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Landscape patterns of soil oxygen and atmospheric greenhouse gases in a northern hardwood forest landscape

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Abstract

The production and consumption of the greenhouse gases, carbon dioxide (CO₂), nitrous oxide (N₂O), and methane (CH₄), are controlled by redox reactions in soils. Together with oxygen (O₂), seasonal and spatial dynamics of these atmospheric gases can serve as robust indicators of soil redox status, respiration rates, and nitrogen cycling. We examined landscape patterns of soil oxygen and greenhouse gas dynamics in Watershed 3 at the Hubbard Brook Experimental Forest, NH, USA. We analyzed depth profiles of soil O₂, CO₂, N₂O, and CH₄ approximately bimonthly for one year. Soil gas depth profiles were obtained from several different soil types encompassing a range of topographic positions, drainage classes, and organic matter content. Soil O₂ was a good predictor of greenhouse gas concentrations. Unsaturated soils always had O₂ concentrations >18%, while saturated soils had O₂ ranging from 0 to 18%. For unsaturated soils, changes in CO₂ were nearly stoichiometric with O₂. High concentrations of CH₄ (>10 μL L⁻¹) were typically associated with saturated soils; CH₄ was typically below atmospheric concentrations (<1.8 μL L⁻¹) in unsaturated soils. High concentrations of N₂O (>5000 nL L⁻¹) were found only in well-aerated soils after summer rainfall events and in marginally-anoxic soils; N₂O was consumed (<200 nL L⁻¹) under anoxic conditions. The production and consumption of greenhouse gases were linked to functionally distinct biogeochemical zones of variable redox conditions (hotspots), which exhibit dynamic temporal patterns of redox fluctuations (hot moments). These soil redox hot phenomena were temporally driven by climate and spatially organized by soil type (reflective of topographic position) further constrained by subsurface hydrology.

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1 Introduction

There remains considerable uncertainty in the magnitude of atmospheric trace gas consumption and production from forest soils. This uncertainty is vexing because controlled studies have shown that much of the variability in trace gas cycling can be explained by soil temperature, moisture, and substrate availability-quality (Skopp et al. 1990; Kirschbaum, 2006). However, expression of these controls in the context of the inherent complexity of forest ecosystem terrain amidst multiple environmental factors produces great variability in trace gas production and consumption and has inhibited our ability to quantify and predict patterns of trace gases in the field.

Soil moisture is of particular importance in the regulation of trace gas dynamics, controlling oxygen (O_2) diffusion at high soil moisture and substrate diffusion at low soil moisture. Topography and climate can organize dynamic spatial gradients of soil moisture, oxygen availability and redox even across upland ecosystems (Magnusson, 1992; Silver et al., 1999). The resulting redox gradients foster different biogeochemical processes (e.g., nitrification, denitrification, methanogenesis) involved in the production and consumption of carbon dioxide (CO_2), nitrous oxide (N_2O), and methane (CH_4) (Davidson and Swank 1986; Teh et al., 2005).

Soil O_2 and greenhouse gases (CO_2 , N_2O , CH_4) have the capacity to function as robust indicators of soil redox and are useful for identifying spatial and temporal transitions in biogeochemical processes across a landscape (Yu et al., 2006). Under optimal environmental conditions, different combinations of soil temperature, moisture, and substrates materialize into biogeochemical hot spots or hot moments (McClain et al., 2003). Understanding the timing and location of such hot phenomena is of fundamental importance towards scaling small biogeochemistry studies up to the landscape level.

Soil O_2 availability is equally critical to the biogeochemistry of upland soils as flooded soils. Studies of soil O_2 availability in upland ecosystems have focused on tropical forests (Silver et al., 1999; Liptzin et al., 2011), but are noticeably lacking for northern

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hardwood forests. Studies that measure multiple trace gases along soil depth profiles in northern hardwood forests are also very rare despite volumes of published surface flux measurements. This is unfortunate as vertical profiling sampling examines trace gas dynamics throughout the entirety of the soil profile, not just cumulative surface flux. Deeper soil horizons are frequently ignored but can play an essential role in the consumption and production of trace gases and overall biogeochemistry in northern hardwood forest soils (Yavitt et al., 1995; Davidson et al., 2006; Fierer et al., 2005; Kellman and Kavanaugh, 2008).

The goals of this study were to (1) capture forest landscape patterns in soil oxygen and trace gas concentrations and (2) examine their relationships to soil moisture and temperature as influenced by climate. We sampled a variety of soil profiles across different landscape positions to assess the challenges associated with prescribing biogeochemical processes based on superficial landscape features. We suspect that subsurface hydrology may limit the use of landscape feature analysis for identifying hot spots of biogeochemical activity, especially in mountainous terrain. We also explored the utility of concomitant measurements of O_2 , CH_4 , and N_2O to examine the mechanism of N_2O production from nitrification versus nitrification. Our objective in this regard was to ascertain which soils expressed the redox conditions (in terms of O_2 and CH_4 concentrations) most conducive for N_2O production or possible consumption.

2 Methods

2.1 Site description and experimental design

Field studies were conducted in Watershed 3 (W3), the hydrologic reference watershed at the Hubbard Brook Experimental Forest (HBEF), New Hampshire, USA ($43^{\circ}56' N$, $71^{\circ}45' W$). Watershed 3 (W3) is a 42 ha south facing catchment with moderate slope (12.1°), ranging from 527 to 732 m in elevation (Fig. 1).

The climate at the HBEF is humid-continental with an average annual precipitation of 1400 mm, of which about 30% falls as snow (Federer et al., 1990). A continual

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snow pack develops almost every year to an average depth of ~1.5 m. Precipitation is evenly distributed throughout the year; annual runoff in the experimental watersheds averages ~870 mm. The mean annual air temperature at the HBEF is 5.6 °C, the mean air temperature in July is 19 °C and in January is -9 °C (Likens and Bormann 1995).

5 At the HBEF, vegetation is characteristic of a developing, northern hardwood forest ecosystem. Due to the intermediate elevation and aspect in W3, the forest type is predominately deciduous and lacks a spruce-fir-birch component at high elevation (Johnson et al., 2000). Sugar maple (*Acer saccharum* Marsh.), yellow birch (*Betula alleghaniensis* Britt.), and American beech (*Fagus grandifolia* Ehrh.) are the major tree species in W3.

10 Soils are underlain by the Rangely formation, a pelitic schist of sillimanite grade, and a mantle of till derived from local bedrock that grades in depth from zero (scattered bedrock outcrops) along the ridge to several meters downslope (Likens and Davis, 1975). Surface topography is generally rough (pit and mound, mostly from wind-thrown trees) and mostly well drained; however, there are some impermeable pan layers (i.e., Cd horizons) at depths of about 0.6 m that restrict vertical water movement and seeps (Likens and Bormann, 1995).

20 Topography and hydrology play a large role in the formation of several soil types within W3. We focused on three contrasting soil types in order to compare dynamics: typical Spodosols (TYPs), “bimodal” Spodosols (BIMS), and umbric Inceptisols (UICP). The majority of the W3 area was dominated by Spodosols, classified as Halpohumods and Haplorthods which exhibit considerable spatial heterogeneity in physical and chemical properties. Typical Spodosols (TYPs) are characterized by moderate podzolization at the pedon scale, well drained, relatively dry, and occupied higher hill-slope positions (i.e., crest, shoulders) (Fig. 2a). Bimodal Spodosols (BIMS) are a variation of TYPs with a second Bh or Bhs horizon at the B/C interface resulting from illuviation in two directions: (i) vertically in the upper, typical portion of the profile; and (ii) laterally by development of a persistent water table. Bimodal Spodosols were found at the transition between TYPs and UICP soil types, were generally well drained

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but exhibited higher moisture contents than TYPS. Umbric Inceptisols are classified as Aquic Humic Dystrudepts characterized by a thin O, a thick A that grades into a Bh over a Cd; umbric epipedons range from 28–82 cm thick. Umbric Inceptisol were mostly poorly drained, frequently saturated, and occupied low lying, gently sloping landscape positions (i.e., local depressions or pits, benches and toeslopes).

2.2 Field Sampling

Soil gas samples were collected at nine soil stations and one seepage zone station for a total of 10 stations.

Three hillslope transects (T1, T2, T3) each with three soil profiles (A, B, C) situated along the length of the hillslope and one seepage zone were established as sampling stations (Fig. 1). Each hillslope transect sequence represented at least two of three predominant soil types (TYPS, BIMS, and UICP) found in W3.

Two methods of soil gas sampling were utilized to determine the depth profiles of O₂, CO₂, N₂O, and CH₄. Soil gas sampling in the seepage zone employed duplicate soil diffusion chambers as described by Yu and DeLaune (2006) with further modification to allow profile sampling to a 60 cm depth (Method 1). For all other stations, a soil pit was excavated down the Cd horizon and soil gas wells installed. Soil gas wells were constructed of nylon tubing (155 cm length, 3 mm o.d., 2 mm i.d. yielding a 5 mL i.v.) (Method 2). Gas well screens, composed of 4–6 lines of perforations 5 cm long, were fabricated by a 22 g needle. A small brass screw fitted at one end prevented soil grains from clogging the gas well upon installation. Gas well installation was facilitated by a 4 mm diameter pilot-hole augured 25 cm into the upslope face of the soil pit. Soil pits were back filled by horizon with gas sampling lines housed in 5 cm o.d. PVC pipe to minimize environmental exposure and wildlife tampering. Red butyl sleeve stoppers, serving as septa on both gas sampler varieties, were zip-tied to the exposed end of the tubing and replaced after each sampling campaign.

Gas profile sampling intervals varied due to variation in soil depth at each station. Gas wells were installed in duplicate and staggered at depths of 5 cm, 10 cm, and

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20 cm; ~15 cm intervals thereafter. Soil profile depth and sampling intervals for all stations are shown in Fig. 1. For Method 1, and Method 2 with unsaturated soil conditions, fine needle polypropylene syringes were used to withdraw 15 mL of soil gas to purge the sampling line and discarded. After the line was purged with fresh sample, two 20 mL gas samples were collected for immediate O₂ analysis with the remainder compressed into an evacuated 10 mL serum bottle fitted with molded PTFE/gray butyl septa and analyzed within 48 h. Sample integrity over prolonged storage for CO₂, N₂O, and CH₄ remained unchanged >10 days. Sampling 60 mL of soil gas collected over three 20 mL aliquots did reveal any significant differences in gas concentrations among the individual aliquots.

In the event of a saturated profile (defined as a continuous stream of extractable soil water; i.e., a water table), soil water was withdrawn directly from the gas sampling line via a 60 mL syringe after removing the septa. Each sample was immediately (<30 s) equilibrated with an equal volume of air (30 mL) in the syringe by vigorously shaking for 1 min; 20 mL of headspace gas was transferred into evacuated storage vials as per the “unsaturated” soil gas samples. Concentrations of dissolved CO₂, N₂O, and CH₄ were corrected for sample volume, equilibration efficiency, and ambient concentrations (monitored at each station). An additional 120 mL of soil water was withdrawn for immediate field determinations of soil water temperature and dissolved O₂.

Winter sampling presented additional challenges when collecting gas samples from the gas wells. Residual soil moisture within the sampling lines would periodically freeze and plug the tubing contained in the PVC housing. To combat ice plugs, hot forced air (1100W heat gun-power inverter-battery setup) was carefully circulated around the outside of the tubing effectively melting the ice within the sampling lines while avoiding damage to the nylon tubing.

Soil gas samples at the nine soil type-hillslope stations collected for one year (2009–2010) every two weeks in the summer (22 June–22 September), fall (23 September–21 December), and spring (21 March–21 June); except during winter months (22 December–20 March) which were sampled monthly. Gas samples in the seepage zone

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were collected every two months (Yu and DeLaune, 2006). Ambient air (~80 mL) was used to re-induce the headspace in the diffusion chambers after sample collection; it was assumed the chambers were equilibrated after two undisturbed months.

2.3 Analytical methods

5 Soil moisture and temperature sensors (Decagon Devices, Pullman, WA) were nested in six of the nine soil pits along the lower (T1) and upper (T3) hillslope transects (Fig. 1). Soil temperature at all other locations was recorded via a long stem thermometer. Temperature was measured at 20 cm below the forest litter layer or 10–16 cm below the surface of the mineral soil.

10 Soil volumetric water content was measured by the charge time of a capacitor in the soil to calculate a dielectric constant. Soil moisture sensors (Decagon ECH2O) were calibrated using manufacturer recommended generic mineral soil equations. Water filled pore space (WFPS) was estimated from volumetric water content from sensors that “leveled out” during the collection period. Leveled out sensor readings were assumed equivalent to relative saturation = 1 and WFPS = 100 %. Volumetric water data were divided by the leveled out sensors readings of the same soil texture to account for differences in porosity across soil horizons.

15 Soil oxygen was measured in the field using an Apogee MO-201 Oxygen Meter with a flow-through head (Apogee Instruments Inc, Logan, UT). The flow-through head was modified to accommodate push button syringe valves, one at each opening, to create an air tight sample introduction chamber. Ambient air and a 15 % O₂ gas standard (Air Liquide America Specialty Gases, Plumsteadville, PA) were used to calibrate the O₂ meter. Before introducing a 20 mL soil gas sample or standard, the sample chamber was flushed with 180 mL of ambient air and re-calibrated. Dissolved O₂ was measured in the field using a Hanna HI9142 Dissolved Oxygen Meter (Hanna Instruments, Woonsocket, RI).

25 Soil CO₂, N₂O, and CH₄ were measured by gas chromatography. Nitrous oxide was detected with an electron capture detector (ECD), and CH₄ and CO₂

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(after methanization) with a flame ionization detector (FID) using an Agilent 6890N GC with a G1888 headspace auto-sampler (Agilent Technologies, Santa Clara, CA). Chromatographic conditions for N₂O, CH₄, and CO₂ provide minimum detection limits of <50 ppbv N₂O (ECD), <0.2 ppmv CH₄ (FID), and <10 ppmv CO₂ (FID). With the exception of the seepage zone, all soil gas concentrations from each duplicate gas well were averaged to derive a single gas concentration per depth per station for use in data analysis.

2.4 Statistical analyses

Differences in soil gas concentrations among soil types were examined using ANOVA on ranks (Kruskal-Wallis) for non-normal distributions. Pair-wise comparison tests on nonparametric data were assessed by Dunn's method. Multivariate comparison of log transformed soil gas concentrations across all soil types were explored with factor analysis using a principal component parameter estimation method. Orthogonal (varimax) rotation was applied in the calculation of factor loadings, values >0.50 were considered significant. All statically analyses were preformed with SAS (version 9.2, SAS Institute, Cary, NC, USA).

3 Results

3.1 Soil properties and chemistry

Both TYPs and BIMS exhibited similar C and N concentrations, however BIMS exhibited a deeper accumulation of C within the second Bh horizon (Table 1). Umbric Inceptisols exhibited the greatest accumulation of C and N of any soil type due to the presence of an umbric epipedon. All soils were acidic, pH <4.3.

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3.2 Spatial patterns of soil O₂ and trace gas concentrations

Over 1500 individual gas profile samples were collected from 30 June 2009 to 21 May 2010 capturing a wide variety of hydrologic and climatic conditions across the different soil types. There was large variation in gas concentrations for individual soil profiles within a particular soil type (Fig. 2). When soil gas concentrations were grouped by soil type statistically significant ($\alpha < 0.05$) differences in soil gas concentrations were apparent. Soil O₂ concentrations amongst soil types ranked highest to lowest TPYS = BIMS > UICP > SEEP (Fig. 2b). Soil CO₂ concentrations ranked UICP > TYPs = BIMS = SEEP (Fig. 2c). Soil N₂O concentrations ranked UICP > BIMS = SEEP > TYPs (Fig. 2d). Soil CH₄ concentrations ranked SEEP > UICP > BIMS > TYPs (Fig. 2e).

Soil GHG concentrations also exhibited considerable variation throughout the soil profile (Fig. 3). Carbon dioxide generally increased with depth across all soil types (Fig. 3a), except after storm events when large pulses of CO₂ were observed at the organic-mineral soil interface. The highest concentrations of N₂O were observed in mineral horizons across all soil types. High concentrations of CH₄ were coincident with the rise and fall of the local water table and generally remained below ambient concentrations above the water table across all soil types (Fig. 3c).

3.3 Soil water content and soil gas concentrations

Variation in soil gas concentrations among and within soil types showed a strong correlation with differences in soil moisture driven by fluctuations in the local water table (Fig. 4). Incidences of significant O₂ depletion (<10 %) and high CH₄ concentrations (>10 $\mu\text{L L}^{-1}$) corresponded with saturated conditions (100 % WFPS), which were driven by changes in the local water table (Fig. 4a and c). Concentrations of O₂ and CH₄ generally followed a strict inverse relationship with WFPS. Production of N₂O seemingly exhibited a unimodal distribution in response to WFPS with local maxima occurring between 50 % and 80 % WFPS (Fig. 4c). High concentrations of CH₄ also

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appeared at >70 % WFPS. However, these distributions were only apparent for BIMS and UICP soil types. Concentrations of N_2O did not exceed 1500 nLL^{-1} when WFPS was >80 %. There was no apparent relationship between CO_2 and WFPS across soil types (Fig. 4b).

Soil moisture among the four UICP soil profiles were highly variable with some profiles very dry and others frequently saturated. Such differences in soil moisture corresponded with differences in the concentrations of soil gases. Soil moisture in station T1A was much lower compared to station T3A whose profile was frequently saturated even to the surface. Correspondingly, station T1A exhibited high O_2 coupled with low CH_4 concentrations compared to station T3A characterized by low O_2 and high CH_4 concentrations. Relative to these two extremes, intermediate concentrations of O_2 and CH_4 were observed at stations T2A and T2B while exhibiting the highest CO_2 and N_2O concentrations of the UICP soils sampled.

3.4 Temperature and soil gas concentrations

Both CO_2 and N_2O showed strong seasonal patterns (Fig. 5a–b). Soil concentrations of CO_2 and N_2O were highest in summer, sharply declined over the fall and winter months, followed by an increase in spring. Soil CO_2 increased exponentially with soil temperature (20 cm depth) across all stations (Fig. 6a). The soil CO_2 -temperature response was highly variable across the different soil types and within each soil type. Soil O_2 closely followed the CO_2 -temperature relationship (data not shown). Concentrations of N_2O > 1000 nLL^{-1} occurred only above 8°C (Fig. 6b). Large pulses of N_2O following spring snowmelt were not observed. There was no apparent relationship between soil CH_4 concentrations and soil temperature.

3.5 Soil O_2 availability and greenhouse gas concentrations

Soil O_2 was generally a good predictor of greenhouse gas concentrations. We examined relationships between O_2 and trace gases separately for saturated and

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unsaturated conditions. Unsaturated soils always had soil O₂ levels >18 %, while saturated soils had O₂ levels ranging from 0 to 18 %. For unsaturated soils, changes in CO₂ were nearly stoichiometric with O₂ (slope = 0.94 ± 0.019, r² = 0.82) (Fig. 7a). High concentrations of CH₄ were typically associated with saturated soils when O₂ < 18%; CH₄ was generally below atmospheric concentrations when O₂ > 18% (Fig. 7b). High concentrations of N₂O (>2000 nLL⁻¹) were found only in unsaturated soils when O₂ > 18% (Fig. 7c).

The 18 % O₂ threshold failed to predict soil greenhouse gas concentrations under all environmental conditions; most notably during the dry down of a previously saturated soil profile. Such a dry down occurred at station T3A during the month of September 2009 (Fig. 8a–b). When the lower soil profile “dried out”, CH₄ concentrations remained above ambient (>3 μLL⁻¹), N₂O significantly increased (>1000 nLL⁻¹), and O₂ was >18 %. Upon re-saturation in October, N₂O sharply decreased to pre-September concentrations. Hence, under certain environmental conditions, high concentrations of both CH₄ and N₂O co-occurred with O₂ > 18%.

3.6 Factor analysis

A conceptual model of landscape-level N₂O cycling was developed using factor analysis. Principal components analysis (PCA) was used to identify the initial eigenvalues: the first factor explained 51 % of the variance, the second factor 32 %, and a third 11 %. Only Factors 1 and 2 had eigenvalues >1.0. Communalities for all soil gas variables were >0.88. Causal naming of Factor 1 was “Aerobic/Anaerobic Respiration” as only O₂ and CH₄ were significant; O₂ and CH₄ had nearly equal but opposite scores (Table 2). We interpreted large positive values as indicative of aerobic respiration (high O₂, below ambient CH₄); large negative values as anaerobic respiration (low O₂, above ambient CH₄). Causal naming of Factor 2 was “Nitrous Oxide Production/Consumption” as only N₂O was significant. We interpreted large positive values as indicative of N₂O production; large negative values as N₂O consumption.

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We identified four quadrants of proposed N₂O production/consumption relative to aerobic and anaerobic respiration processes when plotting Factor 1 vs. Factor 2 by soil type (Fig. 9). Quadrant I: N₂O production under marginally anoxic and/or anoxic conditions. Quadrant II: N₂O production under oxic conditions. Quadrant III: no N₂O production and/or N₂O consumption under oxic conditions. Quadrant IV: N₂O consumption under marginally anoxic and/or anoxic conditions.

Our conceptual model of N₂O cycling proved robust across all soil types. For instance, consumption of N₂O (<200 nLL⁻¹) observed in the seep occurred under anoxic conditions evidenced by high CH₄ (>25 μLL⁻¹) and low O₂ concentrations (<5%) on several occasions. These observations were made apparent as a cluster of three points in Quadrant IV. High concentrations of both N₂O and CH₄ in UICP soil type during a dry down period (i.e., Fig. 8) were evident in Quadrant I. The observed N₂O spikes that followed summer storm events when O₂ remained >18% in BIMS soils clustered within Quadrant II.

4 Discussion

4.1 Soil moisture

The widely held notion that an increase in soil moisture advertently leads to a concomitant decrease in soil oxygen availability appears to be highly dependent on soil type. In HBEF soils, increased soil moisture did not always correspond to low soil O₂ or the onset of anoxic conditions. Rather, even under saturated conditions (i.e., 100% WFPS), soil oxygen concentrations ranged from relatively oxic (>15%) to anoxic (0%). Poorly drained, organic rich soils (i.e., UICP and the seep) were most prone to incidences of significant O₂ depletion and CH₄ production. In contrast, well drained soils remained >10% O₂ despite enduring saturated conditions, apparently lacking the environmental conditions (e.g., hydrologic residence time, biological activity, substrate quality) necessary to significantly deplete O₂.

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Understanding soil O_2 availability with respect to soil moisture must also account for both the physical factors and biological processes controlling re-aeration rates. Physical limitations restrict gas transport into and out of the soil profile (e.g., air permeability as influenced by soil structure, texture, and water content). When biological demand for O_2 exceeds re-aeration rates, O_2 can become depleted resulting in marginally anoxic to anoxic conditions. The same mechanisms that limit O_2 movement into the soil profile also restrict the movement of gases from the profile, leading to a buildup of gaseous respiration byproducts. Aerobic heterotrophic metabolism of labile C substrates should yield a 1:1 molar relationship between O_2 and CO_2 based on the stoichiometry of carbohydrate metabolism (e.g., $C_6H_{12}O_6 + 6O_2 \rightarrow 6CO_2 + 6H_2O$). The slope of soil CO_2 – O_2 linear regressions can be interpreted as proxies for soil gas exchange. Slopes close to unity suggest minimal limitations on soil gas diffusion; alternatively, slopes exhibiting large deviations below unity infer significant gas diffusion limitations. Under unsaturated conditions, across all depths and soil types at HBEF, the slope of soil CO_2 – O_2 regression was very close to unity (0.94) remaining highly correlated ($r^2 = 0.82$) and linear above 18 % O_2 . Under saturated conditions, however, the slope was 0.10 and poorly correlated ($r^2 = 0.36$), closer resembling a humid tropical soil whose slope ranged from 0.25–0.39 (Teh et al., 2005). These results suggest the bulk of the soil atmosphere was well aerated when soil moisture was below field capacity but poorly aerated above field capacity.

The presence of anoxic microsites was apparent by observations of high concentrations of N_2O and CH_4 despite prevailing oxic conditions in some soil profiles (>18 % O_2). Both nitrification and denitrification can produce N_2O as an intermediate product as described in the the “hole-in-the-pipe” conceptual model of Firestone and Davidson (1989). The rate of nitrogen cycling through ecosystems affects the production and/or consumption of N_2O ; the fraction of N converted into N_2O is influenced by soil water and other environmental factors (e.g., O_2 and electron donor availability, temperature). Methanogenesis is carried out by obligate anaerobes in the absence of oxygen. Hence, the production of either N_2O or CH_4 requires at least some degree

of O₂ limitation; however, such periods of O₂ limitation were only established under specific environmental conditions.

Large pulses of N₂O were observed in the upper mineral soil following summer storm events only in BIMS and UICP soil types. These observations are consistent with increased nitrification and/or denitrification rates following rain fall events (Davidson, 1992). However, because such observations clustered in Quadrant II of Fig. 9, we speculate that nitrification was the predominant source of N₂O following summer rainfall events given the lack of appreciable CH₄ concentrations. In contrast, high concentrations of both N₂O and CH₄ were found in a UICP soil during a dry down period, evident in Quadrant I of Fig. 9. We speculate that denitrification under marginally anoxic conditions was the predominant source of N₂O under these environmental conditions because CH₄ production persisted (Bollmann and Conrad, 1998). Although this UICP profile was seemingly well aerated, the associated anoxic microsites were most likely masked by our crude soil O₂ measurements. Nitrous oxide consumption (<200 nL L⁻¹) was only observed in the seep during the fall when CH₄ concentrations peaked (Quadrant IV of Fig. 9). We speculate that denitrifiers reduced N₂O to dinitrogen gas (N₂) under anoxic conditions.

While our soil O₂ measurements at times failed to capture anoxic microsites present in soil profiles, soil water content (as WFPS) did reflect important thresholds in soil redox. Soil water content at 60 % WFPS (near field capacity) has been suggested as a critical transition between aerobic and anaerobic processes (Linn and Doran, 1984; Davidson, 1993; Davidson et al., 1986). Our findings are consistent with 60 % WFPS as a critical transition: (i) the highest concentrations of N₂O were clustered between 50 % and 80 % WFPS (Fig. 4c); and (ii) CH₄ production only appeared when WFPS exceeded 75 %. These results suggest (1) optimal N₂O production via nitrification occurred at WFPS near 50 %; (2) optimal N₂O production via denitrification occurred at WFPS ≤80 %; and (3) anoxic conditions were only found to occur above field capacity. Carbon dioxide exhibited a wide range of concentrations even above field capacity and showed no optimal response to WFPS (Skopp et al., 1990). This suggests CO₂

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concentrations were regulated by environmental factors other than soil moisture (e.g., temperature, root activity, substrate availability) and/or reflects that CO₂ is produced by both aerobic and anaerobic respiration processes.

Continuous soil O₂ measurements would have greatly aided in capturing short term O₂ dynamics following rainfall or snow melt events (see for example, Liptzin et al., 2011). Although our sampling regime captured such events, any significant short-term O₂ depletion (order of hours) would have been missed by our methodology. Advances in soil O₂ probes allow for more discrete and smaller soil atmospheres to be sampled, crucial to understanding soil O₂ dynamics. Continuous monitoring can create a soil O₂ almanac for determining the frequency and durations of specific O₂ thresholds (e.g., hours/days of the year soil O₂ < 10%) with respect to a variety of redox driven soil biogeochemical processes.

4.2 Soil temperature and substrate quality/quantity

Seasonal patterns of CO₂, O₂, and N₂O reflect changes in climate and associated biological activity. Soil O₂ concentrations were tightly coupled to soil respiration as influenced by soil moisture and temperature. Soil temperature, however, appeared to have the largest influence on soil O₂ concentrations via the respiratory demand of aerobic soil respiration in unsaturated soils evident by (1) the strong CO₂ response to temperature; (2) the slope of the CO₂–O₂ regression being very close to unity; and (3) the lack of any apparent relationship between CO₂ and WFPS.

Production of both CO₂ and N₂O peaked during the summer months; moreover, significant production of N₂O occurred only under high soil respiration activity in the upper mineral soil (Fig. 3). The WFPS thresholds on N₂O production were only apparent during summer months suggesting both a link to soil climate and substrate limitations. Microbial biomass and N cycling activities are greater during the summer than any other season at the HBEF due to higher temperatures and large quantities of labile substrate available for microbial respiration (Bohlen et al., 2001). Although new inputs of labile C become available following senescence, N immobilization may limit inorganic

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N availability to either nitrifiers and denitrifiers thus restricting N₂O production despite high soil water content (Dittman et al. 2007). The accumulation of organic matter in UICP and at depth in BIMS soils are important C stores; high concentrations CO₂ and N₂O were observed at depth and suggest that biological activity at depth is significant.

Root and microbial processes are active in cold (0–5 °C) soils; however, our results indicate very little gas production both during the winter and spring snow melt at any depth in the soil profile. Most reports of large trace gas fluxes in northern hardwood forests occur after severe soil frost, whether natural or experimentally induced. Snow pack manipulation studies both at the HBEF and elsewhere show increased N₂O fluxes predominantly due to increases in labile C and inorganic N as a result of several mechanisms: (1) mineralization of deceased roots; (2) decreased N retention due to root mortality and/or injury; (3) physical disruption of soil aggregates and release-mineralization of particulate organic matter; and (4) accumulation of N₂O below ice layers (Goldberg et al., 2010; Groffman et al., 2006) .

Climate change will most likely affect soil temperature, moisture and substrate availability at the HBEF in some way. Uncertainty exists even with knowledge of how such variables ultimately control the production of N₂O and other greenhouse gases. N cycling processes at the HBEF appear to be more sensitive to variation in soil moisture, whereas C cycling processes appeared to be more strongly influenced by temperature (Groffman et al., 2009). Although, the concept of “colder soils in a warmer planet” does increase N₂O fluxes, soil water dynamics during snow melt do not seem to be dramatically altered (Hardy et al., 2001). Still, reduced infiltration may lead to decreased soil moisture thus reducing nitrification and/or denitrification rates. Reduced soil moisture is also expected in a warmer climate in northern hardwood forests due to increases in primary production albeit accompanied by an increase in nitrate leaching due to large increases in net mineralization and nitrification (Campbell et al., 2009). However, most N₂O production appeared to occur after rainfall events or when routinely saturated soils dried out under extended dry conditions. Climate change may also alter the frequency and intensity of rainfall events (IPCC, 2007). Our results demonstrate the importance

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of soil moisture dynamics in governing when and where soil redox hotspots and hot moments emerge across the landscape.

4.3 Significance of greenhouse gas concentrations at Hubbard Brook

The majority of trace gas studies at the HBEF have focused solely on flux measurements between soil surface and the atmosphere. Our results revealed that soil O₂ and GHG concentrations in deeper soil horizons were just as dynamic as in surface organic horizons, especially at the water table interface. The water table interface is a very dynamic zone in terms of soil redox and trace gas cycling (Berglund and Berglund, 2011; Jungkurst et al., 2008). Deeper soil horizons at the HBEF were important zones of GHG production especially in soil profiles (i.e., UICP) experiencing highly fluctuating water tables.

Large spatial and temporal variability existed in soil GHG concentrations across W3 even within the same soil type. Even so, HBEF soils are not large sources of N₂O or CH₄ to the atmosphere at regional or global scales (Keller et al., 1983). Large fluxes of N₂O only seem to occur under significant disturbance such as after a forest clear-cut (Bowden and Bormann, 1986) or severe soil freezing (Groffman et al., 2006; Groffman et al., 2010). Rather, understanding the landscape patterns of soil O₂ and GHG concentrations have value towards better understanding hot spot and hot moment dynamics of soil biogeochemical processes. For example, patterns of soil N₂O concentrations helped reveal that the UICP soils and seeps are dynamic zones of N cycling.

Small areas of the landscape can play a significant role in the overall biogeochemistry of the forest ecosystem. At HBEF, the majority of soils are small sinks for atmospheric CH₄; however, small zones of poorly drained organic rich soils (e.g., Histisols) comprising only a slight portion of the landscape (e.g., 5%), are potentially large sources of atmospheric CH₄. When CH₄ fluxes were weighted by the areal extent of these soil types in a northern hardwood forest in New Hampshire, the ecosystem became a net source of atmospheric CH₄, rather than a CH₄ sink (Yavitt and Fahey,

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1993). In this study, seepage zones demonstrated very dynamic N_2O and CH_4 concentrations and are possibly important hotspots for denitrification. The seepage zone we studied was just of one several small seepage zones throughout W3. The biogeochemical significance, hydrology, and the spatial extent of these seepage zones at Hubbard Brook are largely unknown.

4.4 Hydrology and pedology: Implications at the landscape scale

Surface topography plays a large role in the development and setting of different soil types in W3. However, our results suggest that subsurface hydrology influenced soil oxygen and trace gas concentrations at the HBEF more than surface topography. Diagnosing biogeochemical characteristics of any particular soil type based solely on superficial features proved problematic at the HBEF. For example, station T1A was classified as an UICP soil in a riparian zone but did not exhibit similar hydrology (high moisture content, elevated water table) or the biogeochemistry of other UICP soil profiles. Rather, station T1A was relatively dry due the lack of a Cd horizon to restrict vertical water movement and therefore exhibited much higher soil O_2 concentrations and lower GHG concentrations despite its close proximity to the stream.

Overall our results are consistent with ideas about the organization of hillslope landscapes and pedological units into functionally distinct biogeochemical zones resulting in hotspots and hot moments (Davidson and Swank, 1986; Nishina et al., 2009; Pacific et al., 2008; Webster et al., 2008). Anaerobic processes such as denitrification and methanogenesis were limited by soil moisture which in turn was regulated by precipitation, slope position, but most importantly subsurface hydrology. Aerobic processes, such as nitrification and aerobic metabolism, were regulated by thresholds in WFPS and soil O_2 availability. Therefore, hotspots were not permanent locations, but rather such thresholds were dynamic across the hillslope, shifting the location of hotspots of CO_2 and N_2O up or down the slope depending on soil moisture conditions. During wet conditions, hotspots were present in BIMS mineral horizons identified as a critical transition between well drained TYPS and poorly drained UICP. However, during dry

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conditions, the hotspots shifted downslope into UICP soil types.

Micro-topography can also significantly alter the normal hydrologic and biogeochemical processes along a hillslope (van Verseveld et al., 2009). Pit and mound topography (areas of focused groundwater recharge) are common throughout the HBEF. Such micro-topographic features may escape our current methods of landscape feature classification. Moreover, inclusion of a bottom layer (i.e., underlying geology) would greatly enhance the current surface level approach to understanding landscape biogeochemistry by accounting for subsurface hydrology. The ability to model ecosystem processes (e.g., catchment scale denitrification) requires a mechanistic understanding of biogeochemical cycles at the landscape scale including even the smallest of areas of biogeochemical significance.

5 Conclusions

Redox is fundamental to soil biogeochemistry yet remains cryptic, largely attributed to difficulty in its practical measurement in the field. Soil gas measurements are robust, easily collected, and relatively inexpensive to analyze. Concomitant measurements of multiple gases can reflect important changes in soil redox, providing valuable insight on the relative activity of specific biogeochemical processes from a metabolic perspective. Our results demonstrate that surface flux measurements may at times fail to capture the important soil redox processes reflected in the production/consumption of GHGs of deeper soil horizons. Despite the inherent complexity of forest ecosystem terrain, most of the variability in trace gas production and consumption could be explained in terms of soil temperature, moisture, and substrate availability materializing hotspot and hot moments of biogeochemical activity. Soil redox appeared dynamic and mobile across the HBEF landscape driven by climate and topography, constrained by subsurface hydrologic processes.

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Table 1. Summary of soil horizon characteristics of soil types and associated sampling stations: Typical Spodosols (TYPS); Bimodal Spodosols (BIMS), Umbric Inceptisols (UICP), and seep (SEEP).

Soil Type (Stations)	Horizon	pH (CaCl ₂)	N %	C %	C:N
TYPS (T1 C, T2 C, T3 C)	Oa	3.25	1.63	30.70	19.1
	Bhs	3.87	0.26	3.93	17.4
	B	3.45	0.22	5.54	24.7
BIMS (T2 B, T3 B)	Oa	3.02	1.32	27.17	20.5
	Bhs	3.70	0.19	3.68	19.2
	Bs	4.05	0.32	4.19	13.3
	BC	4.22	0.24	1.13	4.64
	Bh	3.66	0.34	5.79	16.9
UICP (T1 A, T2 A*, T2 B, T3 A)	Oa	3.48	2.28	40.49	17.8
	A	3.67	0.80	12.00	15.1
	Bh	3.91	0.23	4.81	22.0
SEEP	Oa	–	0.75	10.86	14.5
	Bs	–	0.21	3.79	17.9

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Soil Gas	Orthogonally rotated factors			
	Factor Pattern		Standardized Scoring Coefficients	
	Factor 1	Factor 2	“Aerobic/Anaerobic Respiration”	“Nitrous Oxide Production/Consumption”
O ₂	(−0.92)	−0.01	(−0.526)	0.046
CO ₂	0.12	0.29	−0.132	−0.324
N ₂ O	0.01	(0.96)	−0.006	(1.140)
CH ₄	(0.94)	0.02	(0.576)	0.048

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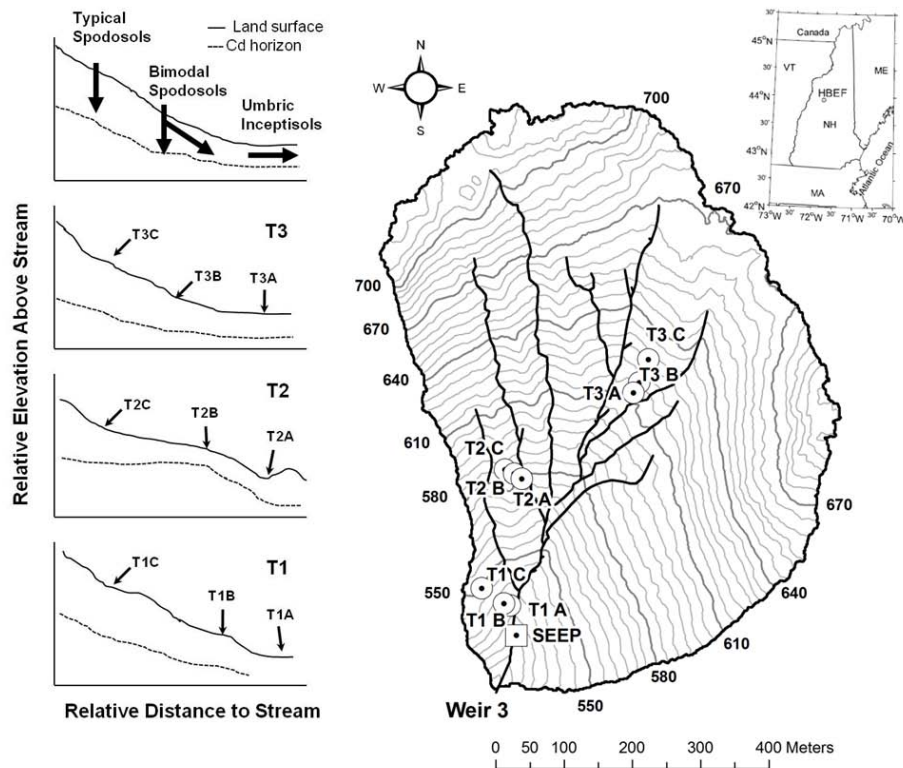


Fig. 1. Site map of watershed 3 (W3) and general location of the Hubbard Brook Experimental Forest (HBEF), New Hampshire (NH), USA. Contour interval is 5 m. Circles denote locations of soil gas sampling stations; square denotes location of the seep gas sampling station.

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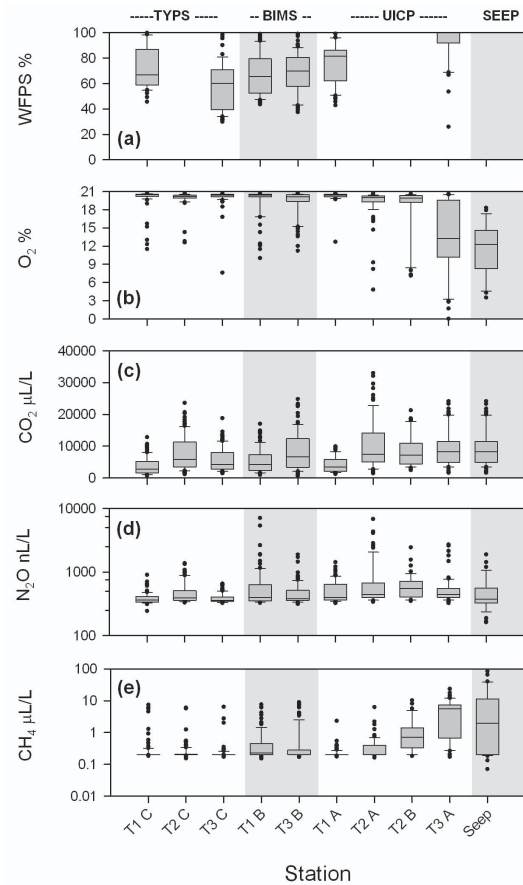


Fig. 2. Summary of (a) water filled pore space (WFPS) and soil concentrations of (b) oxygen, (c) carbon dioxide, (d) nitrous oxide, and (e) methane; across all sampling dates and profile depths for individual stations grouped by soil type: typical Spodosols (TYPs), bimodal Spodosols (BIMS), umbric Inceptisols (UICP), and seep.

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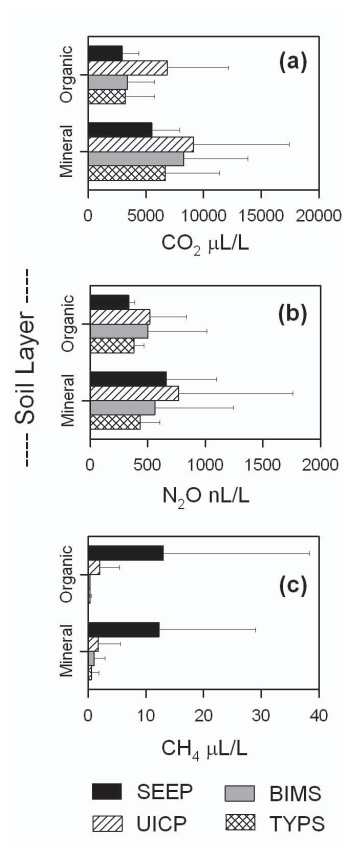


Fig. 3. Soil profile concentrations of (a) carbon dioxide, (b) nitrous oxide, and (c) methane pooled by soil layer across all sampling dates for typical Spodosols (TYPS), bimodal Spodosols (BIMS), umbric Inceptisols (UICP), and seep. Organic layer defined by >10% carbon content by mass; mineral <10% carbon. Values are means ± standard deviation.

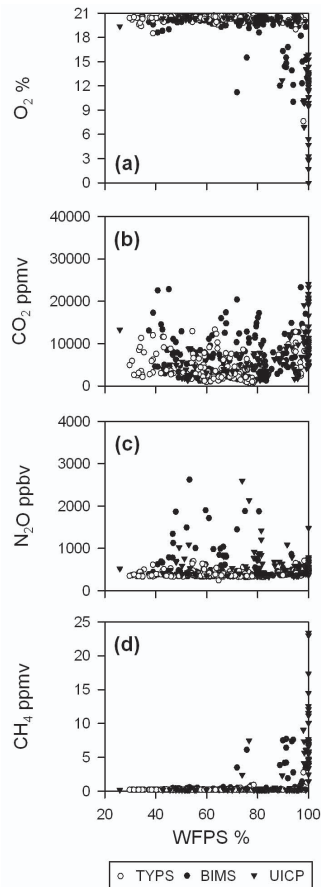


Fig. 4. Relationships of soil concentrations of (a) oxygen, (b) carbon dioxide, (c) nitrous oxide, and (d) methane with water filled pore space across all sampling dates and profile depths for typical Spodosols (TYPS), bimodal Spodosols (BIMS), umbric Inceptisols (UICP).

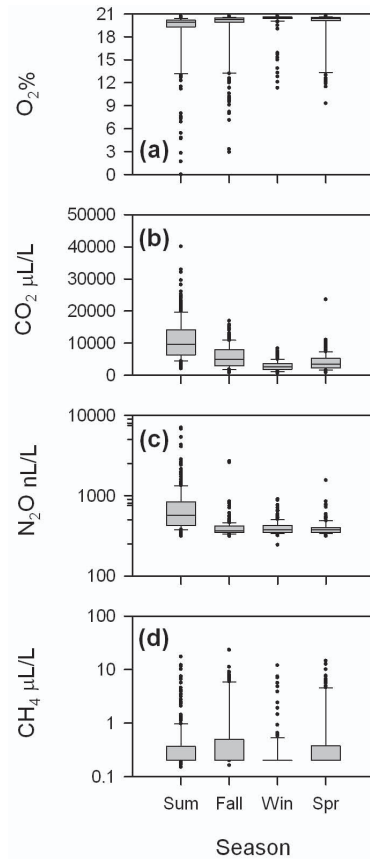


Fig. 5. Seasonal patterns in soil (a) oxygen, (b) carbon dioxide, (c) nitrous oxide, and (d) methane concentrations across all dates, depths, and soil types.

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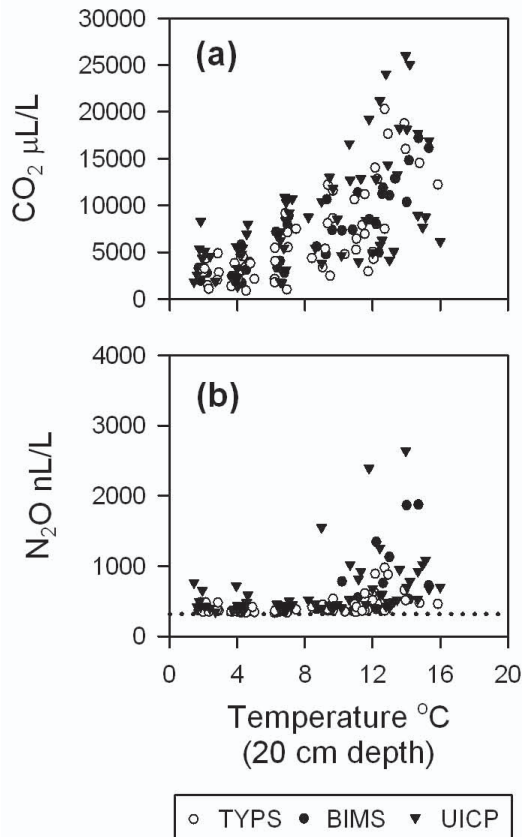


Fig. 6. Correlation between soil temperature and (a) carbon dioxide (b) nitrous oxide concentration by soil type: typical Spodosols ($n = 53$, TYPS), bimodal Spodosols ($n = 36$, BIMS), and umbric Inceptisols ($n = 72$, UICP) at 20 cm depth. Dashed line references the ambient N₂O concentration 315 nL L⁻¹.

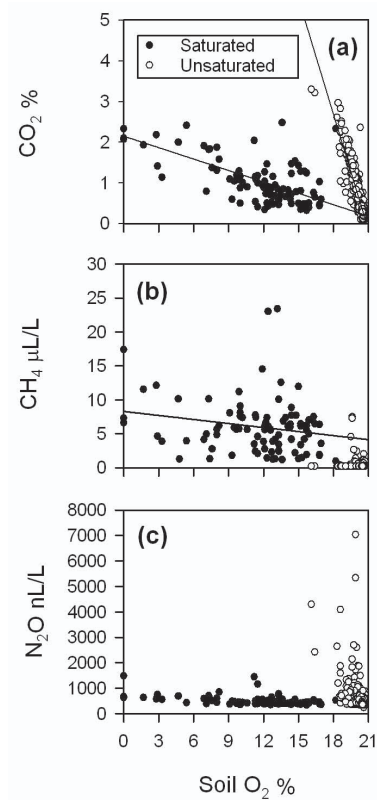


Fig. 7. Correlation between soil oxygen and (a) carbon dioxide (b) nitrous oxide (c) methane for unsaturated soils ($n = 598$, open circles) and saturated soils ($n = 94$, closed circles) across all soil types (excluding seep), depths, and sampling dates.

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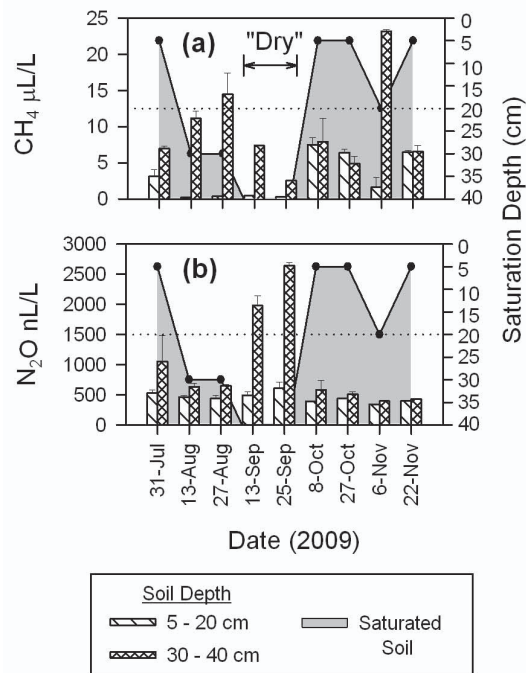


Fig. 8. Bimonthly concentrations of soil (a) methane (b) nitrous oxide over the period of 31 July 2009–22 November 2009 at station T3 A, an umbric Inceptisol. Values are means + standard deviation ($n = 3$ for 5–20 cm; $n = 2$ for 30–40 cm). The dotted line at 20 cm references the transition from organic to mineral soil layers. Gray region indicates saturated soil conditions due the presence of a water table; no water table (i.e., unsaturated conditions) was observed during the “Dry” period from 13 September 2009–25 September 2009.

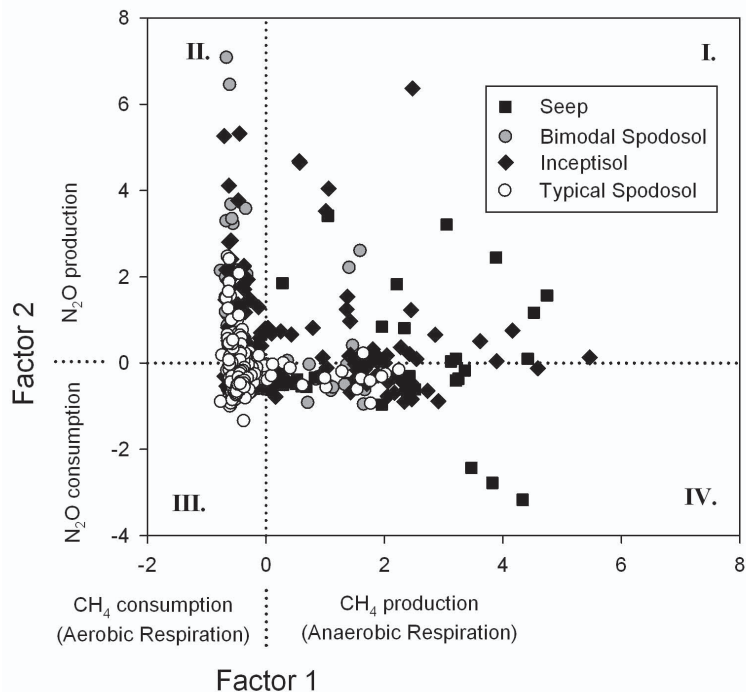


Fig. 9. Factor analysis ($n = 727$) and conceptual model of nitrous oxide (N_2O) production/consumption relative to aerobic and anaerobic respiration processes across different soil types. Quadrant I: N_2O production under marginally anoxic and/or anoxic conditions. Quadrant II: N_2O production under oxic conditions. Quadrant III: no N_2O production and/or N_2O consumption under oxic conditions. Quadrant IV: N_2O consumption under marginally anoxic and/or anoxic conditions.

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