Baltic Sea Keystone Macroalgae (Fucus vesiculosus, Phaeophyceae)

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The brown seaweed *Fucus vesiculosus* is the dominant and the most ecologically crucial primary producer and habitat founder in the Baltic Sea. In the shallow coastal zone, *F. vesiculosus* is particularly exposed to strongly and rapidly changing environmental conditions due to global change.



1. Introduction

Marine seaweeds that inhabit the shallow coastal area of temperate shorelines frequently experience an environment characterized by strong daily and seasonal variations in abiotic drivers, such as high and low irradiances, rapid temperature changes, and pH fluctuations. Due to anthropogenic global change, the continuing warming and its amplification of seasonal fluctuations generates stressful conditions in shallow waters, which seems to be a severe challenge for seaweeds ^{[1][2][3]}. The response of seaweeds to unfavorable environmental conditions is mediated through various physiological and biochemical mechanisms, of which the excessive formation and accumulation of reactive oxygen species (ROS) plays a central role by imposing oxidative stress on the cells (reviewed by ^{[4][5][6]}).

Perennial seaweeds in temperate latitudes can photosynthesize over broad temperature ranges, as they remain photosynthetically active throughout the year. Various metabolic processes in seaweeds induce ROS formation, particularly photosynthesis. Plants and seaweeds accumulate ROS as a concomitant process of the electron transport systems during photosynthesis and respiration, even under normal metabolic conditions ^[Z]. For instance, the main source of ROS in plant and seaweed tissues is the photosynthetic electron transport system that generates singlet oxygen ($^{1}O_{2}$) and superoxide radicals ($^{O_{2}-}$) ^{[B][9]}. Additionally, in a sequential reduction of molecular oxygen (O_{2}), hydrogen peroxide ($H_{2}O_{2}$) as well as hydroxyl radical (^{O}H) are produced. Various environmental factors, e.g., high or low temperature, rapid temperature changes, nutrient (also carbon) deficiency, high irradiance, and ultraviolet radiation (UVR) stimulate, as a general stress response, the gradual and continued production of ROS. Under stressful environmental conditions, photosynthesis is impaired and surplus energy leads to ROS production ^{[10][11][12][13]}. Oxidative stress is recognized as a physiological condition established when ROS formation surpasses the antioxidant defensive systems of organisms, leading to oxidative impairment in lipids, proteins, and DNA ^{[Z][14][15]}. For instance, a direct indicator of oxidative stress and damage is the level of

malondialdehyde (MDA) as a biochemical marker for lipid peroxidation, which is the result of the decomposition of polyunsaturated fatty acids in cell membranes ^[16]. Thus, MDA often accumulates under oxidative stress, and it has widely been used to distinguish between stressed and unstressed seaweeds (e.g., ^{[13][17][18]}).

 H_2O_2 is omnipresent in the oceans worldwide, with concentrations fluctuating temporally and spatially ^{[19][20][21]}. Seawater H_2O_2 concentrations between 10 and 300 nM are reported from different water masses and habitats ^[22] ^{[23][24]}. In shallow and calm coastal areas, seaweeds may also experience direct oxidative stress where H_2O_2 is formed by the photoactivation of dissolved organic material (DOM) due to ultraviolet radiation (UVR) and the release of excited electrons, initiating the reduction of molecular oxygen. The formation of H_2O_2 is mainly observed in surface waters or flat water zones characterized by high concentrations of DOM and oxygen ^{[19][25][26][27][28]}. In surface waters and/or intertidal pools, H_2O_2 can reach even micromolar concentrations (<2 μ M; ^{[29][30]}). H_2O_2 undergoes relatively few reactions with biologically important molecules, but it passes quickly through membranes by diffusion; thus, it is most likely the intracellular preliminary stage for more reactive oxidants (reviewed by Winterbourn ^[31]). However, H_2O_2 directly inhibits photosynthesis by affecting several photosynthetically important enzymes such as RuBisCO ^{[32][33][34]}.

Seaweeds, however, are equipped with various defense mechanisms that effectively remove ROS. Common antioxidative systems in seaweeds consist of several enzymes, e.g., superoxide dismutase (SOD), ascorbate peroxidase (APX), and catalase (CAT), as well as the antioxidants ascorbic acid, glutathione, β -carotene, and α tocopherol [11][35][36]. The antioxidative enzymes transform distinct ROS to less toxic compounds. For example, SOD scavenges and produces ROS at the same time because it catalyzes the conversion of $\cdot O_2^-$ to H_2O_2 and oxygen \square . Then, H₂O₂ is further deprotonated by CAT or APX. SOD is known as "the first line of defense" against ROS and plays a central role in the antioxidative system, as it is a powerful scavenger of O_2^- , which otherwise initiates a ROS cascade $\frac{[6][37]}{2}$. Furthermore, seaweeds are also able to detoxify H₂O₂ by excreting H₂O₂ to reduce intracellular concentrations [38][39]. In recent years, several studies have investigated the underlying molecular processes of ROS acclimation. These include the regulation of gene expression, for example the induction of various ROS scavenging enzymes (e.g., genes encoding for SOD, APX, CAT), heat shock proteins (HSPs), early light-inducible proteins (ELIPs), and the general adjustment of the primary metabolism towards abiotic factors (i.e., high light, high temperature, rapid changes in salinity) in seaweeds [40][41][42][43][44][45]. An overall trend was revealed by Collén et al. [43], who concluded that abiotic stress initiated an increased expression of "stress key genes" (e.g., HSP and ELIP genes), which appear together with decreased expression of energy protein synthesisrelated genes.

Along the rocky and stony shores of the Baltic Sea, the brown seaweed *Fucus vesiculosus* L. forms biomass-rich belts and thereby founds the basis of a productive and structurally complex community [46][47]. *F. vesiculosus* is a keystone species in shallow Baltic coastal habitats, which are characterized by fluctuating environmental conditions, particularly by annual and seasonal variations in pH (7.4–8.5) and temperature (<0 to 20/25 °C), which are tolerated by perennial *F. vesiculosus* [48][49]. The formation and structure of the *F. vesiculosus* ecosystem has been attributed to different abiotic factors and is maintained by fine-tuned biotic interactions [49][50][51][52]. For

example, *F. vesiculosus* populations seem to severely suffer from environmental changes over the past decades, as reflected by their decline in abundance and depth penetration along Baltic shores ^{[53][54]}.

Baltic Sea surface temperature has warmed rapidly during recent decades and is predicted to increase by 3–6 °C until 2100 ^[55]. Additionally, to this continuous warming trend, short-term extreme warming events known as "marine heat-waves" (*sensu* Hobday et al. ^[56]) became also more frequent in this region ^[57]. The simultaneous rise in pCO_2 and the accompanying acidification of the brackish Baltic Sea is challenging to forecast ^[58], but model simulations for the Baltic Proper projected a gradually decreasing mean surface pH until the end of this century ^[59].

Thus, co-occurring changes of environmental variables such as warming and acidification of the Baltic Sea may individually or interactively impact the antioxidative properties of *F. vesiculosus*. Their effect on *F. vesiculosus* may differ seasonally, depending on, for example, growth periods. The present study investigates single and joint effects of increased seawater temperature (Δ + 5 °C) and pCO₂ (1100 ppm) as predicted for shallow shores until the end of this century in the Baltic Sea [58][60][61] on adult *F. vesiculosus* in all four seasons. To simulate these specific global change scenarios, benthic mesocosms (Kiel Outdoor Benthocosms (KOBs)) were used. Temperature and pCO₂ elevation were added on top of the natural fluctuations and variabilities of all abiotic factors present in the KOBs [62]. We hypothesized that higher inorganic carbon availability under elevated pCO₂ may decrease, but higher temperatures may enhance oxidative stress for *F. vesiculosus*. Therefore, the antioxidative properties (SOD activity and lipid peroxidation), as well as the sensitivity of *F. vesiculosus* photosynthetic performance (i.e., effective quantum yield) to artificial oxidative stress resulting from exposure to H₂O₂ under these global change scenarios, were examined for the first time.

2. Antioxidative Potential

Photosynthetic performance measured as effective quantum yield of *Fucus vesiculosus* under short-term H_2O_2 stress was regarded as an indicator for its antioxidative potential. In summer, at increased water temperatures (>26 °C), *F. vesiculosus* deceased, but during the other seasons and treatments, *F. vesiculosus* tolerated up to 5 mM H_2O_2 , resulting in high effective quantum yields. The effective quantum yield of *F. vesiculosus* was significantly reduced, but it was still above 50% of the control in 10 mM H_2O_2 (**Figure 1**). A 50–70% reduction in effective quantum yield of *F. vesiculosus* at 20 mM was observed under all treatments in spring, summer, and autumn. The reduction of the quantum yield was stronger in spring and autumn compared to summer and winter. In winter, especially, the quantum yield was only reduced by 30–40% under all treatments in 20 mM H_2O_2 (**Figure 1**).



■+Temp +CO, □+Temp □+CO, ■Ambient

Figure 1. The effect of ascending H₂O₂ concentrations on effective quantum yield of *Fucus vesiculosus* (expressed as % of the control) grown for three months under various temperature and pCO₂ conditions during different seasons. Seasons: spring: 4 April–19 June 2013; summer: 4 July–17 September 2013; autumn: 10 October–18 December 2013; winter: 16 January–01 April 2014. Temperature and pCO₂ conditions: +Temp +CO₂: elevated temperature Δ + 5 °C with elevated pCO₂; +Temp: elevated temperature Δ + 5 °C with in situ pCO₂; +CO₂: in situ Kiel Fjord temperature with elevated pCO₂; Ambient: in situ Kiel Fjord temperature and pCO₂. Values are means ± SD (standard deviation), *n* = 3. Effective quantum yield values of the controls were between 0.57 and 0.74 for all *F. vesiculosus* apices. *, **: Significant differences in comparison to the paired control value at *p* < 0.05 and *p* < 0.001, respectively (Tukey-HSD). Cross (†) marks death of *F. vesiculosus* in summer under simulated ocean warming.

3. Lipid Peroxidation

Lipid peroxidation was examined by measuring the concentration of the biochemical marker malondialdehyde (MDA). MDA levels of all initial *F. vesiculosus* samples from its native habitat varied slightly but significantly over the course of one year (p < 0.05, Tukey-HSD), with higher levels in April and January compared to July and October (**Figure 2**). During spring, MDA content significantly increased by 20–40% among the measurement dates and under elevated temperatures (**Figure 2** and **Table 1**). During summer, a natural heat-wave increased the Kiel Fjord water temperature dramatically ^[62]. Thus, the water temperature under simulated ocean warming achieved maximum levels (peak temperatures: 27–30 °C for 30 days) that surpassed the thermal tolerance of *F*.

vesiculosus (>26 °C, ^[63]). Therefore, simulated ocean warming in combination with a summer heatwave led to a drastic dieback of the *F. vesiculosus* individuals and resulted in significant differences between the measurement dates (**Figure 2** and **Table 1**). MDA content of *F. vesiculosus* at the end of the summer experiment was neither increased nor decreased under elevated pCO₂ (**Figure 2**). Levels of MDA increased significantly in *F. vesiculosus* until the end of the autumn experiment under simulated ocean warming by 40% (**Figure 2** and **Table 1**). In winter, the MDA content of *F. vesiculosus* almost doubled during the experiment in the increased temperature treatments (**Figure 2** and **Table 1**). This effect of winter warming, resulting in higher MDA content in *F. vesiculosus*, was marginally alleviated at increased pCO₂ levels; however, this effect was not significant (**Figure 2**). The MDA content found during the final sampling of *F. vesiculosus* in the winter experiment revealed an interactive effect of temperature and pCO₂ (two-way ANOVA, *F* = 6.450, *df* = 1, *p* < 0.05).



Figure 2. Malondialdehyde (MDA) concentration of initial *Fucus vesiculosus* growing in its native habitat (n = 12) and at the end of the experiments (n = 3), with controlled temperature and pCO₂ conditions during different seasons. Seasons: spring: 4 April–19 June 2013; summer: 4 July–17 September 2013; autumn: 10 October–18 December 2013; winter: 16 January–1 April 2014. Temperature and pCO₂ conditions: +Temp +CO₂: elevated temperature $\Delta + 5$ °C with elevated pCO₂; +Temp: elevated temperature $\Delta + 5$ °C with in situ pCO₂; +CO₂: in situ Kiel Fjord temperature with elevated pCO₂; Ambient: in situ Kiel Fjord temperature and pCO₂. Values are means ± SD (standard deviation). *: Significant effects of the tested factors revealed by the repeated-measure ANOVA are marked with an asterisk for each season separately. Different uppercase (comparison of initial values) and lowercase (comparison of final values between treatments) letters specify significant differences (p < 0.05; Tukey-HSD, data were ln-transformed in order to meet assumptions of homogeneity of variance). Cross (†) points to the death of *F. vesiculosus* in summer under simulated ocean warming.

Table 1. Repeated-measures ANOVA outcome for temperature, CO_2 , and time effects on malondialdehyde (MDA) concentration in *Fucus vesiculosus* during the different seasonal experiments (n = 3). Seasons: spring: 4 April–19 June 2013; summer: 4 July–17 September 2013; autumn: 10 October–18 December 2013; winter: 16 January–1 April 2014. *p*-values < 0.05 are indicated by bold type.

Source of Variation	DF	F-Value	<i>p</i> -Value
((a) Spring		
Temperature	1	1.078	0.33
CO ₂	1	0.188	0.68
Time	1	0.632	0.45
Temp × CO_2	1	4.164	0.08
Temp × Time	1	5.712	0.04
$CO_2 \times Time$	1	0.536	0.49
Temp × CO_2 × Time	1	0.264	0.62
(k	o) Summer		
Temperature	1	20.979	0.002
CO ₂	1	1.548	0.25
Time	1	22.603	0.001
Temp × CO_2	1	0.002	0.96
Temp × Time	1	22.663	0.001
$CO_2 \times Time$	1	0.059	0.81
Temp × CO_2 × Time	1	2.944	0.13
()	c) Autumn		
Temperature	1	1.910	0.21
CO ₂	1	0.113	0.75
Time	1	24.796	0.002
Temp × CO_2	1	0.717	0.43
Temp × Time	1	13.281	0.008

Source of Variation	DF	F-Value	<i>p</i> -Value
$CO_2 \times Time$	1	0.409	0.54
Temp × CO_2 × Time	1	0.708	0.33
	(d) Winter		
Temperature	1	7.368	0.03
CO ₂	1	0.016	0.93
Time	1	17.644	0.003
Temp \times CO ₂	1	3.047	0.12
Temp × Time	1	18.457	0.003
$CO_2 \times Time$	1	0.381	0.55
Temp × CO_2 × Time	1	1.989	0.19

conditions, but it was not enhanced by increased pCO₂ under ambient temperatures (**Figure 3** and **Table 2**). In autumn, the activity of SOD was not different between the measurement dates under all treatments. However, in winter, SOD activity increased significantly among measurement dates and under warming by 40–60% (**Table 2**). Maximal SOD activity of 400–500 U SOD mg⁻¹ TSP was reached in winter under increased temperatures (**Figure 3**).



Figure 3. Variations of superoxide dismutase (SOD) activities of initial *Fucus vesiculosus* growing in its native habitat (n = 12) and at the end of the experiments (n = 3), with controlled temperature and pCO₂ conditions over

different seasons. Seasons: spring: 4 April–19 June 2013; summer: 4 July–17 September 2013; autumn: 10 October–18 December 2013; winter: 16 January–1 April 2014. Temperature and pCO₂ conditions: +Temp +CO₂: elevated temperature Δ + 5 °C with elevated pCO₂; +Temp: elevated temperature Δ + 5 °C with in situ pCO₂; +CO₂: in situ Kiel Fjord temperature with elevated pCO₂; Ambient: in situ Kiel Fjord temperature and pCO₂. Values are means ± SD (standard deviation). *: Significant effects of the tested factors revealed by the repeated-measure ANOVA are marked with an asterisk for each season separately. Different uppercase (comparison of initial values) and lowercase (comparison of final values between treatments) letters specify significant differences (*p* < 0.05; Tukey-HSD, data were ln-transformed in order to meet assumptions of homogeneity of variance). Cross (†) points to the death of *F. vesiculosus* in summer under simulated ocean warming.

Table 2. Repeated-measures ANOVA outcome for temperature, CO_2 , and time effects on superoxide dismutase (SOD) activity in *Fucus vesiculosus* during the different seasonal experiments (n = 3). Seasons: spring: 4 April–19 June 2013; summer: 4 July–17 September 2013; autumn: 10 October–18 December 2013; winter: 16 January–1 April 2014. *p*-values < 0.05 are indicated by bold type.

Source of variation	DF	F-Value	<i>p</i> -Value
	(a) Spring		
Temperature	1	1.078	0.33
CO ₂	1	0.188	0.68
Time	1	5.712	0.04
Temp × CO_2	1	4.464	0.08
Temp × Time	1	0.632	0.45
$CO_2 \times Time$	1	0.536	0.49
Temp × CO_2 × Time	1	0.264	0.62
(b) Summer		
Temperature	1	13.536	0.006
CO ₂	1	0.583	0.47
Time	1	14.162	0.006
Temp × CO_2	1	0.331	0.58
Temp × Time	1	3.284	0.11
$CO_2 \times Time$	1	1.332	0.28
Temp × CO_2 × Time	1	0.914	0.37

Source of variation	DF	F-Value	<i>p</i> -Value
	(c) Autumn		
Temperature	1	2.070	0.19
CO ₂	1	0.028	0.87
Time	1	0.000	0.99
Temp × CO_2	1	0.212	0.66
Temp × Time	1	0.090	0.77
$CO_2 \times Time$	1	0.019	0.89
Temp × CO_2 × Time	1	0.014	0.91
	(d) Winter		
Temperature	1	9.983	0.01
CO ₂	1	0.012	0.92
Time	1	12.226	0.008
Temp × CO ₂	1	0.044	0.84
Temp × Time	1	4.919	0.06
$CO_2 \times Time$	1	0.897	0.371
Temp × CO_2 × Time	1	0.470	0.512
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