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# Meristematic oxygen variability in eelgrass (*Zostera marina*)

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*Abstract*

We examined the variability in oxygen content of meristematic tissues in eelgrass in order to evaluate its potential role in events of sudden mass mortality within eelgrass beds. Oxygen content within intact eelgrass plants could be described by use of microelectrode techniques at high temporal and spatial resolution in the laboratory and in the field. Under both situations, the meristematic oxygen content was highly variable, ranging from 0 to 200% of air saturation depending on environmental conditions. Changes from steady-state maximum oxygen content to steady-state minimum content occurred within 30 min following experimental manipulation. The internal oxygen content exceeded water column oxygen concentration in the light and was intimately coupled to changes in irradiance because of the photosynthetic oxygen release within the leaves. The photosynthetically produced pool of oxygen could, however, not function as an efficient storage to support nighttime respiration. In the dark, oxygen was primarily supplied from the water column via diffusion into leaves, and the meristem quickly turned anoxic if the water column was anoxic. Experimental reduction of oxygen conditions immediately around the basal plant meristem had no major effect on internal oxygen content. High temperatures had a dramatic effect on the internal oxygen balance of eelgrass. Increasing temperature stimulated plant respiration more than photosynthesis, and the meristem went anoxic, even in the light, at water temperatures above 30°C. We hypothesize that low meristematic oxygen content is a key factor in events of seagrass die-off.

Stochastic events with massive plant mortality in beds of eelgrass (*Zostera marina* L.) are frequently observed in shallow Danish coastal waters. Mass mortality always occurs in late summer under warm, calm weather conditions and is often associated with periods of low oxygen concentrations in the water column. The dying plants are characterized by apparently healthy looking leaves, roots, and rhizomes, but with necrotic tissues in the intercalary meristematic region. A similar scenario can be observed in less successful laboratory cultures of eelgrass at high temperatures or with poor stirring. Within a few days, leaf bundles start to detach from the rhizomes and the plants die. These observations suggest that events of mass mortality among eelgrass stands are caused by degradation of meristematic tissues, which could be induced by poor meristematic oxygen conditions from high temperatures or low water column oxygen concentrations.

The intercalary meristem of eelgrass and other seagrasses is situated in the transition zone between water and sediment, and it initiates the formation of both leaves and rhizome segments. Oxygen must be supplied by radial diffusion from neighboring tissues, especially from the fully developed lacunae of older leaves surrounding the meristematic tissue. Meristems are sites of high metabolic activity, with high oxygen demands that support cell division and growth (Brix and Sorrell 1996). Therefore, the meristematic region likely is more vulnerable to conditions with poor oxygen supply than roots and rhizomes, which also have several physiological and metabolic adaptations to cope with periodic anoxia (Barclay and Crawford 1982; Drew et al. 1994; Vartapetian and Jackson 1997). Aboveground tissues apparently have no special adaptations to anaerobiosis, and both internally produced toxic metabolites and reduced compounds diffusing from the sediment under anoxia might pose a threat to the continuous functioning and survival of meristematic tissues (Pregnall et al. 1984; Smith et al. 1988; Crawford and Braendle 1996). Hence, maintenance of aerobic conditions in the meristematic tissue likely is crucial to eelgrass growth and survival.

Submerged plants, such as seagrasses, have developed a number of anatomical and physiological adaptations to supply belowground tissues with oxygen, the most important being the air-filled lacunae connecting leaves and roots. Oxygen generated by photosynthesis diffuses from leaves to belowground tissues driven by the steep oxygen gradient from leaves to the anoxic sediment. Smith et al. (1984) suggested that eelgrass roots are primarily supplied with oxygen derived from photosynthesis, and that roots, therefore, go anoxic during night. However, recent studies of *Cymodocea rotundata* and *Z. marina* (Pedersen et al. 1998) have revealed efficient oxygen supply to roots in the dark by simple diffusion of oxygen supplied by the water column. The oxygen supply, however, could be highly variable depending on photosynthesis, water column oxygen, and oxygen consumption within tissues and sediment.

The objectives of this study were to analyze the factors controlling meristematic oxygen conditions of eelgrass and to determine whether meristematic oxygen content is sufficiently variable to support the hypothesis for a potential role in eelgrass die-off. We used microelectrode techniques under both laboratory and field situations. Initially we analyzed

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temporal changes in meristematic oxygen as functions of change in light conditions, water column oxygen concentration, and temperature in laboratory experiments. Then we measured in situ variations in meristematic oxygen concentrations in relation to diurnal changes in water column oxygen and light.

## Materials and methods

The oxygen content of the meristematic tissues of eelgrass was examined both in the laboratory and in the field. For laboratory experiments, eelgrass seedlings were gently uprooted, transferred to aquaria (120 liters) with sediment and water from the sampling site, and grown at 14°C in a 14 : 10 h light : dark (LD) cycle at 160 mol photons $m^{-2}$ $s^{-1}$. The water was stirred by submersible pumps and continuously filtered (300 L $h^{-1}$) to prevent blooms of microalgae. The seedlings were acclimated for >1 month.

The meristematic tissue of eelgrass could be recognized as a narrow region immediately above an optically dense zone representing the newest rhizome nodium. Changes in oxygen concentrations were measured by means of Clark-type oxygen microelectrodes (OX10, Unisense). The microelectrodes are fast-responding (90% response within <1 s), are insensitive to stirring (<1%), and provide a spatial resolution of two times the tip diameter (Revsbech 1989). The electrodes were inserted one third into the meristematic region by use of micromanipulators. In the laboratory, the operation was surveyed carefully through a dissection microscope. This could not be done in the field; therefore, the plants were harvested, after taking measurements, for precise location of electrode insertion. Electrodes were connected to a picoammeter (PA2000, Unisense) and a high-resolution analog-to-digital (A-D) converter (ADC16, PicoTech). The electrodes were calibrated to 0 and 100% of air saturation before and after each series of measurements. In addition, the temperature response was characterized for each electrode. Salinity does not affect the signal of the electrode because the electrode measures partial pressure. Water temperature was recorded with a Type K thermocouple connected to a thermocouple converter (TC08, PicoTech). Irradiance was recorded using a LiCor Li-190SA sensor and a LiCor Li-1000 datalogger.

*Laboratory measurements*—In the laboratory, plants were mounted horizontally in an open split chamber containing a leaf compartment and a root–rhizome compartment where oxygen conditions could be individually controlled by bubbling with air or nitrogen ($O_2$ concentrations ranging from 0 to 100% of air saturation; Table 1). The nitrogen gas was mixed with $CO_2$ at 360 ppm to prevent $CO_2$ depletion and, hence, inorganic carbon limitation of photosynthesis. The chamber was placed in a water bath for temperature control. Light was provided by a Tungsten halogen lamp (Schott) at a photon flux density of 350 $\mu$mol photons $m^{-2}$ $s^{-1}$—enough to saturate photosynthesis (Mazzella et al. 1980). The meristematic region of the seedlings was embedded in a 1.5% (wt/v) agar mixture of seawater and agar-agar. In some experiments, the agar was kept anoxic by adding 97.5 mg $Na_2S_2O_4$ $L^{-1}$.

Table 1. Schematic view of the temperature and oxygen conditions around different parts of the plant in the four experiments. Anoxic conditions correspond to ~2% of air saturation. Oxic conditions are 100% of air saturation at any given temperature and salinity.

| Experiment description | Temperature (°C) | Plant part (% air saturation) Root/rhizome | Basal meristem | Shoot |
|---|---|---|---|---|
| 1. Normal conditions | 17 | ~2 | 100 | 100 |
| 2. Anoxic around the meristem | 17 | ~2 | ~2 | 100 |
| 3. Anoxic around the plant | 17 | ~2 | ~2 | ~2 |
| 4. Anoxic around the meristem | 25 | ~2 | ~2 | 100 |

The influence of external oxygen conditions on meristematic oxygen content was analyzed during LD shifts. Four series of experiments with five plants in each were carried out. The first series of experiments simulated a normal situation with anoxic conditions around roots and rhizomes and oxic (100% of air saturation) conditions around the leaves and intercalary meristem. In the second series, the intercalary meristem was placed in the anoxic root chamber to simulate a situation in which the meristem was either buried in the sediment or the anoxic zone invaded the lower part of the water column. The third series simulated a situation with severe oxygen deficiency in the whole water column. The three series were carried out at 17°C. During summer, the temperature of shallow waters can reach 25°C or more. Therefore, a fourth series of experiments were carried out at 25°C; otherwise, conditions resembled the second series with anoxia around both roots and intercalary meristem (*see Table 1 for overview*). Finally, the influence of temperature on oxygen conditions in the meristem was investigated by measuring steady-state oxygen concentrations under light and darkness within a temperature range of 5–35°C. Leaves and intercalary meristem were in 100% air-saturated water and root–rhizomes were in anoxic water.

*Field measurements*—The oxygen content was measured over a diel cycle in two different eelgrass plants at a protected, shallow (~0.5 m deep) locality in the Roskilde Fjord estuary, Denmark. The measurements were performed in early September on a cloudy day with highly variable surface irradiance. Water temperature varied between 17 and 19°C and did not change systematically over the diel cycle. Two microelectrodes with micromanipulators were mounted on aluminium supports anchored in the sediment and were connected to the same data-logging equipment as used in the laboratory. The two sets of microelectrodes with picoammeters had separate power supplies. Sediment around the meristematic region of the eelgrass shoots was gently removed to expose the tissue, and electrodes were inserted carefully into either the meristem or the rhizome of two different plants. The tissues were thereafter gently covered with a thin layer of sediment. Additionally, water column oxygen changes were recorded 20 cm above the sediment. Water and

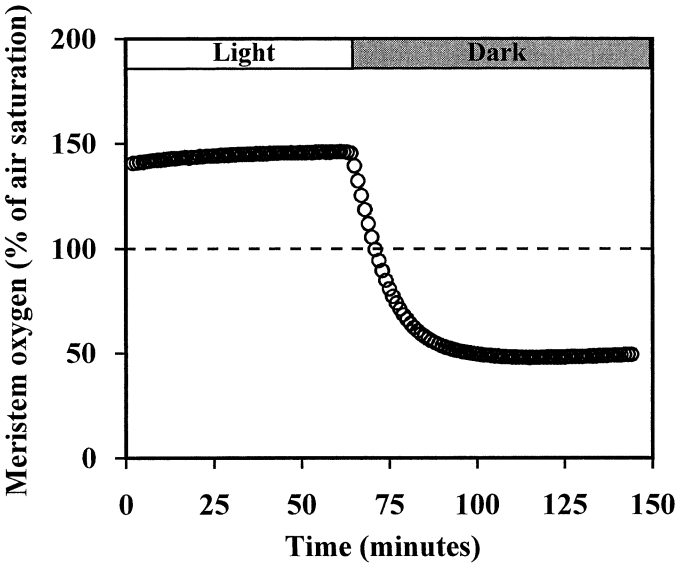


Fig. 1. An example showing the changes in meristematic oxygen content during a LD transition experiment under normal growth conditions with an oxic water column and a moderate temperature. Periods with light and darkness are indicated. The dashed line represents the corresponding oxygen content in the water surrounding the plant.

sediment temperature was measured continuously along with surface irradiance.

*Calculations and statistics*—Electrode signals were converted to oxygen concentrations using the individual calibrations and correcting for variations in temperature. The effects of experimental treatments were compared with respect to obtained maximum and minimum oxygen concentrations in light and dark, respectively. In addition, we compared the response time required to achieve new steady states after LD transitions. Response time was defined as the time from the LD switch to when 90% of the total oxygen decline was reached. Comparisons of two treatments were made by Student's *t*-tests and comparisons of more than two treatments by means of one-way ANOVA and multiple-range tests.

## Results

*Temporal variability in meristematic oxygen content*—The changes in internal oxygen content within the meristematic tissues of eelgrass followed a characteristic pattern during LD shifts (Fig. 1). Under normal conditions with moderate temperature and a fully oxic water column, a high steady-state $O_2$ concentration of up to 150% of air saturation, and substantially exceeding that of the water column $O_2$ concentration, was achieved within 1–2 h in the light. On switching to darkness, the $O_2$ content declined rapidly and reached a minimum concentration of down to 50% of air saturation within less than 1 h. After the minimum concentration had been reached, the oxygen content increased slowly to a new steady state in the dark.

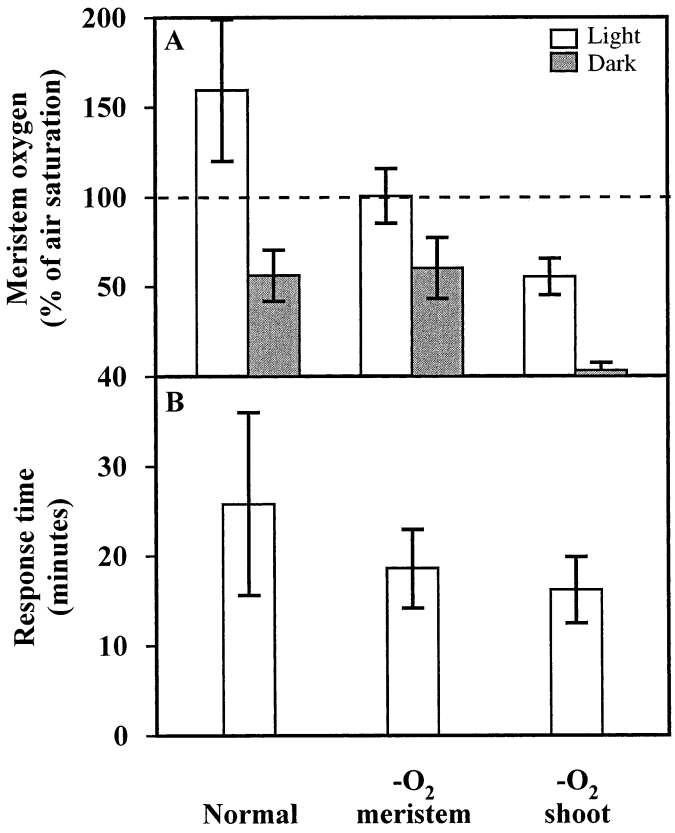


Fig. 2. (A) Maximum and minimum oxygen content of meristematic eelgrass tissues and (B) the 90% response time required to switch from high to low oxygen content as measured during experimental manipulation of oxygen conditions around eelgrass shoots in the laboratory (means ± 95% confidence limit, $n = 5$). Normal conditions represent a situation with oxic water column, anoxic rhizome–root compartment, and moderate temperature (17°C). At $-O_2$ meristem, conditions were as above but the meristem was placed in an anoxic environment. At $-O_2$ shoot, the whole water column was anoxic.

*Responses to variable external oxygen concentrations*—Under conditions simulating normal growth conditions in the field with a moderate temperature and an oxic water column, the mean meristematic oxygen content was ~150% of air saturation in the light (Fig. 2). The oxygen content declined rapidly (a 90% response time of 26 min) after the light had been switched off, but the average minimum oxygen content remained >50% of air saturation (Fig. 2). The meristematic oxygen content was significantly lower (~100% of air saturation) in the light when the water surrounding the meristem was anoxic compared to under normal conditions with a fully oxic water column ($p < 0.05$, Fig. 2). In the dark, the mean level of oxygen saturation was 56–60%, or similar to that under normal growth conditions.

A fully anoxic water column affected meristematic oxygen in both the light and dark significantly compared to the two former conditions ($p < 0.05$, Fig. 2). In the light, internal steady-state oxygen content corresponded to only 50% of air saturation, and in the dark, the meristematic tissues became anoxic within a 90% response time of 16 min, which

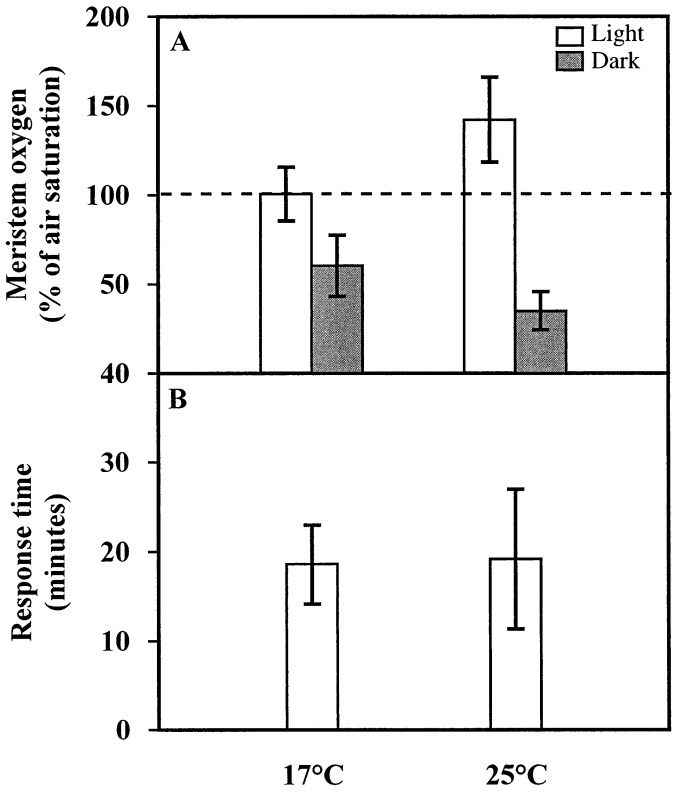


Fig. 3. The effect of temperature (17 vs. 25°C) on (A) maximum and minimum oxygen content and (B) the 90% response time required to switch from high to low oxygen content in eelgrass meristems (means ± 95% CL, $n = 5$). The leaves were in an oxic water column, whereas the meristem and roots–rhizomes were under anoxic conditions.

was significantly faster than under the two former conditions.

*Responses to changing temperature*—The combination of a sudden increase in temperature and keeping the environment around the meristematic region anoxic, but the water column oxic, was intended to simulate summer events with warm and calm weather. The higher temperature (25°C) resulted in a significant increase in the steady-state oxygen content in the light from 100 to 142% of air saturation ($p < 0.05$, Fig. 3). In darkness, the oxygen content was significantly lower at high temperature, reaching a level of only 35% of air saturation at 25°C, compared to 60% of air saturation at 17°C ($p < 0.05$). Although the difference between the oxygen levels in light and dark was higher at 25 than at 17°C, the 90% response time for the decline in oxygen content was about the same, reflecting a much faster depletion of internal oxygen pools at high temperature (Fig. 3).

The steady-state oxygen content of meristematic tissues in light and dark changed systematically with increasing temperature (Fig. 4). In the light, the steady-state oxygen content tended to increase with increasing temperature to a maximum at about 15°C. At higher temperatures, the oxygen content in the meristem decreased and reached zero at 35°C. In darkness the oxygen content decreased linearly with increasing temperature. At 5°C in the dark, the oxygen content was about 80% of air saturation and reached zero at 30°C (Fig. 4).

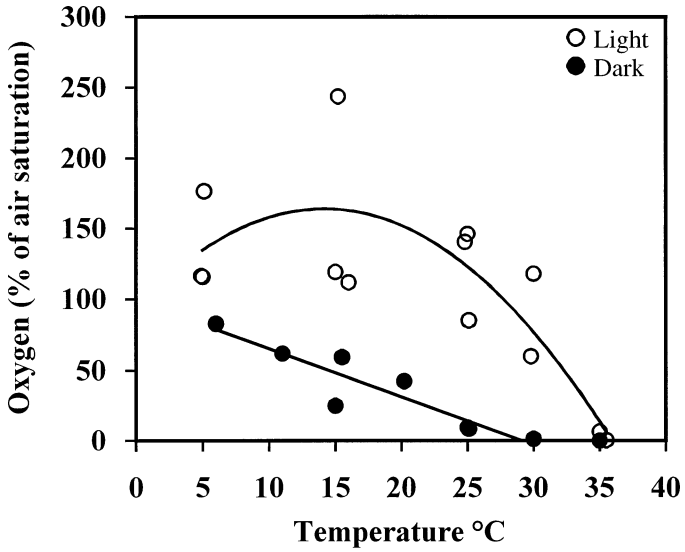


Fig. 4. The effect of changing temperature on steady-state oxygen content in eelgrass meristems in the light and in the dark. Each point represents one measurement. The trend curves were fitted to data measured in the light ($y = -0.35x^2 + 9.83x + 94.3$; $r^2 = 0.65$) and in darkness ($y = -3.42x + 99.6$; $r^2 = 0.85$).

*Field measurements*—Changes in the internal oxygen content measured in the meristematic region of one plant and in the rhizome approximately 1 cm below the meristem in another plant followed very similar patterns over a day–night–day cycle (Fig. 5). The small diel changes in water temperature only had minor influence on oxygen content expressed as percentage of air saturation (up to 4%). During daylight, the oxygen content exceeded water column oxygen concentrations, and the internal oxygen variability was intimately coupled to changes in surface irradiance. On approaching sunset, the internal oxygen content declined quickly to levels below the water column content. The meristematic oxygen content of the one plant was consistently lower than the rhizomatic oxygen content of the other, reflecting differences between plants or tissues.

During the night, the internal oxygen content declined in parallel with the reduction in water column oxygen (Fig. 5). The water column oxygen content was up to 150% of air saturation in the afternoon, declined to about 60% during the night, and started to increase approximately 2 h after sunrise. The intimate coupling between water column and plant oxygen during night was clearly illustrated by the immediate plant response to the sudden decline in water column oxygen shortly after midnight. The minimum oxygen content within the plants was observed around sunrise and corresponded to 6 and 17% of air saturation. The plant oxygen responded with only a short delay to the return of light, and within 3 h, plant oxygen was at the same level, or above, water column oxygen concentration.

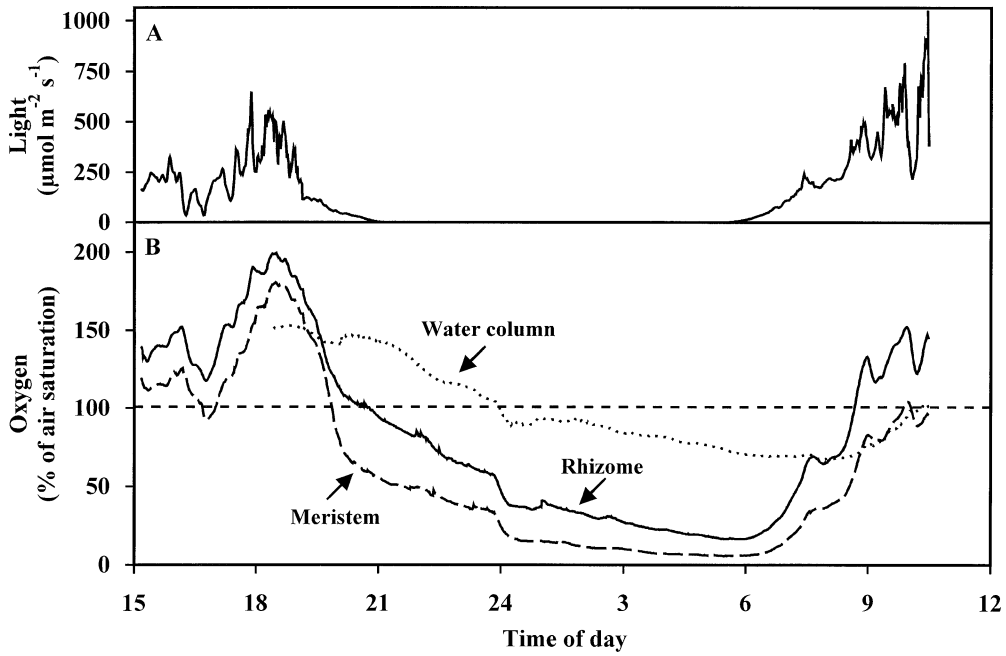


Fig. 5. Diel changes in (A) surface irradiance and (B) oxygen content of water column, meristematic tissue, and rhizomatic tissue in an eelgrass bed in the Roskilde Fjord estuary measured in early September. Water temperature was between 17 and 19° C.

## Discussion

The use of microelectrode techniques to measure internal oxygen variability proved successful under both laboratory and field conditions. In the laboratory, the exact position of the meristematic tissue could be recognized easily, and the microelectrode could be inserted with high precision. Correct positioning was achieved when an almost constant electrode signal was obtained after having passed the zone of the surrounding old leaves with fluctuating oxygen levels. Lacunal oxygen changes in submerged plants have been reported in the literature (Sand-Jensen and Prahl 1982; Roberts and Moriarty 1987), but the techniques have been either destructive or of low sensitivity. The microelectrode technique provides excellent means for describing internal plant oxygen variability with high precision and high spatial and temporal resolution.

The meristematic oxygen content of eelgrass is variable, as was clearly documented during both laboratory experiments and field measurements. The internal oxygen content ranged from 0 to 200% of air saturation depending on external conditions, and changes from steady-state maximum oxygen content to minimum content occurred within 30 min following experimental manipulation. Maintenance of oxic conditions in meristematic and belowground tissues is important for support of rapid growth, nutrient uptake by roots, and translocation of nutrients and carbohydrates between roots and leaves (Smith et al. 1988; Zimmerman and Alberte 1996). The observed variation of in situ meristematic oxygen content suggests that critically low levels of internal oxygen also occur under natural conditions. The critical oxygen level, where tissue switches to the less efficient anaerobic metabolism and starts to accumulate potentially toxic metabolites, is between 1 and 20% of air saturation for fruits, vegetables, and rice (Kubo et al. 1996) but is not known for seagrass tissues. We do, however, expect that the observed minimum oxygen content measured in the field (Fig. 5) is within the critical level for maintenance of aerobic respiration.

The plant oxygen content is dependent on photosynthesis and respiration (Moriarty and Boon 1989), which in turn depend on environmental factors such as light availability and temperature. Meristematic oxygen content also depends on water column oxygen content, loss of oxygen from roots to the anoxic sediment, and the efficiency of internal oxygen transport among tissues. Diffusion distances from leaves to roots of eelgrass are relatively long, and the gas transport would hardly be sufficient to support root respiration if it had to occur by passive diffusion in water. However, oxygen diffusion in air is $10^4$-fold faster than in water, and the maintenance of air-filled lacunae to support gas transport is likely a necessity to allow survival of submerged rooted plants. The fast responses in meristematic oxygen that we observed and the reports of oxic conditions in the rhizomes of *Thalassia testudinum* (Carlson et al. 1988) and of sustained oxic microzones around roots of *C. rotundata* in the dark (Pedersen et al. 1998) suggest that passive diffusion within the air-filled lacunae is a sufficiently efficient transport mechanism for seagrasses under normal environmental conditions.

Oxygen has to be supplied to the meristematic region from the leaves because the meristematic tissues themselves do not have a well-developed photosynthetic apparatus. During daylight, leaf photosynthesis builds up leaf lacunal oxygen concentrations above water column concentrations, and oxygen diffuses to the water column and to neighboring tissues. The high oxygen content observed in the light might

induce photorespiration in leaves (Salisbury and Ross 1992) but also generates a more steep concentration gradient of oxygen between leaves and roots and, hence, a larger flux to the meristem and to belowground tissues.

The water column functioned as a sink to internal leaf oxygen when the oxygen concentration in the water was below that of the leaves in the light. During darkness, the gradient in oxygen concentration was reversed and the water column functioned as a source to plant oxygen. The rate of gas exchange depends on the permeability of the leaf epidermis and the thickness of the diffusive boundary layer around leaves (Sand-Jensen and Prahl 1982). The permeability of the epidermis seemed to be high according to the fast changes from maximum to minimum oxygen content following experimental manipulation. Accordingly, internal pools of plant oxygen cannot function as efficient storage for support of nighttime respiration. The plant depends on a constant supply of oxygen through diffusion across the water–leaf interface, and the flux from water column to eelgrass leaves seemed sufficiently high to supply oxygen to the meristematic regions, as long as water column oxygen remained high and temperature moderate. However, in eutrophic shallow coastal areas, water column oxygen could be substantially reduced during the dark period (Borum 1997), and the flux of oxygen from water to plant might not be sufficient to compensate for plant respiration and for loss of oxygen to the anoxic sediment. During our field measurements, meristematic oxygen content dropped to <10% of air saturation, although water column oxygen remained above 60% of air saturation (Fig. 5).

Fluctuating water column oxygen concentrations are often associated with high water temperature during summer periods of warm and calm weather. Increasing temperature had substantial influence on meristematic oxygen balance. Photosynthesis tended to increase with temperatures up to 15°C. However, respiration apparently increased more than photosynthesis at higher temperatures, resulting in a dramatic decline in meristematic oxygen content that, even in the light, reached zero at 35°C. This pattern is in accordance with the higher $Q_{10}$ value (2.4) observed for respiration than found for photosynthesis of eelgrass (1.5–1.7, Marsh et al. 1986). During darkness, the enhanced respiration caused meristematic tissues to turn anoxic at 25–30°C, which is an ecologically relevant temperature range in shallow water on calm, warm days in the temperate regions inhabited by eelgrass. In addition, the increase in temperature also increases the microbial respiration in the sediment, which consequently increases the diffusion gradient from roots to sediment, resulting in further loss of internal plant oxygen (Moriarty and Boon 1989). Although fluctuations in water column oxygen could cause poor nighttime oxygen conditions, which are replenished during the day, high temperature would likely pose a more serious threat to seagrass survival because the poor oxygen conditions could prevail for several days.

Low oxygen supply to meristematic tissues, rhizomes, and roots has several implications for plant performance and likely also for plant survival. When metabolism shifts to anaerobic respiration, energy harvesting is much less efficient than with aerobic respiration, and translocation of carbohydrates to support metabolism is inhibited by anoxic conditions (Zimmerman and Alberte 1996). Toxic anaerobic metabolites, such as ethanol and lactate, can accumulate within tissues not adapted to anaerobiosis (Smith and ap Rees 1979; Crawford and Braendle 1996; Vartapetian and Jackson 1997), and the absence of oxic microzones around roots and rhizomes (Pedersen et al. 1998) can allow invasion of toxic metabolites (e.g., sulfide) from the sediment into the plant. Although eelgrass roots seem able to excrete ethanol and prevent postanoxic injury (Pregnall et al. 1984; Smith et al. 1988; Crawford and Breandle 1996), no adaptations to anaerobiosis have been observed for aboveground tissues (Pregnall et al. 1984). Meristems might, therefore, be more vulnerable to anoxia than roots and rhizomes.

Although it is known that conditions with hypoxia and high sulfide concentrations have negative effects on eelgrass photosynthesis, growth, and survival (Goodman et al. 1995; Terrados et al. 1999; Holmer and Bondgaard 2001), we are still not able to clearly identify the cause and effects regarding events of seagrass mass mortality. It is not known whether the degradation of meristematic tissues observed under events of die-off is caused directly by the variability in oxygen supply described in this study, is due to accumulation of internally produced anaerobic metabolites and inhibition of carbohydrate translocation (Pregnall et al. 1984; Zimmerman and Alberte 1996), or is caused by the invasion of sulfide from the sediment (Carlson et al. 1994). However, all explanatory models require sustained periods of low internal oxygen content; hence, internal oxygen content is very likely a key factor in understanding the events of seagrass die-off.

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