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IMPACT OF SOIL DROUGHT ON SOIL N DYNAMICS IN A CALIFORNIA GRASSLAND

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1. INTRODUCTION

Due to climate change, extreme events like droughts and heavy rainstorms will become more severe and more frequent in the future (IPCC 2014). For example, California is currently experiencing the most severe dry spell in the last 1,200 years (Griffin and Anchukaitis 2014), and anthropogenic warming has increased the risk of future droughts in this region (Diffenbaugh et al. 2015). Semi-dry Mediterranean grasslands cover 1/3 of the terrestrial surface (Reynolds et al. 2007) and are major sources of CO_2 (Soussana et al. 2007), N_2O (Zhuang et al. 2012) and NO (Davidson and Kingerlee 1997). CO_2 is the major driver of global warming, and N_2O is another potent greenhouse gas (GHG) with a 100-year global warming potential of 265 (Myhre et al. 2013). NO is not a direct GHG, but it regulates the formation of atmospheric O_3 and acts as an air pollutant (Crutzen 1979). Because soil trace gas emissions are controlled by soil moisture (Davidson et al. 1998; Pilegaard et al. 2006; Butterbach-Bahl et al. 2013; Moyano et al. 2013), changes in future precipitation patterns will massively impact trace gas budgets in drought-affected ecosystems.

When soils dry out, water films on soil particle surfaces are disrupted, and diffusion of water-soluble substances is reduced (Manzoni et al. 2014). These substances, however, are substrates for soil microorganisms, who act as major drivers of soil trace gas emissions (Conrad 1996; Schimel and Gulledge 1998). As soil water content decreases, microorganisms become physically separated from their substrates, and microbial growth and metabolism slows down, which leads to a decrease in gas emissions (Stark and Firestone 1995). On the other hand, extracellular enzymes might still be actively decomposing organic matter to dissolved substrates, which accumulate when microorganisms loose access to them as soils dry out (Lawrence et al. 2009; Manzoni et al. 2014).

In addition to substrate limitation, reduced water availability poses osmotic stress on soil microbes. When encountering decreasing water potentials, the cytoplasmatic concentration of osmo-regulatory substances or 'osmolytes' like amino acids (e.g. glutamine, proline) has been shown to increase (Csonka 1989; Lippert and Galinski 1992; Kempf and Bremer 1998; Wood et al. 2001). When soil water potential increases

after rewetting, microorganisms have to rapidly dispose of these osmolytes to prevent uncontrolled influx of excess water into their cytoplasm. However, recent studies found no accumulation of osmolytes after rewetting of dry soil in a California grassland (Boot et al. 2013) or in a forest (Göransson et al. 2013). In a mesocosm study, however, Warren (2014) found elevated concentrations of various osmolytes (ectoine, hydroxyectoine, betaine, proline-betaine, trigonelline, proline, trehalose, arabitol) after 6 weeks of drought, and reported a rapid (3 h) consumption of these substances after rewetting. He suggests that as soon as they are free in the soil solutions, osmolytes are rapidly consumed by plants and microorganisms because these small molecules are rich in N and C and function as substrates.

Rewetting of dry soil reconnects microorganisms with their substrates by reconnecting disrupted water films, and it generates additional substrate from discarded microbial osmolytes and also from death of microorganisms that cannot cope with the sudden change in water potential (Blazewicz et al. 2014). It has been suggested that this increase in substrate availability post-wetting at least partially drives the often reported 'Birch effect' (Evans et al. 2016), which is a spike in soil respiration and N transformation that occurs when dry soils are rewet and that has been named after its discoverer (Birch 1958; Birch 1964). Numerous studies have investigated this phenomenon and found similar results: a massive peak in soil respiration in the first hours post-wetting followed by elevated respiration over the next days (Austin et al. 2004; Borken and Matzner 2009). Similarly, soil NO and N_2O efflux have also been reported to increase after rewetting, with flux rates that remained elevated for hours to days post-wetting (Cárdenas et al. 1993; Harms and Grimm 2012).

NO and N_2O are produced by numerous abiotic and biotic mechanisms (reviewed in Butterbach-Bahl et al. 2013; Medinets et al. 2015), most of which require the availability of N as either NH_4^+, NO_3^- or NO_2^-. Therefore, if emissions of NO and N_2O increase after rewetting of dry soil, it is likely that also the concentrations of these N pools are elevated immediately after rewetting. Soil disturbance during sampling, sieving, transport and storage has been accused to distort measurements of microbial processes (Lee et al. 2007; Cernohlavkova et al. 2009). In conventional soil slurry extraction methods, obtained results strongly depend on the chosen extractant. Most frequently, extraction is

performed either with deionized water, or with strong salt solutions (e.g., 0.5 *M* K_2SO_4, 1 *M* KCl) that yield much higher concentrations of NH_4^+,which strongly adheres to negatively charged clay minerals and can only by extracted in the presence of positively charged counter-ions like K^+. Furthermore, during the extraction soil is usually shaken for 30-120 min on a laboratory shaker. This procedure is very artificial and hardy reflects the *in situ* situation of a soil microorganism, which is almost stationary and only capable of very limited motions. Availability of mineral N primarily has recently been shown to primarily depend on its ability to diffuse through the soil solution (Oyewole et al. 2016). Soil microdialysis has recently been established as an effective tool to monitor soil N dynamics in high temporal and spatial resolution without disturbing the soil matrix (Inselsbacher et al. 2011). Similar to a stationary microorganism, the microdialysis probe depends on substrate diffusion. The present study is the first to combine high-resolution microdialysis measurements of soil N diffusion with flux measurements of CO_2, NO and N_2O to follow the changes in N mobilization and trace gas fluxes *in situ* before and after irrigation of dry soil. We hypothesized that rewetting of dry soil (i) increases the availability of mineral N; (ii) leads to a peak in NO and N_2O emissions that can be related to the increased availability of mineral N, and (iii) produces a short-term pulse of CO_2. To test these hypotheses, a field experiment was conducted in a Mediterranean California grassland in November 2015.

2. Materials and Methods

2.1 Study site

The study site was located 370 m asl in a seasonally dry oak savanna in the University of California Sedgwick Reserve (N 34.7120, W 120.0388) near Santa Barbara, California (Figure 1). Vegetation was dominated by Mediterranean annual grasses (*Bromus diandrus*, *Bromus hordaceous*, and *Avena fatua*). The soil was characterized as Pachic Haploxeroll with silty clay loam texture and granular structure on nearly flat slopes (< 2%). Soil pH was 6.0, with 2.2% C, 0.21% N, and a bulk density of 1.2 g cm^{-3} in the upper 10 cm. Mean annual precipitation was 380 mm, with 90 % of the precipitation falling between November and April, and mean annual temperature was 16.8 °C.

Figure 1: Seasonally-dry oak savanna in the UCSB Sedgwick Reserve near Santa Barbara, California, USA. Vegetation was dominated by Mediterranean annual grasses, which at this time point before onset of the rainy season were dead and dry. The soil was characterized as Pachic Haploxeroll with silty clay loam texture and granular structure and had a pH of 6.0.

2.2 Experimental setup

The field experiment was conducted in early November 2015 before beginning of the wet season. At this time point, the entire vegetation cover was dead and dry. To investigate the impact of rewetting on soil trace gas fluxes and N cycling, an experimental plot measuring 2 m x 1 m was used (Figure 2). In early November 2015, after approximately 6 months of drought, this plot was manually irrigated with 30 L (corresponding to 15 mm rainfall) of local well water (0.003 mg NH_4^+-N L^{-1}, 1.6 m NO_3^--N L^{-1}, 0.4 mg DON L^{-1}). Trace gas fluxes and soil nutrients were monitored over the course of 30 h post-wetting as described below.

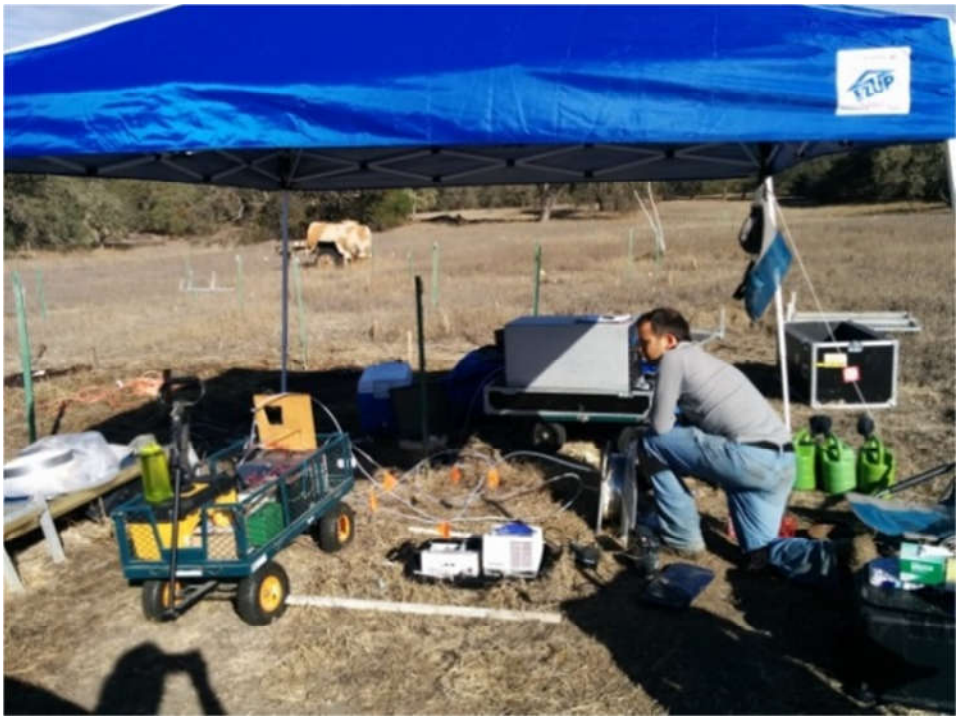

Figure 2: Experimental plot with instrumentation for soil gas flux and nutrient measurement. Left, cart with chemiluminescence NO analyzer and infrared CO_2 analyzer; back, Off-axis ICOS N2O laser; right, mobile gas flux chamber being vented in preparation for the next measurement; center, microdialysis set-up with pump and fraction collector and 4 microdialysis probes.

2.3 TRACE GAS MEASUREMENT

Fluxes of NO, N_2O and CO_2 were determined by chamber methodology (Parkin and Venterea 2010) 1h before and every 2-4 hours after irrigation (n = 4) over the course of 30 h (Figure 4). Briefly, a portable dynamic dark flux chamber with an inner diameter of 30.5 cm and a height of 10 cm (Figure 3) was connected to a chemiluminescence NO analyzer (Scintrex LMA-3, Canada), an infrared CO_2 analyzer (WMA-4, PP Systems, MA, USA) and an Off-axis ICOS N_2O laser (Los Gatos Research, CA, USA). Since the vegetation was dead at this time at the end of the dry season, no plant CO_2 uptake occurred inside the chamber. Fluxes were calculated based on the rate of change in gas concentration inside the chamber as described in Equation 1:

$$\text{Flux} = \frac{dC}{dt} \quad \frac{VN}{ART} \qquad \text{Equation 1}$$

where *dC/dt* is the concentration increase (ppb for NO and N_2O, ppm for CO_2) calculated by linear regression, *V* is the chamber volume (12.6 L), *N* is the atomic weight of N (14.01 g) or C (12.00 g), *A* is the chamber area (730 cm^2), *R* is the universal gas constant (0.0821 L atm $mole^{-1}$ K^{-1}), and *T* is air temperature (K). Units are ng NO-N m^{-2} s^{-1}, ng N_2O-N m^{-2} s^{-1} and µg CO_2-C m^{-2} s^{-1}, respectively.

Figure 3: Mobile flux chamber for trace gas measurement. The plastic 'skirt' is weighed down with a heavy chain to prevent lateral in-blow of wind.

Figure 4: Nightly microdialysis and trace gas measurements.

2.4 MICRODIALYSIS AND SOIL EXTRACTS

The microdialysis system was installed in the center of the experimental plot (Figure 5). Microdialysis probe calibration and soil sampling was performed as described previously (Inselsbacher et al. 2011). Briefly, 4 polyarylethersulphone probes (CMA 20, CMA Microdialysis AB, Kist, Sweden; 100 mm long, 500 µm outer diameter and 400 µm inner diameter, 20 kDa molecular weight cut-off) were installed in a depth of 5 cm in each treatment plot (Figure 6). As perfusate high-purity deionized water (MilliQ) was pumped through the system at a flow rate of 5 µl min^{-1} by a syringe infusion pump (CMA 400), and hourly samples were collected in a refrigerated microfraction collector that was set at 6°C (CMA 470) in 300 µl glass vials. Diffusive N fluxes from the soil solution over the microdialysis membrane surface were calculated as described by Inselsbacher and Näsholm (2012), and expressed as nmol N cm^{-1} h^{-1}.

Figure 5: Set-up of the microdialysis system. On top the CMA 400 pump, on the bottom the CMA 470 refrigerated fraction collector. Orange flags mark positions of the membranes.

Figure 6: Microdialysis membrane inserted into the soil and connected to an inflow tube (blue, contains MilliQ water) and an outflow tube (white, contains dialysate with soil nutrients).

In addition to microdialysis sampling, soil was sampled with steel cylinders (4 cm diameter, 5 cm length) from the treatment plot before the manual irrigation, sieved for 2 mm in the field and transported to the lab on ice. In the lab, 2 sets of soil extracts were prepared within 4 days with either 0.5 M K_2SO_4 or MilliQ water, respectively (n = 3). Extracts were shaken for 1h, filtered with 0.45 µm cellulose acetate filters (Millipore, MA, USA; also see Figure 7) and stored at 4°C for nitrite analysis (Stevens and Laughlin 1995), and at -20°C for ammonium and nitrate analysis, respectively.

Nitrite, nitrate and ammonium in microdialysis samples and soil extracts were analyzed colorimetrically within 5 days on a plate reader (Tecan Infinite 200 PRO, Tecan, Switzerland) as described by Hood-Nowotny et al. (2010).

Figure 7: Water extracts before (right) and after (left) filtration with 0.45 celluloseacetate filters. The cloudy brownish color originates from the high clay content of the soil.

3. RESULTS

3.1 TRACE GAS FLUXES

Rewetting of dry soil lead to an increase in VWC from 5.9 % to 21.7 %, and soil moisture remained elevated over the next 30 h (Figure 8). Following rewetting, NO emissions increased immediately by a factor of 25 from 0.29 ± 0.05 ng NO-N m^{-2} s^{-1} pre-wetting to 7.47 ± 1.26 ng NO-N m^{-2} s^{-1} within 1 h post-wetting. NO fluxes continued to increase over the day and peaked 8 h post-wetting, where flux rates where 41.6 ng NO-N m^{-2} s^{-1} (Figure 8). On the second day following the manual irrigation, NO fluxes dropped slightly but still remained elevated, ranging from 17.5 to 26.7 ng NO-N m^{-2} s^{-1}.

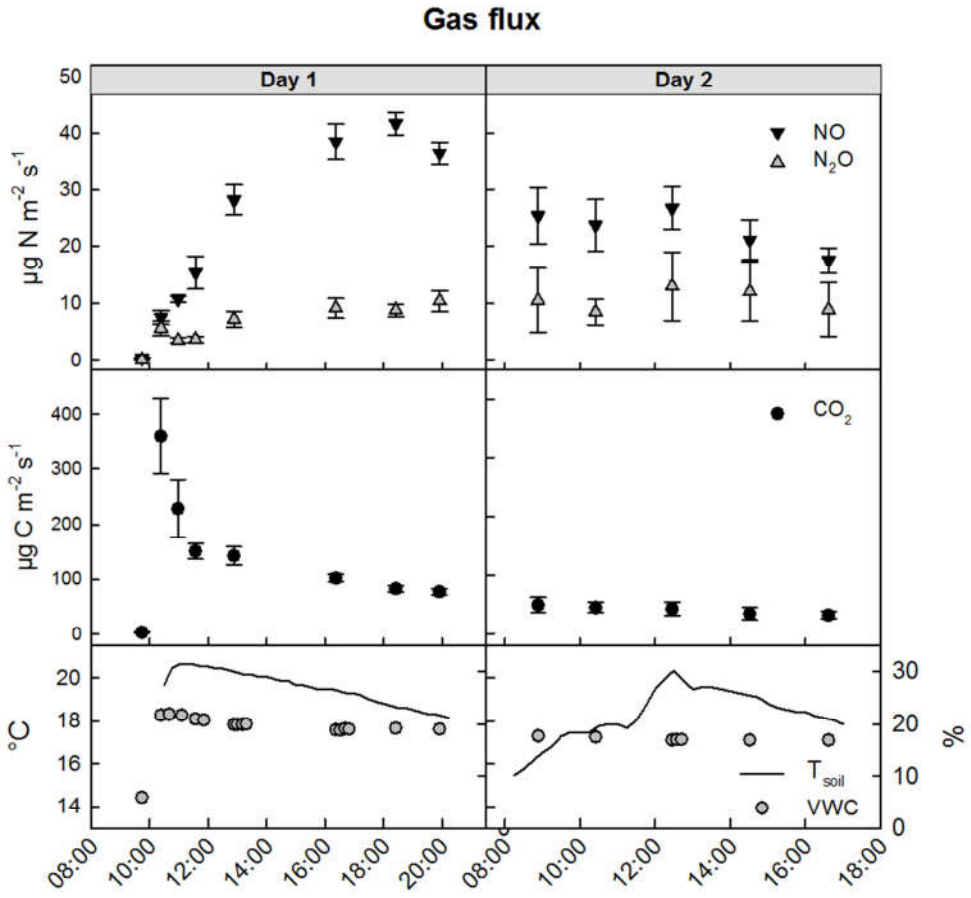

Figure 8: Soil trace gas fluxes (average ± SE, n = 4), soil temperature (T_{soil}) and volumetric water content (VWC) in a California grassland in November 2015. The first time point was measured in dry soil, all consecutive time points follow a manual irrigation with 15 mm well water.

N_2O flux rates constituted only about ¼ of NO flux rates but also increased massively after the rewetting, from almost non-detectable flux rates of -0.04 ± 0.10 ng N_2O-N m^{-2} s^{-1} pre-wetting to 5.57 ± 1.27 ng N_2O-N m^{-2} s^{-1} within 1 h post wetting (Figure 8). In contrast to NO, N_2O did not decrease on day two but kept increasing with a peak of 12.95 ± 6.03 ng N_2O-N m^{-2} s^{-1} 26 h post-wetting.

Soil respiration showed a massive peak with 100-fold increase immediately after rewetting, with maximum flux rates of 360.2 ± 68.3 µg CO_2-C m^{-2} s^{-1} only 1 h after rewetting compared to 3.3 ± 0.8 µg CO_2-C m^{-2} s^{-1} pre-wetting (Figure 8). This pulse was sustained for 2 h, after which flux rates dropped by 58 % to 151.1 µg CO_2-C m^{-2} s^{-1} and then continued to decrease more slowly over the next 30 h to a flux of 31.7 ± 6.7 µg CO_2-C m^{-2} s^{-1} at the end of day two.

3.2 MICRODIALYSIS AND SOIL EXTRACTS

Because microdialysis measurements depend on diffusion of solutes in the soil water to the membrane surface, they require a continuous water film around the dialysis probes. Therefore, it is not possible to deploy this technique in dry soils, so no data of pre-wetting conditions are available. Microdialysis data represent diffusive flux rates over the membrane surface and are shown in Figure 9.

In the first 8 h following the rewetting event, microdialysis results show a mobilization of NO_2^- with values ranging from 0.008 ± 0.005 µg NO_2^--N cm^{-2} h^{-1} to 0.047 ± 0.040 µg NO_2^--N cm^{-2} h^{-1}. On the second day following the rewetting event, diffusive NO_2^- flux had decreased by 50 % and averaged around 0.014 ± 0.003 µg NO_2^--N cm^{-2} h^{-1} compared to an average of 0.028 ± 0.004 µg NO_2^--N cm^{-2} h^{-1} on the day before. Diffusive NO_3^- flux was highest in the first 2 h post-wetting, with flux rates of 0.70 ± 0.47 µg NO_3^--N cm^{-2} h^{-1}, which rapidly declined over the next 8 h to almost non-detectable levels on the following day. Similarly to NO_3^-, diffusive NH_4^+ flux was elevated in the first 2 h post-wetting, with rates of 0.07 ± 0.04 µg NH_4^+-N cm^{-2} h^{-1}, which then dropped to almost zero and remained low for the next 24 h. On the following day, NH_4^+ flux started to rise again 27 h after the rewetting event, and it continued to increase until the end of the measurement where it dominated total mineral N diffusion with a flux rate of 3.56 ± 2.84 µg NH_4^+-N cm^{-2} h^{-1}.

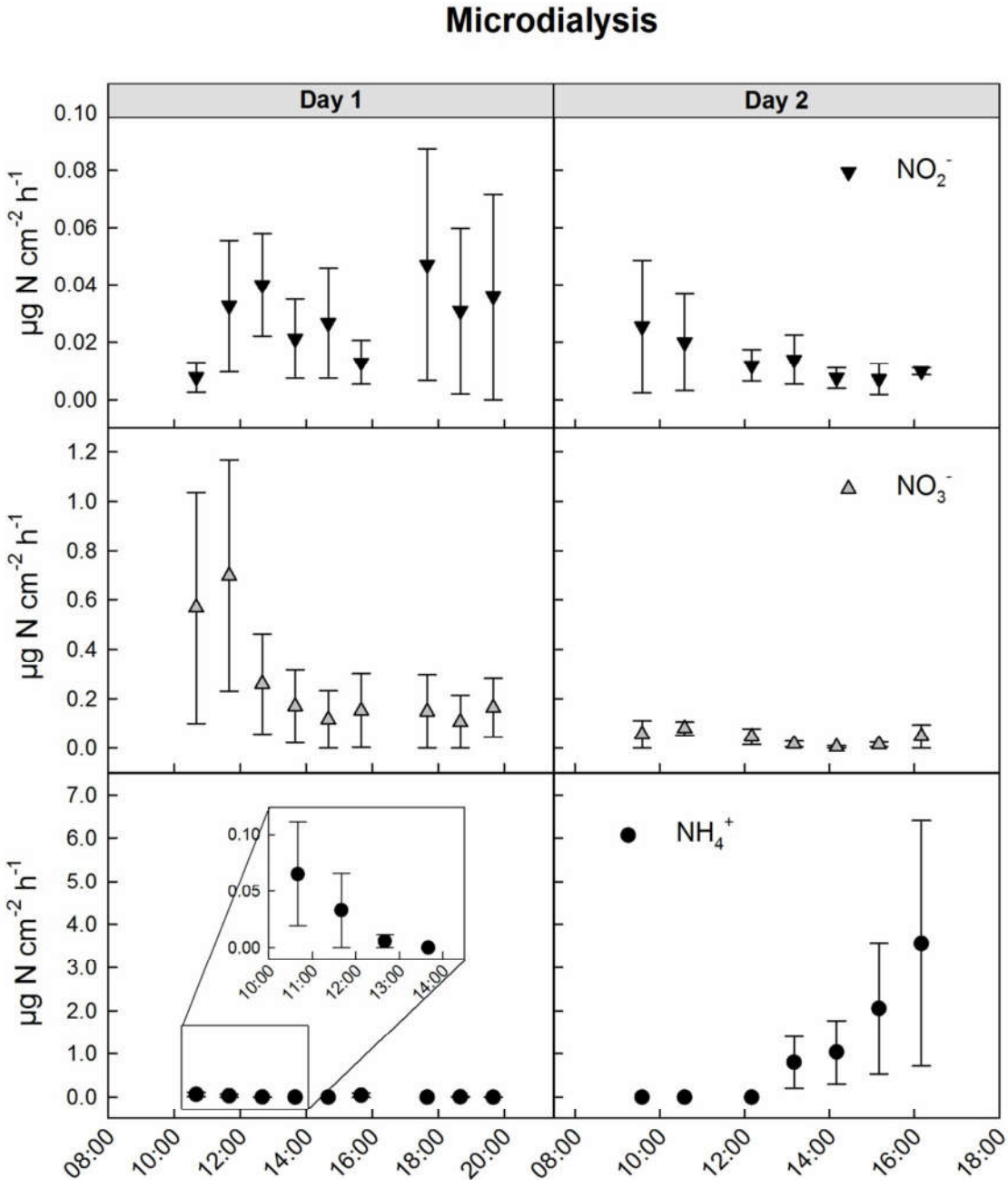

Figure 9: Diffusive flux of different mineral N forms determined with microdialysis over the course of 30 h following a manual irrigation with 15 mm well water (average ± SE, n = 4).

Comparing the relative importance of different mineral N forms immediately after the rewetting event, NO_3^- made up by far the largest fraction of the diffusive N flux, with 0.57 ± 0.47 µg NO_3^--N cm^{-2} h^{-1} compared to 0.07 ± 0.04 µg NH_4^+-N cm^{-2} h^{-1} and 0.008 ± 0.005 µg NO_2^--N cm^{-2} h^{-1} in the first hour post-wetting (Figure 10). This corresponds with the

results of soil water extracts, which show a very high contribution of NO_3^- to the total mineral N pool, with 5.40 ± 0.05 µg NO_3^--N g^{-1} dw compared to only 0.63 ± 0.03 µg NH_4^+-N g^{-1} dw and 1.51 ± 0.11 µg NO_2^--N g^{-1} dw (Figure 10). In contrast to deionized water, 0.5 *M* K_2SO_4 is much more effective in extracting cations like NH_4^+ that are bound to the negatively charged clay minerals by exchanging them with K^+. Consequently, NH_4^+ concentrations in K_2SO_4 extracts were significantly higher compared to water extracts (*t*-test, $P < 0.01$, Figure 11) and made up the largest fraction of the exchangeable mineral N pool, with 6.7 ± 0.5 µg NH_4^+-N g^{-1} dw, followed by 3.5 ± 0.3 µg NO_3^--N g^{-1} dw and 0.9 ± 0.1 µg NO_2^--N g^{-1} dw.

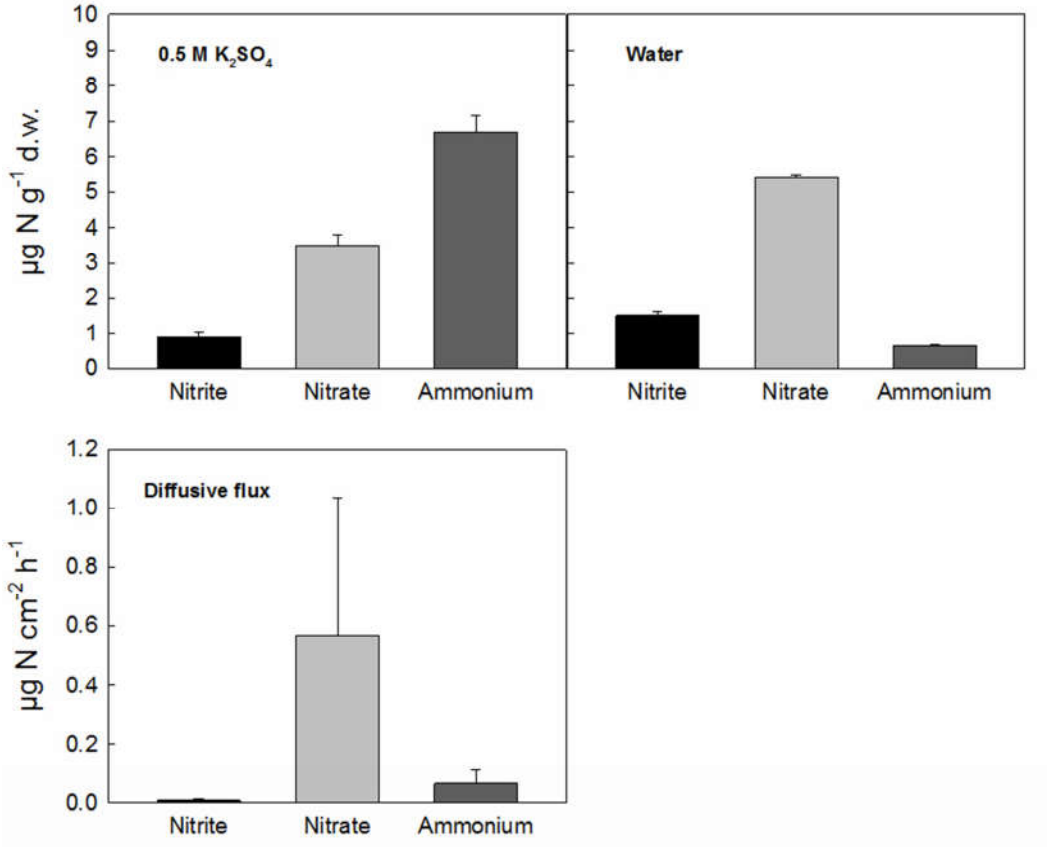

Figure 10: Soil pools of mineral N determined with 0.5 *M* K_2SO_4 and water extracts, respectively, (upper panel, average ± SE, n = 3), and diffusive N flux measured by microdialysis 1 h after a manual irrigation (lower panel, average ± SE, n = 4).

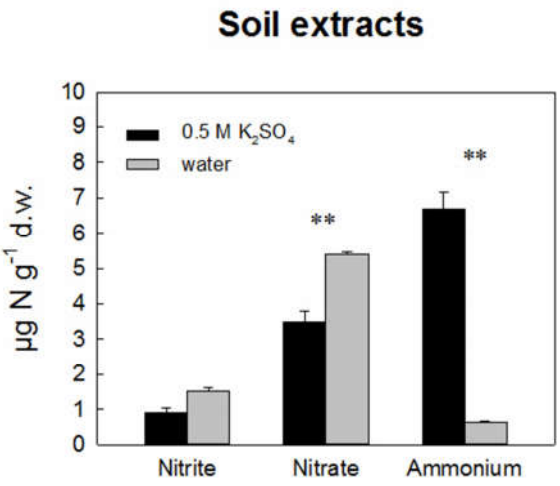

Figure 11: Comparison of soil extracts with 0.5 *M* K_2SO_4 and MilliQ water, respectively. ** indicates significance at $P < 0.01$ (*t*-test, n = 3).

4. Discussion

Emission peaks of trace gases after rewetting of dry soil are a commonly observed phenomenon (Kim et al. 2012). Up to date it has been difficult to link post-wetting emissions to *in situ* substrate mobilization dynamics. In the present study we demonstrate that the novel microdialysis technique is a feasible tool to monitor short-time (hourly) changes in soil N diffusion rates following a rewetting pulse, and that these results can help to explain soil trace gas emissions.

Rates of N gas production depend on the availability of mineral N, which accumulates during long dry periods (Parker and Schimel 2011; Sullivan et al. 2012). This substrate accumulation can be explained by (i) limited microbial accessibility due to reduced diffusion as soil water content decreases (Manzoni et al. 2014); (ii) low microbial activity and thus reduced microbial N demand during drought (Stark and Firestone 1995); (iii) lack of plant N uptake outside the growing season when plants are dead (Parker and Schimel 2011).

In the present study, NO emissions increased immediately after rewetting and continued to increase over the next hours. Nitrifying communities have been shown to take a while to reestablish their metabolism after a long dry spell (Placella and Firestone 2013),

which makes an exclusively biological source of NO emissions within 1 h unlikely. This quick response of NO is most likely caused abiotically via chemo-denitrification (Davidson 1992), which includes chemical decomposition of nitrous acid and reactions between N substrates with reduced metals and humic substances (Donaldson et al. 2014; Medinets et al. 2015). In a preceding study that was conducted at the same site, Homyak et al. (submitted) used ^{15}N-labelled NO_2^-, NO_3^- and NH_4^+ to trace the source of NO emissions after a rewetting event (Figure 12). They showed that following a rewetting event, NO originates from two different sources: first, from a fast 'reactive' abiotic source that is capable of producing NO within minutes via chemo-denitrification; and second from a slower 'emergent' biological NO source that is stimulated by the oxidation of NO_3^- and NH_4^+. This theory was corroborated by our findings, which show rapid increases in NO emissions immediately after rewetting that coincided with mobilization of NO_2^- that might have acted as fuel for chemo-denitrification and could have dominated early NO emissions.

In the first two hours after the rewetting event, soil respiration showed a massive peak with flux rates 100-fold higher than pre-wetting rates. At the same time, within 3 h after the rewetting event diffusive NO_3^- flux was reduced by 70% and diffusive NH_4^+ flux dropped to almost zero. It is conceivable that as the rewetting event alleviated substrate limitation, microorganisms started to grow and produce microbial biomass, which lead to the observed increase in soil respiration, which due to the absence of live plants, was solely of microbial origin. To support microbial biomass production, N was needed which could be the reason for the observed immobilization of mineral N in the initial three hours after the rewetting event. After this initial stage, mineral N diffusion was very low, which might indicate that microbial N uptake exceeded its supply, which, in turn, would have led to microbial N limitation. The reduction in N diffusion coincided with a drop of soil respiration by over 50 %. However, at this stage respiration still exceeded pre-wetting conditions by a factor of 50, which indicates that microorganisms were continuing to grow, albeit probably at a slower rate than in the first 2 hours following rewetting. In support of this assumption, NO and N_2O emissions continued to increase, which could have been caused by an increase in N transformation rates as the microbial biomass recovered. Since gross rates of mineral N supply and uptake were not measured in the present study, we cannot test this assumption. However, in a recent

modelling study, Evans et al. (2016) showed that immediately a rewetting event, the microbial community responded with biomass growth and enzyme production, which lead to an immobilization of mineral N that had accumulated during the preceding drought.

On the second day, approximately 24 h after the rewetting event, diffusive N flux was dominated by NH_4^+. This could indicate the recovery of biological ammonification (Chen et al. 2011) that lead to mineralization of organic N. This NH_4^+ might have served as substrate for nitrifiers and might explain why N gas emissions remained elevated compared to pre-wetting conditions even 24 h after the rewetting event. Evans et al. (2016) showed that the initial phase of N immobilization after a rewetting event was followed by net N mineralization as soon as dissolved organic C (DOC) became limiting, which supports our theory.

5. CONCLUSIONS

The present study demonstrates that microdialysis is a feasible tool to monitor mobilization dynamics of mineral N following rewetting of dry soil in high temporal resolution. Our findings corroborate the theory that in arid environments, immediately after rewetting of dry soil chemo-denitrification of NO_2^- is an important source of N gas emissions. Furthermore, we show that microbial N mineralization recovers within 24 h hours after water availability has been reestablished. These results improve our understanding of how extreme events influence N cycling and production of greenhouse gases and air pollutants.

6. PRELIMINARY RESULTS

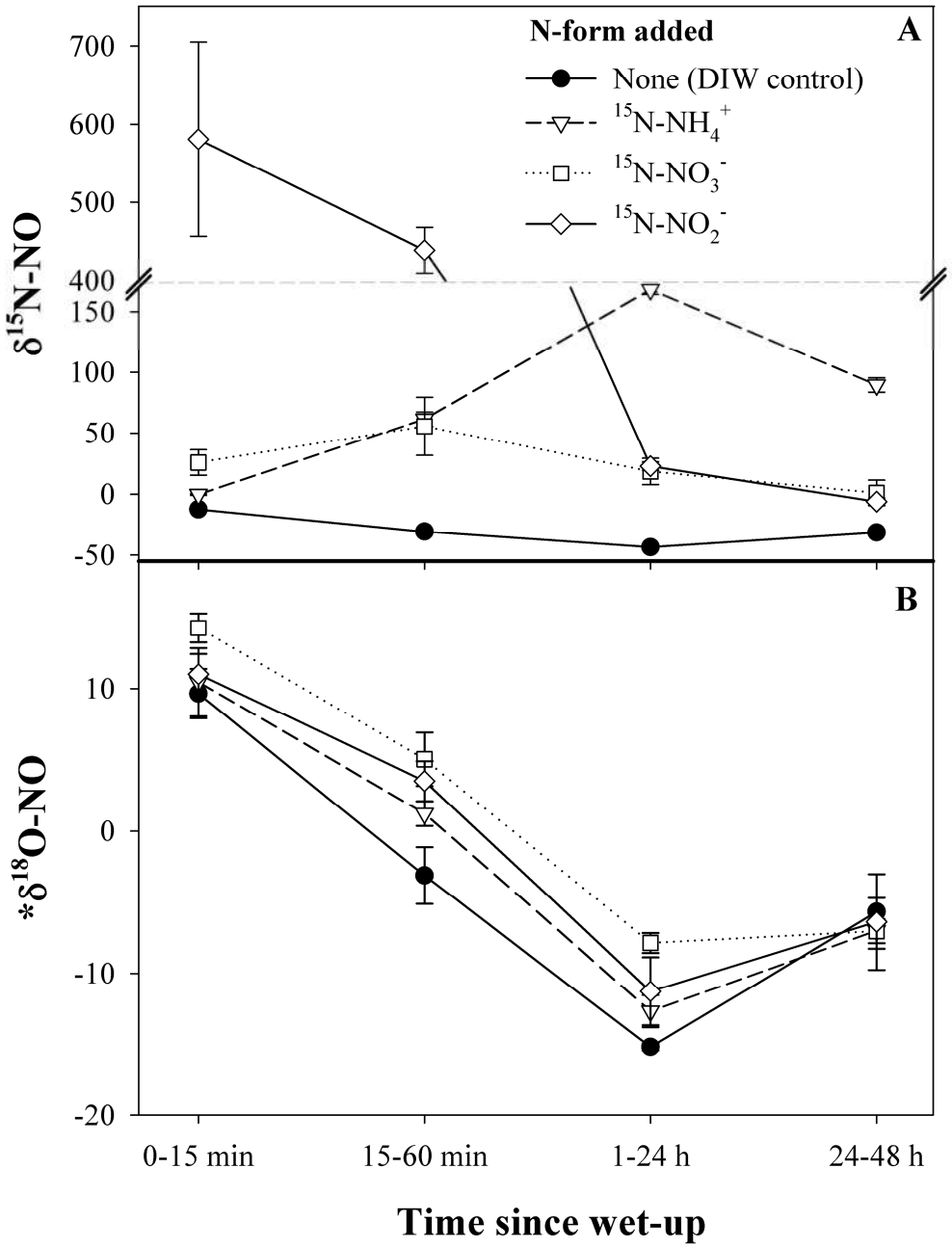

Figure 12: Average (± SE; n=4) $\delta^{15}N$- and $*\delta^{18}O$-NO following the rewetting of dry soils in September 2014. Soils rewetted (500 mL) with deionized water (DIW) are denoted controls, while other soils were rewetted with 1 atom% ^{15}N-NO_2^-, ^{15}N-NO_3^-, and ^{15}N-NH_4^+, respectively. From Homyak et al. (submitted)

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