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LETTER

Regulation of CO2 and N2O fluxes by coupled carbon and nitrogen availability

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Abstract

Carbon (C) and nitrogen (N) interactions contribute to uncertainty in current biogeochemical models that aim to estimate greenhouse gas (GHG, including CO2 and N2O) emissions from soil to atmosphere. In this study, we quantified CO2 and N2O flux patterns and their relationship along with increasing C additions only, N additions only, a C gradient combined with excess N, and an N gradient with excess C via laboratory incubations. Conventional trends, where labile C or N addition results in higher CO2 or N2O fluxes, were observed. However, at low levels of C availability, saturating N amendments reduced soil CO2 flux while with high C availability N amendments enhanced it. At saturating C conditions increasing N amendments first reduced and then increased CO2 fluxes. Similarly, N2O fluxes were initially reduced by adding labile C under N limited conditions, but additional C enhanced N2O fluxes by more than two orders of magnitude in the saturating N environment. Changes in C or N use efficiency could explain the altered gas flux patterns and imply a critical level in the interactions between N and C availability that regulate soil trace gas emissions and biogeochemical cycling. Compared to either N or C amendment alone, the interaction of N and C caused ~60 and ~5 times the total GHG emission, respectively. Our findings suggested that the response of CO2 and N2O fluxes along stoichiometric gradients in C and N availability should be accounted for interpreting or modeling the biogeochemistry of GHG emissions.

1. Introduction

Carbon dioxide (CO2) and nitrous oxide (N2O) are major greenhouse gases (GHGs) that produce a strong positive radiative forcing in the atmosphere. Extensive work has been directed to understanding single substrate dependences of CO2 on organic carbon (C) and N2O to nitrogen (N), both experimentally and through modeling of microbial CO2 and of N2O emissions (Davidson et al 2012, Manzoni et al 2012, Liu et al 2012, Jassal et al 2005, Signor et al 2013, Burzaco et al 2013). However, the plasticity of C and N metabolism in microorganisms (Ter Schure 2000, Horák 1997) produces large uncertainties in coupling of either CO2 or N2O trace gas emissions to single substrate availability.

Recent evidence suggests N availability can influence CO2 production and in turn C availability may influence N2O emissions (Piao et al 2013, Jain et al 2013, Liu and Greaver 2009). Studies have generally not evaluated emissions of both trace gases simultaneously, although potential interactions between substrate availabilities may lead to important connections between the two fluxes through a coupling of the C and N biogeochemical cycles (Sokolov et al 2008, Thornton et al 2009, Bonan and Levis 2010, Zaehe and Dalmonech 2011, Lal 2008). The interactive influence of C and N substrate dependences on the biogeochemical processes mediating soil CO2 and N2O fluxes remains a key uncertainty in understanding the regulation and magnitude of GHG emissions from soils.

As directly measured byproducts of microbial C or N metabolism, CO2 and N2O fluxes provide a window to inspect the energy (C) and nutrient (e.g. N) allocation of soil microorganisms through direct relationships with C and N use efficiency (CUE and NUE). In ecological stoichiometry, CUE or NUE is commonly applied to quantify the balance of C or N between...
biomass growth and consumption (Mooshammer et al. 2014, Manzoni et al. 2012, Roland and Cole 1999). In general, a high CUE or NUE means an increasing microbial biomass but slowed C or N mineralization rate, resulting in low soil CO₂ or N₂O fluxes. In contrast, a low CUE or NUE indicates an inefficient conversion of C or N to biomass, a large return of C or N to the environment, and increased soil CO₂ or N₂O fluxes. A limiting C substrate produces a relatively high CUE while a limiting N source can reduce the CUE, a consequence of coupling or uncoupling of microbial catabolism and anabolism (Sinsabaugh et al. 2013). Microbial NUE is likely controlled and regulated similarly to CUE but directly coupled to the N cycle and associated emissions of N trace gases (Mooshammer et al. 2014). Thus, variation in CO₂ or N₂O flux patterns can be used as an assessment of CUE or NUE under different C or N levels (Eberwein et al. revised). Because of the intrinsic linkage between microbial C and N metabolism (Richardson 2000, Robertson and Groffman 2007), how the overlap between microbial CUE and NUE simultaneously mediates CO₂ and N₂O fluxes needs evaluation.

In this study, we conducted a series of soil incubations to identify the potential interactions between soil CO₂ and N₂O emissions in response to variation in labile C and N amendments. We asked: 1) are soil CO₂ and N₂O soil emissions dependent on the availability of both C and N, and 2) are emissions of the two trace gases correlated in their flux rates? Answering these questions will test alternate hypotheses of trace gas emission regulation, 1) a single-substrate hypothesis currently used in most trace gas emissions models that predicts regulation by a single resource and 2) a dynamic efficiency hypothesis for C and N that predicts interactions between resources will regulate both CO₂ and N₂O fluxes. The results from this study will improve understanding of how both C and N biogeochemical cycles are influenced by multiple limiting resources and demonstrate the potential coupling between these biogeochemical cycles with direct consequences for total GHG emissions.

2. Materials and methods

2.1. Soil characterization
The soil used for our study was collected from an agricultural field (13 ha) located at the University of California Desert Research and Extension Center, El Centro, California (32°N 48’ 42.6”, 115°W 26’ 37.5”). The site is a high temperature, low elevation, desert environment with mean annual precipitation of 5.8 mm and monthly mean air temperatures between 13.9 and 33.9 °C, and extremely high midday temperatures up to 50 °C (www.weather.com). The site has deep alluvial soils (42% clay, 41% silt, 16% sand) with 2.34% C and 0.13% N, and a pH of 8.3 (Oikawa et al. 2014). Prior to soil collection, the field was fallow for 8 months then planted with forage sorghum for two years. Soils were collected between 0–10 cm depths from 5 random locations in the field.

2.2. Laboratory incubations
Prior to incubations, the soil was air dried in the lab, sieved (2 mm mesh), and then homogenized. Soil water holding capacity (WHC) was determined by the gravimetric method (Pansu and Gautheyrou 2006). Three replicate samples (100 g dry weight) were placed in glass jars (~473 ml) and maintained a 40% WHC by weighing the jar every two days and adding de-ionized water as necessary during the incubation period.

To investigate soil CO₂ and N₂O flux responses to C and N amendments and their interaction, two series of laboratory incubations were conducted that included a control (de-ionized water only), dextrose (as a labile carbon source) only, N (ammonium nitrate, NH₄NO₃) only, and both dextrose and N. The first series of incubations (Experiment 1, Exp1) were conducted to quantify soil CO₂ and N₂O fluxes under six levels of N amendment with two levels of C amendment (with and without C). Six levels of N amendment as 0, 10, 50, 200, 700, or 1500 μg N g⁻¹ soil were selected. Along the N gradient, a control and saturating C level (60 g L⁻¹ dextrose, which is equivalent to 18 mg g⁻¹ soil) were selected to investigate C and N interactions. Each treatment included three replicates with 36 samples in total. For the second series of incubations (Experiment 2, Exp2), another 36 samples were used to investigate CO₂ and N₂O fluxes under different C level with saturating N supplement. A C amendment of 0, 1.5, 3, 7, 18, or 30 mg dextrose g⁻¹ soil was set and combined with either no N or a saturating N level (700 μg N g⁻¹ soil). All 72 jars were incubated at 25 °C in the lab for 7 days and CO₂ and N₂O fluxes were measured daily.

2.3. Flux measurements
We used a flux measurement system that allowed simultaneous measurements of both CO₂ and N₂O trace gases within a total sampling period of less than five minutes. Soil N₂O emissions have typically relied on syringe extraction over a thirty minute to one hour sampling period at minimum and subsequent analysis on a gas chromatograph (Alves et al. 2012, Dobbie and Smith 2003). Our system provides the capability to measure the instantaneous fluxes of N₂O and CO₂ and allows investigation of the potential relationships between CO₂ and N₂O fluxes.

We built a dynamic closed system (figure 1) to measure CO₂ and N₂O fluxes simultaneously with a Li-7000 infrared gas analyzer for CO₂ (Licor Biosciences, Lincoln, Nebraska, USA) connected to a N₂O gas analyzer (913-EP, Los Gatos Research, Mountain View, California, USA). The N₂O analyzer uses off-axis integrated cavity output spectroscopy (Off-Axis ICOS) to provide a real-time accurate N₂O concentration measurement with a precision of 0.05 ppb at 1 hz sampling frequency. The CO₂ and N₂O fluxes were...
determined by the linear regression fit between the CO2 or N2O concentration change and the measured time. For CO2 flux calculation, the original model from Licor (Licor 8100 Manual) was adapted for our jar measurements as follows:

\[
F_c = \frac{V R T (1 - \frac{w_0}{1000})}{M (T_0 + 273.15)} \frac{\partial [CO_2]}{\partial t},
\]

where \(F_c\) is CO2 flux (μmol CO2 g\(^{-1}\) soil s\(^{-1}\)) from the soil in the jar, \(V\) (cm\(^3\)) is the volume difference between the jar plus the tubing and the soil (calculated using a bulk density value 1.15 g cm\(^{-3}\) of our soil). \(P_0\) is the initial pressure (kPa), \(w_0\) is initial water vapor in mole fraction (mmol mol\(^{-1}\)). \(R\) is the ideal gas constant (8.314 × 10\(^{-3}\) kPa cm\(^3\) K\(^{-1}\) mol\(^{-1}\)). \(M\) is the mass of soil (g) and \(T_0\) is the initial air temperature (°C). The factor \(\frac{\partial [CO_2]}{\partial t}\) is the changing rate of CO2 concentration along time (μmol mol\(^{-1}\) s\(^{-1}\)). The N2O flux was calculated using the same method but the dry N2O concentration reported from N2O analyzer during the measured intervals was used and thus the water correction term in equation (1) was not needed. Both trace gas measurements were completed within 3–10 mins depending on flux rate. Seven day cumulative CO2 and N2O fluxes were calculated by interpolating the measurements from each day and then integrating.

### 2.4. Statistics

We performed two-way fixed-model ANOVA to test the response of the seven day cumulative CO2 and N2O fluxes to carbon and nitrogen addition. Prior to conducting ANOVA, the normality of the data and the homogeneity of variances were tested using the Shapiro–Wilk test (Royston 1982, Shapiro and Wilk 1965) and the Levene’s test (Brown and Forsythe 1974, Levene 1960), respectively. The Tukey’s honestly significant difference (HSD) test (Tukey 1949) was used to examine intra-group differences. When necessary, Box–Cox transformations (Box and Cox 1964) were applied to meet the assumptions of ANOVA. For N2O fluxes, we added a constant positive value to meet the logarithmic transformation because of some negative values observed during the incubation in association with low rates of net uptake (Majumdar 2013). All statistical analyses and data processing were performed using MATLAB R2011b (The MathWorks Inc., Natick, MA, USA) and the R package (R Core Team 2013).

### 3. Results

#### 3.1. CO2 flux

Cumulative CO2 flux was significantly affected by C (\(p < 0.0001\) in Exp1 and Exp2) and N (\(p < 0.0001\) in Exp1 and Exp2).
in Exp1 and \( p = 0.0006 \) in Exp2) amendments and their interaction effects \((p < 0.0001 \text{ in Exp1 and } p < 0.0001)\) based on a two-way ANOVA. C effects on CO2 flux were positive, indicating a higher dextrose concentration produced higher CO2 flux (figure 2(a)). However, the N effects on CO2 flux were diverse. Under saturating N conditions, the CO2 flux was reduced 39% and 36% at low dextrose levels (1.5 and 3 mg g\(^{-1}\) soil, respectively) compared to treatments without any N amendment (figures 2(a)–(b) without N). But high dextrose levels (18 and 30 mg g\(^{-1}\) soil) resulted in significantly higher CO2 fluxes with N addition compared to without N (figures 2(a)–(b) with N). Although no significant decrease in CO2 flux was found at lower dextrose levels (1.5 and 3 mg g\(^{-1}\) soil) with N addition, there was a significant decrease in CO2 flux at lower N addition when dextrose was saturating (figures 2(c)–(d) with dextrose). CO2 flux increased at a high but sub-toxic N level (700 \( \mu g \) g\(^{-1}\) soil) and decreased at an inhibitory N level (1500 \( \mu g \) g\(^{-1}\) soil). However, there were no significant effects of N addition on CO2 flux when dextrose was not added (figure 2(c) no dextrose).

3.2. N2O flux
Cumulative N2O fluxes were significantly affected by amendments of C \((p < 0.0001)\) and N \((p < 0.0001)\) and their interaction \((p < 0.0001)\) in both experiments. N amendments had consistent positive effects on N2O fluxes (figures 3(a), (b). However, additions of C led to contrasting N2O flux responses. When N additions were low (control, 10 and 50 \( \mu g N g^{-1} \) soil), the additional C source significantly reduced N2O fluxes (figure 3(a) no nitrogen and figure 3(b) with dextrose) but increased fluxes under a higher N level (200 and 700 \( \mu g N g^{-1} \) soil) (figure 3(a) with nitrogen and figure 3(b) with dextrose) until N additions became inhibitory (1500 \( \mu g N g^{-1} \) soil). Thus, N2O fluxes were reduced by adding extra dextrose under a limited N condition but were dramatically increased when both N and C resources were sufficient.

3.3. Relationships between CO2 and N2O fluxes
Comparing CO2 and N2O fluxes under different conditions, there was a clear opposite relationship between cumulative CO2 and N2O fluxes demonstrated in this study (figure 4). When N was not added,
additional C increased CO2 fluxes (figure 2(a) no nitrogen) but reduced N2O fluxes (figure 3(a) no nitrogen), resulting in a negative relationship between them. In contrast, when N availability was saturating, CO2 and N2O fluxes increased with additional C amendments from low to high (figures 2(a) and 2(a) with nitrogen), resulting in a positive relationship. In an unlimited C environment, a negative N effect on CO2 flux and a positive N effect on N2O flux resulted in a positive relationship between CO2 and N2O fluxes. When N crossed a critical level (between 50–200 μg N g⁻¹ soil in our study), the negative N effect on CO2 flux switched and resulted in a positive relationship between CO2 and N2O fluxes.

4. Discussion
Through a series of laboratory experiments we found important connections between C and N biogeochemical cycles with both resources important for CO2 and N2O emissions. Additional C or N substrates caused an increasing soil CO2 or N2O flux because of more C or N resources available for decomposition. The straightforward prediction of the relationship between trace gas fluxes and its primary substrate is true, although it masks substantial contributions from coupled C and N interactions on microbial activity. Our results show that N availability can substantially influence the effect of C availability on CO2 emissions,

Figure 3. Soil N2O flux response to dextrose and nitrogen gradient. The insets zoom into the relatively small N2O fluxes at low levels of the C and N gradient. The significance level is set to $p = 0.05$.

Figure 4. The relationship between CO2 and N2O fluxes in different treatments. The open circles (blue and purple) are the CO2 and N2O fluxes along N gradients (Exp1) and the closed dots (black and red) present the fluxes along the C gradients (Exp2). The N2O flux was logarithmically transferred after addition of a positive constant. The N gradient is marked as 0, 10, 50, 200, 700 and 1500 μg N g⁻¹ soil with C in excess (18 mg dextrose g⁻¹ soil).
and C availability can alter N\textsubscript{2}O flux sensitivity to N addition by more than two orders of magnitude. Notably depending on the stoichiometry of resource amendments, the effects of the secondary resource could both enhance or inhibit emissions of gases. CO\textsubscript{2} emissions were inhibited by N at non-saturating conditions and similarly N\textsubscript{2}O was inhibited by C at non-saturating conditions. However, saturating levels of both C and N accelerated trace gas emissions of both CO\textsubscript{2} and N\textsubscript{2}O. These divergent effects of altered resources with both enhancement and inhibition suggest complex interactions between C and N biogeochemical cycles, with substantial implications for predicting emissions of GHGs.

4.1. Regulating CO\textsubscript{2} flux by carbon use efficiency (CUE)

High CUE is commonly observed in response to C limitation (Sinsabaugh et al 2013), which results in a lower respiration rate. At saturating N and sub-saturated, an increasing CUE could mobilize more C into microbes, leading to relatively lower CO\textsubscript{2} fluxes compared to those without N application (figures 2(a) and (b)). Owing to more N availability, C becomes limiting and soil microorganisms with a relatively fixed organismal stoichiometry require relatively more carbon for growth, which results in a higher CUE and reduced CO\textsubscript{2} fluxes. This dynamic CUE could explain why N addition triggered a decreased CO\textsubscript{2} flux. After C availability increases to a critical level, more C substrate leads to a decreasing CUE and increasing CO\textsubscript{2} fluxes (figure 2(a)). During N limited conditions (figure 2(c)), even when C substrate is saturating, a decreasing CO\textsubscript{2} flux occurs in response to relatively low levels of N addition. Exposed to an excess C source and restricted in growth by N, the microorganisms may adjust their metabolism, i.e., uncoupling catabolism and anabolism via energy spilling pathways associated with decreased CUE (Sinsabaugh et al 2013, Gallmetzer and Burgstaller 2002, Vrabl et al 2009, Larsson et al 1995). However, N amendment will alleviate N limitation and increase CUE. When N is not limiting, the microbes coupled catabolism and anabolism again and the excess C source will introduce a higher CO\textsubscript{2} flux associated with lower CUE (figure 2(c) with dextrose).

Thus, our results support a hypothesis of dynamic CUE that can explain CO\textsubscript{2} flux response to C and N additions. However, the mechanism for soil microbial changes in metabolic pathway under different resource environments that allow adjustment of CUE is unclear and should be targeted for future research. Nevertheless, process models that incorporate a dynamic CUE to estimate CO\textsubscript{2} flux seem warranted.

4.2. Regulating N\textsubscript{2}O flux

From ecological stoichiometry, a higher NUE (related to a lower N\textsubscript{2}O flux) could be expected under N limitation (Mooshammer et al 2014, Sterner and Elser 2002), which implies the limited N would be conserved primarily for growth. The decreasing N\textsubscript{2}O flux associated with low rates of extra C source (figure 3(a) no nitrogen; figure 3(b) with dextrose in lower N levels) suggests that more N has been used to build soil microbial biomass as the extra C is also distributed into growth, which results in a higher NUE and lower N\textsubscript{2}O flux. Alternatively, exogenous C source provides additional electrons (i.e., NADH) via carbon degradation pathways and the TCA cycle to reduce the N\textsubscript{2}O to N\textsubscript{2} by denitrifying enzymes (Giles et al 2012, Richardson 2000). Regardless of how N\textsubscript{2}O is generated from the N cycle pathways (either nitrification or denitrification) (Butterbach-Bahl et al 2013), NADH promotes reduction of N\textsubscript{2}O into N\textsubscript{2} via the electron transport chain. Such a reduction in the N\textsubscript{2}O:N\textsubscript{2} ratio in response to labile carbon substrates has been shown (Morley and Baggs 2010, Giles et al 2012, Lee and Jose 2003, Weier et al 1993), although the magnitude varies because of the divergence in C substrate quality, soil conditions and O\textsubscript{2} availability (Morley and Baggs 2010, Giles et al 2012, Lee and Jose 2003).

N\textsubscript{2}O flux responses to additional C source under limiting N conditions may be regulated by NUE or the interaction between carbon and nitrogen metabolism through nitrification or denitrification pathways. As with CO\textsubscript{2} emissions, while the mechanism for variable NUE is unclear, these findings support the need for improvements in process models that account for resource stoichiometry and C and N interactions rather than N availability alone to estimate N\textsubscript{2}O emissions (Liu et al 2012, Jassal et al 2011).

4.3. Coupled CO\textsubscript{2} and N\textsubscript{2}O flux relationships

Availabilities of C and N substrates simultaneously regulate CO\textsubscript{2} and N\textsubscript{2}O fluxes. From our results, the relationship between soil CO\textsubscript{2} and N\textsubscript{2}O fluxes can be switched from negative to positive (figure 4) based on the N supplement. The critical level for this switch might be a result of the switch in elemental requirement from C to N for microorganism growth. A threshold elemental ratio (TER), which is a parameter in quantifying when growth limitation switches from one element to another (Frost et al 2006, Sterner and Hessen 1994), can control the metabolism of microorganisms (Mooshammer et al 2014). If the C:N ratio is above the TER, the metabolism of soil microbial communities is under N limitation and expresses a relatively higher NUE but lower CUE. The negative relationship between CO\textsubscript{2} and N\textsubscript{2}O fluxes occurs (figure 4 and figures 2(c) and 3(b) when N is low). In contrast, an expected lower NUE but higher CUE would occur when the C:N ratio is below the TER, which is a C limiting condition. The negative relationship still occurs between CO\textsubscript{2} and N\textsubscript{2}O when N is at the control level (figure 4 and figures 2(a) and 3(a) no nitrogen). When C and N availability are both...
available at high levels, elevated CO₂ and N₂O fluxes will be produced and a positive relationship between them is seen (figure 4). Based on the contrary relationship between CO₂ and N₂O fluxes, a critical level of C:N ratio could exist in regulating the response of soil microbial CUE and NUE to substrate availability and controlling the pattern of GHG emissions.

4.4. Implications for total GHG emissions
At global scale, about 80% of N₂O emission is derived from agricultural ecosystems because of synthetic fertilizers used in agricultural soil management (Majumdar 2013, Davidson 2012). In high production agricultural ecosystem, a large amount of carbon substrate can be introduced into the soil via root exudation or residues (Oikawa et al 2014). These substrates have a large influence on CO₂ emissions and as suggested here may also influence N₂O fluxes. Similarly, our results suggest patterns of fertilization may also have direct effects on CO₂ emissions. With N₂O having a much higher warming potential (298 times that of CO₂ over 100 years) (IPCC 2007) than CO₂, these interactions between C and N biogeochemical cycles may have important consequences for net emissions (figure 5). Without additional N, total GHG emissions increased linearly with C additions, while without additional C, total GHG emissions increased minimally with N additions. The largest increases occurred when both C and N were added and total GHG emissions were ~70, ~5 and ~60 times higher than the control samples, C or N amendments, respectively. Extending these findings to the field is a clear research need for understanding how soil emissions of both CO₂ and N₂O contribute to total warming potential in response to coupling between N and C cycles. The divergent effects from limited C or N on CO₂ and N₂O fluxes result in an opposite relationship between them, suggesting the possibility to minimize total GHG emissions by optimizing fertilizer level and timing relative to growth in agricultural management. Moreover, these results highlight the importance of C and N interactions for the ability to understand and predict GHG emissions using biogeochemical models.

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Figure 5. Total GHG equivalent (equivalent CO₂) emissions response to dextrose and nitrogen gradient. The equivalent CO₂ of N₂O emission was calculated using the global-warming potential (GWP) of N₂O as 298 over 100 years based on IPCC (2007).
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