Determination of the adenylate energy charge (AEC) as a tool to determine the physiological status of macroalgal tissues after UV exposure

MARK HÜNKEN1*, ULF KARSTEN2 AND CHRISTIAN WIENCKE3

1Ludwig-Maximilians-University Munich, Department I, Biology, Menzinger Str. 67, D-80638 Munich, Germany
2Institute of Aquatic Ecology, University of Rostock, D-18051 Rostock, Germany
3Foundation Alfred Wegener Institute for Polar and Marine Research, Am Handelshafen 12, D-27570 Bremerhaven, Germany

M. HUNKEN, U. KARSTEN AND C. WIENCKE. 2005. Determination of the adenylate energy charge (AEC) as a tool to determine the physiological status of macroalgal tissues after UV exposure. Phycologia 44: 249–253.

A method was developed to extract adenine nucleotides AMP, ADP, and ATP from marine macroalgal tissue to gain information on the cellular energy charge. Quantification was carried out by high performance liquid chromatography (HPLC). Three species from the rocky shore of the island of Helgoland (German Bight) were examined: Laminaria saccharina (Phaeophyta), Chondrus crispus (Rhodophyta), and Ulva lactuca (Chlorophyta). In L. saccharina and C. crispus, the adenylate energy charge (AEC) was determined in different thallus regions. AEC varied in relation to tissue age and function. Higher AEC values typically occurred in thallus regions with meristic activity. Furthermore, L. saccharina and U. lactuca were exposed to UV-A and elevated UV-B radiation. The AEC was calculated and the maximal quantum yield of photosystem II (Fv/Fm) was determined as indicators for UV stress. In both species, the AEC remained at high values (0.72 ± 0.04), while Fv/Fm dropped rapidly. The results show that the photosynthesis of the phaeophyte is more resistant to UV radiation than the chlorophyte.

INTRODUCTION

In recent decades, UV radiation (UVR) has increased, especially in polar regions due to depletion of the ozone layer and the appearance of so called ‘ozone holes’ over the Antarctic (Crutzen 1992). With the exception of the equatorial region, this depletion also has been observed also in all other latitudes (Björn et al. 1999). Both terrestrial as well as marine life is affected by the resulting higher UVR (Norris 1999). The UV waveband has various deleterious effects on macroalgae, e.g. inhibition of growth (Makarov 1999) and photosynthesis (Wood 1987), leading to changes in the vertical zonation (Franklin & Forster 1997; Hanelt et al. 1997a; Bischof et al. 1998; Hanelt 1998).

Although UVR effects on proteins and DNA in marine organisms have been reported (Bischof et al. 1999), much less is known about energy metabolism. The concentrations of the adenine nucleotides adenosine triphosphate (ATP), adenosine diphosphate (ADP), and adenosine monophosphate (AMP) can be used to calculate the adenylate energy charge (AEC).

According to Atkinson & Walton (1967), the AEC is an index for the amount of metabolically available energy that is actually stored in the adenylate system of a living organism. The AEC can be calculated from the molar levels of ATP, ADP, and AMP using the following formula: \( (0.5 \times \text{ADP + ATP})/(\text{ATP + ADP + AMP}) \). The AEC is a simplification in order to describe the individual effects of ATP, ADP, and AMP on metabolic processes. It is an index without dimension varying between 1, where all adenylates are present as ATP, and 0, where all adenylates are present as AMP. Both extreme values, however, are never obtained under natural conditions (Atkinson 1977).

Adenine nucleotides have stimulating or inhibiting effects on a large number of regulatory enzymes, such as phosphofructokinase, which is inhibited by excess ATP (Ramaiah et al. 1964), or isocitrate dehydrogenase, which is stimulated by AMP (Hathaway & Atkinson 1963).

Since the early 1970s, the AEC has been applied in many ecophysiological studies with different organisms and tissues. Chapman et al. (1971) assumed, on the basis of experiments with Escherichia coli, that cellular growth and reproduction can only be maintained at AEC values >0.7, whereas values <0.5 indicate irreversible damage to the cell.

However, over the years, it has become obvious that the definition of AEC as given above is not valid for all organisms. For instance, in higher plants, the suggested reference points are often lower than in bacteria (Atkinson 1977; Stitt et al. 1982).

For further understanding of the influence of elevated UVR on marine macroalgae of temperate regions, the energy metabolism of these organisms was investigated in the present study. A method was developed to extract adenine nucleotides quantitatively from macroalgal tissue samples and determine their molar levels with high performance liquid chromatography (HPLC) to calculate the AEC.

Changes in metabolically available energy were determined in Laminaria saccharina (Phaeophyta) and Ulva lactuca (Chlorophyta) during 24-h exposure to PAR, UV-A, and enhanced UV-B radiation. In addition, levels of adenine nucleotides and AEC were estimated in different thallus regions of L. saccharina and Chondrus crispus (Rhodophyta).

MATERIAL AND METHODS

Cultivation

Thalli of Ulva lactuca, Chondrus crispus, and Laminaria saccharina were originally collected on the rocky island Helgo-
land (North Sea, German Bight, 54°11’N, 7°53’E). *Chondrus crispus* was collected in 1996 and maintained since then in laboratory culture. *Ulva lactuca* and adult sporophytes of *Laminaria saccharina* were collected in June 2000 and were kept in culture for 2–3 weeks until the start of the experiments.

The algae were cultivated in Provasoli-enriched North Sea water buffered by HEPES-buffer (Provasoli 1986). The algae were kept under continuous light of 25 W/m² at 320 nm (Dring et al. 2001). The *Laminaria saccharina* laboratory culture was collected in 1996 and maintained since then in a water bath for 30 s (Delistraty & Hershner 1983; Koch et al. 1999). The samples were then cooled on ice for 10 min, followed by a 20-min centrifugation at 5500 × g. The residue was resuspended in 1.2 ml of the supernatant was withdrawn and evaporated in a speed-concentrator (SCV 100H, Savant Instruments Inc, USA) at 20°C with a Column thermostat BFO-04 (Techlab, Germany).

**HPLC**

The HPLC analysis was performed in a system consisting of a 600MS system photodiode array controller, a 600 multisolvent delivery system, a 717plus autosampler, and a 996 Detector (Waters, USA). The column was temperature regulated at 20°C with a Column thermostat BFO-04 (Techlab, Germany).

A Luna Column (Phenomenex, 250 mm × 4.6 mm, 5 μm) was used for the separation of the three adenine nucleotides.

**UV experiments**

For the UV experiments, tissue discs (n = 5) from *L. saccharina* and *U. lactuca* of approximately 2.5 cm diameter were punched out from the thalli. The pieces were kept in Petri dishes for wound healing under continuous light at a photon flux of 10–12 μmol photons/m²/s (L58 W/12–950 Lu-milux; De Luxe Daylight lamp; Osram, Germany) at 15°C. The growth medium was changed every two weeks.

**Extraction of adenine nucleotides**

The algal discs were always handled with tweezers to avoid contamination. Thalli were cut into pieces, wrapped in aluminium foil, and immediately shock frozen in liquid nitrogen. The samples were freeze dried in a Lyovac GT2 lyophilizer (Amsco/Finn aqua, Germany). Dried thalli were pulvrised in a mortar, and 20–30-mg aliquots of the powder were filled into 10-ml glass tubes. Boiling EDTA buffer (2 ml 1 mM EDTA, pH 7.5) was added following incubation in a boiling water bath for 30 s (Delistrafty & Hersher 1983; Koch et al. 1990). The samples were then cooled on ice for 10 min, followed by a 20-min centrifugation at 5500 × g. Then 1.8 ml of the supernatant was withdrawn and evaporated in a speed vac-concentrator (SCV 100H, Savant Instruments Inc, USA) at room temperature. The residue was resuspended in 1.2 ml 70% methanol and centrifuged for 10 min at 3500 × g. One millilitre of the supernatant was withdrawn, evaporated as before, and redissolved in 500 μl of the HPLC solvent.

**Chlorophyll fluorescence**

To estimate the effect of UVR on photosynthesis, chlorophyll fluorescence was measured with a PAM fluorometer (PAM-2000, Heinz Walz, Germany). Samples were placed in a dark chamber and the minimum fluorescence level (F₀) was measured after exposure to darkness for 3 min (Hanelt 1998). Afterward, a short saturating flash was provided to determine the maximum fluorescence level (Fₘ). The difference between F₀ and Fₘ gives the variable fluorescence (Fᵥ). According to Schreiber (1997), the ratio Fᵥ/Fₘ can be calculated as Fᵥ/Fₘ = (Fₘ – F₀)/Fₘ. The ratio Fᵥ/Fₘ gives information about the photochemically used energy and hence is a good indicator for the photosynthetic performance.

**Statistical analyses**

The data obtained from the different thallus regions and UV experiments were tested for normal distribution. Experimental effects were analysed using one-way ANOVA (P = 0.05) with SPSS (SPSS Inc, Chicago).

**RESULTS**

**Adenylate content and AEC in different thallus regions**

In *L. saccharina*, the significant highest adenylate content (ng/mg dry weight) was found within the meristematic region, which also agrees with the highest value for the AEC (Table 1).

The stipe had lower, although still comparatively high, levels of adenylate and AEC, whereas the holdfast and the upper and lower part of the blade had the lowest values. Values for AEC and adenylate concentrations in the stipe are statistically significantly lower than in the tips.

As in *L. saccharina*, the upper part of the thallus of *C. crispus*, carrying the meristematic region, also showed the

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**Table 1.** Adenylate energy charge (AEC) and adenylate content in different thallus regions of the brown alga *Laminaria saccharina* and the red alga *Chondrus crispus*.

| Alga               | Thallus region | AEC        | Sum of adenylates (ng·mg⁻¹ dry weight) |
|--------------------|----------------|------------|----------------------------------------|
| *L. saccharina*    | Holdfast       | 0.57 ± 0.06| 30.2 ± 5.6                              |
| n = 20             | Stipe          | 0.68 ± 0.06| 76.0 ± 14.3                             |
|                    | Meristematic region | 0.71 ± 0.03| 90.1 ± 26.0                             |
|                    | Young part of blade | 0.61 ± 0.05| 40.9 ± 6.2                              |
|                    | Old part of blade  | 0.58 ± 0.02| 46.2 ± 6.3                              |
| *C. crispus*       | Thallus basis  | 0.76 ± 0.01| 247.6 ± 17.2                            |
| n = 9              | Thallus tips    | 0.81 ± 0.01| 136.9 ± 4.1                             |
highest value for AEC. However, in contrast with the concentrations in the brown alga, the adenylate content in the non-meristematic part of the thallus was significantly lower compared with the part carrying the meristematic tips (Table 1).

**Effect of UV-A and UV-B radiation on photosynthesis and AEC of* Ulva lactuca *and Laminaria saccharina**

Discs of the blades of *L. saccharina* and *U. lactuca* were exposed to UVR. As shown in Fig. 1A, B, both species responded to the changed radiation conditions with a rapid loss of photosynthetic efficiency. The Fv/Fm ratio of *U. lactuca* was close to 0 after 16 h of exposure, whereas *L. saccharina* exhibited values around 0.15 ± 0.04 after 5–24 h, which represent ~20% of the control.

In both species, AEC values started to increase 5 min after UVR exposure to values around 0.7 and remained on this level until the end of the experiment (Fig. 1C, D). The changes between 0 and 5 min in *L. saccharina* were statistically significant, but not in *U. lactuca*.

![Image](image_url)  
*Fig. 1. Quantum efficiency of photosynthesis (Fv/Fm), adenylate energy charge (AEC) of Laminaria saccharina and Ulva lactuca during 24-h exposure to UV radiation.***

The content of AMP, ADP, and ATP of both algae during UV-A and UV-B exposure is given in Table 2. In *L. saccharina* and in *U. lactuca*, the ATP concentrations decreased within the first 5 min from 23.0 ± 15.0 to a content of 17.8 ± 2.9 ng/mg dry weight (DW) and from 46.8 ± 25.6 to 38.2 ± 15.2 ng/mg DW in *U. lactuca*, followed by a statistically significant increase to a maximum of 37.8 ± 7.3 ng/mg DW after 2 h in *L. saccharina* and to a maximum of 194.4 ± 50.5 ng/mg DW after 3 h (statistically significant) in *U. lactuca*. ATP levels then started to decrease but never reached values below those at the beginning of the experiment. The ADP concentration of *L. saccharina* increased after 30 min of UVR exposure to a maximum of 37.3 ± 7.6 ng/mg DW (statistically significant) and then decreased to values below that at the beginning of the experiment. The ADP level of *U. lactuca* reached a maximum of 106.9 ± 24.6 ng/mg DW after 15 min (statistically significant) following a steady decrease. Here, the final ADP concentration was lower than at the beginning of the treatment.

### Table 2. Concentrations of adenosine triphosphate (ATP), adenosine diphosphate (ADP), and adenosine monophosphate (AMP) of *Laminaria saccharina* and *Ulva lactuca* during 24 h of exposure to ultraviolet (UV) radiation (concentration given in ng·mg⁻¹ dry weight).

| Time  | ATP     | ADP     | AMP     | AEC¹ |
|-------|---------|---------|---------|------|
| 0 min | 22.9 ± 14.9 | 23.0 ± 15.8 | 7.1 ± 3.9 | 0.65 ± 0.02 |
| 5 min | 17.8 ± 2.9 | 26.7 ± 5.5 | 14.7 ± 2.0 | 0.55 ± 0.04 |
| 15 min| 21.3 ± 6.6 | 27.5 ± 6.1 | 14.3 ± 2.7 | 0.55 ± 0.05 |
| 30 min| 25.8 ± 5.7 | 37.3 ± 7.5 | 15.5 ± 2.4 | 0.56 ± 0.04 |
| 1 h   | 30.2 ± 6.8 | 25.4 ± 6.0 | 9.5 ± 2.5  | 0.67 ± 0.03 |
| 2 h   | 37.8 ± 7.3 | 30.9 ± 8.0 | 7.5 ± 1.5  | 0.69 ± 0.04 |
| 3 h   | 37.5 ± 7.0 | 25.7 ± 5.3 | 5.2 ± 0.4  | 0.73 ± 0.03 |
| 6 h   | 34.2 ± 7.4 | 28.8 ± 5.3 | 8.7 ± 1.9  | 0.69 ± 0.05 |
| 16 h  | 28.9 ± 8.0 | 17.3 ± 8.1 | 6.1 ± 1.6  | 0.70 ± 0.03 |
| 24 h  | 31.3 ± 6.2 | 25.7 ± 7.2 | 7.4 ± 0.9  | 0.69 ± 0.03 |
| *Ulva lactuca* |
| 0 min | 46.8 ± 25.6 | 71.3 ± 22.7 | 22.3 ± 5.3  | 0.58 ± 0.07 |
| 5 min | 38.3 ± 15.3 | 90.8 ± 10.0 | 15.0 ± 7.3  | 0.58 ± 0.03 |
| 15 min| 69.0 ± 31.2 | 106.9 ± 24.6 | 9.9 ± 0.3  | 0.66 ± 0.08 |
| 30 min| 78.8 ± 4.5 | 83.2 ± 5.3 | 11.6 ± 2.4 | 0.70 ± 0.05 |
| 1 h   | 148.1 ± 30.5 | 103.1 ± 29.2 | 38.0 ± 24.7 | 0.70 ± 0.05 |
| 2 h   | 147.2 ± 35.6 | 82.5 ± 4.1 | 26.9 ± 1.2 | 0.73 ± 0.03 |
| 3 h   | 194.4 ± 52.4 | 93.4 ± 15.6 | 17.8 ± 4.1 | 0.76 ± 0.07 |
| 6 h   | 138.0 ± 56.6 | 68.5 ± 4.4 | 17.7 ± 4.1 | 0.75 ± 0.04 |
| 16 h  | 69.5 ± 23.2 | 42.0 ± 2.1 | 12.0 ± 1.6 | 0.37 ± 0.05 |
| 24 h  | 62.8 ± 15.9 | 25.1 ± 7.5 | 10.7 ± 3.4 | 0.76 ± 0.04 |

¹ AEC, adenylate energy charge.

As with the other adenylates, the AMP concentrations of *L. saccharina* increased within 30 min of UV exposure to a maximum of 15.5 ± 2.4 ng/mg DW (statistically significant) and then decreased to the lowest level of 5.2 ± 0.4 ng/mg DW after 3 h. Later, the AMP level of *L. saccharina* started to increase again, reaching values between 6.1 ± 1.6 and 8.7 ± 1.9 ng/mg DW. In *U. lactuca*, a significant increase of the cellular AMP level within the first 30 min of the experiment was observed as well. Later, the AMP concentration decreased and remained at this low level until the end of the experiment.

**DISCUSSION**

Variation in the adenine nucleotide content between the three investigated species was observed (see Table 1). This may be explained by the different thallus morphologies of the respective species. While *U. lactuca* resembles a smooth bilayer sheet, *C. crispus* exhibits a cartilaginous and *L. saccharina* a leathery tissue.

The cells of *L. saccharina* contain large amounts of cell wall compounds, polysaccharides, and phenolics, whereas the cells of *U. lactuca* have thin cell walls. Therefore, the different thallus morphology may cause problems in direct comparison of the adenylate content per dry weight in the investigated species.

Thallus morphology may also affect the extraction efficiency of the improved method. However, species-specific variations in adenylate content and AEC may also explain the different concentrations.

The conspicuous variation in adenylates and AEC between different species may also result from different extraction and quantification methods used. Moreover, in green plants, about
47% of adenylates are located within the chloroplast, 44% in the cytoplasm, and only 9% in the mitochondria (Stitt et al. 1982). In animal cells, 90% of the adenylates are located within the cytoplasm (Soboll et al. 1978). Usually, the adenylate levels and AEC in green plants are lower than in microorganisms.

Adenylate contents in different thallus regions of L. saccharina and C. crispus were comparable with those in other aquatic plants. Investigations of the energy metabolism in the marine sea grass Zostera marina (Eelgrass) (Delistraty & Hershner 1983) and the smooth cordgrass Spartina alterniflora (Mendelsson & McKee 1981) showed higher AEC values and adenylate content in tissues with meristematic activities. This was also observed in L. saccharina and C. crispus. In the phaeophyte, the highest values for AEC were found at the basis of the blade, where meristematic tissue provides cells to form the leafy part of the thallus. Meristematic activity in C. crispus is located in the upper part of the thallus. Lower AEC values in the stem-like part of C. crispus, as well as in the stipe and the holdfast of L. saccharina, are explained by the presence of more structural or metabolically inert material (Delistraty & Hershner 1983; Schnettger et al. 1994).

UVR affects photosynthesis and energy metabolism in the two macroalgal species investigated. In both U. lactuca and L. saccharina, the Fv/Fm ratio decreases rapidly within the first 6 h of the experiment. This can be caused by a UVR-induced damage of both photosystems. In particular, UV-B can degrade the D1 protein in the reaction centre core of photosystem II (PS II), resulting in a decrease in the quantum efficiency of PS II (Schnettger et al. 1994; Hanelt et al. 1997b; Bischof et al. 2002).

The cyclic electron flow around PS I is probably regulated by inhibition of the PS II-dependent oxygen generation. Consequently, the occurrence of cyclic electron flow will be forced by damage to PS II. Cyclic electron flow is directly linked with the formation of ATP (Finazzi et al. 1999). The fast decrease of adenylate levels in L. saccharina and U. lactuca can be explained by the initial UVR-induced degradation of the D1 protein and hence damage of PS II, followed by a lower ATP formation via linear electron transport. Formation of ATP increases again when the PS II-dependent oxygen formation decreases and the cyclic electron transport is not further inhibited. The increase of ADP is probably a result of ATP turnover.

Fricoud et al. (1992) suggested the acyl-CoA synthase (also called thikinase) that catalyses formation of actanoyl-CoA as a possible source for AMP in plants. Another explanation for the increase of AMP within the first 2 h of the UV experiment is the Mg2+-dependent forward reaction of adenylate kinase, 2ADP ⇔ ATP + AMP (Busch & Ninnemann 1997).

The AEC of L. saccharina and U. lactuca decreased within the first 5 min of the UV experiment, followed by a recovery and increase to a maximum after 3.3 h of UVR exposure. The Calvin cycle is also inhibited by UVR in algae (Boucher & Prezelin 1996). Therefore, the available energy increases because it cannot be used in carbon fixation. Although photosynthetic efficiency strongly decreased (Fv/Fm), the AEC was maintained at high values, >0.7, in both algae. This has consequences for the enzymatic processes. Enzymes regenerating ATP typically show high activity at low AEC values and decreasing activity at high AEC. These enzymes, of the so-called R type, are taking part in ATP regeneration (Atkinson 1968).

In contrast, ATP-consuming enzymes exhibit low activity at low AEC and increasing activity at high AEC. These enzymes, of the so-called U type, are using ATP. It has been suggested that maintaining the AEC at high values enables plants and bacteria to maintain the activity of ATP-using enzymes (Atkinson 1977).

In U. lactuca, the adenylate content decreased after a maximum at 3.3 h, to 60% of the control while the AEC remained at values >0.7. This was also observed in plants during desiccation and heavy-metal treatment (Sieber & Brändle 1991; Fürtig et al. 1996). The decrease in adenylate content may be caused by the activity of an AMP deaminase, which removes AMP from the adenylate pool (Atkinson 1977). This would keep the AEC at a high level, and enzymes of the U type are still active but with the decrease in the adenylate content leading to a loss of total energy. Consequently, this process guarantees only survival under short-term stress or bridges the time until metabolic adaptation takes place.

In L. saccharina, the situation was somewhat different. Although the AEC was also maintained at a high level, the adenylate content did not drop below the control value. This seems to indicate that the photosynthesis of the phaeophyte is more resistant to UVR than the chlorophyte. The measurements of Fv/Fm are in full agreement with this assumption. The efficiency of the photochemical energy conversion is higher in L. saccharina than in U. lactuca. In addition, the coarse leather-like thallus of L. saccharina provides a better protection by absorbing radiation with the outer cell layers. These cortex cells contain several phenolic compounds in polysomes, which are able to absorb UVR and hence are considered to act as photoprotective substances (Pavia et al. 1997).

CONCLUSION

The AEC is a valuable parameter to determine the general physiological state of all tissues of marine macroalgae. But it is also important to take the concentration of the different adenylates and other physiological parameters, like Fv/Fm, into consideration to understand the processes in energy metabolism during stress situations.

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Received 9 September 2003; accepted 21 October 2004

Communicating editor: J. Beardall