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Short communication

## Flow velocity affects internal oxygen conditions in the seagrass *Cymodocea nodosa*

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## Abstract

The internal oxygen status of seagrass tissues, which is believed to play an important role in events of seagrass die-off, is partly determined by the rates of gas exchange between leaves and water column. In this study, we examined whether water column flow velocity has an effect on gas exchange, and hence on internal oxygen partial pressures  $(pO_2)$  in the Mediterranean seagrass, Cymodocea nodosa. We measured the internal  $pO_2$  in the horizontal rhizomes of C. nodosa in darkness at different mainstream flow velocities, combined with different levels of water column oxygen  $pO_2$  using an experimental flume in the laboratory. Flow velocity clearly had an effect on the internal oxygen status. In stagnant, but fully aerated water the mean internal  $pO_2$  was 6.9 kPa, corresponding to about 30% of air saturation. The internal  $pO_2$  increased with increasing flow velocity reaching saturation of around 12.2 kPa (60% of air saturation) at flow velocities  $\geq$ 7 cm s<sup>-1</sup>. Flow had a relatively larger influence on internal pO2 at lower water column oxygen concentrations. By extrapolating linear relationships between internal and water column  $pO_2$  in this experimental setup, rhizomes would become anoxic at a water column oxygen  $pO_2$  of 4–4.5 kPa (~20% of air saturation) in flowing water, but already at 6.4 kPa ( $\sim$ 30% of air saturation) in stagnant water. Water flow may play an important role for seagrass performance and survival in areas with poor water column oxygen conditions and may, in general, be of importance for the distribution of submerged rooted plants.

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## 1. Introduction

Aquatic, rooted macrophytes normally grow in anoxic sediments, where effective transport of oxygen to roots and rhizomes from the leaves is required to support aerobic metabolism and prevent invasion of potentially toxic metabolites from the sediment (Armstrong, 1979). It has been suggested that low internal oxygen content or anoxia in seagrasses plays a key role in events of sudden seagrass mortality with massive die-offs, which typically occur under warm and calm weather conditions (Plus et al., 2003; Greve et al., 2003; Borum et al., 2005a). While the effect of temperature on seagrass respiration and internal oxygen conditions has been described (Masini and Manning, 1997; Greve et al., 2003), the influence of low water flow on the plant oxygen content has to our knowledge not been studied. In this study, we examine how water flow affects the internal oxygen conditions of the Mediterranean seagrass, *Cymodocea nodosa*.

Seagrasses have, like other aquatic, rooted macrophytes, inter-connected, gasfilled lacunae in leaves and below ground tissues to provide fast and effective exchange of oxygen between the tissues (Sculthorpe, 1967; Armstrong, 1979). The internal oxygen partial pressure  $(pO_2)$  in seagrasses is determined by photosynthetic oxygen production in the leaves, oxygen consumption in the tissues, passive exchange of oxygen with the water column, transport from leaves to roots and rhizomes and by radial oxygen efflux to the sediment (Pedersen et al., 1998; Greve et al., 2003; Borum et al., 2005a, 2005b). Hence, the internal  $pO_2$  is the result of a complex balance between several processes, which partly depend on the internal oxygen content and gradients. During daylight, internal  $pO_2$  may exceed 40 kPa corresponding to about 200% of air saturation (Greve et al., 2003; Borum et al., 2005b), but in darkness the oxygen pool in the aerenchyma rapidly declines due to plant respiration and radial efflux of  $O_2$  from roots to the sediment (Sorrell and Armstrong, 1994; Pedersen et al., 1998). When the  $pO_2$  of the leaf lacunae drops below the water column  $pO_2$ , oxygen will passively diffuse into the leaves from the water column until a new steady state of internal  $pO_2$  is established at a level determined by the balance between losses and gains (Pedersen et al., 2004; Borum et al., 2005b). If the rates of passive oxygen influx from the water column are low, the roots, rhizomes and eventually the meristematic tissues situated in the transition zone between water column and sediment may become anoxic.

The rate of passive oxygen influx is determined by the steepness of the oxygen concentration gradient between the bulk water and the leaf. It has previously been documented that the internal  $pO_2$  in darkness is closely correlated to the  $pO_2$  of the water column (Pedersen et al., 2004). However, the steepness of the oxygen gradient also depends on the thickness of the diffusive boundary layer (DBL) surrounding the leaves, which in turn, is controlled by the flow velocity of the water around the leaves. Measurements on DBLs for different macrophytes have revealed that the DBL thickness may vary 2–5-fold depending on the flow velocities around the leaves (Macfarlane and Raven, 1989; Gonen et al., 1993; Hurd et al., 1996). According to Fick's first law, the flux is inversely proportional to the diffusion path length so that an increase in DBL thickness due to reduced water flow should reduce the influx of oxygen proportionately if the concentration difference between water and leaf is constant. However, with reduced influx the internal  $pO_2$  declines and the concentration gradient between water and leaf increases until a new

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