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Temporal dynamics of CO_2 and CH_4 loss potentials in response to rapid hydrological shifts in tidal freshwater wetland soils

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ABSTRACT

Earth System Models predict climate extremes that will impact regional and global hydrology. Aquatic-terrestrial transition zones like wetlands are subjected to the immediate consequence of climate change with shifts in the magnitude and dynamics of hydrologic flow. Such fluctuating hydrology can alter the nature and rate of biogeochemical transformations and significantly impact the carbon balance of the ecosystem. We tested the impacts of fluctuating hydrology and, specifically, the role of antecedent moisture conditions in determining the dominant carbon loss mechanisms in soils sampled from a tidal freshwater wetland system in the lower Columbia River, WA, USA. Our objective was to understand shifts in biogeochemical processes in response to changing soil moisture, based on soil respiration and methane production rates, and to elucidate such responses based on the observed electron acceptor and metabolite profiles under laboratory conditions. Metabolomics and biogeochemical process rates provided evidence that soil redox was the principal factor driving metabolic function. Fluctuating redox conditions altered terminal electron acceptor and donor availability and recovery strengths of their concentrations in soil such that a disproportionate release of carbon dioxide stemmed from alternative anaerobic degradation processes like sulfate and iron reduction compared to carbon loss due to methanogenesis. Our results show that extended and short-term saturation created conditions conducive to increasing metabolite availability for anaerobic decomposition processes, with a significant lag in methanogenesis. In contrast, extended drying caused a cellular-level stress response and rapid recycling of alternate electron acceptors.
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1. Introduction

Tidally-driven freshwater coastal vegetated wetland systems are currently estimated to store 870 million metric ton or approximately 1 Pg C within the top 1 m of soil, are highly vulnerable to carbon (C) loss through greenhouse gasses like carbon dioxide (CO_2) and methane (CH_4), as result of reduced precipitation and/or sea-level rise (Kirwan et al., 2013; Kirwan and Megonigal, 2013). Notably, the quantitative uncertainties in estimates of CH_4 emissions from vegetated coastal wetlands are ~30%, respectively (EPA, 2017). The directionality and magnitude of changes in C source-sink strengths of these soils remain uncertain as global climate continues to change.

Earth system models predict frequent extreme weather events with longer dry spells or more variable precipitation intensities at regional and global scales (Jentsch et al., 2007; IPCC, 2013), which will significantly influence terrestrial biogeochemical transformations. Soil microbial communities carry out key ecosystem functions, including biogeochemical cycling of major elements like sulfur and iron coupled to the C cycle. These coupled-C processes can be significantly impacted by changes in the abiotic environment, e.g. reduced oxygen availability in saturated soils or complete aeration of soil due to drought. Although well-known functional guilds of bacteria and archaea drive these processes, we lack understanding of their interrelationships to hydrology-driven shifts in the availability of substrate/metabolites and electron acceptors. Predictions of soil C efflux based on current-climate observations will be invalid under altered precipitation regimes without a mechanistic knowledge of key microbially-mediated C-loss processes, at the level of metabolic pathways, to be able to constrain uncertainties (Wieder et al., 2013; Martiny et al., 2017).

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The emissions of carbon dioxide (CO_2) and/or methane (CH_4) are driven by local soil conditions, however the responses vary widely. For example, as non-linear gradients in terminal electron acceptors (TEAs) and substrate concentrations develop over time, ecosystems may experience either rapid losses in C as carbon dioxide (CO_2) and/or methane (CH_4) or experience delays in response to wetting/drying (Joos et al., 2010). As oxygen is depleted upon abrupt wetting or over an extended saturation period, soil respiration is generally predicted to proceed by sequential consumption of nitrate, manganese, iron, and sulfate and ultimately, methanogenesis. How quickly these competitive processes develop from an initial pool of TEAs and substrate concentrations, and if and how they are switched or become limited as moisture regimes shift are underexplored in wetland soils understood. As shifts in TEAs and products of microbial metabolism are integral to determining the temporal dynamics of measured processes, they will, in turn, determine the dominant C loss mechanisms from a soil system. Recent studies ascribe soil C efflux responses to moisture perturbations to "soil moisture legacy effects" (Evans and Wallenstein, 2012; Banerjee et al., 2016) contingent on the extremity and duration of the perturbation. The few studies on the impact of shifting precipitation regimes (extreme wetting and drying) on soil microbiome have focused on upland systems by analyzing microbial community composition (Kieft et al., 1987; Xiang et al., 2008; Evans and Wallenstein, 2012; Barnard et al., 2015) or have concentrated on identifying statistical associations between the microbial and chemical data, e.g. electron acceptor concentrations (Cong et al., 2015). Here, using controlled laboratory incubations, we investigated the degree to which extreme moisture conditions could alter process rates. We developed a conceptual model of competing processes using TEA and metabolite profiles, and the thermodynamic potentials of key processes. Our goal was to use these data types to examine the potential for unquantifiable pathways key to C cycling and/or stress response with rapidly fluctuating moisture, and identify factors that govern the dominant C loss processes in hydrologically influenced soil systems.

We sought to investigate how limitations in TEAs and metabolites central to anaerobic C cycling control the relative dominance of sulfate reduction, iron reduction and methanogenesis in these ecosystems. We hypothesized that (i) an extended saturation will create a "legacy" of conditions primed to increased C loss via methanogenesis (ii) drying of previously saturated soils will induce aerobic C oxidation pathways, and cause osmolytes production, and (iii) wetting of previously dry soil will result in a lag phase in the onset of anaerobic microbial metabolism. Thus, we used controlled laboratory incubations of soils from a tidal wetland in southwestern Washington State (USA) to investigate the degree to which extreme moisture conditions could alter process rates, TEAs, metabolite profiles and thermodynamic potential of competing processes. These data types revealed the potential for unquantifiable pathways key to C cycling and/or stress responses to rapidly fluctuating moisture; from this we developed a conceptual model of the key biogeochemical processes based on observed and estimated stoichiometric relationships between metabolite profiles and TEAs in response to antecedent soil moisture. Such a model construct based on controlled laboratory studies provide process knowledge at a resolution otherwise difficult to obtain from field-based observations.

2. Materials and methods

2.1. Site description and soil collection

One of the largest remaining wetland complexes on the West Coast of the continental United States is on the lower Columbia River and estuary, a 234 km, tidal-fluvial continuum between the Pacific Ocean and Bonneville Dam. The freshwater wetland site is at the widest part of the lowland Columbia near the ocean, at river-kilometer 37 on Grays Bay. The difference between the maximum higher high and minimum lower low for the sampling year (1 Jan–31 Dec 2015) was 3.44 m based on predicted water levels (NOAA, 2017). Grays Bay is in the Energy Minimum reach of the Estuary system zone, near the boundary between tidal freshwater and brackish vegetation zones, where hydrodynamics are strongly affected by both the mixed semi-diurnal tidal regime and river flows (Jay et al., 2016). The Sitka spruce (*Picea sitchensis*) freshwater forested wetland type at the site is characterized by a step-pool channel system where pools alternate with natural log jams and dams built by the North American beaver (*Castor canadensis*) (Diefenderfer and Montgomery, 2009). Modeling indicates that surface water may exceed the bankfull elevation of 2.5 m North American Vertical Datum of 1988 (NAVD 88) as frequently as 17.4% of the time (Coleman et al., 2015). Groundwater dynamics have not been characterized but are assumed to be complex because of the complex channel system and microtopography (Diefenderfer et al., 2008), as well as the root structures of woody plants. At present, the elevation range at which we have surveyed rooted herbaceous, shrub and tree species at the site is 1.8 m to 3.6 m NAVD88 (Borde et al., 2011). The dominant plant species in the 3 m^2 sampling area selected for this study is the obligate wetland plant skunk cabbage (*Lysichiton americanus*), and the sampling area is fringed with salmonberry (*Rubus spectabilis*). The elevation range at which we have surveyed skunk cabbage below river kilometer 70 on the Columbia is 1.9 m to 3.4 m NAVD 88 (Diefenderfer et al., 2013). Of the approximately 8.91 km^2 of the Sitka spruce forested wetland that remains on the Columbia River floodplain (Christy and Putera, 1992), the Secret River forested wetland measures 0.5 km^2 (Coleman et al., 2015). We restricted soil sampling to a relatively small area in order to constrain effects of spatial heterogeneity in micro-elevation driven soil saturation levels for the laboratory investigation.

A grid sampling technique was used to collect soil cores (2.5 cm dia. x 5 cm height) from the mineral horizon after removing the organic layer to a depth of approximately 10 cm. The area of interest (3 m^2, as described above) was divided in to 25 × 25 cm^2 grid cells; 3–4 random samples could be collected from each grid-cell to avoid roots in this densely vegetated area. The cores were carefully lifted out, covered with ethanol-sterilized aluminum foil, stored on ice and transported to the Pacific Northwest National Laboratory, Richland, USA, where they were stored at 4 °C until further use.

Fifteen intact cores were randomly chosen for this study. The average bulk density of the silty soil was 0.97 g cm^{-3}. An experimental unit consisted of a PVC receiving column fitted with two sterilized stainless steel screens (2 and 50 μm openings) placed at the bottom, and closed with PVC caps on both ends (Fig. S1). A sterilized blue-butyl stopper (Bellco Glass Inc.) fitted the top cap was used for headspace gas sampling. All parts in contact with soil were sterilized by autoclaving or by flame sterilization using 80% ethanol.

2.2. Laboratory incubation study

Intact soil cores were subjected to three treatments: two fluctuating moisture regimes to test the effect of antecedent moisture and a continuous saturation/anoxic condition. Cores were pre-incubated at 20 °C for 18 days, and measured daily for headspace CO_2 and CH_4 production rates. At the end of pre-incubation, cores were randomly assigned to the three treatment incubations: Wet-Dry (n = 5), Dry-Wet (n = 4) and continuous Saturation (n = 3). Cores (n = 3) for time-zero (t0) analysis of water-extractable metabolites, sulfate and nitrate concentrations were processed, as described in sections 2.5 and 2.6, within 4 h of end of pre-incubation. Sub-

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