



## Anoxic microsites in upland soils dominantly controlled by clay content

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### ABSTRACT

Recent evidence suggests that oxygen limitations are a critical regulator of soil organic matter mineralization rates, even within seemingly well-drained upland soils. Oxygen limitations may arise in otherwise well-aerated soils when oxygen consumption (via microbial respiration) in soil microsites outpaces oxygen supply (through diffusion). Due to analytical limitations, attempts to parameterize oxygen limitations in models have so far been limited to measures of bulk oxygen concentrations or cm-scale gradients within larger soil structural units (e.g., aggregates or peds). Smaller anoxic microsites may thus have gone undetected, limiting our ability to accurately model and predict anoxic pore volume. Here we quantify the extent of anoxic microsites in soils held at moderate moisture and identify the soil properties that dictate their formation and persistence. Using a planar optode imaging system, we monitored oxygen dynamics during incubations of a range of soils spanning natural and artificial gradients in texture and organic matter availability. While bulk oxygen concentrations ranged from 40 to 100% of saturation, we observed significant micro-scale variability resulting in the formation of anoxic microsites, here defined as soil spaces showing less than 5% saturation. Anoxic microsites comprised 2 and 9% of the total soil volume, or 14–85% of the total pore volume. Bulk oxygen concentrations showed a strong negative correlation with bioavailable organic matter, presumably due to its influence on microbial oxygen consumption. In contrast, the extent of anoxic microsites was negatively correlated to clay content, an effect attributed to limited oxygen supply in clay-rich microstructures. Our results demonstrate that texture-dependent diffusion limitations at moderate moisture conditions cause an abundance of anoxic domains, not only in cm-sized macro-aggregates as current modeling approaches assume, but also within micro-aggregates. Anoxic domain size within these microstructures is at least partially decoupled from bulk oxygen concentrations, challenging the use of bulk oxygen concentrations for predicting microbially available oxygen levels and resulting OM mineralization rates and pathways in upland soils.

### 1. Introduction

Soil plays a critical role in global carbon (C) cycling, representing the largest dynamic C stock on Earth— 3000 Pg of C are stored in soils (Köchy et al., 2015). Soil organic matter (OM) quantities are regulated by the balance between plant inputs and losses through microbial OM mineralization (i.e., complete oxidation of organic compounds to CO<sub>2</sub>) or export of dissolved OM in a given soil. Fundamental drivers of OM mineralization are principally climatic factors, such as temperature and precipitation, combined with OM chemistry (Cotrufo et al., 2015), C and nutrient availability (Fontaine et al., 2007; Klotzbücher et al., 2011; Torn et al., 2005), the formation of protective associations between OM and soil minerals (Oades, 1988; Torn et al., 1997), and physical protection, which constrains the accessibility of substrates to decomposer organisms (Killham et al., 1993; Veen and Kuikman, 1990). What remains elusive is how oxygen limitations in anoxic microsites,

existing within otherwise well-aerated upland soil, impact overall rates of OM mineralization.

Limited oxygen supply into soil structural units (e.g., peds or larger aggregates) can promote the formation of anoxic microsites, even within seemingly aerobic, well-drained soils. Macropores (> 50 μm), with low tortuosity and high pore connectivity, in combination with micropores, with high tortuosity and discontinuity, result in highly-variable flow of gas and water (Jarvis, 2007). If oxygen diffusion through fine-textured micropore domains is slower than its consumption by microbes through respiration, oxygen is depleted and anoxic microsites are established (Sexstone et al., 1985). Interior micropore domains of soil structural units may thus become oxygen depleted relative to the exterior (macropores). Although there is abundant evidence for the existence of anoxic microsites in otherwise well-aerated upland soil (Keiluweit et al., 2016), the relative impact of diffusion limitations and oxygen consumption on the formation of anoxic

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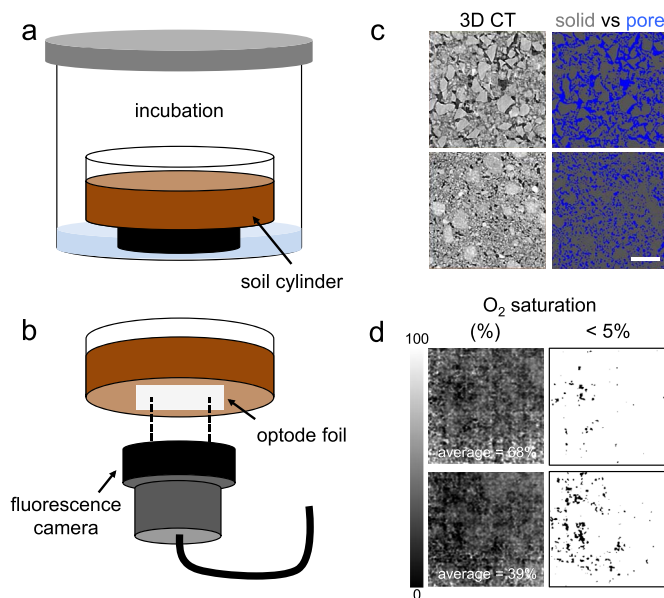
microsites is largely unknown.

The absence of oxygen prompts microbes to switch to alternate electron acceptors, and a diversity of anaerobic metabolic pathways transpire (Hansel et al., 2008). The lack of oxygen in permanently anoxic environments such as marine sediments (Hedges and Keil, 1995) or low-land soils (inclusive of wetlands, peatlands and rice paddies) (Meronigal et al., 2003; Reddy et al., 2000) dramatically reduces OM mineralization rates compared to aerobic environments. This rate-limiting effect is often attributed to the inhibition of oxidative depolymerization reactions (kinetic effects) (Freeman et al., 2001) or the lower energy yields associated with alternate electron acceptors used in anaerobic respiration in the absence of oxygen (thermodynamic constraints) (Arndt et al., 2013; Reddy et al., 1986). We recently showed that anoxic microsites can exert a similarly fundamental control on mineralization rates in upland soils (Keiluweit et al., 2017). In this previous study, mineralization rates in anoxic microsites were reduced by ~90% compared to well-aerated soil environments.

Traditional soil C models (e.g., DayCent and RothC) were not developed to represent the impact of soil microsite differentiation. In upland settings, soils are assumed to be completely aerobic and, hence, mineralization is presented as an exclusively aerobic process (Gottschalk et al., 2012; Parton et al., 1998). In an effort to develop more mechanistic and predictive soil C models, oxygen availability has been incorporated as a factor regulating mineralization rates. For example, Moyano et al. (2012, 2013) predict the influence of diffusion limitations on mineralization rates based on soil moisture content and soil physical properties, an approach that does not specifically isolate the effect of oxygen availability. Davidson et al. (2012) coupled mineralization rate directly to bulk oxygen concentrations, but assumed upland soils to be fully oxygenated, in effect excluding oxygen from their calculations. Further, the focus on bulk oxygen concentrations ignores the potential effects of anoxic microsites in structurally heterogeneous soils.

More recent models (e.g., Koven et al., 2013) address this problem by estimating the anoxic pore volume. Within this anoxic portion, a scaling factor is applied to account for the expected decrease in mineralization rates. The anoxic pore volume is estimated using an approximation of the classic ‘aggregate model’ (Arah and Smith, 1989; Arah and Vinten, 1995; Currie, 1961), which calculates the balance between oxygen diffusion (supply) into the aggregate and microbial oxygen consumption therein (demand) based on pore size distribution and water content as summarized in Keiluweit et al. (2016). However, this approach does not take into account the heterogeneity of soil structural units. For example, microbial activity (and thus oxygen consumption) is considered constant across aggregates. In fact, the ‘aggregate model’ predicts that anoxic microsites are restricted to mm- or cm-sized aggregates (Currie, 1961). Oxygen gradients occurring in soil microsites at smaller spatial scale are thus not currently accounted for in models.

Here we determined the anoxic volume in upland soils experimentally and examined soil factors predicting the abundance of anoxic microsites. We anticipated that soil texture (particle size distribution) couples with OM availability to regulate oxygen supply and demand, and thus the extent of anoxic microsites. To test this hypothesis, we quantified the emergence of anoxic microsites in incubations of homogenized and repacked soil cores varying in texture and C content. We used a series of upland soils with a natural gradient in texture and C content, but otherwise similar characteristics. In addition, we manipulated (i) soil texture by mixing select soils with quartz grains ground to different particle sizes (small = 25–45  $\mu\text{m}$  or large = 150–250  $\mu\text{m}$ ) and (ii) C content by amending soil with ground root material. Soils were incubated over a 35-day period at 60% water filled pore space, a moisture content at which microbial activity is often close to maximum (Franzluebbers, 1999; Linn and Doran, 1984) and many laboratory incubations are conducted. We monitored the extent of anoxic microsites throughout the incubations using a non-invasive



**Fig. 1.** Experimental approach to measuring anoxic microsites. a) Incubation setup consisting of soil cores in air-tight jars. b) Recording of oxygen distribution using planar Optode imaging of sensor foil installed at the bottom of the soil core. c) X-ray CT microtomography images to compare the physical-chemical characteristics of soils in this study; here two soils with strong contrasts in porosity are displayed. Both reconstructed grey scale images (left) and thresholded images highlighting the solid matrix versus pore space (right) are shown. It is important to note that microaggregate structures withstood sieving (lower left image). d) Examples for Optode imaging outputs showing the spatial variations in oxygen concentration (left) and the distribution of anoxic microsites, shown as black areas, using a threshold of < 5% saturation (right). 100% saturation corresponds to the oxygen concentration in fully oxygenated water. Scale bar = 250  $\mu\text{m}$ .

planar optode imaging technique, which quantifies oxygen concentrations at a spatial resolution of 1.35  $\mu\text{m}$  in both air- and water-filled pores (Fig. 1). To assess the impact of anoxic microsites on anaerobic metabolism, we monitored Mn and Fe reduction rates. Finally, we quantified soil factors influencing oxygen supply (texture, porosity, pore size distribution) and demand (microbial biomass and OM bioavailability) to identify the best predictors of bulk oxygen concentrations and the anoxic pore volume.

## 2. Methods

### 2.1. Soil sampling

We chose a series of three arable soils in the Willamette Valley, OR, with natural variations in texture and C content, but otherwise similar C inputs, geochemistry and climate (temperature and precipitation). These soils have developed from stratified, silty glaciolacustrine sediments that were deposited during the late Pleistocene. The brief but intense Missoula flood events created small-scale variability among otherwise very similar parent materials, resulting in a family of soils (Willamette, Woodburn, and Amity series) with distinct variations in texture and OM contents exploited for this study. Taxonomic classification and basic characteristics of each soil can be found in Table 1. We collected top- (depth = 10–30 cm) as well as subsoil (depth 90–110 cm) material, which was sieved (< 250  $\mu\text{m}$ ), air-dried, and stored until further use.

### 2.2. Soil characterization

Particle-size distribution (texture) was determined using a particle size analyzer (Coulter® LS 230). Prior to analysis, air-dried and sieved samples were gently ground using a ceramic pestle and mortar. A 16-part spinning riffler was used to accurately create representative splits

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