

Drought stress, rain and recovery of the intertidal seaweed *Fucus spiralis*

Michael Schagerl · Martin Möstl

Received: 27 January 2011 / Accepted: 24 June 2011 / Published online: 9 July 2011
© Springer-Verlag 2011

Abstract Non-motile organisms of intertidal shores such as seaweeds have to cope with a great variability of environmental factors. In this survey, we studied whether different morphotypes of the intertidal seaweed *Fucus spiralis* L. are also reflected in a characteristic performance. Desiccation and recovery of this Phaeophyceae were investigated in field experiments near Aljezur, Portugal. *Fucus spiralis* is exposed to serious desiccation during periods of falling tide, resulting in a tissue water loss of about 90%. Due to large semidiurnal tidal ranges in this area, two morphotypes can be distinguished: *F. spiralis* growing in the lower intertidal (LZ) is thicker and fleshier compared with plants in the upper intertidal (HZ), and this is reflected in a significant difference in fresh and dry mass. During sunny days and at low tide, effective quantum yields (Φ_{PSII}) decreased significantly after 2 h desiccation. This continued until re-submersion. The photosynthetic performances of HZ and LZ plants also differed significantly after LZ plants were already submerged and photosynthesizing, but the HZ specimens still exposed to air. Recovery experiments after desiccation treatments showed fast recovery within 6 min after re-submersion in both morphotypes. HZ specimens showed a slower recovery, which indicates a protection measure to the adverse conditions in the upper intertidal. In 24 h desiccation treatments, however, HZ specimens expressed a significantly higher maximum fluorescence yield F_v/F_m recovery. Simulated rainfalls during low tides caused photosynthetic

activity to drop to 50% of initial F_v/F_m , independent of the length of the rain period. Treated plants also fully recovered after 6 min re-submersion in seawater. A comparison of single fronds and tufts clearly indicated advantages of the tuft growth strategy: tufts showed higher Φ_{PSII} at prolonged emersion times. Our study indicated a clear relationship between size and drought resistance, which was primarily due to the smaller and hardy HZ plants that withstand longer desiccation times without damage.

Introduction

Around 11% of the aquatic net primary production is generated in coastal ecosystems (Geider et al. 2001). Of this, about 10% (5×10^8 t year⁻¹) originate from seaweeds (Field et al. 1998). In contrast to phytoplankton, which is exposed to strong gradients in the water column due to passive drifting by currents, macroalgae are restricted to the site of growth. They are thus exposed to the ambient conditions in their habitat. Non-motile organisms of the intertidal zone of rocky shores experience adverse environmental conditions during tidal emersion. Within a distance of a few meters, the habitat changes from marine to almost terrestrial and the duration of emersion increases with tidal height. Intertidal algae experience diverse environmental stressors including daily cyclic fluctuations of ambient temperatures, wave exposure, excess irradiance, nutrient limitation, and desiccation combined with salt precipitation on the thallus surface at low tide (Lobban and Harrison 1994; Davison and Pearson 1996). Note that desiccation also has some benefits for intertidal algae and can be seen as a protection measure. Even if photosynthesis stops, thermotolerance increases to the point that the organism is protected from heat-induced

Communicated by P. Kraufvelin.

M. Schagerl (✉) · M. Möstl
Department of Limnology, University of Vienna,
Althanstraße 14, 1090 Vienna, Austria
e-mail: michael.schagerl@univie.ac.at

mortality (Hunt and Denny 2008). Typically, seaweeds growing in the upper intertidal show increased tolerance to environmental fluctuations, whereas those sensitive to ambient stress inhabit the lowermost intertidal zone. This is expressed by a characteristic zonation of the intertidal (Lüning 1990; Ott 1996; Nybakken and Bertness 2005).

Commonly, species distribution limits toward the lower intertidal zone are set by biological interactions, while the upper limits are determined by physical factors (Connell 1972; Menge and Sutherland 1987). One of the major variables controlling the upper growth limit is the ability to cope with desiccation. Unlike vascular plants, macroalgae lack an impermeable cuticle or stomata. As a consequence, seaweeds cannot avoid desiccation (Lüning 1990), but have to cope with air exposure and related adverse conditions. Usually, drying out damages cell membranes and may also cause protein denaturation. Strategies of intertidal seaweeds to retard desiccation include development of cells that are resistant to drying out (Davis 1972), the formation of thick cell walls (McCandless 1981), the production of mucilage envelopes (Berard-Theryault and Cardinal 1973), reduction in size and surface (Bergquist 1959; Schonbeck and Norton 1979), and growth in dense mats (Bewley 1979; Hunt and Denny 2008) referred to as turfs. An additional major strategy to prevent desiccation damage is the accumulation of compatible solutes (CS) as an osmotic adjustment (Kirst 1989; Bäck et al. 1992), which helps to avoid osmotic stress. Moreover, CS protect proteins from denaturation. CS are metabolites of low-molecular mass whose high cellular concentration significantly reduces the cytoplasmatic osmotic potential. Typically, CS are hydrophilic, giving rise to the view that they replace water at the surface of proteins, protein complexes, or membranes (Erdmann and Gademann 2001). One of the most important CS found in Phaeophyceae is D-Mannitol (Karsten et al. 1996); glycine betaine is also present sometimes (Gylle et al. 2009).

The desiccation tolerance of intertidal seaweeds varies greatly among species. The interspecific difference is thought to be related to their vertical distribution. Differences in terms of tolerance against desiccation, changing salinities, and high or low temperatures between species from different heights of the intertidal already reported elsewhere (Biebl 1970; Littler 1980; Dring and Brown 1982; Beer and Kautsky 1992; Boaventura et al. 2002).

In this study, we addressed the question whether also intraspecific differences in desiccation tolerance and recovery exist within the intertidal zone. We focussed on the rockweed *Fucus spiralis* L., one of the most common intertidal macrophytes along the Portuguese Atlantic coast, which is characterized by a warm temperate Mediterranean-Atlantic climate. *F. spiralis* (Phaeophyceae, Heterokontophyta) is a monoecious, perennial seaweed that

receives excess irradiance and high temperatures at low tide periods during summer days. The average life span is around 2 years, and growth rates throughout the year are about $1.2 \text{ cm month}^{-1}$ (Niemeck and Mathieson 1976). Reproduction in fucoids is promoted by water motion, resulting in fertilization success close to 100% (Brawley 1992; Pearson and Brawley 1996; Serraõ et al. 1996). *F. spiralis* survives 2 days drying in air without damage (Schonbeck and Norton 1980) and tolerates salinities from 3 to 32‰ (Niemeck and Mathieson 1976). Niemeck and Mathieson (1976) have described a micro-stratification of biomass, stature, and reproductive activity within this zone.

Our study focused on three questions: (1) How rapidly does *Fucus spiralis* respond to desiccation and how long does recovery take after re-submersion in seawater? Furthermore, how does photosynthesis perform throughout a full tidal cycle on a typical sunny day with low tide at noon? We expected that plants would show a slow decrease in F_v/F_m after 30 min emersion because pilot experiments had shown that the fronds remain quite fleshy during the first half hour of exposure. We also assumed that photosynthetic recovery of re-submerged *Fucus* takes about the same time. Moreover, relative electron transport rates (rETR) and effective quantum yields (Φ_{PSII}) were expected to slightly increase within the first few minutes of emersion because of improved CO_2 supply, followed by a steep decrease in both variables. (2) Heavy rain events that occur especially in wintertime and spring at the Portuguese coast may cause serious osmotic stress to specimens of *F. spiralis* exposed during low tide. We hypothesized that freshwater heavily affects *Fucus* and that no full recovery is possible because *Fucus* is mainly adapted to elevated salt concentrations during desiccation and is not used to salinities below 3‰. (3) Do specimens obtained from the upper and lower intertidal respond differently to desiccation? We expected that specimens from the upper and lower intertidal would respond differently to drying due to variation in their tolerances to desiccation and in their speed of recovery.

Materials and methods

Plant material and collection site

For this study, reproductive *Fucus spiralis* plants were collected in autumn 2005 and spring 2006 near Alljezur, on the Portuguese west coast ($37^{\circ}22'N$ $8^{\circ}50'W$). The tides are semidiurnal here, reaching around 3 m amplitudes at spring tides. Algae growing in the upper intertidal spend about 10 h of one tidal cycle (12.5 h) exposed to air, specimens in the lower intertidal about 7 h. Plants were randomly collected from elevated areas (HZ; ~ 2.5 m above Mean

Lower Low Water = MLLW) and lower areas (LZ; ~ 0.5 m above MLLW). Specimens obtained from the HZ generally showed smaller, more compact thalli compared to organisms of the remaining habitat; we therefore were able to distinguish two morphotypes. Water temperatures during the experiments reached 16–17°C, air temperatures about 30°C at noon. All experiments were conducted under natural solar radiation.

Measurements of solar radiation

Photosynthetic active radiation (PAR = 400–700 nm) was recorded every 5 min during the two-month survey (SKP 240 sensor, Data Hog logging device, Skye Instruments Ltd.). The quantum sensor was positioned so that no shadows would disturb ongoing measurements.

Fluorescence measurements

We applied pulse-amplitude-modulated (PAM) fluorescence to determine stress and recovery during emersion and submersion of *Fucus spiralis* (Diving PAM, Walz). This noninvasive technique yields information about the physiological state of the regulatory processes of in vivo photosynthetic energy allocation (Schreiber and Bilger 1987, 1993; Schreiber et al. 1986), rapidly quantifies changes of photosynthetic efficiency under natural conditions (Maxwell and Johnson 2000) and has already been applied successfully to macroalgae (e.g., Hanelt et al. 1997; Magnusson 1997; Beer et al. 2000; Lamote et al. 2007). For estimating the maximum fluorescence yield $F_v/F_m = (F_m - F_o)/F_m$, the initial fluorescence F_o after 15 min dark adaptation was measured, followed by a saturating pulse of actinic light that induces maximal fluorescence F_m . F_v/F_m is commonly used as a measure for plant photosynthetic performance (Maxwell and Johnson 2000; Rohacek 2002). We considered the algae to be in a healthy, unstressed condition if F_v/F_m exceeded 0.70 (Young et al. 2007). In order to assess Φ_{PSII} at ambient irradiance, the initial fluorescence F_i at ambient irradiance is measured. This is followed by a saturating pulse of actinic light that induces maximal fluorescence F'_m at ambient irradiance. The equation $\Phi_{\text{PSII}} = (F'_m - F_i)/F'_m$ is used to calculate the effective quantum yield (Genty et al. 1989). Relative photosynthetic electron transport rates (rETR) were calculated by $\text{rETR} = \Phi_{\text{PSII}} \times \text{PAR} \times 0.5$, where PAR is the incoming photosynthetic active radiation and the multiplier 0.5 recognizes that transport of a single electron requires two photons. For submerged plants, incoming PAR values were reduced by 5% because of reflection from the water surface (Wetzel and Likens 1990).

Measurements during day time

To investigate diurnal changes in photosynthetic performance, Φ_{PSII} of seven HZ and seven LZ, specimens were measured in situ every 2 h between 8:00 and 20:00. rETRs were calculated by considering ambient PAR recorded by the logging device. This experiment was repeated three times.

Desiccation and recovery

Reproductive thalli between 5 and 10 cm length were collected from both zones in the evening and were allowed to recover fully in seawater for at least 12 h before experiments started. We chose desiccation times of 1, 2, 4, and 24 h in October 2005 and adjusted measurements to 1, 3, 5, and 9 h in April 2006. Before each desiccation period, six thalli from the two zones were weighed and dark-adapted. Then, initial F_v/F_m was determined at final branches of the fronds. Thalli were then attached to a mesh screen to fix their position toward the sun to minimize variations in drying rates. After the respective drying time in the sun, the specimens were dark-adapted for 15 min and reweighed to determine water loss followed by F_v/F_m measurement. For a comparison, submerged thalli were treated in the same way. After treatment, the thalli were put back in seawater (20 L box with seawater, 17°C, and 34.4 psu) and kept shaded for recovery.

For recovery, F_v/F_m of each dark-adapted thallus was measured at 3, 6, 15, 25, 40, and 50 min after specimens were put back in seawater. Thereafter, specimens were reweighed and stored for dry mass determination in the laboratory. For dry mass, tissues were dried at 95°C for 24 h and reweighed. Percent water content was determined as $\text{W}\% = (\text{desiccated mass} - \text{dry mass}) / (\text{fully hydrated mass} - \text{dry mass}) \times 100$ (Björk et al. 1999).

Simulation of rainfall

Eighteen specimens from each zone were collected in the evening and were allowed to acclimate in seawater for at least 12 h. The thalli were put on a mesh screen in the dark, and rainfall was simulated by sprinkling 2 L freshwater (0.0 psu) for 1 min over the thalli every 10 min. F_v/F_m of seven specimens per zone was determined after 1, 3, and 5 h. After treatments, thalli were put back into seawater. For recovery, F_v/F_m of each thallus was measured after 3, 6, 15, 25, 40, and 50 min. This experiment was repeated three times.

Comparison of single thalli and tufts

Fucus spiralis was collected in the morning. For a comparison, 14 single fronds and two tufts consisting of 7–9 fronds of *F. spiralis* were exposed to the sun on a mesh screen. The size of the artificial tufts (fronds tied on their basis) was adjusted to their natural occurrence at the collection site. Φ_{PSII} was measured after 1, 3, 5, and 10 h of desiccation in the sun at different spots of the fronds.

Statistics

Data analysis was done using the software package SPSS 13.0. For comparisons between two independent variables, Mann–Whitney U tests were used. Thalli were grouped according to their growth habitat (HZ, LZ). Comparisons between slopes of regressions followed the z statistics (Clogg et al. 1995).

Results

Photosynthetic characteristics during the day

Within the intertidal, typical communities of wave-exposed shores were observed, including colonies of barnacles and limpets interrupted by Phaeophyceae (*Fucus spiralis*), Chlorophyta (*Enteromorpha* type), and Rhodophyta (*Nemalion* sp.). At the study site, *F. spiralis* showed highest abundances; its distribution ranged from ~ 2.5 m above MLLW to ~ 0.5 m above MLLW. *F. spiralis* occurring in the LZ spends about 45% of the tidal cycle submerged, whereas the HZ thalli are covered by seawater for only 19% of the tidal cycle (at mean tidal height). *F. spiralis* growing in the LZ appears thicker and fleshier and was significantly heavier than HZ plants (fresh mass $P = 0.002$, dry mass $P = 0.003$, $n = 46$; Fig. 1).

On the days of measurements, PAR reached $2,100 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ at noon and the air temperatures rose to 30°C (Fig. 1). Measurements started at 8:00 local time. Thalli of both zones had just become exposed, but were not desiccated because of high air humidity. Initial Φ_{PSII} values of about 0.7 indicated that plants were not stressed (Fig. 2). During the day, Φ_{PSII} decreased to minimum values close to zero at 14:00 h. After 14:00 h, the LZ thalli became re-submerged and Φ_{PSII} responded rapidly with a strong yield increase with significant differences between HZ and LZ specimens ($P \leq 0.001$, $n = 7$ for each group). At 15:30 h, seawater reached HZ thalli, resulting in increased Φ_{PSII} . The rETR data clearly show that primary productivity increased during the first morning hours because of increasing irradiance, even though the plants were already exposed to air (Fig. 2).

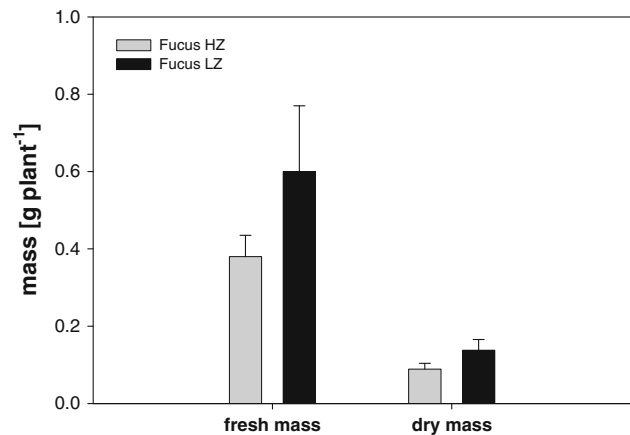


Fig. 1 Fresh and dry mass of randomly selected *F. spiralis* thalli from the upper (gray) and lower (black) intertidal (median + 75% percentile)

Desiccation and recovery

After 1 h air exposure, the specimens had already lost 60% of their tissue water content (Fig. 3). After two more hours, the minimum weight was reached (water loss $\sim 90\%$). Water loss rates of HZ and LZ *Fucus spiralis* did not differ significantly ($P = 0.092$, $n = 14$). F_v/F_m was highly related to the respective tissue water contents (Fig. 4; LZ $r = 0.92$, $n = 56$; HZ $r = 0.95$, $n = 55$); regression coefficients showed no significant differences between the two plants ($Z = -0.566$).

Recovery was tested by measuring F_v/F_m in short time intervals over 50 min after desiccated *Fucus spiralis* material had been re-submerged (Fig. 5). After 1 h desiccation, HZ thalli showed a significantly lower F_v/F_m (~ 0.4) compared to LZ thalli (~ 0.6). Even after longer air exposure and about 90% water loss, however, F_v/F_m reached amounts close to initial values within 6 min recovery. Within the first 9 h, no significant differences in the HZ and LZ recovery rates were estimated, but HZ individuals tended toward lower F_v/F_m (Fig. 6). Nonetheless, prolonged desiccation times caused decreased LZ yields and, finally, HZ significantly exceeded LZ values. After 24 h of desiccation, HZ plants could still recover, but the photosynthetic apparatus of most LZ *Fucus* seemed to be seriously damaged; yield values after 25 min regeneration remained low ($P = 0.001$, Fig. 6).

Effects of heavy rains

Simulated rain for 1 h lowered F_v/F_m values to about 50% of the initial yield. This decrease remained constant for 5 h and longer (Fig. 7), but 6 min after re-submersion in seawater, specimens fully recovered. The experiment was repeated three times with the same results.

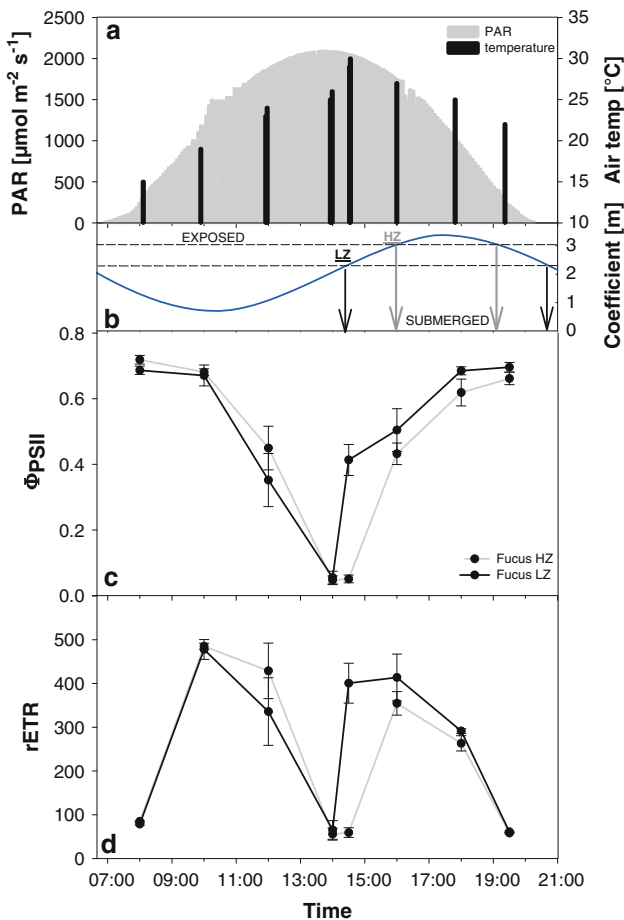


Fig. 2 Incoming irradiance, air temperature (a); tidal height and exposure of *Fucus* (arrows indicate re-submersion of the respective zone due to rising water levels (b)); daily course of the effective quantum yield Φ_{PSII} (c) and of the relative electron transport rates (d) of *F. spiralis* in situ from the upper (gray) and lower (black) intertidal. Data were recorded on 30 April 2006 ($n = 7$, mean \pm SE)

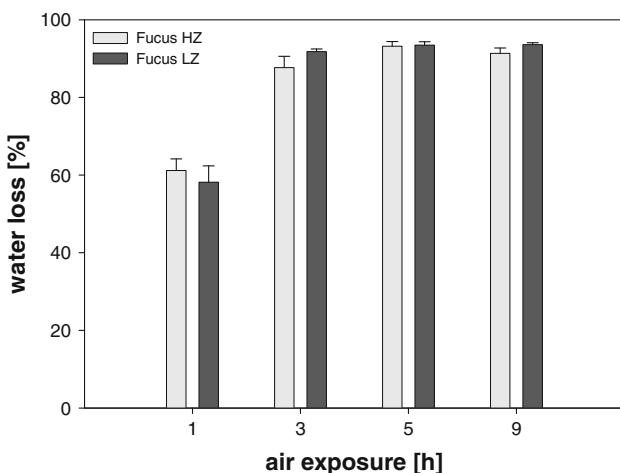


Fig. 3 Percent water loss after 1, 3, 5, and 9 h desiccation on a mesh screen, exposed to the sun, of *Fucus spiralis* from the upper (gray) and lower (black) intertidal (mean \pm SE, $n = 6$)

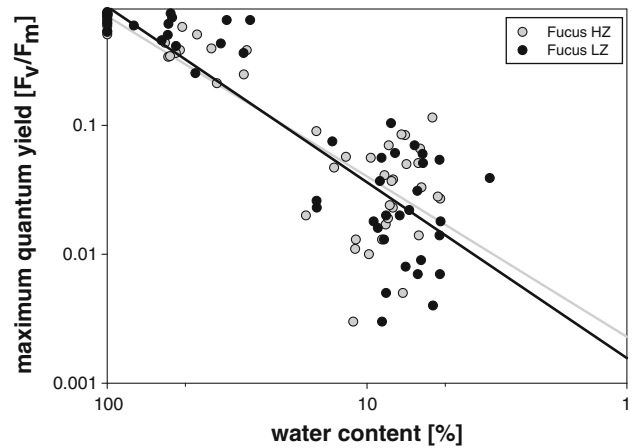


Fig. 4 Relationship between maximum quantum yield F_v/F_m and tissue water content (%) during desiccation

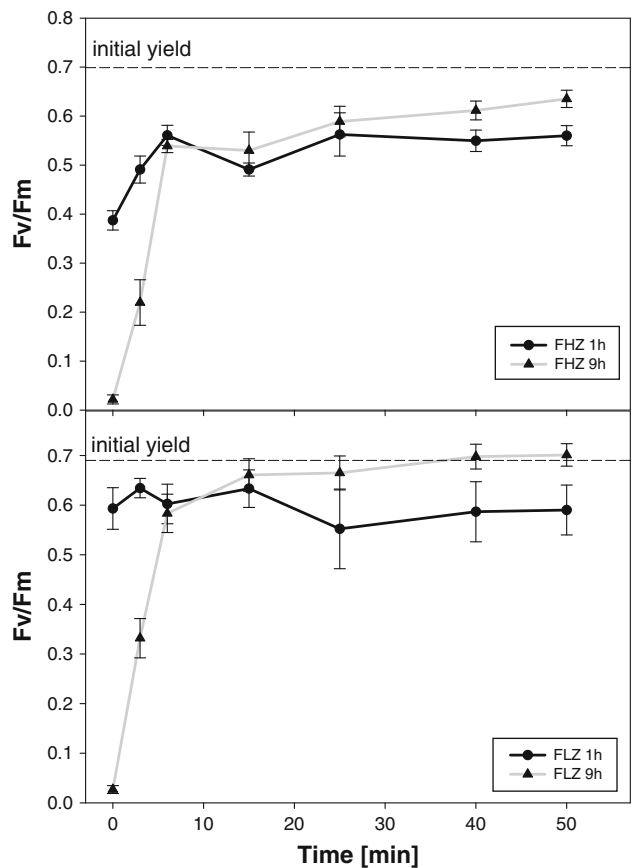


Fig. 5 Maximum quantum yields F_v/F_m after 1 h (filled circle) and 9 h (filled triangle) desiccation of *Fucus spiralis* HZ (top) and LZ (bottom) on a mesh screen exposed to the sun, followed by 50 min regeneration in seawater in the dark. Dashed line indicates the initial yield prior to the experiment (means \pm SE)

Comparison of single thalli and tufts

This experiment compared the desiccation responses of single fronds and tufts. At short desiccation times of 1 h, the photosynthetic performance of the thalli in the tuft was

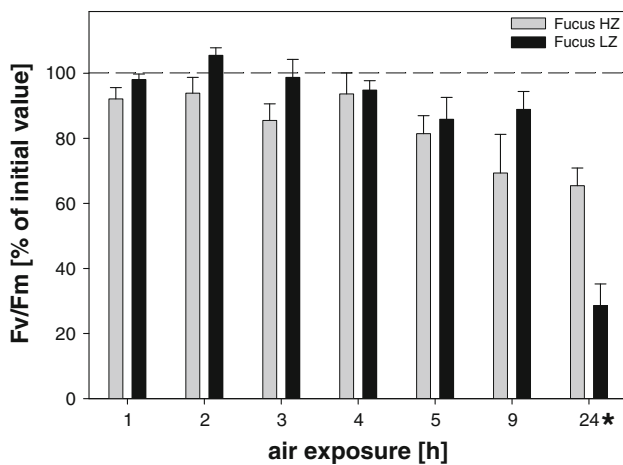


Fig. 6 Maximum quantum yields F_v/F_m normalized to initial values after 25 min re-submersion in seawater after 1, 2, 3, 4, 5, 9, and 24 h desiccation on a mesh screen. *F. spiralis* HZ (gray) and LZ (black). Combined measurements of October 2005 and April 2006 (means \pm SE; $n = 6$ for 2, 3, 4, 5, and 9 h and 12 for 1 and 24 h, respectively, significant differences are indicated with asterisk)

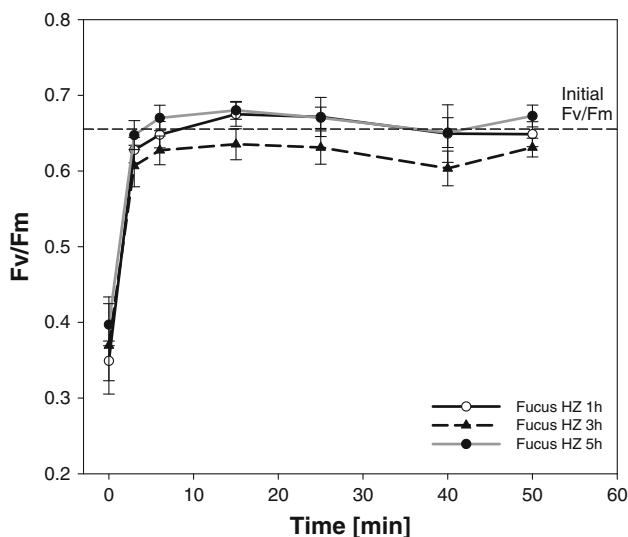


Fig. 7 Maximum quantum yields F_v/F_m of *F. spiralis* thalli, treated with simulated rain. The plants were fixed on a mesh screen in the dark and treated every 10 min for 1 h (circle), 3 h (filled triangle), and 5 h (filled circle) with freshwater. Fluorescence measurements were taken after 1, 3, and 5 h and during recovery (means \pm SE; $n = 7$)

not affected (Fig. 8), while single fronds already showed a steep yield decrease. A major difference in Φ_{PSII} was observed until 5 h desiccation. After 10 h desiccation, however, both values were similar (20% of initial yield).

Discussion

Phenotypes of *Fucus*—Both *Pelvetia canaliculata* (L.) Decaisne and Thuret and *Fucus spiralis* occupy the upper

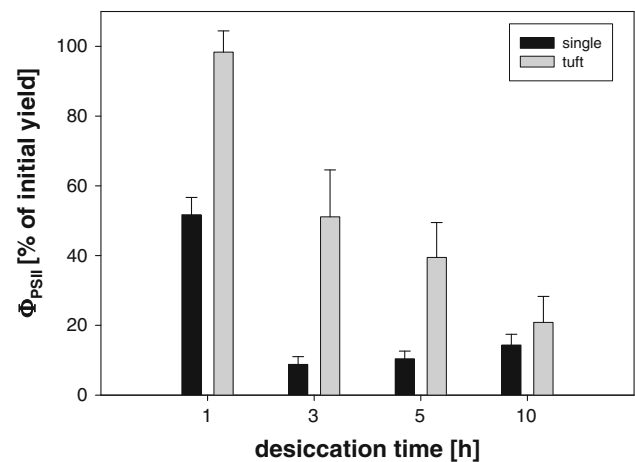


Fig. 8 Effective quantum yields Φ_{PSII} (%) of tufts (gray) compared to single fronds (black) of *F. spiralis* during desiccation lasting 1, 3, 5, and 10 h on a mesh screen exposed to the sun. Values normalized to initial yields (means \pm SE; $n = 14$)

intertidal. Unlike *Pelvetia*, which is unable to tolerate continuous submersion (Rugg and Norton 1987), growth extension of *F. spiralis* to deeper areas is possible in principle, but appears to be limited by competition with faster-growing species (Lüning 1990). Schonbeck and Norton (1980) found that *F. spiralis* showed a higher growth rate when transplanted to sublittoral areas, which supports our findings of significant differences between the fresh and dry mass of HZ and LZ individuals (Fig. 1). Additionally, our measurements of Φ_{PSII} and $rETR_{max}$ during the course of the day indicated a higher productivity for the LZ plants as well.

Scott et al. (2001) studied phenotype variation in *Fucus spiralis* and distinguished two morphotypes designated as *F. spiralis* and *F. spiralis* f. *nanus*. The forma *nanus* thalli were found consistently at elevated areas and differed from the nominate *F. spiralis* in that they were shorter, narrower, and had fewer side branches, but had more fronds originating from a single holdfast. Forma *nanus* did exist within a mosaic of stable phenotypes representing populations specifically adapted to the local environment. Due to the high environmental variability in the intertidal zone, different phenotypes could evolve even within short distances. Similar results were obtained for *Fucus vesiculosus* L. by Pearson et al. (2000), who detected differences in Baltic and North Sea populations in terms of stress and recovery. Different ecotypes of marine and brackish *F. vesiculosus* were also found in the Norwegian Sea and Bothnian Sea, respectively (Gylle et al. 2009). All these results support the hypothesis of Via et al. (1995) on a scaled-down level. Those authors considered that if the geographical range of a species includes a high level of environmental variability, it is unlikely that a single phenotype will confer high fitness in all situations.

The measurements of the daily course of photosynthesis (Fig. 2) showed an initial yield of about 0.7, which is comparable to other studies (Dring et al. 1996; Lamote et al. 2007), followed by a steep and sustained decrease until the rising water level re-submerged the specimens. This decrease was mainly caused by desiccation combined with elevated temperatures. The high incoming irradiance probably played a lesser role because the diurnal course of F_v/F_m is usually less pronounced in green algae (Henley et al. 1991; Magnusson 1997) or even undetectable in *Fucus* (Magnusson 1997). Interestingly, only a single significant difference between the photosynthetic performances of HZ and LZ plants during the day was recorded, i.e., when LZ thalli were submerged but HZ specimens still exposed to air. Figure 2 indicates a phase shift between both zones, although laboratory experiments under defined conditions would be necessary to verify this.

If the incoming radiation is considered (conversion into rETR), a different perspective emerges; rETR increased during the first hours in the morning, even though the specimens were already exposed to air. This increase was mainly caused by raised PAR, which overcompensated the decreasing Φ_{PSII} . The significant yield decrease also indicated that rising rETRs were probably not associated with higher diffusion rates of CO_2 during the early stages of drying. Stocker and Holdheide (1937) and Madsen and Maberly (1990) verified that, in the absence of desiccation, *Fucus spiralis* can photosynthesize more efficiently in air than in water at 15–20°C. This phenomenon is known also from lichens, mosses, and cyanobacteria (Coxson et al. 1983; Titus and Wagner 1984; Fleming et al. 2007) and is explained through the higher diffusion rates of CO_2 in air. Under natural field conditions, however, this characteristic might be masked through rapid water loss and high temperatures during air exposure. This reduces yield and ultimately prevents photosynthesis.

After the plants were submerged by the rising tide, full recovery of Φ_{PSII} was much slower than regeneration experiments suggested. This slow increase, which persisted until the evening (Fig. 2), was probably caused by non-photochemical quenching (recorded PAR from 15:00 to 16:00 still reached 1900 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$). Non-photochemical quenching is a photoprotection measure against excess radiation, which has been related to the reversible de-epoxidation of the carotenoid violaxanthin to zeaxanthin via the intermediate antheraxanthin (Henley et al. 1991; Krause and Weis 1991; Osmond 1994). Zeaxanthin is responsible for heat dissipation of excess energy (Demming et al. 1987; Demmig-Adams 1990). The violaxanthin cycle has been demonstrated in some members of Phaeophyceae (Benet et al. 1994; Lemonie et al. 1995; Harker et al. 1999; Gévaert et al. 2003).

Results of desiccation treatments revealed a lower F_v/F_m of HZ specimens (~ 0.4) after 1 h desiccation time compared to LZ individuals (~ 0.6). This can be interpreted as an acclimation or adaptation to this habitat (Fig. 5). An earlier activation of non-photochemical quenching helps avoid cell damage. Moreover, desiccation also increases thermotolerance (Hunt and Denny 2008), thus protecting HZ thalli from heat-induced mortality. Compared to LZ *Fucus*, HZ specimens also showed a slower recovery in our desiccation measurements with the exception of the 24 h treatment (Fig. 6). This also points to a protection measure against the adverse conditions in the upper intertidal. Such relationships between the extent of recovery from desiccation and vertical distribution have already been reported (Kaltwasser 1938; Dring and Brown 1982; Beer and Kautsky 1992), albeit including other species. For *Fucus serratus* L., a conservation of the photoinhibitory state at the beginning of the desiccation period was assumed (Huppertz et al. 1990), but such a phenomenon was not observed in our study. Generally, the excellent adaptation of *Fucus spiralis* to the intertidal zone is also demonstrated by a rapid recovery of photosynthesis after desiccation. This is an ecological precondition for thalli growing in the upper eulittoral that is covered by water for only 1–2 h in each tidal cycle.

Simulated rains caused a significant decrease in F_v/F_m down to 0.35, while the regeneration time was comparable to that after desiccation (Fig. 7). We did not expect such a fast recovery because *Fucus* mainly experiences elevated salt concentrations at emersion. Clearly, the cell membranes of *F. spiralis* can withstand high osmotic pressure for long times; the constant yield indicates highly developed osmotic regulation capacities.

Differences in the photosynthetic activity of single thalli and tufts during emersion were substantial (Fig. 8) and might explain this growth strategy of many intertidal seaweeds. In dense young populations of *Fucus spiralis*, only 20% of the thalli are exposed to air (Schonbeck and Norton 1979). Moreover, tuft growth protects young stages against strong radiation, including ultraviolet radiation (Hanelt et al. 2007).

Fucus spiralis is well adapted to the harsh environmental conditions of the intertidal. Our desiccation experiments indicated a clear relationship between size and drought resistance, which was primarily due to the smaller and hardy HZ plants that withstand longer desiccation times without damage. Yield recovery after desiccation lasted only 6 min, which was faster than that reported by Dring and Brown (1982), Brown (1987), and Maberly and Madsen (1990) for this and other species. Rain treatments showed that photosynthesis in *F. spiralis* is reduced by about 50% after 1 h rain, but then remained constant even

for longer rain periods. This reflects a high resistance against osmotic pressure as well. Our study raised some questions to be answered in further studies; for example, investigations at a molecular level should be conducted to identify short-term regulations of CS and to examine the response of gene expression to environmental stress. Additionally, genetic studies of neighboring populations would provide further insights into ecotype differentiation and dispersal.

Acknowledgments Thanks to P. Lamprecht for accommodation in Portugal, C. Fesl for statistical hints, and the whole team from the Vienna Team Phycology for their support. Funding for the field study by the KWA University of Vienna is gratefully acknowledged.

References

- Bäck S, Collins JC, Russell G (1992) Comparative ecophysiology of Baltic and Atlantic *Fucus vesiculosus*. Mar Ecol Prog Ser 84:71–82
- Beer S, Kautsky L (1992) The recovery of net photosynthesis during rehydration of three *Fucus* species from the Swedish west coast following exposure to air. Bot Mar 35:487–491
- Beer S, Larsson C, Poryan O, Axelsson L (2000) Photosynthetic rates of *Ulva* (Chlorophyta) measured by pulse amplitude modulated (PAM) fluorometry. Eur J Phycol 35:69–74
- Benet H, Bruss U, Duval JC (1994) Photosynthesis and photoinhibition in protoplasts of the marine brown alga *Laminaria saccharina*. J Exp Bot 45:211–220
- Berard-Therryault L, Cardinal A (1973) Importance de certains facteurs ecologiques sur la resistance a la dessiccation des Fucacees (Phaeophyceae). Phycologia 12:41–52
- Bergquist PL (1959) A statistical approach to the ecology of *Hormosira banksii*. Bot Mar 1:22–53
- Bewley JD (1979) Physiological aspects of desiccation tolerance. Ann Rev Plant Physiol 30:195–238
- Biebl R (1970) Vergleichende Untersuchungen zur Temperaturreisistenz von Meeresalgen entlang der pazifischen Küste Nordamerikas. Protoplasma 69:61–83
- Björk M, Uku J, Weil A, Beer S (1999) Photosynthetic tolerances to desiccation of tropical intertidal seagrasses. Mar Ecol Prog Ser 191:121–126
- Boaventura D, Ré P, Cancela da Fonseca L, Hawkins SJ (2002) Intertidal rocky shore communities of the continental Portuguese coast: analysis of distribution patterns. Mar Ecol 23:69–90
- Brawley SH (1992) Fertilization in natural populations of the dioecious brown alga *Fucus ceranoides* L. and the importance of the polyspermy block. Mar Biol 113:145–157
- Brown MT (1987) Effects of desiccation on photosynthesis of intertidal algae from a southern New Zealand shore. Bot Mar 30:121–127
- Clogg CC, Petkova E, Haritou A (1995) Statistical methods for comparing regression coefficients between models. Am J Soc 100:1261–1293
- Connell JH (1972) Community interactions on marine rocky intertidal shores. Annu Rev Ecol Syst 3:169–192
- Coxson DS, Brown D, Kershaw KA (1983) The interaction between CO₂ diffusion and the degree of thallus hydration in lichens: some further comments. New Phytol 93:247–260
- Davis JS (1972) Survival records in the algae and the survival role of certain algal pigments, fat and mucilaginous substances. The Biologist 54:52–93
- Davison IR, Pearson GA (1996) Stress tolerance in intertidal seaweeds. J Phycol 32:197–211
- Demmig-Adams B (1990) Carotenoids and photoprotection in plants: a role for the xanthophyll zeaxanthin. Biochim Biophys Acta 1020:1–24
- Demming B, Winter K, Krüger A, Czygan FC (1987) Photoinhibition and zeaxanthin formation in intact leaves. Plant Physiol 84:218–224
- Dring MJ, Brown FA (1982) Photosynthesis of intertidal brown algae during and after periods of emersion: a renewed search for physiological causes of zonation. Mar Ecol Prog Ser 8:301–308
- Dring MJ, Wagner A, Boeskov J, Lüning K (1996) Sensitivity of intertidal and subtidal red algae to UVA and UVB radiation, as monitored by chlorophyll fluorescence measurements: influence of collection depth and season, and length of irradiation. Eur J Phycol 31:293–302
- Erdmann N, Gademann M (2001) 11. Salt acclimation of algae and cyanobacteria: a comparison. In: Rai LC, Gaur JP (eds) Algal adaptation to environmental stresses. Springer, Berlin, pp 323–361
- Field B, Behrenfeld J, Randerson T, Falkowski P (1998) Primary production of the biosphere: integrating terrestrial and oceanic components. Science 281:237–240
- Fleming ED, Bebout BM, Castenholz RW (2007) Effects of salinity and light intensity on the resumption of photosynthesis in rehydrated cyanobacterial mats from Baja California Sur, Mexico. J Phycol 43:15–24
- Geider RJ, Delucia EH, Falkowski PG (2001) Primary productivity of planet earth: biological determinants and physical constraints in terrestrial and aquatic habitats. Glob Change Biol 7:849–882
- Genty B, Briantais JM, Baker NR (1989) The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. Biochim Biophys Acta 990:87–92
- Gévaert F, Créach A, Davoult D, Migné A, Levassasseur G, Arzel P, Holl AC, Lemoine Y (2003) *Laminaria saccharina* photosynthesis measured in situ: photoinhibition and xanthophyll cycle during a tidal cycle. Mar Ecol Prog Ser 247:43–50
- Gylle M, Isaksson D, Ekelund NGA (2009) Ecotype differentiation in qualitative content of water soluble organic compounds between marine and brackish *Fucus vesiculosus* L. (Phaeophyceae). Phycol Res 57:127–130
- Hanelt D, Wiencke C, Karsten U, Nultsch W (1997) Photoinhibition and recovery after light stress in different developmental life-history stages of *Laminaria saccharina* (Phaeophyta). J Phycol 33:387–395
- Hanelt D, Wienecke C, Bischof K (2007) Arctic alpine ecosystems and people in a changing environment. Part 3:251–277
- Harker M, Berkaloff C, Lemoine Y, Britton G, Young AJ, Duval JC, Rmiki NE, Rousseau B (1999) Effects of high light and desiccation on the operation of the xanthophyll cycle in two marine brown algae. Eur J Phycol 34:35–42
- Henley WJ, Levassasseur G, Franklin LA, Lindley ST, Ramus J, Osmond CB (1991) Diurnal responses of photosynthesis and fluorescence in *Ulva rotundata* acclimated to sun and shade in outdoor culture. Mar Ecol Prog Ser 75:19–37
- Hunt LJH, Denny MW (2008) Desiccation protection and disruption: a trade-off for an intertidal marine alga. J Phycol 44:1164–1170
- Huppertz K, Hanelt D, Nultsch W (1990) Photoinhibition of photosynthesis in the marine brown alga *Fucus serratus* as studied in field experiments. Mar Ecol Prog Ser 66:175–182
- Kaltwasser J (1938) Assimilation and Atmung von Submersen als Ausdruck ihrer Entquellungsresistenz. Protoplasma 29:498–535
- Karsten U, Mostaert AS, King RJ, Kamiya M, Hara Y (1996) Osmoprotectors in some species of Japanese mangrove. Phycol Res 44:109–112

- Kirst GO (1989) Salinity tolerance of eukaryotic marine algae. *Ann Rev Plant Physiol Plant Mol Biol* 40:21–53
- Krause GH, Weis E (1991) Chlorophyll fluorescence and photosynthesis: the basics. *Ann Rev Plant Physiol Plant Mol Biol* 42:313–349
- Lamote M, Johnson LE, Lemoine Y (2007) Interspecific differences in the response of juvenile stages to physical stress: fluorometric responses of fucoid embryos to variation in meteorological conditions. *J Phycol* 43:1164–1176
- Lemonie Y, Harker M, Rminki NE, Rousseau B, Berkloff C, Duval JC, Young A, Britton G (1995) Xanthophyll cycle operation and photoprotection in brown algae: effects of high light and desiccation. In: Mathis P (ed) *Photosynthesis, from light to biosphere IV*. Kluwer, Dordrecht, pp 119–122
- Littler MM (1980) Morphological form photosynthetic performances of marine macroalgae: tests of a functional/form hypothesis. *Bot Mar* 22:161–165
- Lobban CS, Harrison PJ (1994) *Seaweed ecol and physiology*, 1st edn. Cambridge University Press, Cambridge
- Lüning K (1990) *Seaweeds: their environment, biogeography, and ecophysiology*. Wiley, New York, p 527
- Madsen TV, Maberly SC (1990) A comparison of air and water as environments of photosynthesis by the intertidal alga *Fucus spiralis* (Phaeophyta). *J Phycol* 26:24–30
- Magnusson G (1997) Diurnal measurements of F_v/F_m used to improve productivity estimates in macroalgae. *Mar Biol* 130:203–208
- Maxwell K, Johnson GN (2000) Chlorophyll fluorescence—a practical guide. *J Exp Bot* 51:659–668
- McCandless EL (1981) Polysaccharides of the seaweeds. In: Lobban CS, Wynne MJ (eds) *The biology of seaweeds*. Blackwell, Oxford, pp 559–588
- Menge BA, Sutherland JP (1987) Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *Am Nat* 130:730–757
- Niemeck RA, Mathieson AC (1976) An ecological study of *Fucus spiralis* L. *J Exp Mar Biol Ecol* 24:33–48
- Nybakken JW, Bertness MD (2005) *Marine biology, an ecological approach*, 6th edn. Pearson, Benjamin Cummings, San Francisco
- Osmond CB (1994) What is photoinhibition? Some insights from comparisons of shade and sun plants. In: Baker NR, Bowyer JR (eds) *Photoinhibition of photosynthesis, from the molecular mechanisms to the field*. Bios Scientific, Oxford, pp 1–24
- Ott J (1996) *Meereskunde*, 2nd edn. Ulmer, Stuttgart, p 424
- Pearson GA, Brawley SH (1996) Reproductive ecology of *Fucus distichus* (Phaeophyceae): an intertidal alga with successful external fertilization. *Mar Ecol Prog Ser* 143:211–223
- Pearson G, Kautsky L, Serrao E (2000) Recent evolution in Baltic *Fucus vesiculosus*: reduced tolerance to emersion stresses compared to intertidal (North Sea) populations. *Mar Ecol Prog Ser* 202:67–79
- Rohacek K (2002) Chlorophyll fluorescence parameters: the definitions, photosynthetic meaning, and mutual relationships. *Photosynthetica* 40:13–29
- Rugg DA, Norton DA (1987) *Pelvetia canaliculata*, a seaweed that shuns the sea. Plant life in aquatic and amphibious environments. Blackwell, Oxford, pp 347–358
- Schonbeck MW, Norton TA (1979) An investigation of drought avoidance in intertidal fucoid algae. *Bot Mar* 22:133–144
- Schonbeck MW, Norton TA (1980) Factors controlling the lower limits of fucoid algae on the shore. *J Exp Mar Biol Ecol* 43:131–150
- Schreiber U, Bilger W (1987) Rapid assessment of stress effects on plant leaves by chlorophyll fluorescence measurements. In: Tenhunen JD, Catarino FM, Lange OL, Oechel WD (eds) *Plant response to stress*. Springer, Berlin, pp 27–53
- Schreiber U, Bilger W (1993) Progress in chlorophyll fluorescence research: major developments during the past years in retrospect. *Prog Bot* 54:151–153
- Schreiber U, Schliwa U, Bilger W (1986) Continuous recording of photochemical and non-photochemical chlorophyll fluorescence quenching with a new type of modulation fluorometer. *Photosynth Res* 10:51–62
- Scott GW, Hull SL, Hornby SE, Hardy FG, Owens N (2001) Phenotypic variation in *Fucus spiralis* (Phaeophyceae): morphology, chemical phenotype and their relationship to the environment. *Eur J Phycol* 36:43–50
- Serraõ EA, Pearson G, Kautsky L, Brawley SH (1996) Successful external fertilization in turbulent environments. *Proc Natl Acad Sci USA* 93:5286–5290
- Stocker O, Holdheide W (1937) Die assimilation Helgoländer Gezeitenalgen während der Ebbzeit. *Z Bot* 32:1–59
- Titus JE, Wagner DJ (1984) Carbon balance for two sphagnum mosses: water balance be solves a physiological paradox. *Ecology* 65:1765–1774
- Via S, Gomulkiewicz R, De Jong G, Scheiner SM, Schlichting CD, Van Tienderen P (1995) Adaptive phenotypic plasticity: consensus and controversy. *Trends Ecol Evol* 10:212–217
- Wetzel R, Likens G (1990) *Limnological analyses*, 2nd edn. Springer, Berlin
- Young EB, Dring MJ, Savidge G, Birkett DA, Berges JA (2007) Seasonal variations in nitrate reductase activity and internal N pools in intertidal brown algae are correlated with ambient nitrate concentrations. *Plant Cell Environ* 30:764–774