Ecological Engineering 58 (2013) 414–422

Contents lists available at ScienceDirect

Ecological Engineering

journal homepage: www.elsevier.com/locate/ecoleng

Root effects on the spatial and temporal dynamics of oxygen in sand-based laboratory-scale constructed biofilters

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ARTICLE INFO

Article history:
Received 18 December 2012
Received in revised form 4 May 2013
Accepted 23 June 2013
Available online 14 August 2013

Keywords:
Carex appressa
Planar optode
Oxygen
Radial oxygen loss
Rhizosphere
Macrophyte

ABSTRACT

It is now well known that roots introduce oxygen into the soil environment through radial oxygen loss. The oxygen dynamics surrounding roots in periodically flushed environments, however, remains unstudied. We investigated the impact of roots of the macrophyte *Carex appressa* (Cyperaceae), on the small (rhizosphere) scale spatiotemporal dynamics of sediment oxygen consumption in a periodically flushed soil mimicking natural percolation events. Oxygen dynamics around the roots of *C. appressa* were studied using a planar optode installed in a rhizobox containing sand. A sand-based culture medium was used to simulate conditions in constructed biofiltration wetlands. The use of planar optodes allowed the generation of two dimensional images of sediment oxygen dynamics, that were used to quantify the patterns and kinetics of oxygen consumption. In addition to greatly increasing the spatial heterogeneity of oxygen in the substrate, the area immediately surrounding the roots became sites of both enhanced oxygen consumption, likely due to increased microbial activity associated with the input of carbon-rich rhizodeposits, and radial oxygen loss. This study highlights the profound impact of roots upon sub-surface oxygen dynamics in the rhizosphere.

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1. Introduction

Roots of all plants have a profound effect on the soil environment. Macrophytes, or aquatic plants, are no exception. Macrophytes inhabit complex environments that can undergo periodic or permanent inundation, soil saturation, and long periods of anoxia, which in turn can lead to the accumulation of phytotoxins in the surrounding substrate (Blom, 1999; Mancuso and Boselli, 2002). Oxygen concentrations in sediments are low because the diffusivity of oxygen through water is low (10^4 times lower than through air) (Colmer, 2003) and oxygen in pore water can be rapidly consumed via bacterial respiration (Askaer et al., 2010). Sub-surface oxygen availability is critical to the survival of macrophytes in oxygen-limited sediments. To overcome oxygen limitation in sediments, macrophytes have evolved well developed aerenchyma (Armstrong et al., 1991; Chabbi et al., 2000).

Transport of oxygen from the atmosphere to the roots of macrophytes (via aerenchyma) enables aerobic respiration to continue despite the absence of sediment oxygen (Chabbi et al., 2000; Mainiero and Kazda, 2004; Naiman and Décamps, 1997). In addition to reducing longtitudinal resistance to oxygen diffusion within roots, aerenchyma reduce the proportion of root tissue that is actively respiring, thereby reducing oxygen consumption (Colmer, 2003). Where oxygen transport to root tissue is sufficient, oxygen may be released from roots, creating an oxygenated micro-zone in the rhizosphere. This process has been termed radial oxygen loss (ROL) (Armstrong, 1964, 1971; Pedersen et al., 1998; Penhale and Wetzel, 1983).

Macrophyte roots strongly influence rhizosphere ecology and biogeochemical cycling through the dual processes of rhizodeposition and oxygen release (Gutknecht et al., 2006; Philippot et al., 2009). Whereas ROL can promote nitrification via the aeration of the sediment (Bodelier et al., 1996; Engelaar et al., 1995; Gersberg et al., 1986; Wießner et al., 2005), rhizodeposition can promote denitrification through the addition of labile carbon and subsequent promotion of anoxia (Lin et al., 2002; Weisner et al., 1994). It is well established that macrophytes play an important role in regulating nutrient cycling, and indeed it is for this reason that they are commonly used in water treatment biofilters and riparian restoration (Bratieres et al., 2008; MelbourneWater, 2005; Tanner et al., 1997). However, our understanding of the fine scale effects that they have on sediment oxygen spatiotemporal dynamics is relatively limited. If we are to maximise the efficiency of constructed biofiltration systems, we need a greater understanding of

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0925-8574/$ – see front matter © 2013 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.ecoleng.2013.06.028

such processes around the roots of plants grown under conditions replicating those in (sand-based) biofilters. This can in large part be attributed to the challenges of studying oxygen dynamics, and the effect of roots on them, in situ.

Planar optodes allow the two-dimensional characterisation of a specific analyte, such as oxygen, in high spatial and temporal resolution (Glud et al., 1996). In oxygen sensitive optodes, the fluorescence emission of a fluorophore molecule is dynamically quenched (suppressed) in proportion to the concentration of oxygen present in the sample. This fluorescence is captured by an imaging system, yielding both qualitative and quantitative information on the distribution of oxygen (Frederiksen and Glud, 2006). Planar optodes have been used to study the oxygen dynamics around the roots of a salt-marsh macrophyte (Nordi, 2004), three wetland macrophytes (Blossfeld et al., 2011), and around the roots of a seagrass (Frederiksen and Glud, 2006; Jensen et al., 2005). However, to our knowledge they have not been used to study the spatiotemporal dynamics of oxygen consumption around macrophyte roots following sediment re-oxygenation. This represents an important knowledge gap, because this dynamic exerts an important control over biogeochemical cycling processes such as nitrification and denitrification in dynamically wetted systems such as flood plains, riparian zones and engineered water treatment wetlands (Kadlec and Wallace, 2009; Reddy and DeLaune, 2008).

Here we present results of a study in which we used planar optode imaging to visualise and quantify the spatiotemporal dynamics of oxygen consumption around the roots of the macrophyte *Carex appressa* (Cyperaceae), including after sediment re-oxygenation. This species was selected because it is commonly used in stormwater bio-filtration systems (Blecken et al., 2009; Bratieres et al., 2008; MelbourneWater, 2005), and is particularly effective in nitrogen and phosphorus removal (Fletcher et al., 2007; Read et al., 2010, 2008). In order to replicate conditions in a constructed biofilter, we grew plants in a sand-based culture medium. The rhizosphere within this medium is likely to differ significantly from typical wetland rhizosphere's because it is relatively organic poor and, hence oxidising, compared to more organic rich soils which typify previous rhizosphere studies (Reddy and DeLaune, 2008). We also sought to highlight the potential for the planar optode method to be used to understand how plant roots interact with sediment biogeochemistry. Specifically we aimed to:

1. Quantify the spatial extent of oxygen penetration into sediment surrounding *C. appressa* roots
2. Quantify patterns and kinetics of oxygen consumption following sediment re-oxygenation; and
3. Quantify the radial oxygen loss from *C. appressa* roots.

We hypothesised that, *C. appressa* roots would alter small (rhizosphere) scale oxygen dynamics in sand, via both radial oxygen loss and enhanced rates of microbial respiration around roots.

2. Materials and methods

2.1. Rhizobox and planar optode construction

Oxygen dynamics around the roots of the wetland macrophyte *C. appressa* were studied using a planar optode installed in a rhizobox containing washed river sand. Washed river sand was used to replicate conditions in a constructed biofilter. The rhizobox was constructed of translucent acrylic, and was 280 mm × 100 mm × 100 mm (height × width × depth) in size. The base of the rhizobox had four 9 mm diameter holes, each of which could be blocked with a rubber plug, to allow controlled drainage of pore water. The front wall of the rhizobox was detachable to allow for installation of the planar optode. The planar optode was prepared using a modification of the methods of Larsen et al. (2011), with Pt(II)meso-tetra(pentafluorophenyl)porphine (TFPP) used as the oxygen-sensitive fluorophore due to its superior photosensitivity (Amao et al., 2001). The oxygen-sensitive fluorescent layer of the optode was coated with a silicone-carbon optical insulation layer to protect against sand abrasion in the rhizoboxes and to minimise interference by reflected fluorescence (Larsen et al., 2011). The planar optode was then affixed to the detachable front wall of the rhizobox with plastic tape, on a thin film of water, with an exposed imaging area of 56 mm × 160 mm. This provided direct physical contact between the oxygen sensitive planar optode, and the sediment and roots in the rhizobox.

C. appressa seedlings were sourced from Kuranga Native Nursery, Victoria, Australia. The plants were transferred to a glasshouse on the Clayton campus of Monash University, with supplemental lighting (MK-1 Just-a-shade, Ablite Australia); the mean daily photon flux in the glasshouse was 495.1 ± 108.6 μmol m^{-2} s^{-1}, with a 16/8 h day–night cycle. After 3 weeks, the seedlings were washed free from their substrate and transplanted into PVC tubes (90 mm diameter, by 300 mm long) containing 3.46 kg of coarse sand (porosity = 0.25). The plants were placed in a plastic tub containing reverse osmosis (RO) water to ensure the root zone remained saturated. Twice a week the plants were supplied with 100 mL of 1/10 strength modified Long-Ashton solution (Cavagnaro et al., 2001), plus 2 mM KH_2PO_4. The plants were grown in these tubes for 8 weeks, after which a single healthy specimen was transplanted (with its associated substrate) to the rhizobox. A small amount of additional sand was added to the rhizobox during transplanting, due to the larger volume and different shape of the rhizobox. The rhizobox was then transferred to the glasshouse, where it was tilted forward at an angle of 45° for a period of 7 days to encourage root development along the optode surface. An overlying water column was maintained in the rhizobox throughout this period. At the time of imaging, the *C. appressa* specimen had reached an age of 6 months.

2.2. Quantification of oxygen dynamics

All oxygen imaging was completed in an imaging laboratory, lit with grow lights (Sylvania Gro-Lux ®) on a 12:12 day–night cycle at 22 °C. Plant-free control images were generated using a rhizobox containing saturated sand treated in the same manner as when the rhizobox contained the plant specimen. Two-dimensional oxygen imaging and data processing were undertaken as described by Larsen et al. (2011). Oxygen dynamics in both the *C. appressa* and plant-free control imaging series were studied by draining the anoxic pore water from the rhizobox by removing the plugs from its base, with the oxygenated water of the overlying water column allowed to percolate down, re-oxygenating the substrate. The consumption of this oxygen was recorded until the profile had returned to anoxia. The oxygen consumption rate was extracted from oxygen images in two regions; the rhizosphere (planted treatment only), and the bulk sediment (planted and un-planted treatments).

Radial oxygen loss (ROL) was calculated for four roots visible on the planar optode by summing the oxygen concentration at each point within the oxic zone multiplied by the first order rate constant for oxygen consumption measured within the sediment. More specifically, the oxic zone around the root was approximated as a prolate ellipsoid, where the root runs along the major axis. As the root diameter was much less than the oxic zone diameter, it was assumed that the planar optode image represented a cross-section of the oxic zone. Radial and longitudinal profiles of oxygen were extracted from the data (See Fig. 5) and the ROL

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