidal cycle from 10:00 to 18:30 h, and different light conditions due to variations of water depth and position of the sun. The Φ_{PSII} decreased strongly during the ebb tide, essentially due to a drop in the maximal fluorescence level for light-adapted samples (F_m'). This was the result of increasing non-photochemical quenching (NPQ). Algae totally recovered during the rising tide, indicating that no significant photosynthetic damage occurred at ebb tide. *L. saccharina* responded to high light stress with photoprotective processes such as the xanthophyll cycle. The de-epoxidation ratio (DR) (i.e. conversion of violaxanthin into antheraxanthin and zeaxanthin) increased during the ebb tide and decreased during the rising tide. However, in spite of the development of a photoprotective mechanism, the overall photosynthetic activity (rETR) declined strongly at the highest irradiance level. This result indicates that primary production levels have been overestimated in the past.

KEY WORDS: *Laminaria saccharina* · Photoprotection · Xanthophyll cycle · Chlorophyll fluorescence · Diurnal tidal cycles · Diving PAM

INTRODUCTION

Laminariales are among the most abundant macroalgae in the upper subtidal zone of rocky shores in Northern France. They are located in a large belt between 6 m below and 2 m above bathymetrical zero. However, laminarian stocks, especially *Laminaria digitata* and *L. saccharina* have been decreasing in the last few years (Cosson 1999, Arzel 2000) for reasons that are not understood. This decrease leads to economic problems, as laminariales are used either as food or, more significantly, for the industrial extraction of valuable compounds such as alginate, laminarin, mannitol and iodine. To understand this decrease, the physiological behaviour that results from environmental variations or stresses needs to be explored in more detail.

Laminaria is sessile, attached by holdfasts in the intertidal or upper subtidal zones. It is exposed to considerable variations in irradiance because of (1) continuously changing water depth during the tidal cycle, and (2) natural variations in irradiance caused by weather conditions and by the sun's changing position during the day (Dring & Lüning 1994). At our study site

(Brittany), tides are semidiurnal; during spring tides, the low tide is around midday and thus coincides with maximal ambient irradiance. *Laminaria* acclimated to low irradiance are then exposed to high incident light levels. Exposure to excessive irradiance may lead to photoinhibition in macroalgae, reducing photosynthetic efficiency but avoiding, in most cases, photo-oxidative damage (Hanelt et al. 1993, 1997, Bruhn & Gerard 1996, Schofield et al. 1998, Ensminger et al. 2000, Rodrigues et al. 2000). Under such circumstances, algae are able to develop protective mechanisms that dissipate excess excitation energy as heat. This phenomenon could be partially controlled by the xanthophyll cycle, which consists of the de-epoxidation of violaxanthin to, first, antheraxanthin, and then zeaxanthin (Demmig-Adams & Adams 1996). The alga's xanthophyll cycle is triggered by light stress, as shown in green macroalgae by Ensminger et al. (2000), in brown macroalgae by Uhrmacher et al. (1995) and Schofield et al. (1998), and in *L. saccharina* in *in vitro* experiments by Duval et al. (1992), Benet et al. (1994), Harker et al. (1999), and Gévaert et al. (2002).

The photosynthetic performance of several marine macroalgae has been estimated using oxygen exchange, and more recently in the field, using a portable pulse amplitude modulated (PAM) fluorometer. This instrument provides information such as quantum yield, relative electron transport rate (rETR), and photochemical and non-photochemical quenching (NPQ). Using this technique, Hanelt et al. (1997) showed that gametophytes and old sporophytes of *Laminaria saccharina* are less sensitive to high light levels than younger thalli. Harker et al. (1999) showed that *L. saccharina* can develop NPQ of fluorescence, correlated with an increase in the de-epoxidation ratio (DR) of violaxanthin to zeaxanthin. Nevertheless, experimental irradiances used in that study were higher than the highest irradiances found in the field. No study has been done *in situ* to investigate the photosynthetic responses of *L. saccharina* to light variation and the development of photoprotective mechanisms during a tidal cycle. A recently developed submersible PAM fluorometer (Diving PAM, Walz) has been used to study *in situ* photosynthesis in seagrass (Ralph et al. 1998, Beer & Björk 2000), sponges (Beer & Ilan 1998) and corals (Beer et al. 1998, Jones & Hoegh-Guldberg 2001), but not in seaweeds.

In this study, a series of *in situ* measurements were undertaken using the Diving PAM to determine whether *Laminaria saccharina* growing in the upper subtidal zone on rocky shores of Northern Brittany are sensitive to photoinhibition during a tidal cycle, and whether they are able to develop photoprotective mechanisms such as the xanthophyll cycle. To this end, experiments were carried out at ambient light, temperature and water conditions.

MATERIALS AND METHODS

Experiments were carried out on the brown kelp *Laminaria saccharina* (Lamouroux) in the upper subtidal zone of a Northern Brittany rocky shore near Roscoff (France) during the spring tide of September 2000. A total of 8 sporophytes with blade lengths of about 1 m were marked the day before the experiment with a coloured thread attached to their stipe. Fluorescence parameters were followed during the tidal cycle for 3 of these 8 sporophytes; 3 other thalli were used for pigment analysis and 2 other thalli were used to estimate photosynthetic parameters from rapid light curves (i.e. rETR variations vs increasing irradiance).

The seawater temperature during the experiment was about 16°C. Photosynthetically active radiation (PAR) was measured in air during the tidal cycle (1 measurement every 15 s, averaged over 1 min) using an SA-190 quantum sensor connected to a datalogger (Li-Cor, Li-1400). *In situ* ambient radiation was measured underwater close to the algae with the Diving PAM quantum sensor, calibrated in air with the SA-190 light meter.

Fluorescence measurements. *In vivo* chlorophyll fluorescence properties were measured *in situ* by SCUBA divers using a submersible PAM fluorometer. The fluorescence signal was always taken from the middle of the frond in the same place for 3 sporophytes. Thalli were dark-adapted for 5 min using the 'Dark Leaf Clip Diving L-C' (Walz) to which the fiber optic of the fluorometer was applied and maintained to perform each measurement. First, the initial fluorescence (F_0) was induced by the low irradiance of the red measuring light, and maximal fluorescence (F_m) was determined following a single saturating light pulse (0.8 s). Variable fluorescence (F_v) was calculated as the difference between F_m and F_0. The optimal quantum yield was calculated as F_v/F_m. After these initial measurements, the effective quantum yield of photosystem II (Φ_{PSII}) was followed on the 3 sporophytes at 5 stages of the tidal cycle: S_1 and S_2 during the ebb tide (algae at 5.4 and 3.1 m depth, respectively), S_3 at low tide (1.6 m depth), and S_4 and S_5 during the rising tide (4.2 and 8.4 m depth, respectively). In contrast to F_v/F_m, Φ_{PSII} was measured under ambient light. The fiber optic was mounted in a home-made transparent Plexiglas holder applied to one side of the thallus in such a way that the distance between the fiber optic and the algal tissue was constant and standard. The fiber optic forms a 60° angle with the sample, avoiding awkward shading or darkening.

Φ_{PSII} was calculated as $(F_m' - F_t)/F_m'$ (Genty et al. 1989), where F_m' is the maximal fluorescence level measured during a single saturating light pulse (0.8 s) for light-adapted samples, and F_t is the fluorescence

steady-state level immediately prior to the flash. Then, the apparent photosynthetic rETR was estimated according to Genty et al. (1989) using the following equation:

$$\text{rETR} = \Phi_{\text{PSII}} \times \text{PPFD} \times 0.5 \qquad (1)$$

where PPFD (PAR photon flux density) is the value of the actinic light (directly measured close to the sample by the Diving PAM quantum sensor, which was also fixed to the holder), and 0.5 is a correction factor based on the assumption that the incident photons are absorbed equally by the pigments of the 2 photosystems.

Rapid light curves. Rapid light curves were also determined with the Diving PAM in 2 other *Laminaria saccharina* thalli at S_1, S_3 and S_5 (beginning of the ebb tide, low tide, and end of the flood tide, respectively). They were generated by applying and maintaining the light guide of the Diving PAM on the thalli via the Dark Leaf Clip. The initial F_0 and F_m were measured after 5 min darkness as described above for each sporophyte before monitoring commenced. The algae were then exposed to 8 steps (10 s each) of increasing artificial actinic light from the internal light source of the Diving PAM. The fluorescence parameters were measured using an automatic run and Φ_{PSII}, rETR and NPQ were calculated at each step. The apparent photosynthetic rETR was calculated as described above, but in this case as a function of the artificial actinic light provided by the internal light source of the Diving PAM. We checked that the irradiance of the internal light source did not decrease over the whole series of measurements by recording the light intensities (using an SA-190 light meter) during 6 rapid light curves (corresponding to our experiments) and used the averaged values of these measurements: 10, 40, 79, 150, 234, 333, 513, 715 µmol quanta m^{-2} s^{-1}. The irradiation period (10 s) and the number of replicates and stages were limited by the power of the battery in the Diving PAM.

NPQ, which correlates positively and linearly to energy dissipation as heat, was calculated according to Bilger & Björkman (1990):

$$\text{NPQ} = \frac{F_m - F_m{'}}{F_m{'}} \qquad (2)$$

where F_m is the maximum fluorescence for each sporophyte at the beginning of the experiment (at S_1).

Photosynthetic parameters, i.e. maximum rETR (rETR$_m$), initial slope of the non-saturated photosynthetic rate (α_I), saturation onset parameter (I_k) and irradiance for rETR$_m$ (I_m) were estimated from the rapid light curves using the model described by Eilers & Peeters (1988).

Pigments analysis. Thallus disks (8 mm diameter) were sampled at the 5 stages of the tidal cycle (S_1 to S_5)

from 3 separate thalli. The disk samples were immediately frozen and kept in liquid nitrogen until pigment extraction and analysis by HPLC in the laboratory. Before the extraction, epiphytic diatoms were removed by rinsing the samples with distilled water and drying with filter paper. Samples were then ground in a mortar with methanol under dim light. Following extraction, homogenates were centrifuged at $15\,000 \times g$ for 5 min. Supernatants were filtered on PTFE Millex membrane (0.45 µm) (Millipore) and dried under a stream of nitrogen. Pigments were extracted with a mixture of methylene chloride/distilled water (50/50 v/v) and after decanting, the non-pigmented aqueous phase was discarded to remove the salt. The pigment phase was then evaporated under a stream of nitrogen and recovered with methanol for injection.

Reversed-phase HPLC was performed according to Arsalane et al. (1994) using a Waters system equipped with a 1091 diode array detector on a Zorbax ODS column (25.0 cm × 4.6 mm, 5 µm particles). Extinction coefficients used for external calibration of our system were as in Berkaloff et al. (1990). The xanthophyll cycle DR, determined at the different stages of the tidal cycle, was calculated as:

$$\text{DR} = \frac{A + Z}{V + A + Z} \qquad (3)$$

where V, A, and Z are violaxanthin, antheraxanthin and zeaxanthin concentration, respectively (moles per 100 moles chlorophyll *a*).

RESULTS

Time course of light

The experiment was performed under mostly clear sky with some irregular occurrence of clouds. Irradiance gradually increased during the morning, reached its maximum value at 14:00 h (UT + 2) and then progressively declined until sunset (Fig. 1). Maximum irradiance thereby corresponded to the period of low tide (about 13:30 h) when algae were at 1.6 m depth; this is commonly the case during spring tides in Northern Britanny. During this period, algae were therefore subjected to rather high irradiances of 559 µmol quanta m^{-2} s^{-1}.

Time course of fluorescence parameters

The mean F_v/F_m, determined at the beginning of the experiment, was 0.74 ± 0.01 (mean ± SD). Fig. 2 illustrates the time course of the mean effective quantum yield (Φ_{PSII}) in *Laminaria saccharina* measured under-

water. During the ebb tide, Φ_{PSII} declined by 82%, essentially due to decreases in the F_m' values (data not shown). This illustrates the initiation of the NPQ increase and photoprotective reactions during the ebb tide. However, during the rising tide, the Φ_{PSII} returned to the initial value, as the thalli recovered their photosynthetic efficiency. The PSII of *L. saccharina* did not appear to be irreversibly damaged at low tide. A significant negative linear correlation was observed between Φ_{PSII} levels and the corresponding underwater irradiances:

$$\Phi_{PSII} = 0.660 - 0.001 \times \text{(underwater irradiance)};$$
$$r = 0.822, n = 15, p < 0.001$$

In order to follow more precisely the overall photosynthetic capacity of *Laminaria saccharina* during the tidal cycle we calculated the rETR (Fig. 3). The mean rETR increased during the ebb tide with the increase in irradiance measured at the surface of the thallus and reached its maximum value at midday (irradiance at the thallus surface: 309 µmol quanta m^{-2} s^{-1}). However, with maximum irradiance (559 µmol quanta m^{-2} s^{-1}) at low tide, the rETR was only half of the previous value. The rETR subsequently continued to decrease with decreasing irradiance until sunset.

Time course of pigment content

During the ebb tide, violaxanthin was progressively converted into zeaxanthin, and DR increased from 0.100 to 0.213 at low tide (Fig. 4). During the rising tide, the DR returned to about the initial value. The amounts of other pigments (chlorophyll *c*, fucoxanthin, chlorophyll *a* and β carotene) did not change (data not shown).

A significant negative linear correlation was observed between the effective quantum yields of PSII and DR:

$$DR = 0.231 - 0.225 \, \Phi_{PSII};$$
$$r = 0.773, n = 15, p < 0.001$$

Rapid light curves

Fig. 5 shows the variation in rETR versus irradiance (µmol quanta m^{-2} s^{-1}) in 2 sporophytes at 3 different tidal stages, and corresponding curves obtained by fitting the

data to the model of Eilers & Peeters (1988). The photosynthetic parameters at the 3 stages of the tidal cycle are given in Table 1. Whereas α_I and I_k did not vary significantly in the course of the tide (Kruskal-Wallis test: $H_c = 4.191$, p = 0.123 and $H_c = 3.714$, p = 0.156, respectively; $n_1 = 2$, $n_2 = 2$, $n_3 = 2$), rETR$_m$ and I_m values were significantly higher at S_1 than at S_5 but lower than at S_3 (Kruskal-Wallis test: $H_c = 4.571$; p = 0.102, the lowest significant probability available for $n_1 = 2$, $n_2 = 2$, $n_3 = 2$ and obtained with the most favorable case corresponding to a complete separation of each pair within the 3 groups S_1, S_3 and S_5. At low tide, rETR$_m$ was 49 ± 3 (mean ± SD) and I_m, 427 ± 18 µmol quanta m^{-2} s^{-1}. NPQ curves for sporophytes 1 and 2 are pre-
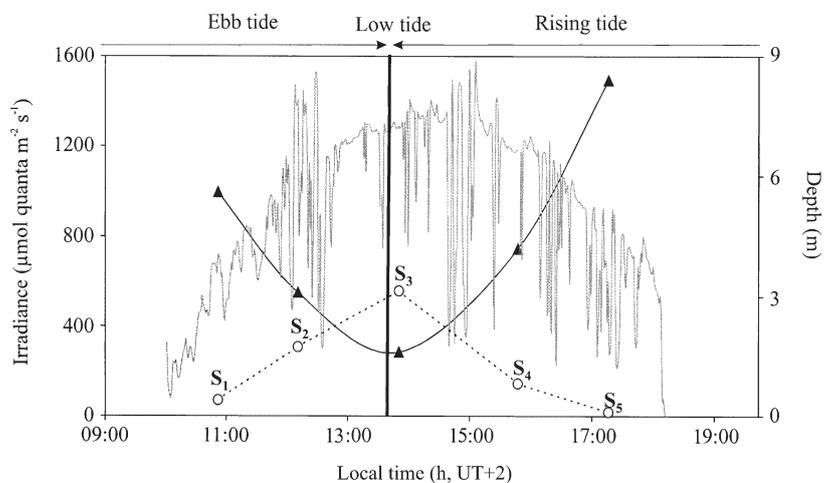
Fig. 1. Diurnal course of incident irradiance (PAR, solid line), underwater irradiance (···○···) and depth (–▲–) during the tidal cycle (S_1 to S_5)
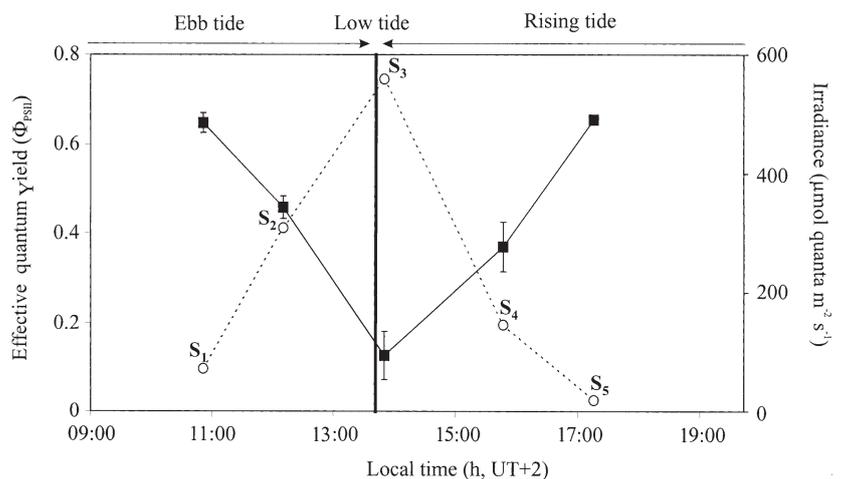

Fig. 2. *Laminaria saccharina.* Diurnal course of mean effective quantum yield (Φ_{PSII}) measured in 3 sporophytes during the 5 stages of the tidal cycle, S_1 to S_5 (–■–; vertical bars: SD) and underwater irradiance measured at the surface of the algae (···○···)

sented in Fig. 6. NPQ values increased progressively with the irradiance applied regardless of the state of the tide, but nevertheless remained relatively low. The NPQ values during the rising tide (S_5) were significantly lower than at low tide (S_3), but higher than at ebb tide (S_1) (1-way ANOVA: *F*-ratio = 276.85, p < 0.001, n = 48; Tukey post-hoc test: p < 0.001 between S_1 and S_3, as well as S_1 and S_5, and S_3 and S_5). At the beginning of the ebb tide (S_1), *Laminaria saccharina* developed negligible thermal energy dissipation, regardless of the irradiance applied.

DISCUSSION

Laminaria saccharina has been the subject of physiological and ecological studies which have led to a better understanding of the maintenance of ecologically important *L. saccharina* populations in many different environments (water depth and latitude), but all have been carried out in the laboratory, either on cultivated *L. saccharina* or on collected algae which could have been subject to stress due to the treatment. We considered that it was important to follow the light variations to which *L. saccharina* can be subject during diurnal tidal cycles and to study their physiological responses *in situ*.

The seaweeds studied were located at a rather high shore level (1.6 m depth at low tide). Nevertheless, the thalli never emerged and therefore never experienced full solar radiation or desiccation.

The optimal quantum yield, a measure widely used to assess the importance of light stress, was first calculated from F_v/F_m of dark-adapted *Laminaria saccharina*
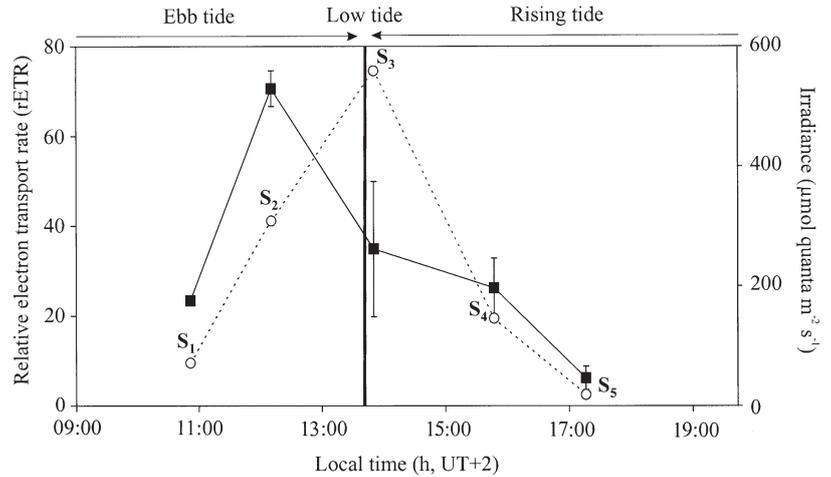

Fig. 3. *Laminaria saccharina.* Diurnal course of mean relative electron transport rate (rETR) measured in 3 sporophytes during the 5 stages of the tidal cycle, S_1 to S_5 (–■–; vertical bars: SD) and underwater irradiance measured at the surface of the algae (···○···)
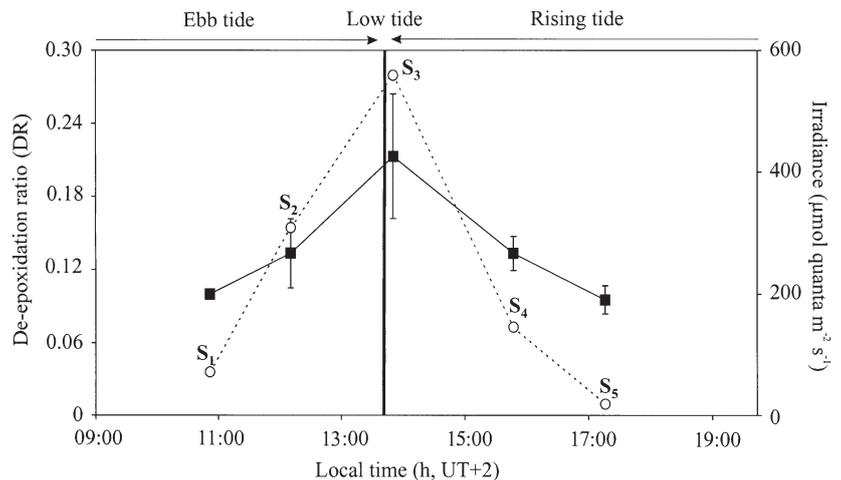

Fig. 4. *Laminaria saccharina.* Diurnal course of mean de-epoxidation ratio (DR) measured in 3 sporophytes during the 5 stages of the tidal cycle, S_1 to S_5 (–■–; vertical bars: SD) and underwater irradiance measured at the surface of the algae (···○···)

Table 1. *Laminaria saccharina.* Photosynthetic parameters assessed with the model of Eilers & Peeters (1988) at different stages of the tidal cycle, measured in 2 sporophytes (8 levels of irradiance). α_I = initial slope of the photosynthetic rate; $rETR_m$ = maximum relative electron transport rate; I_k = saturation onset parameter; I_m = irradiance for $rETR_m$. r^2 = 0.998 to 0.999 in all cases

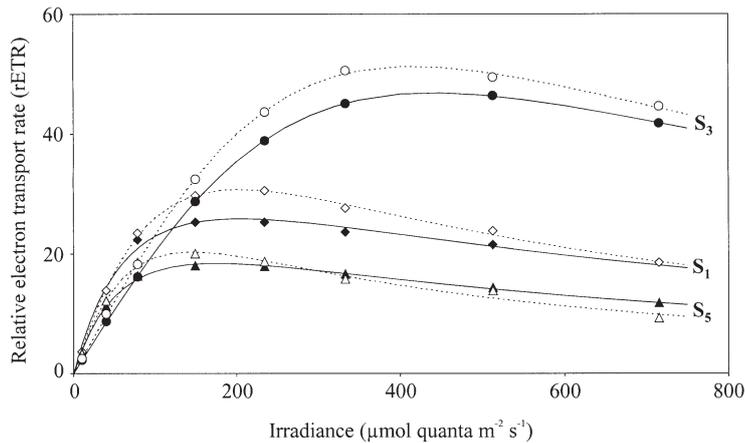| Stage of the tidal cycle	Depth (m)	α_I	$rETR_m$	I_k ($\mu mol\ m^{-2}\ s^{-1}$)	I_m ($\mu mol\ m^{-2}\ s^{-1}$)
Ebbing tide (S_1)	5.6	0.48 (0.43–0.53)	28.5 (26–31)	60 (49–72)	203.5 (203–204)
Low tide (S_3)	1.6	0.23 (0.22–0.24)	49 (47–51)	215 (212–218)	427 (414–440)
Rising tide (S_5)	8.4	0.42 (0.41–0.43)	19 (18–20)	46 (43–50)	161 (146–176)

Fig. 5. *Laminaria saccharina.* Rapid light curves, expressed as relative electron transport rate (rETR) at different stages of the tidal cycle, S_1, S_3 and S_5. Black symbols and solid line: sporophyte 1, open symbols and dotted line: sporophyte 2. Data are fitted to the model of Eilers & Peeters (1988)

thalli in the morning. The high value, about 0.75 is commonly obtained with brown macroalgae (Büchel & Wilhelm 1993, Dring et al. 1996) and indicated that the algae were photochemically efficient despite exposure to 4 successive sunny days during the spring tide, suggesting that they were acclimated to high light.

Increasing light during the ebb tide (due both to the ambient light increase during the morning and to decreasing water depth) led to an immediate decrease in photosynthetic quantum yield, and the seaweeds responded to the maximum light (559 µmol quanta m^{-2} s^{-1}) by a 82% reduction in the effective quantum yield (Fig. 2). The reduction is essentially due to the drop in

F_m' which could be the result of an increasing NPQ. Recovery was complete at the end of the rising tide, contrary to laboratory experiments (Bruhn & Gerard 1996). The diurnal course of the effective quantum yield (Φ_{PSII}) was directly correlated to underwater irradiance. The rapid recovery of the quantum yield suggested that the responses of *Laminaria saccharina* to high light intensity are linked to a down-regulation of PSII (now usually termed 'dynamic photoinhibition') rather than to the onset of photosynthetic damage ('chronic photoinhibition'), which reduces photosynthesis for longer periods (Henley et al. 1991, Osmond & Grace 1995, Jones & Hoegh-Guldberg 2001, Werner et al. 2001). Photoprotection after exposure to solar radiation has been observed in other macroalgae (Hanelt et al. 1997, Ensminger et al. 2000, Rodrigues et al. 2000). It occurs when light energy input exceeds the capacity for energy utilization and usually results in thermal dissipation of excess excitation energy in the pigment antenna of PSII. This regulatory process is still not fully understood, but it is known to limit accumulation of reactive oxygen species, protecting algae against photo-oxidative damage.

Several mechanisms in algae divert excess energy. First, they are able to reduce absorption by re-arranging the chloroplasts into a low-absorbing position (Hanelt & Nultsch 1991). Moreover, older, thicker sporophytes are more resistant to high light than younger, thinner thalli (Hanelt et al. 1997). In this way, the chloroplasts could be protected by increasing self-shading. When these mechanisms are insufficient to avoid excess energy absorption, algae and higher plants may develop a photoprotective process such as the xanthophyll cycle, resulting in thermal energy dissipation. It involves the de-epoxidation of violaxanthin to antheraxanthin and zeaxanthin (Demmig-Adams & Adams 1996).

Bruhn & Gerard (1996) studied the xanthophyll cycle during high light stress treatments on *Laminaria saccharina*. They found that the photoinhibition responses are not affected in the presence of the inhibitor dithiothreitol (DTT), but that recovery from photoinhibition is slower. In our experiment, DR varied during the tidal cycle as shown in Fig. 4: it increased during the ebb tide, reached its maximal value at low tide and then decreased during the rising tide. We show here that in *L. saccharina*, the xanthophyll cycle occurs *in situ* during the tidal
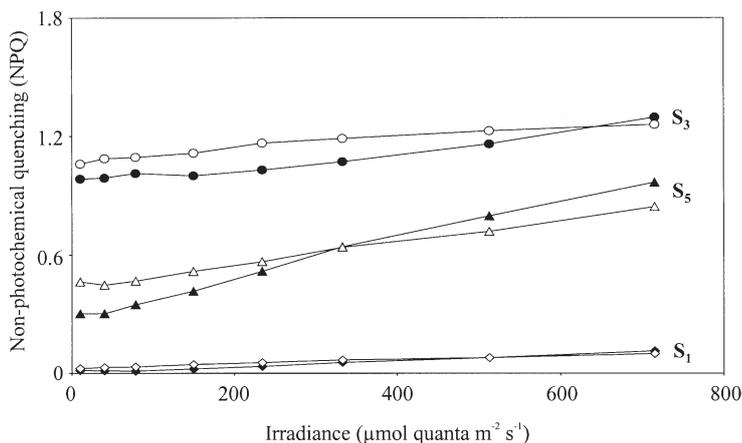

Fig. 6. *Laminaria saccharina.* Changes in non-photochemical quenching (NPQ) in response to increased irradiance. NPQ was calculated from the fluorescence parameters of the rapid light curves at different stages of the tidal cycle: S_1, S_3 and S_5. Black symbols: sporophyte 1, open symbols: sporophyte 2

cycle and that its development is directly correlated with the daily course of effective quantum yield. However, the converted pool of violaxanthin is rather low (about 21%) in comparison to the conversion ratio (60%) in *Lobophora variegata* in coral reefs (Franklin et al. 1996), but our data are in agreement with the results obtained during photoinhibition of *Cladophora glomerata* (Ensminger et al. 2000). Harker et al. (1999) obtained an *in vitro* DR of 0.41 when *L. saccharina* were submitted to 450 µmol quanta m^{-2} s^{-1} for 45 min, which caused photoinhibition by suppression of oxygen evolution (Lemoine et al. 1995).

The initial DR in our study is quite high (0.1) suggesting that zeaxanthin and antheraxanthin are an important protection against high light stress, or that some conversion occurred even when irradiance was low (72 µmol quanta m^{-2} s^{-1}). The DR obtained *in vitro* by Harker et al. (1999) in dark incubated *Laminaria saccharina* was 0.07, similar to our *in situ* initial value.

The rETR increased during the morning ebb tide, indicating increasing photon capture, but it decreased sharply at the low tide peak of light, and then slowly declined with falling PPFD during the afternoon rising tide, showing that *Laminaria saccharina* can undergo photoinhibition of photosynthetic efficiency and performance under midday low tide irradiance conditions.

Rapid light curves measured at early ebb tide (S_1), low tide (S_3) and the later rising tide (S_5) allowed us to determine photosynthetic response to light variations. At S_3, *Laminaria saccharina* exhibited photosynthetic characteristics of high light adapted algae. At this stage, the rETR$_m$ was double the values obtained at S_1 and S_5. These results are consistent with those obtained for the daily rETR variation (Fig. 3), i.e. the rETR value was higher in S_3 than in S_1 and S_5. It would have been interesting to conduct a rapid light curve at S_2 when the rETR of the diurnal course was at its maximum.

An increased photosynthetic rate is typically observed with acclimation to higher irradiance (Henley 1993). The increase in ETR$_m$ indicates an activation of photosynthesis, most likely via increased rate of 'dark' carbon-fixing enzymes such as RUBISCO. This is a common phenomenon in macrophytes. Similar activation and increased ETR is also seen in corals (Ralph et al. 1999). Some differences were observed in measures of photosynthetic activity (rETR$_m$ and I_m) between S_1 and S_5 (cf. Table 1). They could be due to the differences in depth and irradiance: at S_1 the depth was 5.4 m and irradiance was 72 µmol quanta m^{-2} s^{-1}, and at S_5 the depth was 8.4 m and irradiance was 19 µmol m^{-2} s^{-1}. Variations of NPQ calculated from the fluorescence parameters during the rapid light curves at S_1, S_3 and S_5 agree with the values of Φ_{PSII} and DR (Figs. 2 & 4 respectively): under strong light at low tide

(S_3), *Laminaria saccharina* exhibited the highest NPQ, consistent with the lowest Φ_{PSII} value (Fig. 2) and highest DR value (Fig. 4). The response of the algae at S_1, i.e. a low NPQ, suggests that they were not adapted to high light and therefore not able to develop a high NPQ.

In conclusion, *in situ* experiments demonstrated that *Laminaria saccharina* is strongly photoinhibited at ebb tide and fully recovers its photosynthetic capacities during the rising tide, because it has developed photoprotective mechanisms such as the xanthophyll cycle during periods of light stress. However, the strong decrease in rETR at the highest irradiance level should be taken into account in estimates of primary production.

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