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Patterns and Mechanisms of Trace Gas Pulses Following Soil Rewetting in Drylands

A Dissertation submitted in partial satisfaction
of the requirements for the degree of

Doctor of Philosophy

in

Evolution, Ecology, and Organismal Biology

by

Holly Andrews

June 2021

Dissertation Committee:

Dr. G. Darrel Jenerette, Chairperson

Dr. Lorelee Larios

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The Dissertation of Holly Andrews is approved:

Committee Chairperson

University of California, Riverside

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The text of Chapter 1 of this dissertation is a re-print of the material as it appears in: “Exotic grass litter modulates seasonal pulse dynamics of CO₂ and N₂O, but not NO, in Mediterranean-type coastal sage scrub at the wildland-urban interface” *Plant and Soil* 2020. The co-author listed in this publication, G. Darrel Jenerette, directed and supervised the research which forms the basis for this dissertation.

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Dedication

To my furry Ph.D. companions:

Bunny, who started this crazy adventure with me

and

Brie, who is helping with the final steps.

ABSTRACT OF THE DISSERTATION

Patterns and Mechanisms of Trace Gas Pulses Following Soil Rewetting in Drylands

by

Holly Andrews

Doctor of Philosophy, Graduate Program in Evolution, Ecology, and Organismal Biology
University of California, Riverside, June 2021
Dr. G. Darrel Jenerette, Chairperson

Drylands compose approximately 40% of the earth's land surface; a hallmark of these systems is low average soil moisture and infrequent precipitation (or irrigation) which limit biogeochemical cycling rates. However, following a re-wetting event, soil metabolism can recover within minutes, leading to discrete pulses of high rates of carbon dioxide and nitrogen oxide trace gas flux that can exceed those of more mesic systems. Although evidence suggests that moisture, temperature, and substrate availability are predominant abiotic predictors of soil metabolism, these mechanisms have not been well-described interactively and in the context of re-wetting pulses.

In this dissertation, I utilized a unique network of soil chambers and trace gas analyzers to quantify patterns of carbon dioxide (CO₂), nitrous oxide (N₂O), and nitric oxide (NO) pulses driven by temperature-moisture-substrate interactions. In an urban shrubland context (Chapter 1), I investigated pulse consequences of exotic grass litter accumulation during shrubland-grassland ecosystem type conversion. I showed that rewetting pulses of CO₂, N₂O, and NO differ across seasonal wetting history, and that

invasive grass litter may provide a labile C source that stimulates CO₂ and N₂O, but not NO, emissions from soils in this system. In a high-temperature agricultural context (Chapter 2), I explored the potential for subsurface drip irrigation to reduce soil trace gas emissions compared to traditional furrow irrigation management. I found substantial evidence that drip irrigation reduced water use, irrigation-induced pulses, and per-yield emissions of CO₂, N₂O, and NO from alfalfa and sudangrass fields. Particularly, the benefits of drip irrigation were strongest for fertilized sudangrass and in hot summer months, suggesting that irrigation is a strong control over emissions in optimal temperature and substrate conditions. In a desert context (Chapter 3), I tested interactive mechanisms limiting CO₂ pulses by explicitly manipulating temperature and coupled carbon-nitrogen availability. I found evidence that C and N stoichiometry, not strictly limitation, determined CO₂ pulse responses to soil re-wetting, and pulse responses to temperature were complicated by interactions with soil moisture immediately following rewetting. My dissertation research identifies a theme that temperature-moisture-substrate interactions drive pulse responses to dryland soil rewetting.

Table of Contents

Introduction	1
References.....	6
Chapter 1: Exotic grass litter modulates seasonal pulse dynamics of CO ₂ and N ₂ O, but not NO, in Mediterranean-type coastal sage scrub at the wildland-urban interface	
Abstract	10
Introduction	11
Methods	15
Results	21
Discussion	25
References	35
Tables and Figures	43
Chapter 2: Subsurface drip irrigation reduces per-yield water use and emissions of CO ₂ , N ₂ O, and NO in an arid forage cropping system	
Abstract	48
Introduction	49
Methods	55
Results	62
Discussion	66
Conclusion	73
References	74
Tables and Figures	80

Chapter 3: Soil CO₂ rewetting pulses driven by interactions among soil temperature, carbon, and nitrogen limitation in deserts

Abstract	89
Introduction	90
Methods	93
Results	99
Discussion	104
References	112
Tables and Figures	117
Conclusion	
Synthesis and Future Directions	128
References	131

List of Tables

Chapter 1	Page
Table 1.1	43
Change in soil moisture content and soil-extractable nitrogen pools following wet-season experimental wetting in plots that differ in dominant plant cover type (CSS shrub vs. exotic grass) and litter amendment treatments (added litter (+) vs. control). Extractable N (NH_4^+ and NO_3^-) concentrations were compared using 3-way ANOVA across all combinations of land cover type, litter treatment, and collection timepoint (pre-wet/48-hr post-wet). Bolded values indicate significant changes in variable conditions from pre-wet to 48-hour post-wet with 95% confidence ($p < 0.05$). Note that while NO_3^- did not change by individual treatments, 48-hour post-wet concentrations were significantly higher than pre-wet when all plots were combined ($p = 0.002$).	
Table 1.2	44
Drivers of peak and 48-hour total fluxes of CO_2 , N_2O , and NO . For each dependent variable, a general linear model (GLM) was generated using season, litter, plant community, and all possible interactions among them. Each full model was analyzed using analysis of variance (ANOVA); shown are fixed effects with p-values $p < 0.15$. Statistically significant p-values ($\alpha = 0.95$, $p < 0.05$) are indicated by *.	
Chapter 2	
Table 2.1	80
Upscaled water usage associated with crop production. Because growing season lengths and irrigation cycles differ between crops, irrigation treatment comparisons should be made within each crop type but are not necessarily comparable between crops. Alfalfa was harvested ~monthly; sudangrass was harvested every ~3 months.	
Table 2.2	81
Experimental predictors of soil climate conditions and trace gas emissions in irrigated agricultural fields. Variance of each dependent variable was explained using a reduced general linear model (GLM) with the lowest Akaike Information Criterion (AICc). Statistical significance of each independent variable in the best model was tested using analysis of variance (ANOVA) at 95% confidence, and separation of individual treatment groups was identified using post-hoc t-tests or Tukey's tests.	
Table 2.3	82
Upscaled soil trace gas emissions associated with crop production. Per-yield emissions were calculated by multiplying 10-day total emissions by the number of irrigation events, and dividing the total by per-area harvested yield. Values are reported as averages (standard deviations) for each treatment group.	

Chapter 3

- Table 3.1 117
Experimental predictors of CO₂ 24-hour total flux from rewetted desert soils. Only treatment sets testing a full nutrient addition suite (wet, wet+C, wet+N, wet+C+N) were used (n=2 field campaigns). Variance in CO₂ flux was explained using a reduced general linear model (GLM) with the lowest Akaike Information Criterion (AICc). Statistical significance of each independent variable in the best model was tested using analysis of variance (ANOVA) at 95% confidence, and separation of individual treatment groups was identified using post-hoc t-tests or Tukey's tests. Results describe boxplots displayed in Figure 3.4.
- Table 3.2 118
Temperature, moisture, and nitrogen dependence of CO₂ peak and 24-hour total flux from rewetted desert soils in amended and saturated nutrient conditions. Statistical significance of each independent variable was tested using analysis of variance (ANOVA) at 95% confidence.
- Table 3.3 119
Nitrogen dependence of CO₂ peak and 24-hour total flux from rewetted desert soils along a N deposition gradient. Statistical significance of each independent variable was tested using analysis of variance (ANOVA) at 95% confidence.
- Table 3.2 120
High CO₂ fluxes reported for various ecosystem types, primarily in drylands.

List of Figures

Chapter 1	Page
Figure 1.1	45
Instrumentation diagram of my custom array of gas analyzers (top) and sample instrument output from which fluxes were calculated (bottom). Arrows indicate direction of airflow in this chamber system, which is closed for CO ₂ and open for both N ₂ O and NO, and grey shaded regions of graphs indicate the area of linear increase that was used to calculate flux of each gas.	
Figure 1.2	46
Soil moisture (a) and trace gas pulse (b-d) responses to experimental wetting in CSS shrub (“CSS”) and exotic grass (“Grass”) plant cover types during a dry and wet season. Points and standard deviation bars indicate timepoint measurements and dotted lines indicate extrapolated time series curves. Colors indicate litter amendment treatments.	
Figure 1.3	47
48-hour peak (a,c,e) and cumulative (b,d,f) fluxes following experimental wetting in CSS shrub (“CSS”) and exotic grass (“Grass”) plant cover types treated with grass litter amendments (“+”) or not (“Control”) during a dry and wet season. Peak fluxes were calculated as maximum fluxes during the 48-hour measurement period and cumulative fluxes were interpolated using area-under-the-curve integration from each 48-hour time series. Quantile outliers are notated as dots above or below boxes and whiskers; refer to Table 1 for statistical significance of relationships.	
Chapter 2	
Figure 2.1	83
Extractable NH ₄ ⁺ and NO _x (NO ₂ ⁻ + NO ₃ ⁻) following soil irrigation. Points and error bars indicate means and standard errors of extractable soil N at time points following irrigation. Colors delineate irrigation type; dotted lines connecting points are for visualization only and do not indicate statistical significance.	
Figure 2.2	84
Instantaneous carbon dioxide (CO ₂) fluxes measured in each sampling campaign. Drip-irrigated chambers are colored red and flood-irrigated chambers are colored blue; specific shades of each color indicate individual chambers. Dotted lines delineate scheduled irrigation events within each campaign.	
Figure 2.3	85
Instantaneous nitrous oxide (N ₂ O) fluxes measured in each sampling campaign. Drip-irrigated chambers are colored red and flood-irrigated chambers are colored blue; specific shades of each color indicate individual chambers. Dotted lines delineate scheduled irrigation events within each campaign.	

Figure 2.4 86
Instantaneous nitric oxide (NO) fluxes measured in each sampling campaign. Drip-irrigated chambers are colored red and flood-irrigated chambers are colored blue; specific shades of each color indicate individual chambers. Dotted lines delineate scheduled irrigation events within each campaign. Note the range of fluxes for sudangrass (top) is 10x larger than for alfalfa (bottom).

Figure 2.5 87
Post-wetting responses of instantaneous CO₂, N₂O, and NO fluxes to flood (left) or drip (right) irrigation in sudangrass (top) and alfalfa (bottom) fields. Colors and symbols delineate responses of each gas, adjusted to comparable units; points within each color indicate average fluxes across all replicates for each hour post-irrigation.

Figure 2.6 88
Total soil emissions of trace gases (left) and average climate conditions (right) over 10 days following scheduled irrigation. Colors indicate flood (blue) and drip (red) irrigation treatments. Totals were calculated using area-under-the-curve integration for the 10-day time series of each chamber.

Chapter 3

Figure 3.1 121
CO₂ pulse behavior following soil rewetting for all field campaigns (n=8). The dotted line at x=0 indicates the soil rewetting event; each point indicates an instantaneous CO₂ flux measurement.

Figure 3.2 122
CO₂-temperature (a,c,e) and CO₂-moisture (b,d,f) relationships under rewetting only (no nutrient amendment) conditions. Instantaneous CO₂ flux plotted against instantaneous soil climate (a,b) were not tested for statistical significance. Peak instantaneous CO₂ flux for each pulse were compared to corresponding soil temperature (c) and moisture (d). 24-hour total CO₂ fluxes for each pulse, calculated using area-under-the-curve integration, were also compared to 24-hour average soil temperature (e) and moisture (f). Statistically significant (p<0.05) regression curves are indicated in red; temperature correlations were generally exponential (c,e) compared to linear correlations to moisture (f).

Figure 3.3 123
CO₂ pulse-temperature relationships under rewetting (no nutrient amendment) conditions for Summer 2019 campaign, in which temperature at time of wetting was most explicitly manipulated. *Top*: Instantaneous CO₂ fluxes at time post-wetting. Points are colored by time of day at which soils were rewetted and figure panels are separated by daytime and nighttime hours. *Bottom*: 24-hour total CO₂ flux as explained by soil temperature at time of rewetting; points are colored to match top panels. The statistically significant (p<0.05) regression line is indicated in black.

Figure 3.4 124
24-hour total CO₂ flux responses to experimental carbon and nitrogen amendments (left) and seasonal magnification of those amendments (right). Field campaigns were only included if they manipulated C and N in a fully-factorial suite (n=2 field campaigns); inlaid boxplot indicates differences in 24-hour total CO₂ fluxes in wet-only conditions (no amendments) between wet and dry seasons (n=5 field campaigns). Colors separate nutrient amendment treatments; statistical significance of season*amendment interactions are displayed in Table 3.1.

Figure 3.5 125
Peak (a,c,d) and 24-hour total (b,e,f) CO₂ flux responses to experimental nitrogen amendments at Boyd Deep Canyon (a,b) and in desert sites spanning a nitrogen deposition gradient (c-f). Solid lines indicate significant correlations and dashed lines indicate marginal significance at 95% confidence; colored lines represent site- or N type-specific relationships while black lines indicate significant relationships when all data are pooled. At Boyd Deep Canyon (a,b), colors indicate type of N amendment; in other plots (c-f), sites in the N deposition gradient are colored to indicate low (yellow) to high (red) throughfall N deposition.

Figure 3.6 126
Co-limitation in CO₂ flux-temperature relationship (a,c,e) and contrasting flux-moisture interactions (b,d,f) introduced under nutrient amendments. Points are colored by experimental nutrient addition treatments. Instantaneous CO₂ flux plotted against instantaneous soil climate (a,b) were not tested for statistical significance. Peak instantaneous CO₂ flux for each pulse were compared to corresponding soil temperature (c) and moisture (d). 24-hour total CO₂ fluxes for each pulse, calculated using area-under-the-curve integration, were also compared to 24-hour average soil temperature (e) and moisture (f). For subsequent analyses, the “limited” wet-only, wet+C, and wet+N treatments were pooled and compared to the “unlimited” wet+C+N conditions. Statistically significant (p<0.05) regression curves are indicated as solid lines (“limited” group) and dashed (“unlimited” group); correlations were generally linear (d,e,f) except for when comparing peak CO₂ flux to corresponding temperature (c).

Figure 3.7 127
Conceptual diagram linking soil conditions at time of rewetting (blue) and longer-term soil conditions (red) to the CO₂ pulse response to rewetting that were tested in this study. I do not make predictions about the relative sizes of effects contributing to CO₂ pulses but indicate the direction of effect with arrows and +/- signs.

Introduction

Over 40% of the earth's terrestrial surface is classified as a "dryland" system, characterized by low average soil moisture and infrequent precipitation (Pravalie, 2016). Because soil metabolism and nutrient cycling rates are generally low in dry soils, biogeochemical and emissions models often estimate drylands as small contributors to carbon (C) and nitrogen (N) budgets (Schlesinger & Bernhardt, 2013). However, increasing evidence suggests that these models underestimate nutrient cycling rates in drylands because they do not well describe mechanistic responses to infrequent soil rewetting events (Li et al., 2006). Field- and lab-based studies show that rewetting of dry soils in a number of contexts induces pulses -- rapid increases followed by slower decreases -- of biological activity and accompanying metabolic processes (Austin et al., 2004; Collins et al., 2008; Schimel, 2018). This phenomenon has been described as the "Birch effect," based on the foundational work which quantified increases in soil respiration and nitrogen mineralization in response to multiple soil drying-rewetting events (Barnard et al., 2020; Birch, 1958). Pulse behavior has since been ascribed to other soil metabolic responses to rewetting, including the emission of other trace gases (Eberwein et al., 2020; Galbally et al., 2008; Harms & Grimm, 2012; Homyak et al., 2016; Leitner et al., 2017), nitrification/denitrification (Guo et al., 2014; Miller et al., 2005), and most recently the activation of microbial genes (Barnard et al., 2015; Evans & Wallenstein, 2012). Increasing evidence suggests that pulses triggered by re-wetting (precipitation, irrigation) events are stereotypical and account for significant rates of C

and N transformation in dryland soils. However, mechanisms contributing to the timing, size, and duration of metabolic pulses still remain largely unclear for the diverse group of ecosystems housed under the umbrella term "drylands" (Butterbach-Bahl et al., 2013; Collins et al., 2014; Schimel, 2018).

Pulsed trace gas emissions from dryland soils are a dominant pathway of C and N loss from soils and can have substantial consequences for atmospheric chemistry. Carbon dioxide (CO₂), the dominant biogenic greenhouse gas (IPCC 2019), is a primary product of soil respiration and has been studied most extensively in pulse literature (Barnard et al., 2020; Evans et al., 2016; Fan et al., 2015; Jarvis et al., 2007). However, re-wetting can also generate anaerobic soil microsites that produce pulses of nitrous oxide (N₂O) (Abed et al., 2013; Guo et al., 2014), a greenhouse gas with almost 300 times the warming potential of CO₂ (IPCC 2019), which has become particularly problematic in desert agriculture (Kuang et al., 2021; Sapkota et al., 2020). Finally, dryland soils are a major source of nitric oxide (NO), a precursor to ozone that negatively impacts air quality at high concentrations and is highly susceptible to N additions via fertilizer and atmospheric N deposition (Schlesinger & Bernhardt, 2013); some of the highest pulses of NO in literature have been observed in re-wetted dryland soils (Eberwein et al., 2020; Homyak et al., 2016). The timing and magnitudes of N₂O and NO pulses from soils are likely tied to moisture (and correspondingly oxygen (O₂)) availability (Sihi et al., 2020); however, specific microbial mechanisms driving production of these gases are complex and remain unclear (Firestone & Davidson, 1989).

Two critical and interacting regulators of biological metabolism are climate and substrate availability; therefore, soil trace gas pulses should also be limited by these mechanisms. Temperature is positively correlated to kinetic energy and reaction rate of reactants with microbial enzymes; therefore, higher temperatures tend to increase microbial respiration (Bond-Lamberty & Thomson, 2010; Lloyd & Taylor, 1994; Wang et al., 2021) and other metabolic processes (Marusenko et al., 2013; Stark, 1996) which result in higher flux rates of trace gases. Coupled moisture-temperature interactions can mediate metabolic recovery; I therefore hypothesized that temperature would modulate the size of trace gas pulses following soil rewetting. Similarly, enzymatic reaction rates tend to increase in higher concentrations of nutrient substrates if those substrates are required for specific metabolic processes (Sirulnik et al., 2007), resulting in higher fluxes of trace gases to the atmosphere (Leitner et al., 2017). In the context of rewetting, substrate availability to soil microbes is often described within the "pulse-reserve" paradigm (Collins et al., 2008). When soils are dry, C and N substrates accumulate in soil "reserves" that are inaccessible to microbes; rewetting increases microbial access to these substrates, and access to additional substrates will generally increase metabolic rates and trace gas pulses (Evans et al., 2016; Jenerette & Chatterjee, 2012; Leitner et al., 2017). However, indirect mechanisms that control soil C and N substrate availability and accessibility, such as decomposing plant litter, fertilizer inputs, plant physiology and life history traits, and stoichiometric relationships, have not been well-tested within the pulse-reserve framework, and I hypothesized that these mechanisms additionally modulate trace gas responses to rewetting.

Although temperature, moisture, and substrate availability are important individual predictors of trace gas pulses, the interactions among these mechanisms are arguably more reliable for characterizing responses to rewetting in a field context. Dual-Arrhenius-Michaelis-Menten (DAMM) models are frequently used to describe CO₂ fluxes as interactions between temperature and C availability (Davidson et al., 2012), whereby the strongest rates of respiration occur in high temperature-high C conditions with the highest potential for enzymatic reactions. Similar interactive models exist for N₂O (Xu-Ri et al., 2012) and NO (Hudman et al., 2012), but all of these models are based on limited field data and do not well capture soil drying-rewetting dynamics that are dominant in dryland systems. Lab-based studies demonstrate a synergistic effect of temperature, moisture, and substrates for driving trace gas pulses (Liang et al., 2016) but do not capture variation in these mechanisms over time. I hypothesized that rewetting pulses of CO₂, N₂O, and NO would be driven by non-additive temperature-moisture-substrate interactions that could not be explained by any mechanism alone.

The goals of this dissertation were to identify patterns of CO₂, N₂O, and NO pulse responses to rewetting in dryland systems, and to quantify individual and interacting temperature, moisture, and substrate mechanisms in driving these pulses in field conditions. Simultaneously, I aimed to address soil and atmospheric consequences of regional anthropogenic land-use and land-cover changes in three ecosystem contexts. I asked three sets of research questions corresponding to three dissertation chapters: 1) How does an increase in exotic grass litter, expected to occur during shrubland-grassland conversion, influence seasonal pulse dynamics of CO₂, N₂O, and NO soil emissions? 2)

How do two contrasting irrigation strategies, traditional surface flood irrigation and water-conservative subsurface drip irrigation, affect crop yield, water usage, and pulsed emissions of CO₂, N₂O, and NO, and does this effect change with crop species and season? and 3) How do soil temperature, C availability, and N availability individually and interactively modulate CO₂ pulses from re-wetted desert soils?

References

- Abed, R. M. M., Lam, P., de Beer, D., & Stief, P. (2013). High rates of denitrification and nitrous oxide emission in arid biological soil crusts from the Sultanate of Oman. *The ISME Journal*, 7(9), 1862–1875.
- Austin, A. T., Yahdjian, L., Stark, J. M., Belnap, J., Porporato, A., Norton, U., Ravetta, D. A., & Schaeffer, S. M. (2004). Water pulses and biogeochemical cycles in arid and semiarid ecosystems. *Oecologia*, 141(2), 221–235.
- Barnard, R. L., Blazewicz, S. J., & Firestone, M. K. (2020). Rewetting of soil: revisiting the origin of soil CO₂ emissions. *Soil Biology & Biochemistry*, 107819.
- Barnard, R. L., Osborne, C. A., & Firestone, M. K. (2015). Changing precipitation pattern alters soil microbial community response to wet-up under a Mediterranean-type climate. *The ISME Journal*, 9(4), 946–957.
- Birch, H. F. (1958). The effect of soil drying on humus decomposition and nitrogen availability. *Plant and Soil*, 10(1), 9–31.
- Bond-Lamberty, B., & Thomson, A. (2010). A global database of soil respiration data. *Biogeosciences*, 7(6), 1915–1926.
- Butterbach-Bahl, K., Baggs, E. M., Dannenmann, M., Kiese, R., & Zechmeister-Boltenstern, S. (2013). Nitrous oxide emissions from soils: how well do we understand the processes and their controls? *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 368(1621), 20130122.
- Collins, S. L., Belnap, J., Grimm, N. B., Rudgers, J. A., Dahm, C. N., Odorico, P. D., Litvak, M., Natvig, D. O., Peters, D. C., Pockman, W. T., Sinsabaugh, R. L., & Wolf, B. O. (2014). A Multiscale, Hierarchical Model of Pulse Dynamics in Arid-Land Ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, 45, 397–419.
- Collins, S. L., Sinsabaugh, R. L., Crenshaw, C., Green, L., Porras-Alfaro, A., Stursova, M., & Zeglin, L. H. (2008). Pulse dynamics and microbial processes in aridland ecosystems. *The Journal of Ecology*, 96(3), 413–420.
- Davidson, E. A., & Kanter, D. (2014). Inventories and scenarios of nitrous oxide emissions. *Environmental Research Letters: ERL [Web Site]*, 9(10), 105012.
- Davidson, E. A., Samanta, S., Caramori, S. S., & Savage, K. (2012). The Dual Arrhenius and Michaelis-Menten kinetics model for decomposition of soil organic matter at hourly to seasonal time scales. *Global Change Biology*, 18(1), 371–384.

- Eberwein, J. R., Homyak, P. M., Carey, C. J., Aronson, E. L., & Jenerette, G. D. (2020). Large nitrogen oxide emission pulses from desert soils and associated microbiomes. *Biogeochemistry*, *149*(3), 239–250.
- Evans, S., Dieckmann, U., Franklin, O., & Kaiser, C. (2016). Synergistic effects of diffusion and microbial physiology reproduce the Birch effect in a micro-scale model. *Soil Biology & Biochemistry*, *93*, 28–37.
- Evans, S. E., & Wallenstein, M. D. (2012). Soil microbial community response to drying and rewetting stress: does historical precipitation regime matter? *Biogeochemistry*, *109*(1), 101–116.
- Fan, Z., Neff, J. C., & Hanan, N. P. (2015). Modeling pulsed soil respiration in an African savanna ecosystem. *Agricultural and Forest Meteorology*, *200*, 282–292.
- Firestone, M. K., & Davidson, E. A. (1989). Microbiological basis of NO and N₂O production and consumption in soil. In *Exchange of Trace Gases between Terrestrial Systems and the Atmosphere* (pp. 7–21).
- Galbally, I. E., Kirstine, W. V., Meyer, C. P., & Wang, Y. P. (2008). Soil–Atmosphere Trace Gas Exchange in Semiarid and Arid Zones. *Journal of Environmental Quality*, *37*, 599–607.
- Guo, X., Drury, C. F., Yang, X., Daniel Reynolds, W., & Fan, R. (2014). The extent of soil drying and rewetting affects nitrous oxide emissions, denitrification, and nitrogen mineralization. *Soil Science Society of America Journal*. *Soil Science Society of America*, *78*(1), 194–204.
- Harms, T. K., & Grimm, N. B. (2012). Responses of trace gases to hydrologic pulses in desert floodplains: Trace gas fluxes from desert floodplains. *Journal of Geophysical Research*, *117*(G1), 221.
- Homyak, P. M., Blankinship, J. C., Marchus, K., Lucero, D. M., Sickman, J. O., & Schimel, J. P. (2016). Aridity and plant uptake interact to make dryland soils hotspots for nitric oxide (NO) emissions. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(19), E2608–E2616.
- Hudman, R. C., Moore, N. E., Mebust, A. K., Martin, R. V., Russell, A. R., Valin, L. C., & Cohen, R. C. (2012). Steps towards a mechanistic model of global soil nitric oxide emissions: implementation and space based-constraints. *Atmospheric Chemistry and Physics*, *12*(16), 7779–7795.

- IPCC, 2019: Climate Change and Land: an IPCC special report on climate change, desertification, land degradation, sustainable land management, food security, and greenhouse gas fluxes in terrestrial ecosystems [P.R. Shukla, J. Skea, E. Calvo Buendia, V. Masson-Delmotte, H.-O. Pörtner, D. C. Roberts, P. Zhai, R. Slade, S. Connors, R. van Diemen, M. Ferrat, E. Haughey, S. Luz, S. Neogi, M. Pathak, J. Petzold, J. Portugal Pereira, P. Vyas, E. Huntley, K. Kissick, M. Belkacemi, J. Malley, (eds.)]. In press.
- Jarvis, P., Rey, A., Petsikos, C., Wingate, L., Rayment, M., Pereira, J., Banza, J., David, J., Miglietta, F., Borghetti, M., Manca, G., & Valentini, R. (2007). Drying and wetting of Mediterranean soils stimulates decomposition and carbon dioxide emission: the “Birch effect.” *Tree Physiology*, 27(7), 929–940.
- Jenerette, G. D., & Chatterjee, A. (2012). Soil metabolic pulses: water, substrate, and biological regulation. *Ecology*, 93(5), 959–966.
- Kuang, W., Gao, X., Tenuta, M., & Zeng, F. (2021). A global meta-analysis of nitrous oxide emission from drip-irrigated cropping system. *Global Change Biology*. <https://doi.org/10.1111/gcb.15636>
- Leitner, S., Homyak, P. M., Blankinship, J. C., Eberwein, J., Jenerette, G. D., Zechmeister-Boltenstern, S., & Schimel, J. P. (2017). Linking NO and N₂O emission pulses with the mobilization of mineral and organic N upon rewetting dry soils. *Soil Biology & Biochemistry*, 115, 461–466.
- Liang, L. L., Grantz, D. A., & Jenerette, G. D. (2016). Multivariate regulation of soil CO₂ and N₂O pulse emissions from agricultural soils. *Global Change Biology*, 22(3), 1286–1298.
- Li, X., Meixner, T., Sickman, J. O., Miller, A. E., Schimel, J. P., & Melack, J. M. (2006). Decadal-scale dynamics of water, carbon and nitrogen in a California chaparral ecosystem: DAYCENT modeling results. *Biogeochemistry*, 77(2), 217–245.
- Lloyd, J., & Taylor, J. A. (1994). On the temperature dependence of soil respiration. *Functional Ecology*, 8, 315–323.
- Marusenko, Y., Huber, D. P., & Hall, S. J. (2013). Fungi mediate nitrous oxide production but not ammonia oxidation in aridland soils of the southwestern US. *Soil Biology & Biochemistry*, 63, 24–36.
- Miller, A. E., Schimel, J. P., Meixner, T., Sickman, J. O., & Melack, J. M. (2005). Episodic rewetting enhances carbon and nitrogen release from chaparral soils. *Soil Biology & Biochemistry*, 37(12), 2195–2204.

- Pravalie, R. (2016). Drylands extent and environmental issues. A global approach. *Earth-Science Reviews*, 161, 259–278.
- Sapkota, A., Haghverdi, A., Avila, C. C. E., & Ying, S. C. (2020). Irrigation and Greenhouse Gas Emissions: A Review of Field-Based Studies. *Soil Systems*, 4(2), 20.
- Schimel, J. P. (2018). Life in Dry Soils: Effects of Drought on Soil Microbial Communities and Processes. *Annual Review of Ecology, Evolution, and Systematics*, 49(1), 409–432.
- Schlesinger, W. H., & Bernhardt, E. S. (2013). *Biogeochemistry Third Edition* (pp. 135–172). Academic Press.
- Sihi, D., Davidson, E. A., Savage, K. E., & Liang, D. (2020). Simultaneous numerical representation of soil microsite production and consumption of carbon dioxide, methane, and nitrous oxide using probability distribution functions. *Global Change Biology*, 26(1), 200–218.
- Sirulnik, A. G., Allen, E. B., Meixner, T., & Allen, M. F. (2007). Impacts of anthropogenic N additions on nitrogen mineralization from plant litter in exotic annual grasslands. *Soil Biology & Biochemistry*, 39(1), 24–32.
- Stark, J. M. (1996). Modeling the temperature response of nitrification. *Biogeochemistry*, 35(3), 433–445.
- Wang, C., Morrissey, E. M., Mau, R. L., Hayer, M., Piñeiro, J., Mack, M. C., Marks, J. C., Bell, S. L., Miller, S. N., Schwartz, E., Dijkstra, P., Koch, B. J., Stone, B. W., Purcell, A. M., Blazewicz, S. J., Hofmockel, K. S., Pett-Ridge, J., & Hungate, B. A. (2021). The temperature sensitivity of soil: microbial biodiversity, growth, and carbon mineralization. *The ISME Journal*. <https://doi.org/10.1038/s41396-021-00959-1>
- Xu-Ri, Prentice, I. C., Spahni, R., & Niu, H. S. (2012). Modelling terrestrial nitrous oxide emissions and implications for climate feedback. *The New Phytologist*, 196(2), 472–488.

Chapter 1

Exotic grass litter modulates seasonal pulse dynamics of CO₂ and N₂O, but not NO, in Mediterranean-type coastal sage scrub at the wildland-urban interface

Abstract

Mediterranean shrublands adjacent to urbanization experience nitrogen deposition and exotic grass invasions which likely have downstream consequences for carbon and nitrogen emissions from soils. I tested a hypothesis that soil wetting produces trace gas pulses modified by seasonal wetting history, grass litter availability, and cover type in these systems. Over two seasons, I conducted 48-hour wetting experiments and measured CO₂, N₂O, and NO pulses at an invaded, polluted California shrubland following grass litter addition to sites dominated by either an invasive grass (*Schismus barbatus*) or a native shrub (*Eriogonum fasciculatum*). CO₂ and N₂O pulses consistently appeared 15 minutes post-wetting and diminished within twelve hours; NO peaked later and remained elevated at 24 hours. All pulses were stronger in the dry season than wet season. Grass litter amendments increased CO₂ and dry-season N₂O pulses without significantly modifying NO pulses. Grass cover reduced CO₂ pulses compared to shrub cover. My results support the hypothesis that shrubland soils produce stronger pulses of CO₂, N₂O, and NO during the dry season when wetting is less frequent. I show that invasive grass litter can provide a labile C source that stimulates CO₂ and N₂O, but not NO, emissions from shrubland soils.

Introduction

Carbon (C) and nitrogen (N) cycling in dryland soils are often described using a pulse-reserve model, whereby most nutrient processes occur in discrete “pulses” catalyzed by the wetting of dry soils (Collins et al. 2008; Loik et al. 2004; Ogle and Reynolds 2004; Reynolds et al. 2004). Pulses – rapid increases and subsequent decreases of nutrient fluxes – occur following soil wetting, when microbial communities recover their metabolic activities within minutes (Austin et al. 2004). Carbon dioxide (CO₂) is the main product of soil microbial respiration and is a prominent trace gas pulse emitted when dry soils are rewetted, frequently described as the “Birch effect” (Birch 1958; Jarvis et al. 2007). However, increasing evidence suggests soil wetting produces pulses of other trace gases with additional consequences for ecosystem function. While loss of N through hydrologic pathways is common in many ecosystems, gaseous emissions of N, including both nitrous oxide (N₂O) and nitric oxide (NO), can be an important loss pathway in drylands (Eberwein et al. 2020; Harms and Grimm 2012; Leitner et al. 2017; Peterjohn and Schlesinger 1990). Further, N₂O, like CO₂, is a greenhouse gas that contributes to global climate forcing. NO is a precursor to tropospheric ozone formation, reducing regional air quality, and is also the largest component of atmospheric N deposition, fertilizing drylands near cities (Fenn et al. 2010). Understanding mechanisms that drive trace gas emissions following soil wetting can therefore improve the accuracy of biogeochemical models and climate forecasting.

Once triggered by wetting, the magnitude of a particular trace gas pulse can be mediated by substrate availability and wetting history (Homyak and Sickman 2014;

Jenerette and Chatterjee 2012; Liang et al. 2016). Theory suggests that emissions of N₂O and NO increase with soil N availability as they are byproducts of both microbial nitrification and denitrification (Firestone and Davidson 1989; Davidson et al. 2000). Additionally, CO₂ and N₂O emissions are both limited by C substrates (Liang et al. 2016), and the relative impact of C on N₂O production depends on the extent to which it is produced by heterotrophic denitrification compared to autotrophic nitrification (Firestone and Davidson 1989). Labile C and N reserves accumulate during extended periods of drought and soil drying, resulting in pulse responses to wetting (Noy-Meir 1973). In Mediterranean-type ecosystems, wetting patterns are seasonally divergent: in the cool wet season, rains are more frequent and pulses tend to be small, and in the warm dry season, rains are infrequent but pulses are large (Homyak and Sickman 2014; Hudman et al. 2012; Jenerette and Chatterjee 2012; Reynolds et al. 2004). However, little attention has been given to how multiple trace gases simultaneously respond to biotic disturbances that fundamentally alter soil structure and substrate availability, or the legacies that these changes have for ecosystem function through time.

Many drylands adjacent to urbanization, including Mediterranean-type shrublands, are increasingly undergoing type conversion to exotic annual grasslands, which alters rates of nutrient exchange between plants, soil, and the atmosphere (Cleland et al. 2016; Sirulnik et al. 2007; Wolkovich et al. 2010). Grasses employ faster life history strategies than native perennial shrubs, such that grass encroachment into native systems tends to increase rates of litterfall (Wolkovich et al. 2010) and decomposition (Liao et al. 2008; Mack and D'Antonio 2003), resulting in larger labile C and N pools

near the soil surface. Grasses tend to increase available C in soils through production of C-rich litter that decomposes more quickly and accumulates in higher volumes than that of native species (Mack and D'Antonio 2003; Zhang et al. 2014). Effects of exotic grass litter on soil N are less certain; grass litter may not change soil N directly (Wolkovich et al. 2009), although interactions between litter quality and atmospheric N deposition may increase rates of N leaching from litter to soils (Sirulnik et al. 2007). Grass-invaded systems can undergo higher rates of N mineralization and nitrification (Dickens and Allen 2014; Norton et al. 2008; Yelenik and D'Antonio 2013), resulting in faster N cycling (Sirulnik et al. 2007). In invaded shrublands, the summer dry season corresponds with senescence and litter deposition by exotic annual grasses, effectively decoupling newly available litter substrates from adequate soil moisture for microbial decomposition. Because litterfall rates are higher in invaded shrublands compared to intact counterparts (Wolkovich et al. 2010), decoupling these processes can generate larger C and N “reserves” in invaded compared to native soil that could be lost as trace gases.

Greater nutrient availability at the soil surface and the microbial capacity to process these nutrients can increase the magnitude of C and N losses from shrubland soils following a wetting event. For example, in a drought study tracking effects of exotic grasses on shrubland N dynamics, soils under grass cover and severe drought had larger losses of N by leaching upon soil rewetting (Pérez et al. 2020). Shrub-grass conversion may correspondingly increase pulsed trace gas losses of C and N from soils (Mauritz and Lipson 2013; Norton et al. 2008). However, mechanistic links between invasive grasses and trace gas pulses have not been well quantified and mechanisms controlling NO and

N₂O, such as soil moisture availability, are understudied (Butterbach-Bahl et al. 2013). In addition to individual effects of elevated C and N on emissions from soils, coupled additions of C and N can produce even stronger responses of CO₂ and N₂O (Eberwein et al. 2015; Liang et al. 2015; Sokolov et al. 2008; Zaehle 2013) than either nutrient alone, suggesting that alterations to soil nutrient stoichiometry during grass invasion may produce interactive as well as individual effects on trace gas fluxes. By alleviating both C and N substrate limitation directly, grass litter may increase C and N cycling rates in soils, ending in higher emissions of gaseous C and N to the atmosphere (Esch et al. 2017; Zhang et al. 2014). More directed field studies are needed to link increases in grass litter to CO₂, N₂O, and NO fluxes from Mediterranean shrublands, including coastal sage scrub (CSS), for which we have a limited understanding of trace gas emissions.

To address uncertainties in the effect of exotic grasses on soil trace gas emissions from Mediterranean shrublands, I conducted a litter addition experiment in a historically CSS ecosystem to answer the question: how does an increase in exotic grass litter, expected to occur during shrubland-grassland conversion, influence seasonal pulse dynamics of CO₂, N₂O, and NO soil emissions? I hypothesized that the magnitude of trace gas pulses would be mediated by interactions with the seasonal climate regime (Hartley and Schlesinger 2000; Zhang et al. 2014), litter quantity (Austin et al. 2004; Noy-Meir 1973), and dominant plant cover type (Norton et al. 2007; Rau et al. 2011), all of which have been proposed to affect C and N availability to soil microbial communities. Based on these hypotheses, I predicted that the magnitude of CO₂, N₂O, and NO pulses would be stronger following wetting in the dry season compared to the

wet season; that pulses would be greater from soils with grass litter amendments compared to unamended plots; and that pulses would be stronger from soils in exotic grass cover compared to those in unconverted shrub cover. By quantifying trace gas pulse responses to interactions among climate, litter availability, and dominant plant cover type, I aimed to better understand the ecosystem consequences of grass invasion in Mediterranean shrublands at large.

Methods

Study site

I conducted my study at Motte Rimrock Reserve (33.80° N, 117.26° W, 482 m elevation), a suburban constituent of the University of California Reserve System located in Perris, California, USA. Soils consist of sandy clay loam of the Cieneba-Fallbrook association derived from granitic rock (Knecht 1971). The native plant community is Riversidean CSS, dominated by *Artemisia californica*, *Eriogonum fasciculatum*, and *Salvia mellifera* shrubs (Cleland et al. 2016); exotic grasses and forbs have been steadily invading the reserve since its establishment in 1976. Motte Rimrock Reserve receives atmospheric deposition of up to 35 kg N ha⁻¹ yr⁻¹, predominantly as dry deposition during the dry season, which is likely contributing to grass invasion success (Allen et al. 1998; Fenn et al. 2010; Fenn et al. 2003; Valliere et al. 2017). Following a wildfire in the southern half of the reserve in 2011, large patches of reserve land have effectively type-converted to exotic annual grassland dominated by aggressive exotic species such as *Avena barbata*, *Bromus tectorum*, and *Schismus barbatus* (Allen et al. 1998). The reserve experiences a Mediterranean-type climate with mild-wet winters and hot-dry summers;

annual temperatures range from 2 to 37 °C, and over 75% of the reserve's 33 cm average annual rainfall occurs in the wet season between November and April. I conducted my study in August 2016 and April 2017, which were the end of the dry and wet season, respectively; these dates served as endpoints of wetting history that I expected would produce maximum differences in pulses. My study also coincided with California's return to historic normal rainfall following a multi-year, extreme drought (Griffin & Anchukaitis 2015).

Litter addition plot design

Throughout the reserve, I established 16 1-m by 1-m plots; 8 plots were established under canopies of *E. fasciculatum* ("CSS"), and 8 plots were established in areas of the reserve dominated by *S. barbatus* ("Grass"). I chose these species as endmembers of plant life history traits: *E. fasciculatum* is a perennial, evergreen shrub while *S. barbatus* is an annual bunchgrass that senesces at the onset of first drought entering the dry season. Within each plot, I installed two pairs of polyvinyl chloride (PVC) soil collars to a depth of 10 cm which remained installed in the plots for the entirety of the study. Each pair consisted of a large collar measuring 25 cm in diameter and a small collar measuring 10 cm in diameter. One pair per plot, hereafter "+" collars, was amended with the equivalent of 47.75 g m⁻² *S. barbatus* litter, an amount that covered the entirety of the soil surface of each collar but which may be modest compared to other litterfall estimates in invaded CSS (Wolkovich et al. 2010). Grass litter was procured by clipping stands of senesced *S. barbatus* from outside study plots, but within Motte Rimrock Reserve, during the August 2016 dry season. The other pair of soil collars

in each plot served as a control (“Control”) and received no grass litter amendments during the study period. To prevent wind and animal removal of litter, I fastened wire cages over soil collars which were only removed for soil and trace gas measurements. To simulate natural grass senescence cycles, no new litter was added prior to the wet season campaign.

Measurement of soil climate parameters and CO₂, N₂O, and NO fluxes following experimental wetting

I measured NO and N₂O fluxes from large collars and CO₂ fluxes from small collars; prior to sampling, I removed live standing biomass from collars to limit interference with instruments. I did not attempt to separate autotrophic and heterotrophic sources of respiration; because the fluxes I measured from dry soils were low, I assumed that CO₂ flux responses to wetting were primarily heterotrophic. Following gas measurements, soil climate parameters were measured in small collars. Trace gas fluxes were measured using a custom array of gas analyzers. CO₂ measurements were made on small collars using a 10-cm diameter closed-chamber system (LI-8100A; LI-COR Bioscience, Lincoln, NE, USA; Fig. 1.1). To measure NO and N₂O, I constructed an open-chamber system (Fig. 1.1) connected by Teflon tubing and consisting of: (1) a 25-cm PVC collar top equipped with a fan to accelerate air mixing and a rubber gasket to create a tight seal with the soil collar; (2) a N₂O/CO cavity ringdown infrared analyzer (Los Gatos Research, San Jose, CA, USA); and (3) a combined nitrogen dioxide (NO₂) converter/NO monitor system (Model 401/410, 2B Technologies, Boulder, CO, USA). To quantify each flux, I measured concentrations of CO₂, N₂O, and NO every 1, 1, and

10 seconds, respectively, for approximately 5 minutes inside the sealed chambers. NO₂ and NO concentrations were measured simultaneously, but NO₂ concentrations were small compared to NO and were not included in subsequent analyses. Fluxes of each gas were calculated as the regression coefficient of the linear change in concentration within the sealed chamber over the 5-minute measurement period, corrected for soil collar area and meteorological parameters using the Ideal Gas Law (Davidson et al. 2000). This system has the advantage of measuring fluxes with higher temporal resolution than most previous measurements (Davidson et al. 2000; Oikawa et al. 2015), allowing us to visualize real-time fluxes in the field and to repeat measurements within minutes of experimental wetting.

I quantified trace gas fluxes in my study following two experimental wetting campaigns: one during a dry season (August 2016) and one during a wet season (April 2017). Before wetting, I measured ambient, “pre-wet” fluxes of CO₂, N₂O, and NO. I then simulated a 3-cm rain event in each plot by adding 1.47 L and 240 mL deionized water in large and small collars, respectively, during morning hours. I took flux readings again at 15 minutes, 6 hours, and 48 hours post-wetting. Individual rain events in the Motte Reserve can range 0.18 to 6.17 cm (Western Regional Climate Center 2019), so my simulated rain was representative of a mid-size event. During the dry season, I made additional measurements at 1, 12, and 24 hours post-wetting, but eliminated these timepoints during the wet season campaign because they did not alter calculations of peak and 45-hour cumulative fluxes for any gas species. For each gas species in each wetting campaign, I constructed time series of observed fluxes, which were used for

subsequent analysis. Concurrent to each trace gas measurement, I also measured soil temperature (ProCheck soil temperature probe, Decagon Devices, Pullman, WA, USA) and soil moisture (Hydrosense II, Campbell Scientific, Logan, UT, USA) and constructed similar time series.

Measurement of soil extractable N pools during experimental wetting

From records in the TRY and BIEN Plant Trait Databases, I estimate that *S. barbatus* litter contained an average C:N ratio of 16.25 g g⁻¹ (Frenette-Dussault et al. 2012), twice that of *E. fasciculatum* at 8.86 g g⁻¹ (Maire et al. 2016). Additional records report total litter N content of *E. fasciculatum* and *S. barbatus* as 29.44 and 22.74 mg g⁻¹ dry mass (Butterfield & Briggs 2011; Sheremetev, *unpublished*), respectively, and total litter C for *S. barbatus* as 453.94 mg g⁻¹ dry mass (Frenette-Dussault et al. 2012). I therefore assumed *S. barbatus* litter to be predominantly a source of organic C while contributing proportionally less N. To investigate potential N sources for NO and N₂O, I quantified soil pools of extractable N (ammonium (NH₄⁺) and nitrate (NO₃⁻)) before and after wetting. During the wet season campaign, I collected soil cores 2.5 cm in diameter and 10 cm deep from small soil collars prior to 48 hours post-wetting and transported cores on ice for subsequent processing in lab. Each core was homogenized and subsampled for pools of extractable NH₄⁺ and NO₃⁻. Briefly, a 2.5 mg subsample of homogenized soil was extracted with 25 mL of 2M KCl, then quantified using a discrete analyzer (AQ2 Discrete Analyzer, SEAL Analytical, Mequon, WI, USA). I only measured extractable soil N pools during the wet season; however, changes in NH₄⁺ and NO₃⁻ in response to wetting were used to assess mobilization of soil N.

Data analysis

From each time series of soil climate and gas flux, I extracted peak and cumulative fluxes over each 48-hour measurement period. Peak fluxes were calculated as maximum emission across the 48-hour time series. I calculated 48-hour cumulative flux as the integrated area under each time series curve using linear trapezoidal methods. Only the timepoints shared by dry and wet seasons (pre-wet, 15 min, 6 hour, 48 hour) were used to calculate peak and cumulative fluxes to avoid measurement differences between seasons. I assessed effects of season, plant cover type, and litter amendments on time series by constructing a linear mixed model for each gas species (CO₂, N₂O, and NO) and climate variable (soil temperature, soil moisture), using soil collar ID and measurement date as random variables. Each model contained all possible interactions of season (dry/wet), plant cover type (shrub/grass), and litter amendment (+/control). To evaluate peak and 48-hour cumulative flux responses of each gas, I constructed a general linear model (GLM) for each response of interest and tested all combinations of season, cover type, and litter addition using 3-way analysis of variance (ANOVA). I also used this method to compare peak and average soil temperature and moisture across all treatment combinations. Wet-season soil extractable N (NH₄⁺ and NO₃⁻) concentrations were compared using 3-way ANOVA across all combinations of cover type, litter treatment, and collection timepoint (pre-wet/48-hr post-wet). I constructed regressions of gas fluxes vs. soil climate variables but did not extract information not already explained by seasonal differences in soil moisture. All statistical tests were performed in JMP Version

13.0 (SAS Institute Inc., Cary, NC) and plotted using *ggplot2* (Wickham 2016) and *cowplot* packages in RStudio (RStudio Team 2018).

Results

Soil extractable N response to wet-season wetting

Soil extractable NO_3^- increased by an average of 0.47 g g^{-1} dry soil in response to wetting in the wet season (Table 1; $p < 0.001$); conversely, NH_4^+ did not change significantly from dry conditions (Table 1; $p = 0.113$). I did not measure soil N pools during the dry season but suspect similar wetting-induced increases in available NO_3^- likely occurred, given previous assays conducted in similar systems (Leitner et al. 2017; Vourlitis et al. 2007; Vourlitis and Zorba 2007). Soil NH_4^+ varied marginally in a cover*litter interaction ($p = 0.065$), where grass litter amendments reduced NH_4^+ in shrub plots but enhanced NH_4^+ in grass plots compared to controls. Differences in soil NO_3^- between litter-amended plots and controls were not observed (Table 1; $p = 0.135$).

Soil temperature and moisture responses to wetting

I did not observe differences in measured average soil temperatures across season, litter, or cover type treatments ($p = 0.286$). Minimum measured soil temperatures also did not differ across seasons ($p = 0.304$) or treatments, averaging $22.70 \text{ }^\circ\text{C}$ and $24.81 \text{ }^\circ\text{C}$ in the dry and wet season, respectively. However, peak temperatures, taken 6 hours post-wetting and coinciding with midday, averaged $3 \text{ }^\circ\text{C}$ higher in the dry season ($40.79 \text{ }^\circ\text{C}$) compared to the wet season ($37.72 \text{ }^\circ\text{C}$; $p = 0.049$). Peak soil temperatures also averaged $3 \text{ }^\circ\text{C}$ higher in grass cover ($40.91 \text{ }^\circ\text{C}$) compared to shrub cover ($37.60 \text{ }^\circ\text{C}$; $p = 0.034$). The

measured soil temperature range averaged 5.5 °C larger in the dry season than the wet season ($p=0.032$).

Pre-wet soil moisture in all plots was significantly higher in the wet season (4.78%) than in the dry season (3.55%; $p<0.001$) (Figure 1.2a). As expected, soil moisture increased following experimental wetting but never exceeded 30%. Although moisture decreased over 48 hours, it did not return to pre-wet conditions (Figure 1.2a; $p<0.001$). Following wetting, peak ($p<0.001$) and average ($p<0.001$) soil moisture were higher in the wet season compared to the dry season campaign; in some plots, average moisture was three times higher in wet than dry season. Soils in shrub cover produced marginally higher moisture responses to wetting compared to those in *S. barbatus* grass cover (Figure 1.2a; $p=0.090$), particularly during the wet season.

CO₂ pulse following wetting

Pre-wet CO₂ fluxes did not differ across seasons ($p=0.148$; Table 2) and averaged 4.2 $\mu\text{g CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. Across all treatments, CO₂ fluxes following wetting responded with a pulse consistent with the Birch effect: fluxes peaked within 15 minutes of wetting, decreased over the next 6 hours, and returned to almost pre-wet levels by 48 hours post-wetting (Figure 1.2b). CO₂ pulses were stronger and remained elevated for longer following wetting in the dry season than in the wet season (Figure 1.2b): peak fluxes averaged twice as high (Figure 1.3a; $p<0.001$), and 48-hour cumulative fluxes were up to 10 times greater (Figure 1.3d; $p<0.001$). Plant cover type modulated the seasonality of CO₂ pulse responses; the highest fluxes of CO₂ in the study were observed 15 minutes post-wetting in dry-season shrub plots, averaging 137.88 $\mu\text{g CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (Figure 1.2b). In

both seasons, shrub cover also produced marginally higher CO₂ fluxes at 6 hours post-wetting (Figure 1.2b). Although peak CO₂ fluxes did not differ by cover type, shrub cover produced higher 48-hour cumulative soil CO₂ fluxes compared to grass cover (Figure 1.3a; Table 1.2; p=0.040). Additional litter enhanced CO₂ pulses regardless of season or cover type (Figure 1.2b). Litter-amended plots produced higher fluxes of CO₂ than did control plots at 15 minutes and 6 hours post-wetting (Figure 1.2b). 48 hours after wetting, CO₂ fluxes from litter-amended plots also remained elevated above pre-wet levels but only during the dry season. Peak and cumulative CO₂ fluxes were marginally (Figure 1.3a; Table 1.2; p=0.078) and significantly (Figure 1.3d; Table 1.2; p=0.016) higher, respectively, from litter-amended plots compared to controls.

N₂O pulse following wetting

Pre-wet N₂O fluxes were consistent across seasons (Table 1.2; p=0.407), averaging 0.17 ng N₂O-N m⁻² s⁻¹. N₂O produced pulses following wetting: fluxes increased within the first 15 minutes of wetting and peaked between 15 minutes (wet season) and 6 hours (dry season). Fluxes sharply declined following peak, in most cases returning to pre-wet conditions by 48 hours (Figure 1.2c). While seasonal effects on N₂O pulses appeared early post-wetting, litter effects appeared at 6 and 48 hours (Figure 1.2c), during which litter-amended, dry-season soils maintained high N₂O fluxes compared to declining trends in other treatments. N₂O pulses did not differ across plant cover types. Peak N₂O fluxes were significantly higher during the dry compared to wet season with average rates of 2.10 and 1.46 ng N₂O-N m⁻² s⁻¹, respectively (Figure 1.3b; Table 1.2; p=0.032), and litter-amended conditions produced similarly high peak N₂O fluxes

compared to controls (Table 1.2; $p < 0.050$). The dry season also contributed to greater 48-hour cumulative fluxes of N_2O (Table 1.2; $p = 0.010$), and added litter marginally increased N_2O cumulative fluxes over controls (Table 1.2; $p = 0.099$). In addition to the individual effects of season and litter, N_2O pulses responded to a season*litter interaction in which dry-season, litter-amended conditions produced peak fluxes 1.77 times higher than other treatment combinations (Season*litter $p < 0.050$). 48-hour cumulative fluxes of N_2O were also influenced by a season*litter interaction (Figure 1.3e; Table 1.2; $p = 0.010$), in which added litter enhanced 48-hour flux responses to wetting during the dry, but not the wet, season.

NO pulse following wetting

Pre-wet NO fluxes were marginally higher during the dry season (Table 1.2; $p = 0.091$), averaging $10.30 \text{ ng NO-N m}^{-2} \text{ s}^{-1}$ compared to 2.28 during the wet season. NO produced pulses following wetting but over a longer time duration than those for CO_2 and N_2O . Peak NO fluxes occurred at 6-12 hours post-wetting and at levels up to five times higher than pre-wet fluxes, averaging $147.69 \text{ ng NO-N m}^{-2} \text{ s}^{-1}$; by 48 hours post-wetting, fluxes declined but remained elevated above pre-wet conditions, particularly during dry months (Figure 1.2e). Dry-season wetting produced larger NO pulses than did wet-season wetting; peak and 48-hour cumulative fluxes both differed by as much as seven orders of magnitude between seasons (Figure 1.3c,f; Table 2; $p < 0.001$). Plant cover type and litter treatments modulated seasonal NO pulse responses but not considerably. During the dry season, litter amendments resulted in higher NO fluxes prior to wetting (Figure 1.2c), and in both seasons, litter amendments also produced strong immediate responses to wetting

as indicated by higher fluxes at 15 minutes post-wetting. CSS shrub cover also produced larger NO fluxes than did grass cover 15 minutes post-wetting (Figure 1.2c).

Discussion

My results provide new evidence that CO₂, N₂O, and NO emissions from Mediterranean-type soils exhibit seasonally-distinct pulse responses to wetting, that exotic grass litter enhances pulses of CO₂ and N₂O, and that a shift from shrub to grass cover reduces CO₂ pulses without altering N pulses. For all three trace gases, the strongest driver of pulse size was season, where one wetting event in the dry season induced pulses up to 10 times greater in magnitude than wet-season counterparts (Figure 1.2). Observed seasonal differences in pulses are consistent with an inverse relationship between wetting frequency and changes to both microbial activity and substrate availability post-wetting. By simultaneously quantifying pulses of multiple trace gases in response to experimental wetting treatments, my findings build on previous studies of individual trace gas emissions from other arid systems (Adair and Burke 2010; Blazewicz et al. 2014; Huxman et al. 2004), including California shrublands (Esch et al. 2017; Homyak and Sickman 2014). For CO₂ and N₂O, seasonal effects on pulses were modulated by the influx of litter in the dry season, a prominent effect of exotic grass invasion into CSS (Evans et al. 2001; Gill and Burke 1999; Wolkovich et al. 2010). Although I hypothesized invasion-induced changes in plant cover would increase nutrient cycling in CSS, cover type was the weakest driver of pulse responses, only constraining CO₂ pulses in grass compared to shrub cover. My findings suggest that both intact and

grass-invaded CSS produce trace gas pulses following wetting that are seasonally divergent and modulated by quantity of litter.

Timing of trace gas pulses

The coupling of rapid CO₂ and N₂O pulses, contrasted with lagging NO pulses, has not been previously observed in dryland experimental wetting studies. Although pulses of CO₂ occurring within an hour of wetting have been repeatedly reported (Bowling et al. 2011; Fraser et al. 2016; Jenerette and Chatterjee 2012), the timing of N trace gas pulses is less certain in dryland systems (Schimel 2018). Other studies have reported rapid NO responses to wetting (Harms and Grimm 2012) that can occur simultaneously to N₂O pulses (Leitner et al. 2017), providing support that nitrification and denitrification are both water-limited processes, but my results suggest NO may not respond as quickly as N₂O in shrubland soils.

CO₂ and N₂O pulses peaked within 6 hours of wetting and diminished to almost pre-wet levels after 12-24 hours, indicating a quick recovery of biological respiration and enzyme activity in response to increases in soil moisture but subsequent reduction independent of moisture availability (Figure 1.2a-c). Substrate availability and the frequency of wetting can determine the timing of trace gas responses to wetting (Austin et al. 2004; Galbally et al. 2008); at my site, abundant N and limited C could constrain the CO₂ and N₂O pulses I observed while promoting longer pulses of NO. Because soils were still moist after 24 hours (Figure 1.2a), CO₂ and N₂O pulses ended likely not because of water limitation but because of C limitation for respiration and denitrification. Pulses of NO were less immediate but lasted much longer than CO₂ and N₂O (Figure

1.2d), particularly during the dry season, and may be explained by sustained soil moisture and N availability during the 48-hour measurement period (Table 1.1; Figure 1.2a).

Although I did not directly quantify the sources of N₂O and NO, I suspect NO was predominantly formed through nitrification, a process which occurs independent of C availability and in larger magnitudes in most arid systems (Hartley & Schlesinger 2000). However, the much smaller and faster pulses of N₂O I observed may be attributed to denitrification in short-lived anoxic soil microsites (Galbally et al. 2008; Sexstone et al. 1985), as N₂O emissions are highly sensitive to respiration-induced reductions in soil oxygen levels (Butterbach-Bahl et al. 2013).

Seasonal drivers of C and N pulses

The strongest driver of CO₂, N₂O, and NO pulses was season, with larger pulses of all three trace gases occurring in the dry season compared to the wet season (Figure 1.2,1.3). My experimental wetting treatments were meant to simulate one rain event within the context of seasonal patterns of infrequent rain (dry season) compared to frequent rain (wet season) legacies. My site received a total of 9.9 mm and 198.4 mm rainfall in the three months prior to dry-season and wet-season measurements, respectively (Western Regional Climate Center 2019), highlighting substantial seasonal variability in wetting that could differentially prime soil microbes and physical access to litter and soil substrates. Wetting during the dry season could increase microbial access to labile C and N that had accumulated in spatially isolated reserves during prolonged drought (Homyak et al. 2018). Conversely, frequent precipitation during the wet season may have sustained soil microbial metabolism and access to C and N (Miller et al. 2005),

limiting the accumulation of large labile C and N reserves. My site also receives high levels of atmospheric N deposition, predominantly as dry deposition in the dry season (Fenn et al. 2010), which could magnify dry N reserves at the soil surface (Allen et al. 1998) and, subsequently, N trace gas responses to wetting.

I found strong dry-season and weak wet-season C and N gas pulses in CSS, despite nonsignificant seasonal differences in pre-wet fluxes (Figure 1.2). Peak NO fluxes I observed in the dry season were within the range of values that have been reported for other artificial wetting experiments in drylands, which have ranged 140-250 ng NO-N m⁻² s⁻¹ (Davidson et al. 1991; Davidson et al. 1993; Hall et al. 2008; Homyak and Sickman 2014). Conversely, N₂O peaks I observed across both seasons were lower compared to other dryland studies, which have reported fluxes as high as 1.5 μg N₂O-N m⁻² s⁻¹ (Eberwein et al. 2020; Harms and Grimm 2012, Leitner et al. 2017). Lack of seasonal differences in pre-wet NO fluxes that I observed contrast with previous results showing higher dry-season NO fluxes (Homyak and Sickman 2014) but were not unexpected given that moisture was low immediately prior to wetting in both seasons of my study. All other patterns I observed are consistent with observations in dry systems including forests, deserts, chaparral, and grasslands (Austin et al. 2004; Harms and Grimm 2012; Homyak and Sickman 2014; Jarvis et al. 2007; Jenerette and Chatterjee 2012; Leitner et al. 2017; Miller et al. 2005; Norton et al. 2008).

The inverse relationship between frequency of soil wetting and magnitude of pulses across multiple ecosystems suggests the importance of precipitation history as a predictor for “hot moments” of large wetting-induced losses of C and N from California

soils during dry months (Leitner et al. 2017) but smaller losses in periods with more recent precipitation. While trace gas pulses also tend to increase with temperature (Bowling et al. 2011; Hudman et al. 2012; Liang et al. 2016), soil temperatures during my study period only differed by 3 °C at peak daytime temperature and by 2 °C at minimum measured temperature across seasons. My spot measurements may underestimate the influence of temperature on trace gas pulses broadly; however I would still expect differences in temperature-gas flux relationships to be apparent in my timed sampling regimen. Therefore, I expect seasonal effects of temperature on pulses to be negligible within the context of this study, and I interpret differences in pulse magnitudes primarily as an effect of seasonal wetting history. The stronger dry-season N₂O pulses I observed contrast with DAYCENT estimations of stronger wet-season N emissions (Li et al. 2006), and my empirical observations may be used to inform future biogeochemical models that relate soil processes to precipitation events. In addition to wetting history, future work should characterize the contribution of seasonal temperature and substrate availability to pulse dynamics in shrublands more explicitly.

Grass litter drivers of C and N pulses

Grass litter amendments increased pulses of CO₂ and N₂O, but not NO (Figure 1.3). I expected *S. barbatus* litter to contribute substantial quantities of C based on its higher C:N ratio compared to *E. fasciculatum*; however, I expected that the high quantity of litter I added would increase N availability as well. Other studies report either promotion (Marcos et al. 2016) or suppression (Che et al. 2018) of microbial nitrifying genes following litter addition to arid soils, so I expected NO pulses to respond to grass

litter in a similar fashion to N₂O. At my site, grass litter did not significantly enhance already-high soil N availability (Table 1). I suspect that high rates of background atmospheric N deposition, which is common in Mediterranean shrublands adjacent to urbanization, overwhelmed any effect that grass litter may have had on soil N dynamics that have been observed in systems where background N deposition is lower (Norton et al. 2008; Wolkovich et al. 2010) and C and N limitation is more apparent (Hartley and Schlesinger 2000). I also did not observe differences in soil available N pools across litter treatments in the wet season (Table 1), further evidence that litter was not a significant source of N over seasonal timescales.

Importantly, litter-amended plots produced stronger CO₂ and N₂O pulses, suggesting that grass litter provided a labile C source for wetting-induced respiration and denitrification within the context of elevated background N (Davidson and Swank 1987; Peterjohn and Schlesinger 1991). Whether labile C was provided purely as a result of higher litter quantity in amended plots or because grass litter differed in quality from evergreen shrub litter is unclear and should be addressed in future studies. However, a C budget in grass-invaded CSS reports higher rates of C leaching and larger soil labile C pools, driven by litter pools that are over 40 times larger than uninvaded counterparts (Wolkovich et al. 2010), and I suspect this mechanism applies to my study as well.

The strongest CO₂ and N₂O pulse responses to litter were during the dry season, when amendments were added and litter was freshest. Previous studies have shown that CO₂ emissions from substrate-amended soils tend to be strongest during the first wetting after litter is added, and that pulses diminish during subsequent re-wettings, when most

labile C has been lost and remaining litter is more difficult to decompose (Birch 1958; Lado-Monserrat et al. 2014). Single inputs of C-rich litter can also produce a priming effect for greater microbial respiration and turnover in arid soils with low organic matter content, such as occur in CSS (Bastida et al. 2019), which would explain the strong CO₂ and N₂O responses to wetting in plots with added litter. I performed my dry-season experimental wetting three days after litter addition, so the pulses I observed coincided with the maximum potential effect of litter-derived C. Grass litter may also interact with other organisms at the soil surface that accelerate incorporation of litter nutrients into the soil (e.g. invertebrates; Dipman et al. 2019) or reduce rates of photosynthesis (e.g. biological crusts) during the dry season (Serpe et al. 2013), all of which would promote net emission of C. Although I still observed intact litter in plots during the wet season, I expect that it contained proportionally more recalcitrant than labile C, contributing less to alleviating C limitation and dampening CO₂ and N₂O pulses. To better understand the mechanisms by which litter influences trace gas pulses, it will be important to separate effects of litter quantity and quality explicitly.

Plant cover drivers of C and N pulses

Plant cover type contributed to differences in CO₂ pulses but did not significantly alter N trace gas pulses. I hypothesized that C and N pulses would be stronger in exotic grass compared to native CSS shrub cover, given evidence that C and N pools tend to be constrained to shallower soil depths and cycling rates increase in other invaded shrublands (Evans et al. 2001; Hawkes et al. 2005; Kramer et al. 2012; Rau et al. 2011; Wolkovich et al. 2009). However, I observed weaker CO₂ pulses from soils in exotic

grass cover compared to shrub cover, and I detected no significant differences in N trace gas pulses between cover types (Figure 1.3). The lack of N response suggests that grass cover did not appreciably change soil components (e.g. soil physics, resources, and/or microbial communities) compared to those in native shrub cover, as have been observed in other invaded ecosystems (Dickens et al. 2013; Hawkes et al. 2005; Kourtev et al. 2002). Previous studies that have explored contributions of grass invasion to N cycling have often been done in areas of low background N deposition (Norton et al. 2008; Wolkovich et al. 2010). High N deposition often associated with CSS sites adjacent to urbanization such as mine (Fenn et al. 2010; Allen et al. 1998; Norton et al. 2007) may limit the effects of cover and litter on N availability that have been observed elsewhere. Conversely, simplification of root architecture from deeper-rooted shrub to shallow-rooted grass may limit water infiltration through the soil profile (Goldstein & Suding 2014) and decrease root respiration, producing the smaller CO₂ pulses I observed in grass cover.

The effects of plant cover on CO₂ pulses were particularly strong during the dry season, when grasses were senesced and shrubs were dormant (Figure 1.3a,b). The shift from a perennial to annual system can cause intra-annual divergence in soil C and N pools (Adair and Burke 2010), affecting their availability for microbial uptake and respiration (Mauritz and Lipson 2013). During the wet season, growing plant biomass sequesters C and N, equalizing the losses of these nutrients to the atmosphere (Adair and Burke 2010; Homyak et al. 2016) in both cover types. During the dry season, native shrubs may still maintain low levels of root respiration and exudation after annual grasses

have senesced, contributing to higher autotrophic and total respiration under shrub cover during wetting events. Although dry CO₂ fluxes did not differ between cover types, shrub cover produced larger wetting-induced increases in CO₂ compared to more muted responses in grass cover, suggesting that some priming effects of soils under shrub cover – of root and/or microbial origin – may be minimized during conversion to exotic grasses (Bastida et al. 2019).

Synthesis and implications for C and N cycling in drylands

The pulse dynamics of N₂O that I observed differ from other studies in drylands, while NO dynamics were consistent with previously reported values. Compared to synthesized trace gas fluxes across multiple dryland ecosystems (Eberwein et al. 2020; Soper et al. 2016), peak N₂O fluxes that I measured were low, particularly in the wet season and in control plots. Conversely, peak measured NO fluxes were consistent with those measured from other dry systems; in the dry season, NO peaks were most similar to those measured in desert (Hartley and Schlesinger 2000) and chaparral (Homyak and Sickman 2014) systems, which have ranged 200-350 ng NO m⁻² s⁻¹. These comparisons suggest that NO is the dominant N gas loss pathway in CSS, and N₂O pulses may be suppressed here more than in other dryland systems. I suspect my study site is more invaded and polluted than other shrubland systems where pulses have been measured, additionally highlighting my study's importance for understanding N cycling at the wildland-urban interface.

Although only 25% of rain events occur during the dry season at my site (based on 7-year averages, Western Regional Climate Center 2019), emissions of an order of

magnitude higher in this season may have larger ecosystem effects than those occurring during more frequent precipitation in the wet season. Therefore, dry-season emissions may be more likely to be affected by other plant and soil properties. Using California CSS as a case study, I show that although a shift from shrub to grass cover reduces wetting-induced pulses of soil CO₂ respiration, inputs of labile grass litter at the onset of the dry season elevate CO₂ and N₂O pulses from soils, potentially through an alleviation of soil C limitation at a site with high background soil N. NO did not respond to plant cover or litter amendments, but differences in NO pulses between a Mediterranean wet and dry season were much stronger than for CO₂ or N₂O, suggesting that losses via NO are driven by factors (e.g. atmospheric N deposition) at scales larger than the invaded patch. Given the roles of trace gas species in atmospheric chemistry, I expect that exotic grass invasion is not likely to alter air quality patterns in adjacent urban centers, but accelerated life history traits of grasses may enhance the production of climate-altering greenhouse gases. Strong trace gas pulse responses to wetting are a key feature of many drylands globally; higher inputs of grass litter associated with exotic grass invasion into Mediterranean-type shrublands can increase dry-season pulses without producing carry-over effects in the subsequent wet seasons.

References

- Adair, C. E., & Burke, I. C. (2010). Plant phenology and life span influence soil pool dynamics: *Bromus tectorum* invasion of perennial C3–C4 grass communities. *Plant and Soil*, 335(1), 255–269.
- Allen, E. B., Padgett, P. E., Bytnerowicz, A., & Minnich, R. (1998). *Nitrogen Deposition Effects on Coastal Sage Vegetation of Southern California*. Retrieved from USDA Forest Service website:
https://www.fs.fed.us/psw/publications/documents/psw_gtr166/psw_gtr166_002_allen.pdf
- Austin, A. T., Yahdjian, L., Stark, J. M., Belnap, J., Porporato, A., Norton, U., Ravetta, D. A., & Schaeffer, S. M. (2004). Water pulses and biogeochemical cycles in arid and semiarid ecosystems. *Oecologia*, 141(2), 221–235.
- Bastida, F., García, C., Fierer, N., Eldridge, D. J., Bowker, M. A., Abades, S., Alfaro, F. D., Asefaw Berhe, A., Cutler, N. A., Gallardo, A., García-Velázquez, L., Hart, S. C., Hayes, P. E., Hernández, T., Hseu, Z.-Y., Jehmlich, N., Kirchmair, M., Lambers, H., Neuhauser, S., ... Delgado-Baquerizo, M. (2019). Global ecological predictors of the soil priming effect. *Nature Communications*, 10(1), 3481.
- Birch, H. F. (1958). The effect of soil drying on humus decomposition and nitrogen availability. *Plant and Soil*, 10(1), 9–31.
- Blazewicz, S. J., Schwartz, E., & Firestone, M. K. (2014). Growth and death of bacteria and fungi underlie rainfall-induced carbon dioxide pulses from seasonally dried soil. *Ecology*, 95(5), 1162–1172.
- Bowling, D. R., Grote, E. E., & Belnap, J. (2011). Rain pulse response of soil CO₂ exchange by biological soil crusts and grasslands of the semiarid Colorado Plateau, United States. *Journal of Geophysical Research*, 116(G3), 2197.
- Butterbach-Bahl, K., Baggs, E. M., Dannenmann, M., Kiese, R., & Zechmeister-Boltenstern, S. (2013). Nitrous oxide emissions from soils: how well do we understand the processes and their controls? *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 368(1621), 20130122.
- Butterfield, B.J. & Briggs, J.M. (2011). Regeneration niche differentiates functional strategies of desert woody plant species. *Oecologia*, 165:477-487.
- Che, R., Qin, J., Tahmasbian, I., Wang, F., Zhou, S., Xu, Z., & Cui, X. (2018). Litter amendment rather than phosphorus can dramatically change inorganic nitrogen pools in a degraded grassland soil by affecting nitrogen-cycling microbes. *Soil Biology & Biochemistry*, 120, 145–152.

- Cleland, E. E., Funk, J. L., & Allen, E. B. (2016). Coastal Sage Scrub. In H. Mooney & E. Zavaleta (Eds.), *Ecosystems of California* (pp. 429–448). Berkeley, United States: Univ of California Press.
- Collins, S. L., Sinsabaugh, R. L., Crenshaw, C., Green, L., Porrás-Alfaro, A., Stursova, M., & Zeglin, L. H. (2008). Pulse dynamics and microbial processes in aridland ecosystems. *The Journal of Ecology*, *96*(3), 413–420.
- Davidson, E. A., Keller, M., Erickson, H. E., Verchot, L. V., & Veldkamp, E. (2000). Testing a conceptual model of soil emissions of nitrous and nitric oxides: using two functions based on soil nitrogen availability and soil water content, the hole-in-the-pipe model characterizes a large fraction of the observed variation of nitric oxide and nitrous oxide emissions from soils. *AIBS Bulletin*, *50*(8), 667–680.
- Davidson, E. A., Vitousek, P. M., Matson, P. A., Riley, R., Garcia-Mendez, G., Maass, J. M. (1991). Soil emissions of nitric oxide in a seasonally dry tropical forest of Mexico. *Journal of Geophysical Research* *96*:15439–15445.
- Davidson, E. A., Matson, P. A., Vitousek, P. M., Riley, R., Dunkin, K., Garcia-Mendez, G., Maass, J. M. (1993). Processes regulating soil emissions of NO and N₂O in a seasonally dry forest. *Ecology* *74*:130–139.
- Davidson, E. A., & Swank, W. T. (1987). Factors limiting denitrification in soils from mature and disturbed southeastern hardwood forests. *Forest Science*, *33*(1), 135–144.
- Dickens, S. J. M., & Allen, E. B. (2014). Soil nitrogen cycling is resilient to invasive annuals following restoration of coastal sage scrub. *Journal of Arid Environments*, *110*, 12–18.
- Dickens, S. J. M., Allen, E. B., Santiago, L. S., & Crowley, D. (2013). Exotic annuals reduce soil heterogeneity in coastal sage scrub soil chemical and biological characteristics. *Soil Biology & Biochemistry*, *58*, 70–81.
- Dipman, M. M., & Meyer, W. M. (2019). Type conversion from native California sage scrub to non-native grassland accelerates decomposition processes. *Applied Soil Ecology: A Section of Agriculture, Ecosystems & Environment*, *144*, 68–71.
- Eberwein, J. R., Homyak, P. M., Carey, C. J., Aronson, E. L., & Jenerette, G. D. (2020). Large nitrogen oxide emission pulses from desert soils and associated microbiomes. *Biogeochemistry*.
- Eberwein, J. R., Oikawa, P. Y., Allsman, L. A., & Jenerette, G. D. (2015). Carbon availability regulates soil respiration response to nitrogen and temperature. *Soil Biology & Biochemistry*, *88*, 158–164.

- Esch, E. H., Lipson, D., & Cleland, E. E. (2017). Direct and indirect effects of shifting rainfall on soil microbial respiration and enzyme activity in a semi-arid system. *Plant and Soil*, *411*(1-2), 333–346.
- Evans, R. D., Rimer, R., Sperry, L., & Belnap, J. (2001). Exotic plant invasion alters nitrogen dynamics in an arid grassland. *Ecological Applications*, *11*(5), 1301–1310.
- Fenn, M. E., Baron, J. S., Allen, E. B., Rueth, H. M., Nydick, K. R., Geiser, L., Bowman, W. D., Sickman, J. O., Meixner, T., Johnson, D. W., & Neitlich, P. (2003). Ecological effects of nitrogen deposition in the western United States. *Bioscience*, *53*(4), 404–420.
- Fenn, M. E., Allen, E. B., Weiss, S. B., Jovan, S., Geiser, L. H., Tonnesen, G. S., ... Bytnerowicz, A. (2010). Nitrogen critical loads and management alternatives for N-impacted ecosystems in California. *Journal of Environmental Management*, *91*(12), 2404–2423.
- Firestone, M. K., & Davidson, E. A. (1989). Microbiological basis of NO and N₂O production and consumption in soil. *Exchange of Trace Gases between Terrestrial Systems and the Atmosphere*, pp. 7–21.
- Fraser, F. C., Corstanje, R., Deeks, L. K., Harris, J. A., Pawlett, M., Todman, L. C., ... Ritz, K. (2016). On the origin of carbon dioxide released from rewetted soils. *Soil Biology & Biochemistry*, *101*, 1–5.
- Frenette-Dussault, C., Shipley, B., Léger, J.F., Meziane, D. & Hingrat, Y. (2012). Functional structure of an arid steppe plant community reveals similarities with Grime's C-S-R theory. *Journal of Vegetation Science* *23*: 208-222.
- Galbally, I. E., Kirstine, W. V., Meyer, C. P., & Wang, Y. P. (2008). Soil–atmosphere trace gas exchange in semiarid and arid zones. *Journal of Environmental Quality*, *37*, 599–607.
- Gill, R. A., & Burke, I. C. (1999). Ecosystem consequences of plant life form changes at three sites in the semiarid United States. *Oecologia*, *121*(4), 551–563.
- Goldstein, L. J., & Suding, K. N. (2014). Intra-annual rainfall regime shifts competitive interactions between coastal sage scrub and invasive grasses. *Ecology*, *95*(2), 425–435.
- Griffin, D., & Anchukaitis, K. J. (2015). How unusual is the 2012–2014 California drought? *Geophysical Research Letters*, 9017–9023.
- Hall, S. J., Huber, D., & Grimm, N. B. (2008). Soil N₂O and NO emissions from an arid, urban ecosystem. *Journal of Geophysical Research*.

- Harms, T. K., & Grimm, N. B. (2012). Responses of trace gases to hydrologic pulses in desert floodplains: trace gas fluxes from desert floodplains. *Journal of Geophysical Research*, *117*(G1), 221.
- Hartley, A. E., & Schlesinger, W. H. (2000). Environmental controls on nitric oxide emission from northern Chihuahuan desert soils. *Biogeochemistry*, *50*(3), 279–300.
- Hawkes, C. V., Wren, I. F., Herman, D. J., & Firestone, M. K. (2005). Plant invasion alters nitrogen cycling by modifying the soil nitrifying community. *Ecology Letters*, *8*(9), 976–985.
- Homyak, P. M., Blankinship, J. C., Marchus, K., Lucero, D. M., Sickman, J. O., & Schimel, J. P. (2016). Aridity and plant uptake interact to make dryland soils hotspots for nitric oxide (NO) emissions. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(19), E2608–E2616.
- Homyak, P. M., & Sickman, J. O. (2014). Influence of soil moisture on the seasonality of nitric oxide emissions from chaparral soils, Sierra Nevada, California, USA. *Journal of Arid Environments*, *103*, 46–52.
- Homyak, P. M., Blankinship, J. C., Slessarev, E. W., Schaeffer, S. M., Manzoni, S., & Schimel, J. P. (2018). Effects of altered dry season length and plant inputs on soluble soil carbon. *Ecology*, *99*(10), 2348–2362.
- Hudman, R. C., Moore, N. E., Mebust, A. K., Martin, R. V., Russell, A. R., Valin, L. C., & Cohen, R. C. (2012). Steps towards a mechanistic model of global soil nitric oxide emissions: implementation and space based-constraints. *Atmospheric Chemistry and Physics*, *12*(16), 7779–7795.
- Huxman, T. E., Snyder, K. A., Tissue, D., Leffler, A. J., Ogle, K., Pockman, W. T., Sandquist, D. R., Potts, D. L., & Schwinning, S. (2004). Precipitation pulses and carbon fluxes in semiarid and arid ecosystems. *Oecologia*, *141*(2), 254–268.
- Jarvis, P., Rey, A., Petsikos, C., Wingate, L., Rayment, M., Pereira, J., Banza, J., David, J., Miglietta, F., Borghetti, M., Manca, G., & Valentini, R. (2007). Drying and wetting of Mediterranean soils stimulates decomposition and carbon dioxide emission: the “Birch effect.” *Tree Physiology*, *27*(7), 929–940.
- Jenerette, G. D., & Chatterjee, A. (2012). Soil metabolic pulses: Water, substrate, and biological regulation. *Ecology*, *93*(5), 959–966.
- Knecht, A. A. (1971). *Soil Survey, Western Riverside Area, California*. U.S. Soil Conservation Service.

- Kourtev, P. S., Ehrenfeld, J. G., & Häggblom, M. (2002). Exotic plant species alter the microbial community structure and function in the soil. *Ecology*, 83(11), 3152–3166.
- Kramer, T. D., Warren, R. J., Tang, Y., & Bradford, M. A. (2012). Grass invasions across a regional gradient are associated with declines in belowground carbon pools. *Ecosystems*, 15(8), 1271–1282.
- Lado-Monserrat, L., Lull, C., Bautista, I., Lidón, A., & Herrera, R. (2014). Soil moisture increment as a controlling variable of the “Birch effect”: interactions with the pre-wetting soil moisture and litter addition. *Plant and Soil*, 379(1), 21–34.
- Leitner, S., Homyak, P. M., Blankinship, J. C., Eberwein, J., Jenerette, G. D., Zechmeister-Boltenstern, S., & Schimel, J. P. (2017). Linking NO and N₂O emission pulses with the mobilization of mineral and organic N upon rewetting dry soils. *Soil Biology & Biochemistry*, 115, 461–466.
- Li, X., Meixner, T., Sickman, J. O., Miller, A. E., Schimel, J. P., & Melack, J. M. (2006). Decadal-scale dynamics of water, carbon and nitrogen in a California chaparral ecosystem: DAYCENT modeling results. *Biogeochemistry*, 77(2), 217–245.
- Liang, L. L., Eberwein, J. R., Allsman, L. A., Grantz, D. A., & Jenerette, G. D. (2015). Regulation of CO₂ and N₂O fluxes by coupled carbon and nitrogen availability. *Environmental Research Letters*, 10(3), 034008.
- Liang, L. L., Grantz, D. A., & Jenerette, G. D. (2016). Multivariate regulation of soil CO₂ and N₂O pulse emissions from agricultural soils. *Global Change Biology*, 22(3), 1286–1298.
- Liao, C., Peng, R., Luo, Y., Zhou, X., Wu, X., Fang, C., ... Li, B. (2008). Altered ecosystem carbon and nitrogen cycles by plant invasion: a meta-analysis. *The New Phytologist*, 177(3), 706–714.
- Loik, M. E., Breshears, D. D., Lauenroth, W. K., & Belnap, J. (2004). A multi-scale perspective of water pulses in dryland ecosystems: climatology and ecohydrology of the western USA. *Oecologia*, 141(2), 269–281.
- Mack, M. C., & D’Antonio, C. M. (2003). The effects of exotic grasses on litter decomposition in a Hawaiian woodland: the importance of indirect effects. *Ecosystems*, 6(8), 723–738.
- Maire, Vincent et al. (2016), Data from: Global effects of soil and climate on leaf photosynthetic traits and rates, v2, Dryad, Dataset, <https://doi.org/10.5061/dryad.j42m7>

- Marcos, M. S., Bertiller, M. B., Cisneros, H. S., & Olivera, N. L. (2016). Nitrification and ammonia-oxidizing bacteria shift in response to soil moisture and plant litter quality in arid soils from the Patagonian Monte. *Pedobiologia*, *59*(1), 1–10.
- Mauritz, M., & Lipson, D. L. (2013). Altered phenology and temperature sensitivity of invasive annual grasses and forbs changes autotrophic and heterotrophic respiration rates in a semi-arid shrub community. *Biogeosciences Discussions*, *10*, 6335–6375.
- Miller, A. E., Schimel, J. P., Meixner, T., Sickman, J. O., & Melack, J. M. (2005). Episodic rewetting enhances carbon and nitrogen release from chaparral soils. *Soil Biology & Biochemistry*, *37*(12), 2195–2204.
- Norton, J. B., Monaco, T. A., & Norton, U. (2007). Mediterranean annual grasses in western North America: kids in a candy store. *Plant and Soil*, *298*(1), 1–5.
- Norton, U., Mosier, A. R., Morgan, J. A., Derner, J. D., Ingram, L. J., & Stahl, P. D. (2008). Moisture pulses, trace gas emissions and soil C and N in cheatgrass and native grass-dominated sagebrush-steppe in Wyoming, USA. *Soil Biology & Biochemistry*, *40*(6), 1421–1431.
- Noy-Meir, I. (1973). Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics*, *4*(1), 25–51.
- Ogle, K., & Reynolds, J. F. (2004). Plant responses to precipitation in desert ecosystems: integrating functional types, pulses, thresholds, and delays. *Oecologia*, *141*(2), 282–294.
- Oikawa, P. Y., Ge, C., Wang, J., Eberwein, J. R., Liang, L. L., Allsman, L., ... Jenerette, G. D. (2015). Unusually high soil nitrogen oxide emissions influence air quality in a high-temperature agricultural region. *Nature Communications*, *6*, 8753.
- Peterjohn, W. T., & Schlesinger, W. H. (1990). Nitrogen loss from deserts in the southwestern United States. *Biogeochemistry*, *10*(1), 67–79.
- Peterjohn, W. T., & Schlesinger, W. H. (1991). Factors controlling denitrification in a Chihuahuan desert ecosystem. *Soil Science Society of America Journal*, *55*, 1694–1701.
- Pérez Castro, S., Esch, E. H., Eviner, V. T., Cleland, E. E., & Lipson, D. A. (2020). Exotic herbaceous species interact with severe drought to alter soil N cycling in a semi-arid shrubland. *Geoderma*, *361*, 114111.

- Rau, B. M., Johnson, D. W., Blank, R. R., Lucchesi, A., Caldwell, T. G., & Schupp, E. W. (2011). Transition from sagebrush steppe to annual grass (*Bromus tectorum*): influence on belowground carbon and nitrogen. *Rangeland Ecology & Management*, *64*(2), 139–147.
- Reynolds, J. F., Kemp, P. R., Ogle, K., & Fernández, R. J. (2004). Modifying the “pulse-reserve” paradigm for deserts of North America: precipitation pulses, soil water, and plant responses. *Oecologia*, *141*(2), 194–210.
- RStudio Team (2018). RStudio: Integrated development for R. RStudio, Inc., Boston, MA. <http://www.rstudio.com/>.
- Schimel, J. P. (2018). Life in dry soils: effects of drought on soil microbial communities and processes. *Annual Review of Ecology, Evolution, and Systematics*, *49*(1), 409–432.
- Serpe, M. D., Roberts, E., Eldridge, D. J., & Rosentreter, R. (2013). *Bromus tectorum* litter alters photosynthetic characteristics of biological soil crusts from a semiarid shrubland. *Soil Biology & Biochemistry*, *60*, 220–230.
- Sexstone, A. J., Parkin, T. B., & Tiedje, J. M. (1985). Temporal response of soil denitrification rates to rainfall and irrigation. *Soil Science Society of America Journal*, *49*, 99–103.
- Sirulnik, A. G., Allen, E. B., Meixner, T., & Allen, M. F. (2007). Impacts of anthropogenic N additions on nitrogen mineralization from plant litter in exotic annual grasslands. *Soil Biology & Biochemistry*, *39*(1), 24–32.
- Sokolov, A. P., Kicklighter, D. W., Melillo, J. M., Felzer, B. S., Schlosser, C. A., & Cronin, T. W. (2008). Consequences of considering carbon–nitrogen interactions on the feedbacks between climate and the terrestrial carbon cycle. *Journal of Climate*, *21*(15), 3776–3796.
- Soper, F. M., Boutton, T. W., Groffman, P. M., & Sparks, J. P. (2016). Nitrogen trace gas fluxes from a semiarid subtropical savanna under woody legume encroachment. *Global Biogeochemical Cycles*, *30*(5), 614–628.
- Valliere, J. M., Irvine, I. C., Santiago, L., & Allen, E. B. (2017). High N, dry: experimental nitrogen deposition exacerbates native shrub loss and nonnative plant invasion during extreme drought. *Global Change Biology*, *23*(10), 4333–4345.
- Vourlitis, G. L., Zorba, G., Pasquini, S. C., & Mustard, R. (2007). Carbon and nitrogen storage in soil and litter of southern Californian semi-arid shrublands. *Journal of Arid Environments*, *70*(1), 164–173.

- Vourlitis, G. L., & Zorba, G. (2007). Nitrogen and carbon mineralization of semi-arid shrubland soil exposed to long-term atmospheric nitrogen deposition. *Biology and Fertility of Soils*, 43(5), 611–615.
- Western Regional Climate Center. (2019). *Motte Rimrock Reserve California*. Retrieved from <https://wrcc.dri.edu/weather/ucmo.html>.
- Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York. ISBN 978-3-319-24277-4, <https://ggplot2.tidyverse.org>.
- Wolkovich, E. M., Bolger, D. T., & Cottingham, K. L. (2009). Invasive grass litter facilitates native shrubs through abiotic effects. *Journal of Vegetation Science*, 20(6), 1121–1132.
- Wolkovich, E. M., Lipson, D. A., Virginia, R. A., Cottingham, K. L., & Bolger, D. T. (2010). Grass invasion causes rapid increases in ecosystem carbon and nitrogen storage in a semiarid shrubland. *Global Change Biology*, 16(4), 1351–1365.
- Yelenik, S. G., & D’Antonio, C. M. (2013). Self-reinforcing impacts of plant invasions change over time. *Nature*, 503(7477), 517–520.
- Zaehle, S. (2013). Terrestrial nitrogen - carbon cycle interactions at the global scale. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 368(ii), 9.
- Zhang, L., Wang, H., Zou, J., Rogers, W. E., & Siemann, E. (2014). Non-native plant litter enhances soil carbon dioxide emissions in an invaded annual grassland. *PloS One*, 9(3), e92301.

Tables

Table 1.1 Change in soil moisture content and soil-extractable nitrogen pools following wet-season experimental wetting in plots that differ in dominant plant cover type (CSS shrub vs. exotic grass) and litter amendment treatments (added litter (+) vs. control). Extractable N (NH_4^+ and NO_3^-) concentrations were compared using 3-way ANOVA across all combinations of land cover type, litter treatment, and collection timepoint (pre-wet/48-hr post-wet). Bolded values indicate significant changes in variable conditions from pre-wet to 48-hour post-wet with 95% confidence ($p < 0.05$). Note that while NO_3^- did not change by individual treatments, 48-hour post-wet concentrations were significantly higher than pre-wet when all plots were combined ($p = 0.002$).

<i>Measured variable</i>	<i>Plant community</i>	<i>Litter treatment</i>	<i>Pre-wet (sd)</i>	<i>48-hr post-wet (sd)</i>	<i>Δ (sd)</i>
Moisture content (g g ⁻¹ soil)	CSS	Control	0.03 (0.02)	0.09 (0.04)	0.08 (0.04)
		+	0.01 (0.00)	0.09 (0.07)	0.06 (0.06)
	Grass	Control	0.01 (0.01)	0.05 (0.02)	0.03 (0.02)
		+	0.02 (0.02)	0.05 (0.03)	0.02 (0.02)
NH_4^+ (g g ⁻¹ soil)	CSS	Control	0.52 (0.22)	0.79 (0.27)	0.41 (0.36)
		+	0.44 (0.14)	0.58 (0.21)	0.07 (0.21)
	Grass	Control	0.39 (0.09)	0.67 (0.19)	0.10 (0.30)
		+	0.78 (0.55)	0.67 (0.48)	-0.02 (0.75)
NO_3^- (g g ⁻¹ soil)	CSS	Control	0.95 (0.51)	1.28 (0.40)	0.72 (0.43)
		+	0.61 (0.14)	1.10 (0.32)	0.29 (0.48)
	Grass	Control	0.64 (0.12)	1.43 (1.02)	0.73 (1.13)
		+	0.77 (0.29)	0.96 (0.29)	0.09 (0.38)

Table 1.2 Drivers of peak and 48-hour total fluxes of CO₂, N₂O, and NO. For each dependent variable, a general linear model (GLM) was generated using season, litter, plant community, and all possible interactions among them. Each full model was analyzed using analysis of variance (ANOVA); shown are fixed effects with p-values $p < 0.15$. Statistically significant p-values ($\alpha = 0.95$, $p < 0.05$) are indicated by *.

<i>Dependent variable</i>	<i>Significant fixed effects</i>	<i>F-value</i>	<i>p-value</i>
Peak CO ₂ flux ($\mu\text{g CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	Season	12.964	< 0.001*
	Litter	2.676	0.110
Peak N ₂ O flux ($\text{ng N}_2\text{O-N m}^{-2} \text{ s}^{-1}$)	Season	4.920	0.032*
	Litter	4.253	0.046*
	Season*Litter	3.344	0.075
Peak NO flux ($\mu\text{g NO-N m}^{-2} \text{ s}^{-1}$)	Season	63.959	< 0.001*
48-hour CO ₂ flux ($\mu\text{g CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	Season	84.873	< 0.001*
	Litter	6.433	0.016*
	Community	4.567	0.040*
	Season*Community	2.590	0.117
48-hour N ₂ O flux ($\text{ng N}_2\text{O-N m}^{-2} \text{ s}^{-1}$)	Season	5.891	0.021*
	Litter	2.247	0.144
	Season*Litter	7.439	0.010*
48-hour NO flux ($\mu\text{g NO-N m}^{-2} \text{ s}^{-1}$)	Season	50.439	< 0.001*

Figures

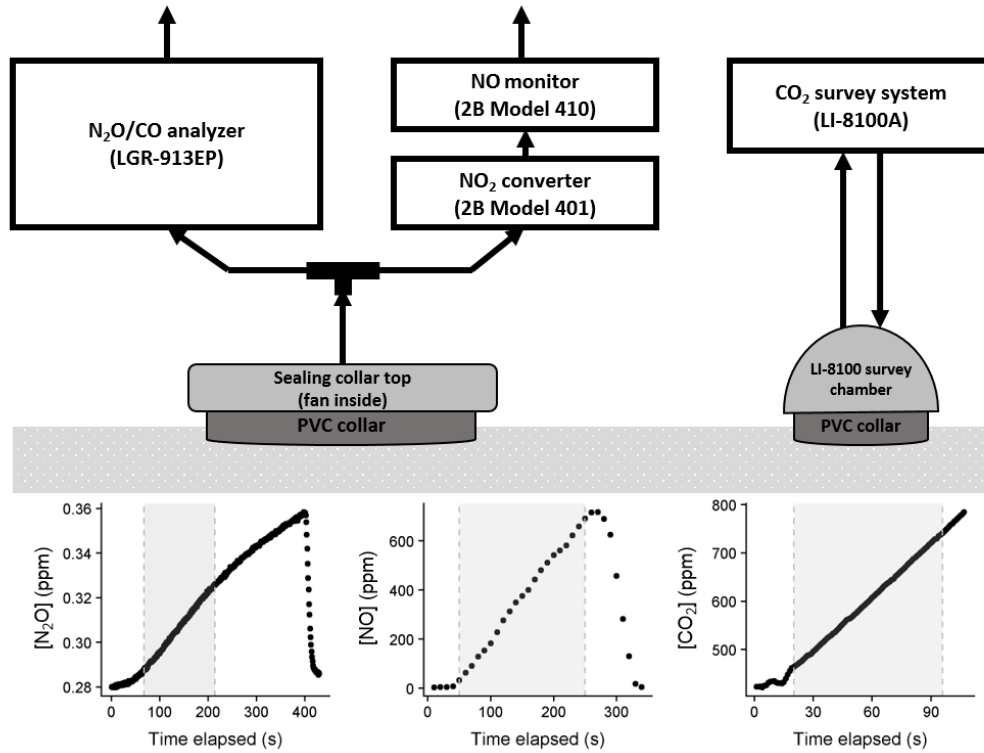


Fig. 1.1 Instrumentation diagram of my custom array of gas analyzers (top) and sample instrument output from which fluxes were calculated (bottom). Arrows indicate direction of airflow in this chamber system, which is closed for CO₂ and open for both N₂O and NO, and grey shaded regions of graphs indicate the area of linear increase that was used to calculate flux of each gas

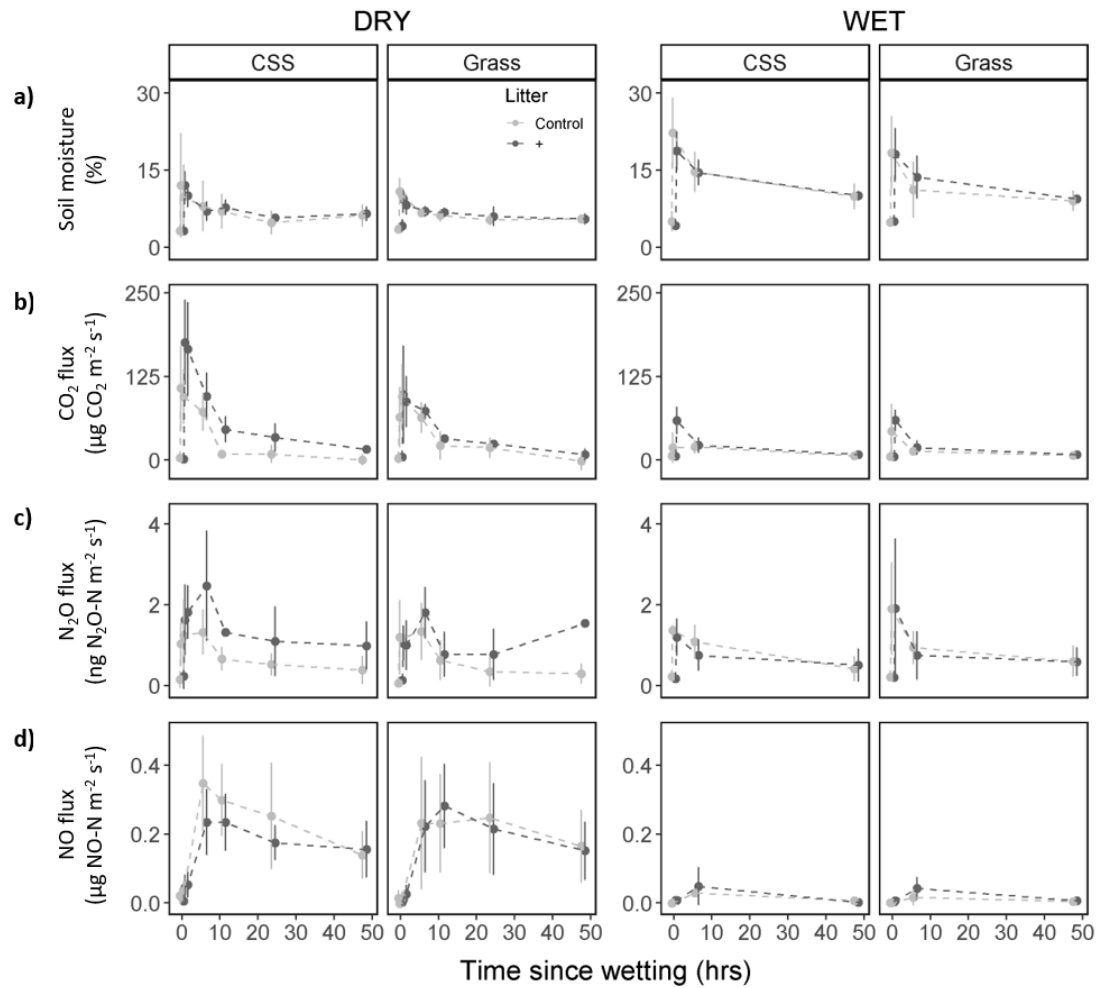


Fig. 1.2 Soil moisture (a) and trace gas pulse (b-d) responses to experimental wetting in CSS shrub (“CSS”) and exotic grass (“Grass”) plant cover types during a dry and wet season. Points and standard deviation bars indicate timepoint measurements and dotted lines indicate extrapolated time series curves. Colors indicate litter amendment treatments

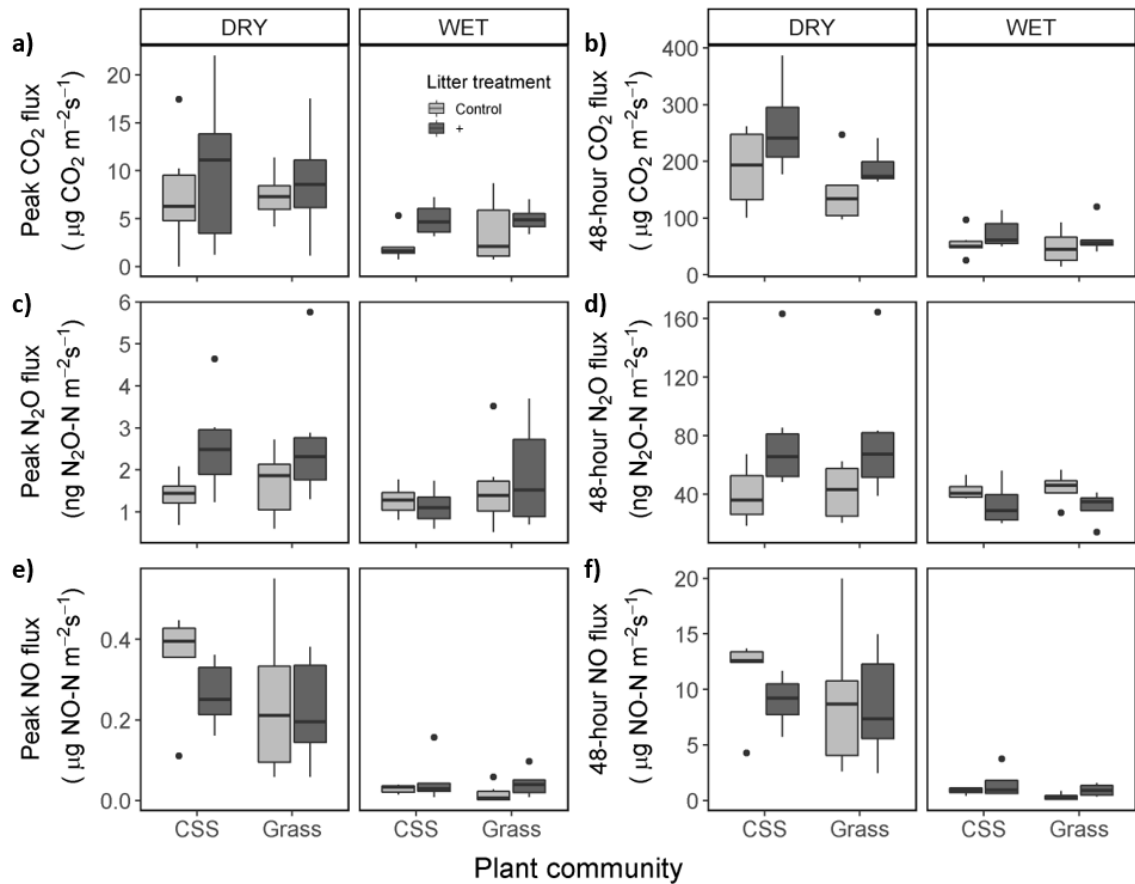


Fig. 1.3 48-hour peak (a,c,e) and cumulative (b,d,f) fluxes following experimental wetting in CSS shrub (“CSS”) and exotic grass (“Grass”) plant cover types treated with grass litter amendments (“+”) or not (“Control”) during a dry and wet season. Peak fluxes were calculated as maximum fluxes during the 48-hour measurement period and cumulative fluxes were interpolated using area-under-the-curve integration from each 48-hour time series. Quantile outliers are notated as dots above or below boxes and whiskers; refer to Table 1 for statistical significance of relationships

Chapter 2

Subsurface drip irrigation reduces per-yield water use and emissions of CO₂, N₂O, and NO in a high-temperature forage cropping system

Abstract

Agricultural irrigation is traditionally applied at the soil surface; however, in high-temperature regions, surface irrigation in furrows can result in inefficient water use and large emissions of carbon dioxide (CO₂), nitrous oxide (N₂O), and nitric oxide (NO). A potential management solution to increase water infiltration and reduce soil emissions is to adopt subsurface drip irrigation, a method which increases rhizosphere access to water more continuously through time. In a multi-year field study, I compared crop yield, water usage, and soil emissions for flood- and drip-irrigated field plots in southern California in two seasons and between two forage crops, N-fixing alfalfa and non-N fixing sudangrass. I monitored soil climate and emission responses to irrigation using a custom array of automated chambers multiplexed to trace gas analyzers which measured gas fluxes on a 30-minute cycle. Post-irrigation instantaneous and 10-day integrated fluxes were compared across irrigation type, season, crop type, and their interactions and then scaled by harvested yield. I found that, compared to flood-irrigated fields, drip irrigation in alfalfa produced 106.9% yield, used 89.3% water, and produced 41.1% CO₂, 85.8% N₂O, and 72.8% NO emissions. Drip irrigation in sudangrass produced 106.1% yield of flooded fields, used 31.6% water, emitted 103.4% CO₂, 37.5% N₂O, and 38.3% NO. 10-day integrated emissions of all gases were lower in alfalfa compared to sudangrass, despite higher soil moisture in alfalfa plots. In both crops, differences between irrigation

types were strongest in the summer season when flooded soil produced the strongest pulses of N₂O and NO compared to small drip-irrigated pulses. As agriculture continues to intensify in warmer climates, implementation of subsurface drip irrigation may reduce feedbacks of agriculture to climate change and air quality.

Introduction

Agricultural lands are responsible for a large portion of annual soil emissions of carbon (C) and nitrogen (N) trace gases (Aneja et al., 2009), consisting of both greenhouse gases and those which, at high concentrations, degrade local and regional air quality (Sha et al., 2021). Carbon dioxide (CO₂), the dominant biogenic greenhouse gas (IPCC 2019), is a primary product of the agricultural life cycle (Paustian et al., 2000); however, agricultural soils are now also the largest anthropogenic source of nitrous oxide (N₂O), a greenhouse gas with almost 300 times the warming potential of CO₂ (IPCC 2019, (Davidson & Kanter, 2014). Additionally, soils in agricultural regions are a major source of ozone-forming nitric oxide (NO) (Almaraz et al., 2018; Davidson & Kinglerlee, 1997; Sha et al., 2021), particularly in fields that are fertilized with N (Davidson, 2009) and that are located in high-temperature regions (Oikawa et al., 2015). Over one-third of cultivated lands, consisting largely of livestock forage crops, are situated in dryland ecosystems which are characterized by low and inconsistent water availability (White & Nackoney, 2003); scheduled irrigation is often used for popular high-quality forage crops grown in desert regions that require considerable water inputs (Putnam & Kallenbach, 1997), such as alfalfa (*Medicago sativa* L.) and sudangrass (*Sorghum bicolor* ssp. Sudanese). However, re-wetting of dry soils can trigger pulses of metabolic activity that release

gaseous emissions to the atmosphere at high rates, particularly if the transition from dry to wet soil conditions is rapid and large. To reduce agricultural feedbacks to climate change and air quality in dryland regions, links between irrigation and trace gas pulses need to be established and contextualized within broader patterns of climate and crop management.

Pulsed emissions of C and N trace gases have been repeatedly observed following soil rewetting in arid natural ecosystems (Andrews & Jenerette, 2020; Eberwein et al., 2020; Homyak et al., 2016; Miller et al., 2005) and their agricultural counterparts (Liang et al., 2016; Oikawa et al., 2014). Although soil re-wetting is a trigger for pulse occurrence, the magnitude and duration of pulses can be additionally modulated by interactions between temperature and nutrient availability, with the strongest pulsed emissions occurring in hot, nutrient-saturated soils (Liang et al., 2016; Oikawa et al., 2015) that occur frequently in arid agriculture. CO₂ pulses have been described as the "Birch effect," whereby rewetting of dry soils stimulates a spike in soil respiration by reactivating soil metabolism and increasing microbial access to C and N substrates, followed by decline in respiration as soils dry (Barnard et al., 2020; Birch, 1958; Schimel, 2018). However, recent evidence from high-temperature agriculture shows the opposite response of CO₂ fluxes to re-wetting, where fluxes are initially suppressed from limited O₂ availability (Oikawa et al., 2014). These findings suggest that the Birch effect may not be a universal response in drylands, particularly for soils with high clay content. Pulses of N₂O and NO following soil re-wetting have also been identified in dryland soils (Andrews & Jenerette, 2020; Eberwein et al., 2020; Galbally et al., 2008; Leitner et al.,

2017; Liang et al., 2016; Q. Wei et al., 2018; Yan et al., 2005) driven by similar microbial activation and substrate access. N₂O is generally produced in high-moisture, anaerobic soils or soil microsites via denitrification; conversely, NO is predominantly produced via nitrification in lower-moisture, aerobic soils (Schlesinger & Bernhardt, 2013). Therefore, N₂O and NO pulses may be asynchronous, with N₂O pulses occurring earlier when high-moisture conditions favor anaerobic soil microsites, followed by later occurrence of NO when soil moisture falls below a certain threshold. Irrigation strategies that manipulate the range and timing of soil moisture will likely alter the proportions of N₂O and NO production; however, microbial mechanisms driving N₂O and NO pulses are complex and less understood (Firestone & Davidson, 1989; Schimel, 2018), and studies comparing timing and magnitude of N₂O and NO pulses simultaneously in dry systems are sparse (Andrews & Jenerette, 2020; Eberwein et al., 2020).

Because re-wetting is the primary trigger for trace gas pulses, irrigation strategy is likely a major contributor to annual emissions from agricultural soils. Most agricultural fields are irrigated with traditional "flood" or "furrow" surface irrigation; however, flood irrigation applied to slow-draining clay soils in high-temperature regions results in extensive surface evaporation, exceeding 50% of irrigation inputs in some cases (Lu et al., 2017). Additionally, high temperatures coupled with rapid shifts in soil moisture during flooding are likely to stimulate pulses of soil C and N loss through trace gas emission pathways (Leon et al., 2014; Liang et al., 2016). Because surface irrigation promotes high losses of water and nutrients at the soil surface, subsurface drip irrigation has become a popular, water-conservative alternative (Velasco-Muñoz et al., 2019). By

installing drip-line infrastructure directly in the plant rhizosphere and releasing smaller quantities of water more continuously over time, growers can engineer more spatially and temporally efficient water usage. Proportionally less water is expected to be lost to evaporation by reducing surface pooling and less extreme shifts in soil moisture should correspondingly reduce, but not eliminate, trace gas pulses of C and N. Some evidence from vegetable and nut crops suggests drip irrigation reduces CO₂ emissions across the growing season (C. Wei et al., 2021), N₂O pulses following irrigation (Suddick et al., 2011; Q. Wei et al., 2018), and annual N₂O emissions (Deng et al., 2018; Kennedy et al., 2013; Kuang et al., 2021), compared to traditional flooding. Impacts on NO emissions are less conclusive, with studies reporting consistent NO emissions regardless of irrigation strategy (Sanchez-Martín et al., 2010) or only modest reductions in drip-irrigated emissions (Sánchez-Martín et al., 2008). However, whether drip irrigation can also reduce trace gas emissions from soils of forage crops, a dominant crop type grown in dryland regions, remains unclear.

Irrigation-induced pulses may differ throughout the growing season and across crops of differing nutrient acquisition strategies, complicating our understanding of irrigation effects on agricultural soil emissions. Most forage crops, such as sudangrass, require exogenous N inputs to produce competitive yields; a common practice is to apply fertilizer together with irrigation as "fertigation." Because fertilizers are applied as sporadic, large events, they can be a leaky source of N to hydrologic and gaseous emissions pathways (Davidson, 2009; Liu & Greaver, 2009; Suddick et al., 2011; Yan et al., 2005), compounding the impacts of fertigation on trace N pulses. Biogenic N fixation,

a strategy used by alfalfa, is a more continuous mechanism of N addition than fertigation that is somewhat decoupled from irrigation events. Studies in alfalfa have indicated the potential for drip irrigation to improve yield, save water, and retain soil nutrients (Fu et al., 2021; Zaccaria et al., 2017); sudangrass has received less research attention for irrigation improvements, but infrastructure targeting reduced runoff has resulted in higher, albeit less water-efficient, yields (Grismer & Bali, 2001). Whether these crop-specific water-nutrient interactions translate to reduced gaseous losses from dryland forage soils is not well understood; however, drip irrigation may be most beneficial for reducing trace gas emissions in fertigated crops like sudangrass. Although alfalfa and sudangrass differ in fertilizer requirements, both crops are harvested multiple times over the course of a growing season, and each successive stand will experience different ranges of soil temperature and potentially other soil conditions. Prior evidence demonstrates a positive correlation between temperature and trace gas pulses from agricultural soils, even in high-temperature regions (Liang et al., 2016; Oikawa et al., 2014, 2015); therefore, I expect hotter temperatures produced in the summer growing season (July-September) would result in larger pulses than the cooler, spring season (April-June). Similarly, temperature-emissions relationships in soils are modulated by soil moisture (Sihi et al., 2020; C. Wei et al., 2021; Zhao et al., 2020), indicating that differences in irrigation strategy effectiveness could be magnified in summer when temperatures are highest.

To investigate how agricultural irrigation influences trace gas emissions in drylands, I conducted a set of field experiments in the Imperial Valley, a region that

serves as a model for future agriculture under climate warming projections (IPCC 2019). As of 2018 (Ortiz, 2018), alfalfa (*Medicago sativa* L.) is the largest forage crop commodity for Imperial County, grown on 62,795 hectares (155,171 acres). Sudangrass (*Sorghum bicolor* spp. Sudanese), a high-biomass-producing grass, is the third most prevalent forage crop in the Imperial Valley, encompassing 21,675 hectares (53,562 acres). I chose to compare these two crops not only because of their popularity in the county but also because of differences in their N acquisition strategies. Alfalfa, an N-fixing legume, is generally not amended with fertilizer; conversely, sudangrass receives a large fertilizer application at planting (100–150 kg N ha⁻¹) followed by smaller applications (50 kg N ha⁻¹) throughout the growing season (Meister, 2004; Oikawa et al., 2015). Within this model system, I asked: how do two contrasting irrigation strategies, traditional surface flood irrigation and water-conservative subsurface drip irrigation, affect crop yield, water usage, and pulsed emissions of CO₂, N₂O, and NO, and does this effect change with crop species and season?

To answer these questions, I utilized a custom array of automated soil chambers, probes, and analyzers to quantify trace gas fluxes and corresponding soil conditions, *in situ* and at high temporal resolution, in a series of irrigation experiments. First, I predicted that, like other dryland systems, arid agricultural soils would experience drying-rewetting cycles that generate large, pulsed emissions of CO₂, N₂O, and NO. I expected that irrigated arid soils would produce CO₂ and N₂O pulses first followed by NO pulses as soils re-dry; however, given previous evidence from my study site, CO₂ fluxes could be suppressed rather than accelerated. Second, I predicted that drip irrigation

would produce smaller pulses and per-yield emissions of CO₂, N₂O, and NO compared to those produced by flooding and would increase water use efficiency while maintaining consistent crop yield. Third, I predicted that less N would be lost as N₂O and NO from soils containing N-fixing alfalfa compared to soils from fertilized sudangrass fields. Finally, I predicted that increasing seasonal temperatures from spring to summer would consequently increase CO₂, N₂O, and NO pulses and per-yield emissions. Testing hypotheses that compare surface flood and subsurface drip irrigation in crop-dependent and seasonal contexts improves our understanding of mechanisms driving trace gas emissions from dryland agriculture and explores the potential systemic benefits of water-conserving infrastructure in a hotspot of agricultural production.

Methods

Study site, focal species, and field setup

All field data were collected from experimental agricultural fields at the University of California Desert Research and Extension Center (DREC), located in Holtville, Imperial County, CA (32°N 480 42.6, 115°W 260 37.5, -18 m ASL elevation). Experimental agricultural fields at DREC, including my study fields, have been active since 1912 and have been used in previous studies that have explored alternative irrigation strategies for desert forage (Grismer & Bali, 2001; Zaccaria et al., 2017) and have reported high trace gas emissions from soils (Eberwein et al., 2015; Liang et al., 2016; Oikawa et al., 2014, 2015). Soils are characterized as deep alluvial (42% clay, 41% silt and 16% sand) with average pH of 8.3 and C and N content of 2.34% and 0.13%,

respectively (Oikawa et al., 2015). DREC experiences average annual precipitation of 38 mm and monthly mean air temperatures ranging 1 to 42°C (Oikawa et al., 2015).

I conducted a series of four campaigns in 2018-2020 that tested effects of irrigation type between two points of the calendar growing season (spring and summer) and between two valuable forage crop species, alfalfa and sudangrass, in a fully-factorial design. To accommodate fertilizer applications, sudangrass plants were grown in beds separated by 1.5 m with 20-cm deep furrows. Two adjacent 0.20-acre fields, separated by a 15-meter strip of bare soil, were used as experimental testbeds to evaluate irrigation inputs for each crop. One field was irrigated by gravity-fed flood irrigation, the most prevalent irrigation practice in the Imperial Valley; the other field was irrigated via subsurface rubber drip tape installed 10 to 15 cm below the soil surface and within crop rows. Alfalfa was not grown in a furrow system and so received flood irrigation across the whole field; conversely, sudangrass was grown in beds and received flood irrigation in furrows. Fields were irrigated as needed, usually every 10-14 days or when soil surface volumetric water content fell below $0.10 \text{ cm}^3 \text{ cm}^{-3}$. Fertilizer applications to sudangrass were as ammonia (NH_3) in flood-irrigated furrows, and urea (UN) was applied as fertigation in drip-irrigated beds.

Experimental design

Sudangrass seeds were planted April 17, 2018 and received initial irrigation. Both flood- and drip-irrigated fields were irrigated on April 18, May 4, and May 17 prior to first harvest on June 25. During this time, flood-irrigated fields were fertilized with 100 kg N ha^{-1} on April 18; drip-irrigated fields were fertilized during each irrigation event

with 25 kg N ha⁻¹ each (75 kg N ha⁻¹ total). Aboveground biomass was harvested again August 28 following no fertilizer additions and five and seven irrigation events in flood and drip, respectively, between June 25 and August 28. A final harvest took place November 28; both fields received four irrigation events prior to harvest (August 28 to November 28). The flood-irrigated field was fertilized with 100 kg N ha⁻¹ on September 7 and the drip-irrigated field was fertilized with two applications of 25 kg N ha⁻¹ each on September 7 and October 5 (50 kg N ha⁻¹ total). I measured soil emissions during the first fertilization event (April 16-May 21) and the growth period prior to the last harvest (August 28 to September 25).

In 2019, fields were tilled and alfalfa was planted in fields on March 15; hay was harvested on May 17, June 24, July 31, August 26, and October 12. As a perennial crop, alfalfa continued to be harvested in 2020 on January 17, March 10, April 13, May 27, and June 24. No fertilizer was added to alfalfa plots. During each growth period, flood-irrigated fields received between one and three large irrigation events and drip-irrigated fields received between one and seven small irrigation events. I measured soil emissions prior to the third (June 26-July 14, 2019) and tenth (May 29-June 27) harvests; during the third growth period, flood and drip fields both received two irrigations each. During the tenth growth period, flood and drip fields received one and seven irrigations, respectively; however, one drip event was unintentional due to a damaged water pipe, and another event was small compared to other drip events (<0.01 acft).

Soil climate and trace gas measurements

At the beginning of each sampling campaign, eight polyvinyl chloride (PVC) soil collars (20-cm diameter) were installed (n=4 collars per field). Collars were positioned in crop rows and pushed into the ground to 5-cm depth; plant biomass was removed from inside the collars to avoid plant interference with sensors housed inside automated chambers. An automated long-term chamber (LI-8100-104; LI-COR Bioscience, Lincoln, NE, USA) was fitted on each soil collar, and accompanying 5-cm soil temperature (LI-8150-203 thermistor probe; LI-COR Bioscience, Lincoln, NE, USA) and moisture (LI-GS1 probe; LI-COR Bioscience, Lincoln, NE, USA) probes were inserted into soils adjacent to each collar. All eight automated chambers were then connected to a custom trace gas analyzer array housed inside an insulated, air-conditioned box stationed between the two fields.

Air collected from an actively-measuring chamber was passed through a multiplexer (LI-8150; LI-COR Bioscience, Lincoln, NE, USA) followed by a sequence of three trace gas analyzers: 1) a N₂O/CO cavity-ringdown infrared analyzer (Los Gatos Research, San Jose, CA, USA); 2) a CO₂ infrared gas analyzer system (LI-8100A; LI-COR Bioscience, Lincoln, NE, USA); and 3) a coupled nitrogen dioxide (NO₂) converter and NO monitor (Model 401/410, 2B Technologies, Boulder, CO, USA). The multiplexer, N₂O/CO analyzer, and the CO₂ system formed a closed loop that returned sample air to the active chamber which was sealed over the soil collar; however, the NO₂/NO monitor is an open system, so a portion of air was siphoned from the sample loop through a one-way check valve and was measured as NO (and NO₂). By

incorporating an NO "leak" in the sample loop, I assumed a small amount of error was introduced into my flux calculations from dilution of trace gas concentrations.

Concentrations of CO₂, N₂O, and NO were measured simultaneously at rates of 1, 1, and 10 seconds, respectively; I did not examine NO₂ or CO in this study. The measurement procedure for each chamber included a 30-second pre-measurement purge, a 2.5-minute active measurement period for trace gas concentrations and soil climate status, and a 30-second post-measurement purge before cycling to the next chamber. Inactive chambers remained open and away from collars to minimize interference with soil-atmosphere exchanges; during active measurement, a chamber swiveled and closed over the collar to form a seal. Each measurement cycle through all eight chambers took place every 30 minutes and was controlled by the LI-8100A.

Ancillary soil chemistry sampling

In conjunction with each emissions campaign, I collected 5-cm² x 10-cm deep soil cores from rows/beds adjacent to each soil collars at timepoints prior to and following irrigation to track changes in extractable N (ammonium NH₄⁺ and nitrate/nitrite NO₂⁻ + NO₃⁻). In alfalfa fields, I collected cores immediately before irrigation (day 0) and 2 days post-irrigation. In sudangrass plots, I collected cores more frequently at pre- and 1, 3, 5, and 7 days post-irrigation. I collected additional cores at 2 and 10 days post-wetting in early-season sudangrass to capture changes in N following initial fertilization of the fields. Each core was homogenized in a plastic bag, transported to the lab on ice, and extracted in 1:10 soil weight:solution volume ratio of 2M KCl solution following standardized methods for inorganic N analysis (Carter & Gregorich, 2006). Briefly,

extracts were shaken for 1 hour, centrifuged, and gravity-filtered through 11-micron filter paper at room temperature followed by analysis via phenate method for ammonium and via acidification and automated cadmium coil reduction for nitrate/nitrite (Seal Analytical Inc., AQ2 Discrete Analyzer; Mequon, Wisconsin).

Data processing and statistical methods

Harvested biomass and water use data were collected at field scale; therefore, I statistically compared individual crop type, season, and irrigation type using 3-way analysis of variance (ANOVA) but without including interactions among groups. From biomass and water data, I calculated water use efficiency (WUE) of productivity for by dividing harvested biomass by total water use for each field. I tested all combinations of crop, season, and irrigation effects for predicting WUE using 3-way ANOVA. Finally, I tested all treatment combination effects for predicting soil extractable NH_4^+ and NO_3^- using repeated-measures ANOVA.

I batch processed instantaneous flux and climate data for each emissions collection campaign using methods adapted from Andrews & Jenerette (2020) and Krichels et al. (*in review*). Briefly, instantaneous fluxes of CO_2 , N_2O , and NO were calculated as the regression coefficient of linear increase in gas concentration data during the 2.5-minute active chamber measurement period, corrected for soil collar dimensions and atmospheric parameters following the Ideal Gas Law (Davidson et al., 2000). Instantaneous fluxes of each gas were compiled and integrated with instantaneous soil temperature and moisture measurements using a publicly-accessible R script (Andrews & Krichels 2021). My final dataset consisted of measurements of CO_2 , N_2O , NO , soil

temperature, and soil moisture for each chamber, with one replicate set of eight chamber measurements occurring every 30 minutes. From these high-resolution measurements, I can capture interactive responses to rapid changes in soil conditions, such as during re-wetting, that could be missed or misinterpreted at coarser temporal scales.

In addition to instantaneous measurements, I extracted the magnitude and timing of each peak instantaneous flux and climate parameter, calculated as the maximum instantaneous measurement recorded over a 10-day time series. I extracted 10-day average temperature and moisture values as well as 10-day cumulative flux values, the latter of which were calculated as the integrated area under each time series curve using linear trapezoidal method. I assessed effects of irrigation type (flood vs. drip), crop type (alfalfa vs. sudangrass), and part of growing season (spring vs. summer) on 10-day peak and total fluxes and peak and average temperature and moisture by constructing a general linear model (GLM) for each response of interest. I tested all combinations of crop, season, and irrigation using 3-way ANOVA and selected reduced models with the lowest Akaike Information Criterion (AICc).

To estimate emissions across an entire harvest period, and thereby extract per-yield emissions values, multiplied my integrated total fluxes by the number of irrigation events for that harvest and divided the total by the per-area yield harvested; the result was the estimated amount of each trace gas emitted per amount of biomass harvested. Representing emissions in this way produced scalable data for county-level agricultural emissions in each crop and irrigation type and allowed us to compare the effectiveness of drip irrigation more directly across crop types and seasons.

Results

Harvested biomass, water use, and soil N pools across crop, season, and irrigation type

Total water usage did not significantly differ across crop ($p=0.76$), season ($p=0.61$), or irrigation ($p=0.52$) individually; however, water use in flooded fields tended to be higher for sudangrass plots compared to alfalfa plots while the opposite trend occurred in drip-irrigated fields (Table 1). Within each crop*season pair, harvested yield differed by less than 50 kg across irrigation treatments was generally higher in drip plots. Water use efficiency (WUE) of productivity did not significantly differ across crop ($p=0.14$), season ($p=0.53$), or irrigation ($p=0.14$) treatments individually but was highest in sudangrass drip plots, 3-4 times higher than sudangrass flood plots and 2-10 times higher than all alfalfa plots (Table 1). WUE in early-season alfalfa was higher in flood plots, but drip plots in late-season alfalfa had the highest WUE of all alfalfa treatment combinations.

Soil extractable NH_4^+ was higher in spring sudangrass samples than all other crop*season combinations (Crop $p=0.007$; Season $p<0.001$; Crop*Season $p=0.03$), coinciding with initial fertilization of sudangrass fields (Figure 2.1). Irrigation did not have a significant overall effect on extractable NH_4^+ ($p=0.10$); however, extractable NH_4^+ in the spring season was lower in drip than flood plots (Season*Irrigation $p=0.01$). Soil extractable NO_3^- was higher in summer plots than spring plots ($p=0.03$), particularly in drip-irrigated treatments (Season*Irrigation $p=0.04$).

Responses of CO₂, N₂O, and NO fluxes to scheduled irrigation in two forage crops

CO₂ fluxes ranged from near-zero to 991 $\mu\text{g CO}_2\text{-C m}^{-2} \text{ s}^{-1}$ in sudangrass and near-zero to 862 $\mu\text{g CO}_2\text{-C m}^{-2} \text{ s}^{-1}$ in alfalfa, with high spatial heterogeneity across chambers (Figure 2.2). N₂O fluxes were also spatially-variable and ranged near-zero to 3.53 $\mu\text{g N}_2\text{O-N m}^{-2} \text{ s}^{-1}$ in sudangrass and near-zero to 2.76 $\mu\text{g N}_2\text{O-N m}^{-2} \text{ s}^{-1}$ in alfalfa (Figure 2.3). NO fluxes ranged 0 to 893 $\text{ng NO-N m}^{-2} \text{ s}^{-1}$ in sudangrass and near-zero to 88.2 $\text{ng NO-N m}^{-2} \text{ s}^{-1}$ in alfalfa (Figure 2.4).

CO₂ fluxes were generally suppressed in response to irrigation followed by substantial ramp-up at ~200 hours post-irrigation (Figure 2.2,2.5). In sudangrass, flood-irrigated plots produced more consistent CO₂ fluxes through time while experiencing a larger range of soil moisture (7-59%). Conversely, drip-irrigated plots initially suppressed CO₂ more but under drier conditions produced larger CO₂ fluxes than flood plots, while experiencing a soil moisture range (7-32%) almost half that of flood plots (Figure 2.5). Alfalfa plots experienced similar maximum soil moisture levels but flood plots experienced more complete soil drying and therefore a larger soil moisture range (10-57%) than drip plots (19-58%). CO₂ fluxes tended to be lower in alfalfa than sudangrass plots, and drip irrigation suppressed CO₂ fluxes in alfalfa for longer and at lower magnitudes (Figure 2.5).

Rapid N₂O pulses occurred almost simultaneously to CO₂ suppression and dissipated by 100 hours post-irrigation (Figure 2.5). N₂O pulses were on average stronger in alfalfa than sudangrass and in flood- than drip-irrigated plots ($p < 0.001$). Following N₂O pulses, NO pulses occurred between 50 and 300 hours post-irrigation. NO pulses

were much stronger in sudangrass than alfalfa ($p < 0.001$), reaching peak fluxes that differed by almost a magnitude on average (Figure 2.5). NO pulses were also stronger in flood- than drip-irrigated plots.

10-day mean temperature and moisture conditions and pulse responses of CO₂, N₂O, and NO across crop, season, and irrigation treatments

Mean soil temperatures during 10-day post-irrigation periods were 4-6 °C cooler in spring sudangrass plots than other crop*season treatments (Crop*season $p < 0.001$; Figure 2.6). Mean soil moisture was higher in alfalfa (41%) compared to sudangrass (25%; $p < 0.001$) and in spring (38%) compared to summer (29%; $p = 0.017$; Figure 2.6, Table 2.2). Irrigation effects on soil moisture diverged between crop types (Crop*Irrigation $p < 0.001$); flood irrigation resulted in similar soil moisture between alfalfa (36%) and sudangrass (31%), but drip irrigation decreased soil moisture in sudangrass plots (20%) while increasing moisture in alfalfa plots (46%).

Differences in total CO₂, N₂O, and NO emissions over the 10-day measurement period were quantified using a fully-factorial generalized linear model (Table 2.2, Figure 2.6). Total CO₂ pulsed emissions were larger ($p < 0.001$) in sudangrass (113 (15.3) g CO₂-C m⁻²) than in alfalfa (52.9 (6.17) g CO₂-C m⁻²). Pulses were also higher ($p = 0.01$) from flood-irrigated plots (90.8 (12.3) g CO₂-C m⁻²) compared to drip-irrigated plots (76.4 (14.22) g CO₂-C m⁻²). In a crop*irrigation interaction ($p = 0.03$), alfalfa drip plots produced lower 10-day CO₂ emissions (39.1 (6.12) g CO₂-C m⁻²) compared to all other groups (67.9-114 (9.32-23.6) g CO₂-C m⁻²). Conversely, in a crop*season interaction ($p = 0.008$), summer sudangrass plots produced higher 10-day CO₂ emissions (171 g CO₂-

C m⁻²) than all other groups (51.0-83.8 (3.98-13.4) g CO₂-C m⁻²). In a marginally-significant (p=0.06) crop*season*irrigation interaction, the highest CO₂ 10-day emissions were from summer sudangrass flooded plots (173 (42.9) g CO₂-C m⁻²) while the lowest emissions were from summer alfalfa drip plots (28.7 (17.7) g CO₂-C m⁻²).

Total N₂O emissions over the 10-day measurement period were larger (p<0.001) in sudangrass (62.7 (13.7) mg N₂O-N m⁻²) than in alfalfa (35.3 (12.2) mg N₂O-N m⁻²). N₂O pulses were also higher (p=0.02) from flood-irrigated plots (64.1 (15.4) mg N₂O-N m⁻²) compared to drip-irrigated plots (35.1 (10.2) mg N₂O-N m⁻²). In a season*irrigation interaction (p=0.02), flood and drip irrigation produced similar N₂O emissions in spring (53.8 and 42.8 mg N₂O-N m⁻², respectively) but diverged in summer, with flood plots (87.8 (41.8) mg N₂O-N m⁻²) increasing N₂O emissions and drip plots (19.6 (8.03) mg N₂O-N m⁻²) decreasing N₂O emissions.

Total NO emissions over the 10-day measurement period responded similarly to those of N₂O. Pulses were larger (p<0.001) in sudangrass (19.9 (5.28) mg NO-N m⁻²) than in alfalfa (2.80 (0.289) mg NO-N m⁻²) and were higher (p=0.01) from flood-irrigated plots (14.8 (5.77) mg NO-N m⁻²) compared to drip-irrigated plots (8.49 (1.68) mg NO-N m⁻²). In a season*irrigation interaction (p=0.002), flood and drip irrigation produced similar NO emissions in spring (9.46 and 10.3 mg NO-N m⁻², respectively) but diverged in summer, with flood plots increasing NO emissions (26.9 (18.4) mg NO-N m⁻²) and drip plots decreasing in NO emissions (4.93 (1.59) mg NO-N m⁻²).

Discussion

When I compared the sizes of trace gas pulses, water use, and hay yield across two alternative locations of irrigation, surface flood and subsurface drip, I found high potential of drip irrigation for alleviating hydrologic and atmospheric consequences of forage agriculture in arid climates. My study provides field-based evidence that irrigated agriculture produces CO₂, N₂O, and NO pulses using data collected at among the highest temporal resolutions to date. Compared to traditional surface irrigation, subsurface drip increased yield of both alfalfa and sudangrass and simultaneously reduced per-yield water use and per-yield soil emissions of CO₂, N₂O, and NO. In my study, drip irrigation in alfalfa produced 106.9% hay yield, used 89.3% water, and produced 41.1% CO₂, 85.8% N₂O, and 72.8% NO emissions of flood-irrigated soils. Similarly, drip irrigation in sudangrass produced 106.1% hay yield, used 31.6% water, and produced 103.4% CO₂, 37.5% N₂O, and 38.3% NO emissions of flood-irrigated soils. The benefits of drip irrigation for reducing nitrogenous soil emissions were particularly strong for sudangrass, a crop requiring fertigation N inputs, and in summer harvests, when average soil temperature and moisture were also high. Coupled high temperature-high substrate conditions are known to produce strong C and N pulse responses in agricultural soils in a laboratory setting (Liang et al., 2016); I report that irrigation is also a control over pulses of CO₂, and especially of N₂O and NO, such that more water-conservative methods produce smaller pulses even in optimal pulse environments.

CO₂, N₂O, and NO pulse emissions in arid forage agriculture

Soil irrigation triggered emission pulses (N₂O and NO) or suppression (CO₂) of trace gases which lasted hours (N₂O) to days (NO and CO₂). I observed immediate suppression of CO₂ following irrigation, which does not follow the traditional Birch effect response but has been reported previously at this site (Oikawa et al., 2014) and is indicative of O₂ limitation. Following CO₂ (and O₂) suppression, N₂O pulses occurred, peaking between 24 and 48 hours, followed by NO pulses at 50-200 hours post-wetting. Because N₂O pulses were synchronized with CO₂ suppression and NO pulses coincided with CO₂ recovery, I suspect that O₂ depletion was a primary mechanism driving soil metabolic processes following irrigation (Sihi et al., 2020; Yong Wang et al., 2017) and suggest that future work investigate these mechanisms more explicitly. NO, and to a lesser extent CO₂, also displayed diel emissions patterns that increased during the day and decreased at night. Few studies have explored diel fluctuations of NO (Meixner et al., 1997) and as a result may be inaccurately estimating daily emission rates that I capture here. N₂O followed by NO pulses can occur within minutes to hours of rewetting in non-agricultural drylands (Andrews & Jenerette, 2020; Eberwein et al., 2020); I suspect that the slower and longer pulses of N₂O and NO that I observed were due to more thorough saturation of soils maintained for a longer period of time in my clay-rich fields.

Effects of irrigation type on pulses and per-yield emissions of CO₂, N₂O, and NO

In almost all field campaigns, drip irrigation reduced total and per-yield emissions of CO₂, N₂O, and NO compared to flood irrigation. Consistent with my hypothesis, soils experiencing less extreme shifts in moisture resulted in weaker pulse responses; in both

crop types, drip-irrigated soils experienced smaller soil moisture ranges than did their flooded counterparts and soil moisture was slower to peak. Although N₂O emissions reductions in drip irrigation are well-documented (Kuang et al., 2021), my results in sudangrass show much stronger reductions than the estimated global average of 32% lower N₂O emissions, further indicating that drip irrigation should be a standard practice for forage grasses grown in high-temperature systems. For the campaign (spring alfalfa) that experienced infrastructural malfunctions, elevated water use during that harvest period still elevated trace N emissions, particularly of N₂O, further supporting my hypothesis that consistently lower water use decreased soil trace gas emissions. Drip-irrigated soils generally had more consistent extractable N pools over time than did flood-irrigated soils as well, particularly in fertilized sudangrass plots. I suspect that targeted, slow-release drip irrigation retained more N for biological use, while flood irrigation flushed soils with N over a shorter time period and caused more N to leak through trace gas (and hydrologic) pathways (Homyak et al., 2016; Leitner et al., 2017; Yahui Wang et al., 2020). Although drip-irrigated soils tended to be hotter than flood-irrigated soils, particularly in summer, the magnitude of soil drying-rewetting cycles and incorporation of fertilizer were primary determinants of trace gas pulse size.

Crop type contributions to irrigation effectiveness

Differences in plant physiology and corresponding management strategies between sudangrass and alfalfa resulted in a different effectiveness of drip compared to flood irrigation. Although alfalfa and sudangrass have similar water requirements (Grismer, 2001), irrigation in alfalfa fields was applied to the whole field as opposed to

concentrated in furrows in sudangrass fields. Drip irrigation in alfalfa maintained high soil moisture longer, while in sudangrass drip reduced overall soil moisture, preventing unnecessary evaporative losses from flooded furrows. Therefore, drip irrigation increased WUE over flood irrigation, consistent with my predictions, and was most effective at reducing per-yield water use in sudangrass plots while producing modest reductions in alfalfa. I did not expect to observe (small) increases in yield from drip-irrigated plots; however, increased yield and water use efficiency are consistent with other studies testing drip irrigation in alfalfa (Zaccaria et al., 2017).

In terms of per-yield trace gas emissions, drip irrigation in alfalfa primarily reduced CO₂ emissions compared to flood irrigation, while in sudangrass it predominantly reduced N₂O and NO emissions. In alfalfa, CO₂ suppression was maintained longer in drip compared to flooded fields, which I attribute to sustained high soil moisture and hypoxic conditions in soil (Davidson et al., 2012; Sihi et al., 2020). These same conditions would also be favorable for N₂O production via denitrification, but I observed smaller N₂O pulses and accumulation of extractable N in alfalfa drip soils, suggesting that alfalfa N₂O production may have been limited by substrate availability (Liang et al., 2015). In sudangrass, drip irrigation reduced trace gas N emissions by 60-70%, suggesting that N was less leaky from drip-irrigated soils where fertigation was slower, in lower amounts, and in a readily-accessible location in the rhizosphere. Conversely, extractable NH₄⁺ measured in sudangrass flood fertigation showed much larger increases that I expect were immediately lost rather than being incorporated into plant biomass, resulting in lower hay yields compared to drip-irrigated counterparts. In

sudangrass, drip irrigation did not reduce CO₂ emissions and increased spatial variability of CO₂ pulses; since soil moisture was overall lower in these plots, anaerobic conditions that would favor CO₂ suppression and N₂O production were likely present for a shorter time and/or in a smaller number of microsites compared to flooded plots. However, large reductions in both N₂O and NO in drip fertigation more than offset unchanged or slightly increased CO₂ emissions from sudangrass plots. My findings are partially supported by a recent review of irrigation effects on greenhouse gas emissions (Sapkota et al., 2020) which reported either no change or higher CO₂ emissions from reduced irrigation practices, depending on crop of interest. Based on these findings, drip-line implementation lowered overall emissions from alfalfa and sudangrass compared to surface irrigation but predominantly reduced CO₂ emissions in alfalfa and N emissions in sudangrass.

Seasonal contributions to irrigation effectiveness

CO₂ emissions were larger in soils measured in summer compared to spring; these findings are consistent with my hypothesis that seasonal soil temperature and moisture interactions drive soil respiration patterns. As expected, over the course of the growing season, average temperatures generally increased. Interestingly, average soil moisture also increased later in the growing season, particularly in sudangrass, which could be a consequence of soil compaction and slower rates of water infiltration with subsequent harvests (de Lima et al., 2017) as well as slight increases in amount of water added during irrigation. The combination of increases to both temperature and moisture explain most clearly the seasonal increases in CO₂ pulses from both flood and drip irrigated soils,

as microbial enzyme kinetics and substrate availability would both be expected to increase in these conditions (Bowling et al., 2011; Davidson et al., 2012; Liang et al., 2016). However, in terms of per-yield emissions, seasonal patterns suggest CO₂ emissions were maintained in drip irrigation compared to increasing in flood-irrigated conditions.

N₂O and NO emissions from flood-irrigated soils also increased from spring to summer, supporting my hypotheses that higher temperature and moisture would induce stronger pulse responses and per-yield emissions. However, N emissions from drip generally diverged from flood-irrigated soils in summer months, resulting in decreased per-yield emissions of N₂O and sustained per-yield NO for these fields. I expect that the targeted nature of drip lines reduced the number of anaerobic microsites for N₂O production and reduced the spread of N outside of the rhizosphere, even in fertilized sudangrass, during subsequent harvests. Because root structures were left intact through the entire growing season, rhizosphere size may also have increased at higher rates in drip compared to flood fields (Xiao et al., 2015) and stabilized a larger portion of soil N from drip lines. Larger belowground biomass in drip-irrigated plots could result in higher root carbon use efficiency that maintained lower CO₂ emissions and reduced losses of N from the soil. In fields with less targeted flood irrigation, root structures that increased more slowly over time would still be less efficient at capturing N, thereby promoting higher N losses as N₂O and NO in high temperature and moisture conditions. I note that because both forage crops experienced multiple harvests over one growing season, I cannot necessarily separate effects of seasonal differences in weather from effects of

harvesting history. I suggest future work to explore each of these factors individually to identify whether the benefits of drip irrigation in late season are more strongly linked to seasonal weather regimes or harvest practices.

Potential effectiveness of drip irrigation at the county and state scale

Using county-level agricultural land data collected for Imperial County in 2018 (Ortiz, 2018), I estimated growing-season yield, water use, and emissions that would be produced by alfalfa and sudangrass land area in flood-irrigated and drip-irrigated scenarios from my small-field measurements. I note that while my estimates of sudangrass yield are comparable to those reported, my estimates of alfalfa yield in both irrigation scenarios are much higher than reported. Alfalfa and sudangrass production span 62,795 hectares and 21,675 hectares, respectively; together, these crops account for 61% of county land dedicated to field crops and 39% of county agricultural land. County-wide implementation of drip irrigation for these two crops could increase alfalfa yield by 120,800 metric tons (MT) yr⁻¹ and sudangrass yield by 20,330 MT yr⁻¹ while reducing irrigation requirements by 0.383 km³, approximately 10% of Imperial County's 3.824 km³ annual water allotment. Extrapolating from my small-field data, I estimate that drip implementation in both alfalfa and sudangrass could decrease the global warming potential (GWP) of Imperial County by 1,488,149 MT CO₂e yr⁻¹ (0.003% global annual emissions (EIA, 2020)) and reduce emitted NO by 63.48 MT yr⁻¹. Although there are costs associated with additional infrastructure, I find that county-wide drip implementation for two popular crops has large potential benefits for reducing

greenhouse gas emissions and modest benefits for improving air quality in Imperial County and similar high-temperature regions.

Conclusion

Agricultural soils in drylands are a large source of trace gas emissions, which include greenhouse gases (CO₂ and N₂O) and air pollutants (NO); the majority of emissions from these systems occur following scheduled irrigation events which also put pressure on limited water resources in dryland regions. I show that traditional surface irrigation produces large pulses of CO₂, N₂O, and NO in two popular forage crops in the Imperial Valley; however, implementation of water-conservative subsurface drip irrigation can reduce trace gas emission pulses, and corresponding annual emissions, of these gases while simultaneously reducing water use and improving yield. In crop-specific contexts, drip irrigation in unfertilized alfalfa largely reduced per-yield CO₂ emissions while in fertilized sudangrass it reduced N₂O and NO emissions to rates 37.5% and 38.3% of flooded fields, respectively. Drip irrigation also proved more advantageous with seasonal increases in temperature and moisture, avoiding the increases in pulses that were experienced in flood-irrigated fields. To meet climate change mitigation scenarios (IPCC 2019) and to improve public health (Hall et al., 1996), regional management strategies for agriculture must be improved; for dryland regions like the Imperial Valley, I find subsurface drip irrigation to be a win-win-win alternative for food production, water use, and harmful soil emissions.

References

- Almaraz, M., Bai, E., Wang, C., Trousdell, J., Conley, S., Faloona, I., & Houlton, B. Z. (2018). Agriculture is a major source of NO_x pollution in California. *Science Advances*, 4(1), eaao3477.
- Andrews, H. M., & Jenerette, G. D. (2020). Exotic grass litter modulates seasonal pulse dynamics of CO₂ and N₂O, but not NO, in Mediterranean-type coastal sage scrub at the wildland-urban interface. *Plant and Soil*, 456(1), 339–353.
- Andrews, H.M., & Krichels, A. (2021). TraceGasArray: Calculation and integration of trace gas fluxes and soil climate data for high-resolution *in situ* chamber array. GitHub repository: <https://github.com/handr003/TraceGasArray>.
- Aneja, V. P., Schlesinger, W. H., & Erisman, J. W. (2009). Effects of agriculture upon the air quality and climate: research, policy, and regulations. *Environmental Science & Technology*, 43(12), 4234–4240.
- Barnard, R. L., Blazewicz, S. J., & Firestone, M. K. (2020). Rewetting of soil: revisiting the origin of soil CO₂ emissions. *Soil Biology & Biochemistry*, 107819.
- Birch, H. F. (1958). The effect of soil drying on humus decomposition and nitrogen availability. *Plant and Soil*, 10(1), 9–31.
- Bowling, D. R., Grote, E. E., & Belnap, J. (2011). Rain pulse response of soil CO₂ exchange by biological soil crusts and grasslands of the semiarid Colorado Plateau, United States. *Journal of Geophysical Research*, 116(G3), 2197.
- Carter, M. R., & Gregorich, E. G. (Eds.). (2006). *Soil Sampling and Methods of Analysis: Second Edition*. Taylor & Francis Group.
- Davidson, E. A. (2009). The contribution of manure and fertilizer nitrogen to atmospheric nitrous oxide since 1860. *Nature Geoscience*, 2(9), 659–662.
- Davidson, E. A., & Kanter, D. (2014). Inventories and scenarios of nitrous oxide emissions. *Environmental Research Letters: ERL [Web Site]*, 9(10), 105012.
- Davidson, E. A., Keller, M., Erickson, H. E., Verchot, L. V., & Veldkamp, E. (2000). Testing a conceptual model of soil emissions of nitrous and nitric oxides: using two functions based on soil nitrogen availability and soil water content, the hole-in-the-pipe model characterizes a large fraction of the observed variation of nitric oxide and nitrous oxide emissions from soils. *AIBS Bulletin*, 50(8), 667–680.

- Davidson, E. A., & Kinglerlee, W. (1997). A global inventory of nitric oxide emissions from soils. *Nutrient Cycling in Agroecosystems*, 48, 37–50.
- Davidson, E. A., Samanta, S., Caramori, S. S., & Savage, K. (2012). The Dual Arrhenius and Michaelis-Menten kinetics model for decomposition of soil organic matter at hourly to seasonal time scales. *Global Change Biology*, 18(1), 371–384.
- de Lima, R. P., da Silva, A. P., Giarola, N. F. B., da Silva, A. R., & Rolim, M. M. (2017). Changes in soil compaction indicators in response to agricultural field traffic. *Biosystems Engineering*, 162, 1–10.
- Deng, J., Guo, L., Salas, W., Ingraham, P., Charrier-Klobas, J. G., Froelking, S., & Li, C. (2018). Changes in irrigation practices likely mitigate nitrous oxide emissions from California cropland. *Global Biogeochemical Cycles*, 32(10), 1514–1527.
- Eberwein, J. R., Homyak, P. M., Carey, C. J., Aronson, E. L., & Jenerette, G. D. (2020). Large nitrogen oxide emission pulses from desert soils and associated microbiomes. *Biogeochemistry*, 149(3), 239–250.
- Eberwein, J. R., Oikawa, P. Y., Allsman, L. A., & Jenerette, G. D. (2015). Carbon availability regulates soil respiration response to nitrogen and temperature. *Soil Biology & Biochemistry*, 88(June), 158–164.
- EIA. (2020). *U.S. Energy-Related Carbon Dioxide Emissions, 2019*. e U.S. Energy Information Administration (EIA), U.S. Department of Energy.
- Firestone, M. K., & Davidson, E. A. (1989). Microbiological basis of NO and N₂O production and consumption in soil. In *Exchange of Trace Gases between Terrestrial Systems and the Atmosphere* (pp. 7–21).
- Fu, B., Li, Z., Gao, X., Wu, L., Lan, J., & Peng, W. (2021). Effects of subsurface drip irrigation on alfalfa (*Medicago sativa* L.) growth and soil microbial community structures in arid and semi-arid areas of northern China. *Applied Soil Ecology: A Section of Agriculture, Ecosystems & Environment*, 159, 103859.
- Galbally, I. E., Kirstine, W. V., Meyer, C. P., & Wang, Y. P. (2008). Soil–Atmosphere Trace Gas Exchange in Semiarid and Arid Zones. *Journal of Environmental Quality*, 37, 599–607.
- Grismer, M. E. (2001). Sudangrass uses water at rates similar to alfalfa, depending on location. *California Agriculture*, 55(4), 44–48.

- Grismer, M. E., & Bali, K. M. (2001). Reduced-runoff irrigation of Sudan grass hay, Imperial valley, California. *Journal of Irrigation and Drainage Engineering*, 127(5), 319–323.
- Hall, S. J., Matson, P. A., & Roth, P. M. (1996). NO_x emissions from soil: Implications for Air Quality Modeling in Agricultural Regions. *Annual Review of Energy and the Environment*, 21(1), 311.
- Homyak, P. M., Blankinship, J. C., Marchus, K., Lucero, D. M., Sickman, J. O., & Schimel, J. P. (2016). Aridity and plant uptake interact to make dryland soils hotspots for nitric oxide (NO) emissions. *Proceedings of the National Academy of Sciences of the United States of America*, 113(19), E2608–E2616.
- IPCC, 2019: Climate Change and Land: an IPCC special report on climate change, desertification, land degradation, sustainable land management, food security, and greenhouse gas fluxes in terrestrial ecosystems [P.R. Shukla, J. Skea, E. Calvo Buendia, V. Masson-Delmotte, H.-O. Pörtner, D. C. Roberts, P. Zhai, R. Slade, S. Connors, R. van Diemen, M. Ferrat, E. Haughey, S. Luz, S. Neogi, M. Pathak, J. Petzold, J. Portugal Pereira, P. Vyas, E. Huntley, K. Kissick, M. Belkacemi, J. Malley, (eds.)]. In press.
- Kennedy, T. L., Suddick, E. C., & Six, J. (2013). Reduced nitrous oxide emissions and increased yields in California tomato cropping systems under drip irrigation and fertigation. *Agriculture, Ecosystems & Environment*, 170, 16–27.
- Krichels, A., Homyak, P., Aronson, E., Sickman, J., Botthoff, J., Shulman, H., Piper, S., Andrews, H., & Jenerette, G.D. (*in review*). Rapid nitrate reduction produces pulsed NO and N₂O emissions following wetting of dryland soils. *Biogeosciences*.
- Kuang, W., Gao, X., Tenuta, M., & Zeng, F. (2021). A global meta-analysis of nitrous oxide emission from drip-irrigated cropping system. *Global Change Biology*. <https://doi.org/10.1111/gcb.15636>
- Leitner, S., Homyak, P. M., Blankinship, J. C., Eberwein, J., Jenerette, G. D., Zechmeister-Boltenstern, S., & Schimel, J. P. (2017). Linking NO and N₂O emission pulses with the mobilization of mineral and organic N upon rewetting dry soils. *Soil Biology & Biochemistry*, 115, 461–466.
- Leon, E., Vargas, R., Bullock, S., Lopez, E., Panosso, A. R., & La Scala, N. (2014). Hot spots, hot moments, and spatio-temporal controls on soil CO₂ efflux in a water-limited ecosystem. *Soil Biology & Biochemistry*, 77, 12–21.

- Liang, L. L., Eberwein, J. R., Allsman, L. A., Grantz, D. A., & Jenerette, G. D. (2015). Regulation of CO₂ and N₂O fluxes by coupled carbon and nitrogen availability. *Environmental Research Letters: ERL [Web Site]*, 10(3), 034008.
- Liang, L. L., Grantz, D. A., & Jenerette, G. D. (2016). Multivariate regulation of soil CO₂ and N₂O pulse emissions from agricultural soils. *Global Change Biology*, 22(3), 1286–1298.
- Liu, L., & Greaver, T. L. (2009). A review of nitrogen enrichment effects on three biogenic GHGs: the CO₂ sink may be largely offset by stimulated N₂O and CH₄ emission. *Ecology Letters*, 12(10), 1103–1117.
- Lu, X., Liang, L. L., Wang, L., & Jenerette, G. D. (2017). Partitioning of evapotranspiration using a stable isotope technique in an arid and high temperature agricultural production system. *Agricultural Water Management*.
<https://www.sciencedirect.com/science/article/pii/S0378377416302967>
- Meister, H. S. (2004). *Sample Costs to Establish and Produce Sudangrass*. University of California Cooperative Extension.
- Meixner, F. X., Fickinger, T., Marufu, L., Serça, D., Nathaus, F. J., Makina, E., Mukurumbira, L., & Andreae, M. O. (1997). Preliminary results on nitric oxide emission from a southern African savanna ecosystem. *Nutrient Cycling in Agroecosystems*, 48(1), 123–138.
- Miller, A. E., Schimel, J. P., Meixner, T., Sickman, J. O., & Melack, J. M. (2005). Episodic rewetting enhances carbon and nitrogen release from chaparral soils. *Soil Biology & Biochemistry*, 37(12), 2195–2204.
- Oikawa, P. Y., Ge, C., Wang, J., Eberwein, J. R., Liang, L. L., Allsman, L. a., Grantz, D. a., & Jenerette, G. D. (2015). Unusually high soil nitrogen oxide emissions influence air quality in a high-temperature agricultural region. *Nature Communications*, 6, 8753.
- Oikawa, P. Y., Grantz, D. A., Chatterjee, A., Eberwein, J. E., Allsman, L. A., & Jenerette, G. D. (2014). Unifying soil respiration pulses, inhibition, and temperature hysteresis through dynamics of labile soil carbon and O₂: Soil C and O₂ regulate soil respiration. *Journal of Geophysical Research: Biogeosciences*, 119(4), 521–536.
- Ortiz, C. (2018). *Crop and Livestock Report*. Imperial County Office of the Agricultural Commissioner.
- Paustian, K., Six, J., Elliott, E. T., & Hunt, H. W. (2000). Management options for reducing CO₂ emissions from agricultural soils. *Biogeochemistry*, 48, 147–163.

- Putnam, D., & Kallenbach, R. (1997). Growers face critical juncture in desert forage production. *California Agriculture*, 51(3), 12–16.
- Sánchez-Martín, L., Arce, A., Benito, A., Garcia-Torres, L., & Vallejo, A. (2008). Influence of drip and furrow irrigation systems on nitrogen oxide emissions from a horticultural crop. *Soil Biology & Biochemistry*, 40(7), 1698–1706.
- Sanchez-Martín, L., Mejjide, A., Garcia-Torres, L., & Vallejo, A. (2010). Combination of drip irrigation and organic fertilizer for mitigating emissions of nitrogen oxides in semiarid climate. *Agriculture, Ecosystems & Environment*, 137(1), 99–107.
- Sapkota, A., Haghverdi, A., Avila, C. C. E., & Ying, S. C. (2020). Irrigation and Greenhouse Gas Emissions: A Review of Field-Based Studies. *Soil Systems*, 4(2), 20.
- Schimel, J. P. (2018). Life in Dry Soils: Effects of Drought on Soil Microbial Communities and Processes. *Annual Review of Ecology, Evolution, and Systematics*, 49(1), 409–432.
- Schlesinger, W. H., & Bernhardt, E. S. (2013). *Biogeochemistry Third Edition* (pp. 135–172). Academic Press.
- Sha, T., Ma, X., Zhang, H., Janecek, N., Wang, Y., Wang, Y., Castro García, L., Jenerette, G. D., & Wang, J. (2021). Impacts of Soil NO_x Emission on O₃ Air Quality in Rural California. *Environmental Science & Technology*.
<https://doi.org/10.1021/acs.est.0c06834>
- Sihi, D., Davidson, E. A., Savage, K. E., & Liang, D. (2020). Simultaneous numerical representation of soil microsite production and consumption of carbon dioxide, methane, and nitrous oxide using probability distribution functions. *Global Change Biology*, 26(1), 200–218.
- Suddick, E. C., Steenwerth, K., Garland, G. M., Smart, D. R., & Six, J. (2011). Discerning Agricultural Management Effects on Nitrous Oxide Emissions from Conventional and Alternative Cropping Systems: A California Case Study. In *Understanding Greenhouse Gas Emissions from Agricultural Management* (Vol. 1072, pp. 203–226). American Chemical Society.
- Velasco-Muñoz, J. F., Aznar-Sánchez, J. A., Batlles-de-laFuente, A., & Fidelibus, M. D. (2019). Sustainable Irrigation in Agriculture: An Analysis of Global Research. *WATER*, 11(9), 1758.

- Wang, Y., Li, S., Liang, H., Hu, K., Qin, S., & Guo, H. (2020). Comparison of Water- and Nitrogen-Use Efficiency over Drip Irrigation with Border Irrigation Based on a Model Approach. *Agronomy*, *10*(12), 1890.
- Wang, Y., Uchida, Y., Shimomura, Y., Akiyama, H., & Hayatsu, M. (2017). Responses of denitrifying bacterial communities to short-term waterlogging of soils. *Scientific Reports*, *7*(1), 803.
- Wei, C., Ren, S., Yang, P., Wang, Y., He, X., Xu, Z., Wei, R., Wang, S., Chi, Y., & Zhang, M. (2021). Effects of irrigation methods and salinity on CO₂ emissions from farmland soil during growth and fallow periods. *The Science of the Total Environment*, *752*, 141639.
- Wei, Q., Xu, J., Li, Y., Liao, L., Liu, B., Jin, G., & Hameed, F. (2018). Reducing Surface Wetting Proportion of Soils Irrigated by Subsurface Drip Irrigation Can Mitigate Soil N₂O Emission. *International Journal of Environmental Research and Public Health*, *15*(12), 2747.
- White, R. P., & Nackoney, J. (2003). *Drylands, people, and ecosystem goods and services: a web-based geospatial analysis*. Washington, DC: World Resources Institute.
- Xiao, Y., Zhang, J., Jia, T. T., Pang, X. P., & Guo, Z. G. (2015). Effects of alternate furrow irrigation on the biomass and quality of alfalfa (*Medicago sativa*). *Agricultural Water Management*, *161*, 147–154.
- Yan, X., Ohara, T., & Akimoto, H. (2005). Statistical modeling of global soil NO_x emissions: Global soil NO_x emissions. *Global Biogeochemical Cycles*, *19*(3), 921.
- Zaccaria, D., Carrillo-Cobo, M. T., Montazar, A., Putnam, D. H., & Bali, K. (2017). Assessing the Viability of Sub-Surface Drip Irrigation for Resource-Efficient Alfalfa Production in Central and Southern California. *WATER*, *9*(11), 837.
- Zhao, P., Pumpanen, J., & Kang, S. (2020). Spatio-temporal variability and controls of soil respiration in a furrow-irrigated vineyard. *Soil and Tillage Research*, *196*, 104424.

Tables

Table 2.1 Upscaled water usage associated with crop production. Because growing season lengths and irrigation cycles differ between crops, irrigation treatment comparisons should be made within each crop type but are not necessarily comparable between crops. Alfalfa was harvested ~monthly; sudangrass was harvested every ~3 months.

<i>Crop</i>	<i>Growing season</i>	<i>Irrigation type</i>	<i>Total water used (m³)</i>	<i>Harvest yield (kg)</i>	<i>WUE of productivity (kg m⁻³ water)</i>
Sudangrass	Spring	Drip	138.433	435.4487	3.146
Sudangrass	Spring	Flood	326.342	434.54149	1.332
Sudangrass	Summer	Drip	103.859	508.0235	4.891
Sudangrass	Summer	Flood	419.383	444.5205	1.060
Alfalfa	Spring	Drip	530.396*	245.756346	0.463
Alfalfa	Spring	Flood	222.026	281.953017	1.270
Alfalfa	Summer	Drip	123.348	230.515642	1.869
Alfalfa	Summer	Flood	283.700	192.413883	0.678

Table 2.2 Experimental predictors of soil climate conditions and trace gas emissions in irrigated agricultural fields. Variance of each dependent variable was explained using a reduced general linear model (GLM) with the lowest Akaike Information Criterion (AICc). Statistical significance of each independent variable in the best model was tested using analysis of variance (ANOVA) at 95% confidence, and separation of individual treatment groups was identified using post-hoc t-tests or Tukey's tests.

Dependent variable	Best model AICc	Best model independent variable	DF	F-value	p-value ($\alpha = 0.05$)	Post-hoc test results (in decreasing order)
10-day mean temperature (°C)	176.08	Crop	1	34.282	<0.001	A = alfalfa; B = sudangrass
		Season	1	37.500	<0.001	A = summer; B = spring
		Crop*Season	1	15.787	<0.001	A = all others; B = sudangrass spring
10-day mean soil moisture (%)	-89.10	Crop	1	41.455	<0.001	A = alfalfa; B = sudangrass
		Season	1	6.230	0.017	A = summer; B = spring
		Irrigation	1	0.029	0.865	
		Crop*Irrigation	1	18.816	<0.001	A = alfalfa drip; B = alfalfa flood, sudangrass flood; C = sudangrass drip
10-day total CO ₂ flux (log g CO ₂ -C m ⁻²)	97.66	Crop	1	20.677	<0.001	A = sudangrass; B = alfalfa
		Season	1	2.935	0.095	
		Irrigation	1	7.312	0.010	A = flood; B = drip
		Crop*Irrigation	1	5.221	0.028	A = all others; B = alfalfa drip
		Season*Irrigation	1	3.214	0.081	
		Crop*Season	1	7.957	0.008	A = sudangrass summer; B = all others
10-day total N ₂ O flux (log mg N ₂ O-N m ⁻²)	141.95	Crop	1	12.700	<0.001	A = sudangrass; B = alfalfa
		Season	1	0.606	0.441	
		Irrigation	1	5.824	0.020	A = flood; B = drip
		Season*Irrigation	1	5.291	0.021	A = summer flood; AB = spring flood, spring drip; B = summer drip
10-day total NO flux (log mg NO-N m ⁻²)	85.72	Crop	1	85.180	<0.001	A = sudangrass; B = alfalfa
		Season	1	0.043	0.837	
		Irrigation	1	7.135	0.011	A = flood; B = drip
		Season*Irrigation	1	10.90	0.002	A = summer flood; AB = spring drip, spring flood; B = summer drip
		Crop*Season	1	2.880	0.097	

Table 2.3 Upscaled soil trace gas emissions associated with crop production. Per-yield emissions were calculated by multiplying 10-day total emissions by the number of irrigation events, and dividing the total by per-area harvested yield. Values are reported as averages (standard deviations) for each treatment group.

Crop	Season	Irrigation type	Mean irrigation interval (days)	Mean (SE) CO ₂ flux per irrigation (g CO ₂ -C m ⁻²)	Mean (SE) N ₂ O irrigation flux per (mg N ₂ O-N m ⁻²)	Mean (SE) NO irrigation flux per (mg NO-N m ⁻²)	# irrigation events to produce yield	Harvest yield (g m ⁻²)	Mean (SE) CO ₂ emissions per yield (g CO ₂ -C g yield ⁻¹)	Mean (SE) N ₂ O emissions per yield (mg N ₂ O-N g yield ⁻¹)	Mean (SE) NO emissions per yield (mg NO-N g yield ⁻¹)
Sudan-grass	Spring	Drip	13	145.47 (43.73)	48.09 (7.36)	19.60 (2.32)	3	537.560	0.812 (0.244)	0.268 (0.041)	0.109 (0.013)
Sudan-grass	Spring	Flood	13	123.58 (27.40)	71.41 (19.59)	19.36 (3.30)	3	536.888	0.691 (0.153)	0.399 (0.109)	0.108 (0.018)
Sudan-grass	Summer	Drip	10	226.99 (51.41)	35.63 (12.01)	8.98 (3.29)	4	627.677	1.447 (0.328)	0.227 (0.077)	0.057 (0.021)
Sudan-grass	Summer	Flood	10	223.39 (51.56)	137.74 (70.45)	48.31 (34.58)	4	549.217	1.627 (0.376)	1.003 (0.513)	0.352 (0.252)
Alfalfa	Spring	Drip	12	52.55 (3.29)	49.63 (30.04)	2.92 (0.27)	2	289.180	0.363 (0.023)	0.343 (0.208)	0.020 (0.002)
Alfalfa	Spring	Flood	12	63.61 (7.06)	43.86 (19.56)	2.68 (0.26)	2	331.772	0.383 (0.043)	0.264 (0.118)	0.016 (0.002)
Alfalfa	Summer	Drip	14	52.46 (33.84)	5.94 (2.77)	3.69 (0.44)	2	271.246	0.387 (0.250)	0.044 (0.020)	0.027 (0.003)
Alfalfa	Summer	Flood	14	177.56 (35.77)	24.73 (1.28)	6.05 (1.96)	2	226.412	1.568 (0.316)	0.218 (0.011)	0.053 (0.017)

Figures

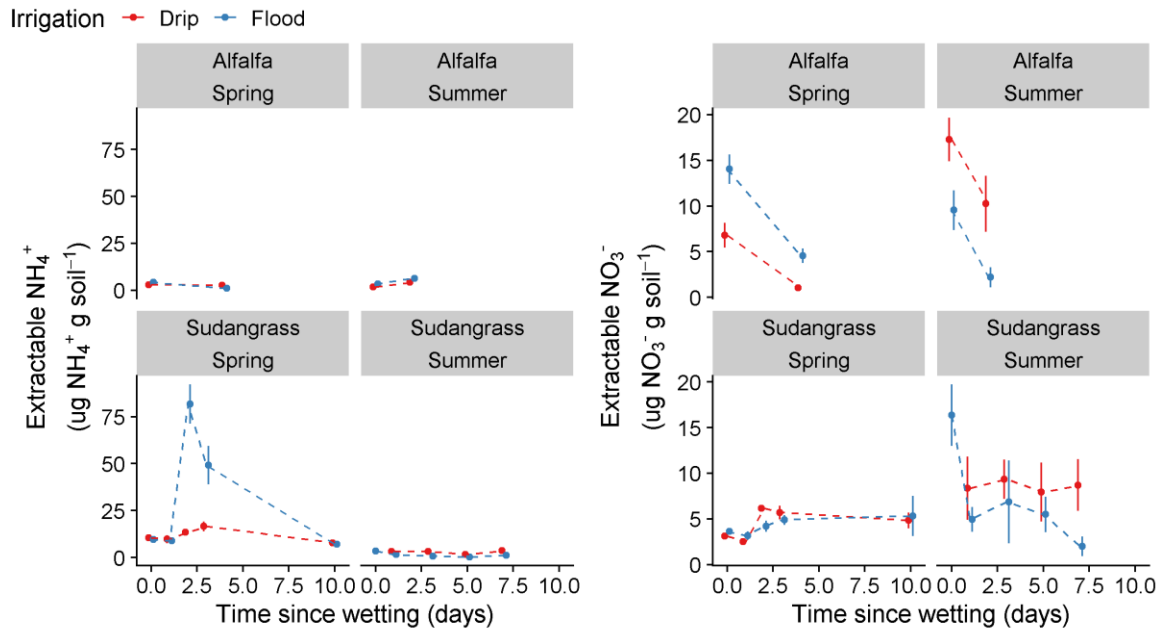


Figure 2.1 Extractable NH_4^+ and NO_x ($\text{NO}_2^- + \text{NO}_3^-$) following soil irrigation. Points and error bars indicate means and standard errors of extractable soil N at time points following irrigation. Colors delineate irrigation type; dotted lines connecting points are for visualization only and do not indicate statistical significance.

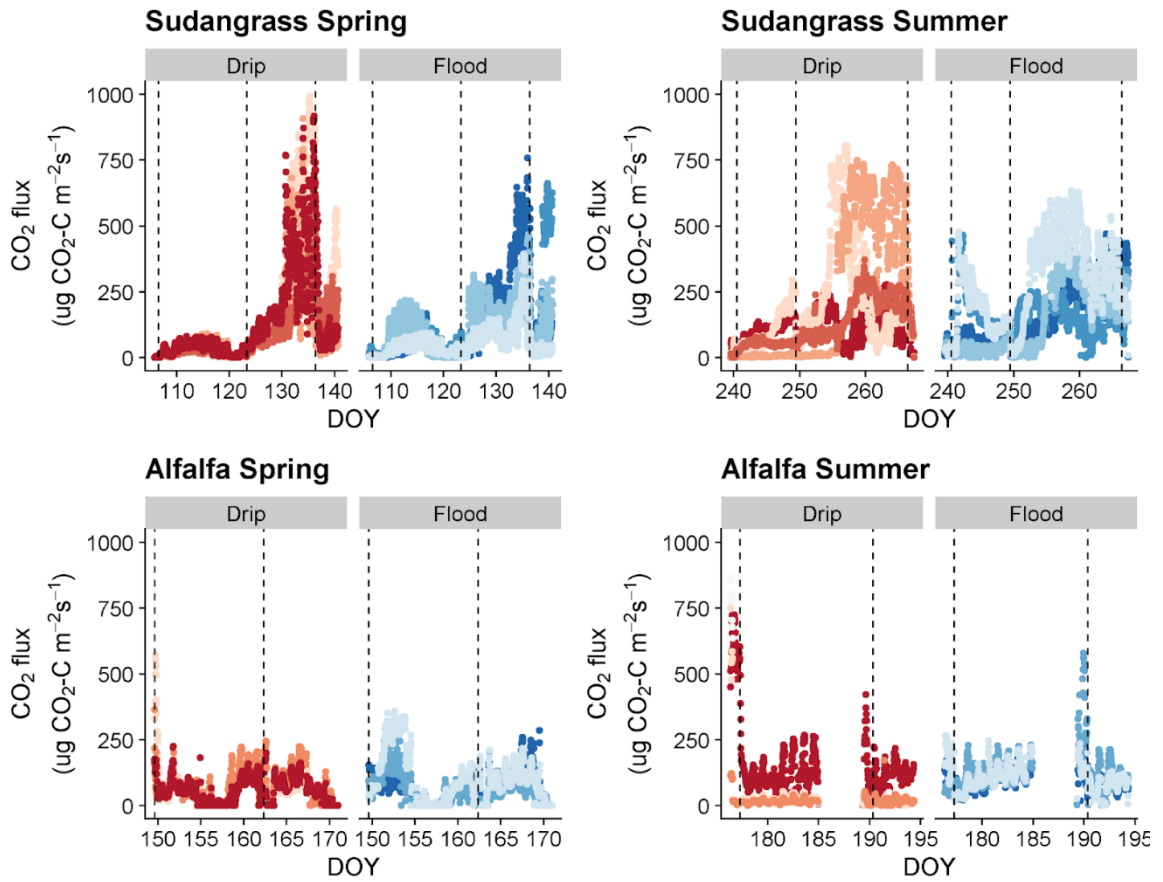


Figure 2.2 Instantaneous carbon dioxide (CO₂) fluxes measured in each sampling campaign. Drip-irrigated chambers are colored red and flood-irrigated chambers are colored blue; specific shades of each color indicate individual chambers. Dotted lines delineate scheduled irrigation events within each campaign.

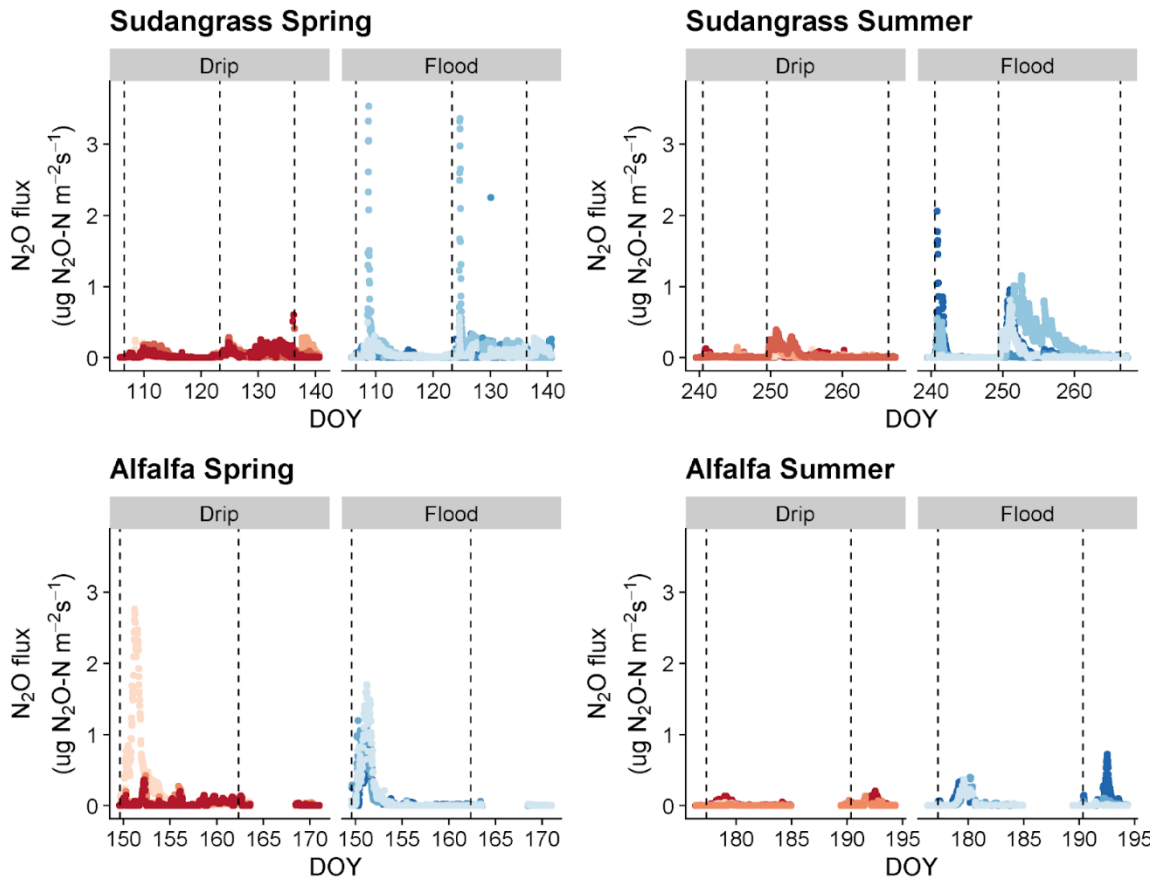


Figure 2.3 Instantaneous nitrous oxide (N_2O) fluxes measured in each sampling campaign. Drip-irrigated chambers are colored red and flood-irrigated chambers are colored blue; specific shades of each color indicate individual chambers. Dotted lines delineate scheduled irrigation events within each campaign.

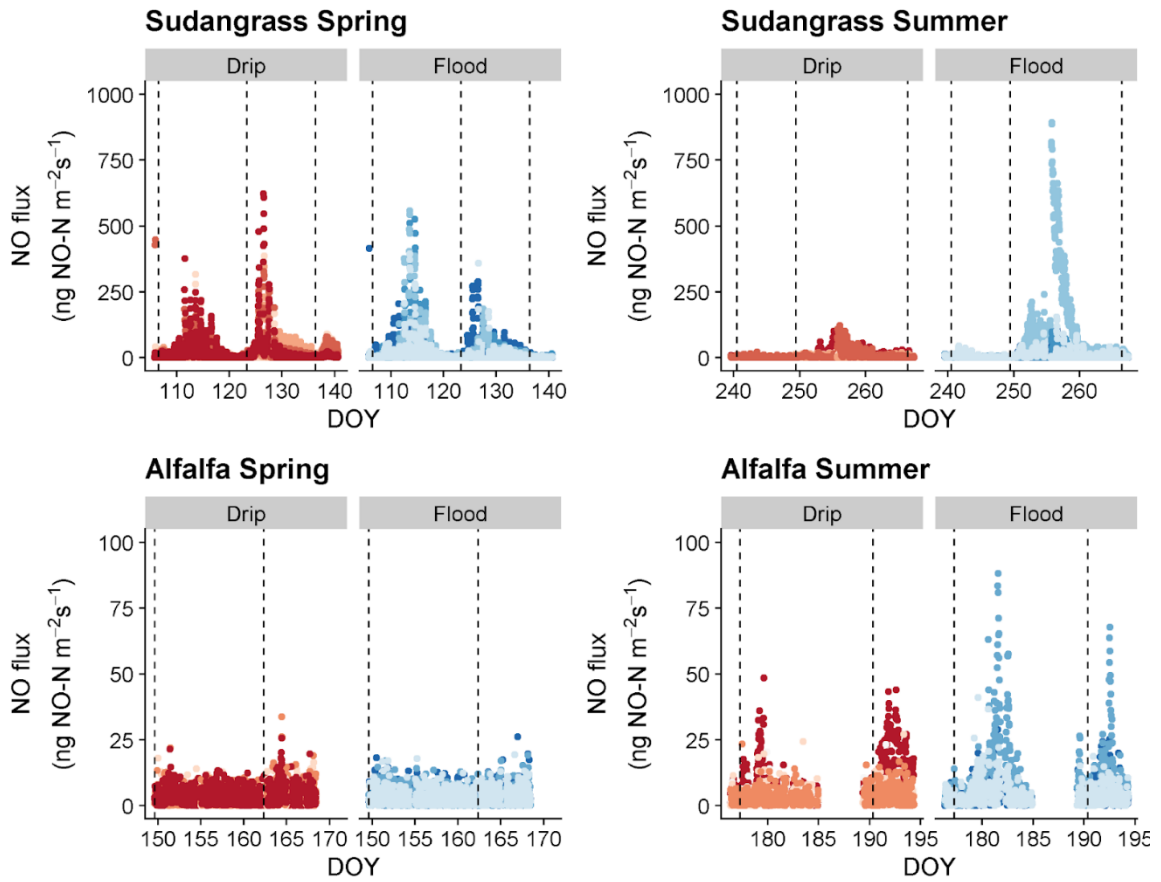


Figure 2.4 Instantaneous nitric oxide (NO) fluxes measured in each sampling campaign. Drip-irrigated chambers are colored red and flood-irrigated chambers are colored blue; specific shades of each color indicate individual chambers. Dotted lines delineate scheduled irrigation events within each campaign. Note the range of fluxes for sudangrass (top) is 10x larger than for alfalfa (bottom).

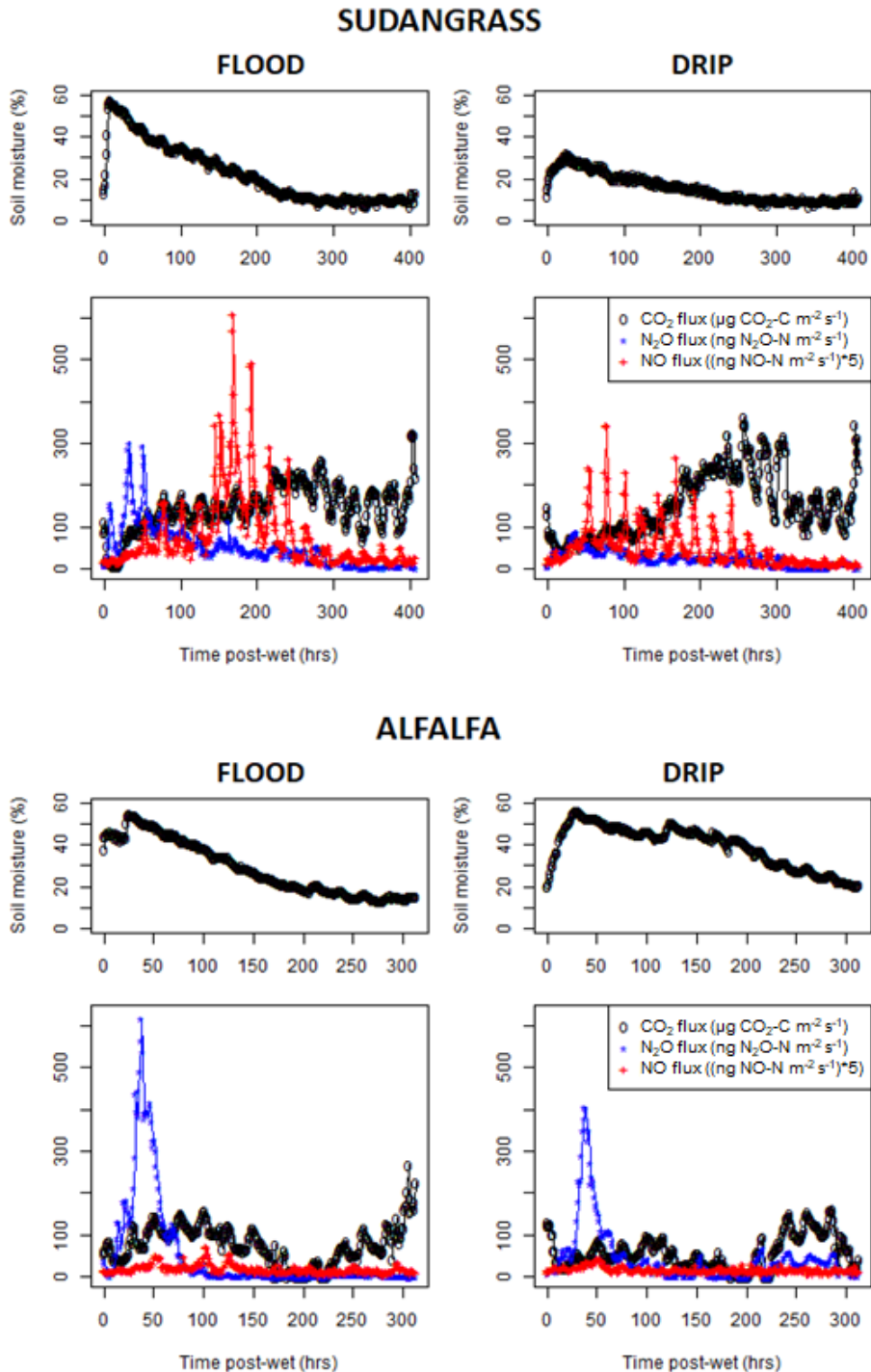


Figure 2.5 Post-wetting responses of instantaneous CO₂, N₂O, and NO fluxes to flood (left) or drip (right) irrigation in sudangrass (top) and alfalfa (bottom) fields. Colors and symbols delineate responses of each gas, adjusted to comparable units; points within each color indicate average fluxes across all replicates for each hour post-irrigation.

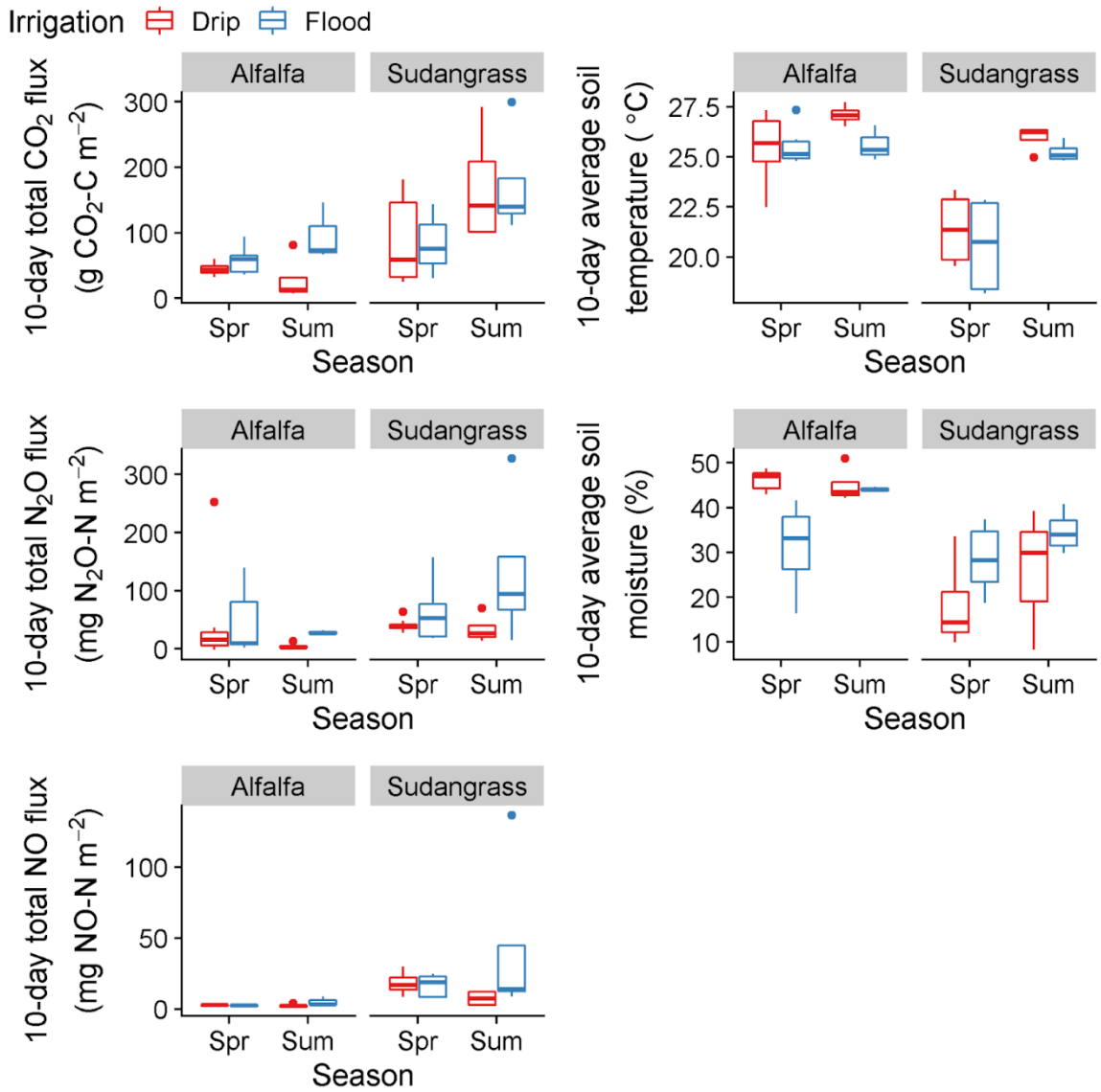


Figure 2.6 Total soil emissions of trace gases (left) and average climate conditions (right) over 10 days following scheduled irrigation. Colors indicate flood (blue) and drip (red) irrigation treatments. Totals were calculated using area-under-the-curve integration for the 10-day time series of each chamber.

Chapter 3

Soil CO₂ rewetting pulses driven by interactions among soil temperature, carbon, and nitrogen limitation in deserts

Abstract

Pulses of soil CO₂ respiration, consistent with the Birch effect, are triggered by soil re-wetting in desert soils; following re-wetting, CO₂ pulses are additionally limited by interactions between average temperature and carbon substrate availability. Other mechanisms may additionally limit CO₂ respiration indirectly, such as nitrogen availability and fine-scale temperature patterns, but these have not been well tested in field conditions. I conducted a series of re-wetting experiments at a focal desert site to quantify interactive relationships among temperature, C, N, and CO₂ pulse size at multiple temporal scales; I compared these findings to data from an N addition experiment conducted in desert sites along a N deposition gradient. As expected, temperature and C addition increased CO₂ pulses at my focal site; interestingly, CO₂ pulses were larger during daytime re-wetting compared to nighttime, but these patterns were only partially explained by temperature. I also observed a switch in CO₂ pulse responses to N addition along my N deposition gradient; added N at cleaner sites resulted in larger CO₂ pulses, while additional N at N-polluted sites decreased CO₂ pulses. Therefore, C and N stoichiometry, not strictly limitation, determine CO₂ pulse response to soil re-wetting, and microbial respiration responses to temperature are complicated by rapid soil moisture shifts during re-wetting of desert soils.

Introduction

Carbon (C) cycling in deserts and other dryland systems is strongly regulated by soil moisture, whereby infrequent re-wetting events simultaneously trigger re-activation of biological metabolism and spatial redistribution of soil resources (Miller et al., 2005; Schimel, 2018). In dry soils, respiration rates of greenhouse gas carbon dioxide (CO₂) are generally low; re-wetting increases microbial access to C, the main energetic substrate for metabolism and CO₂ production, and can generate pulses of high CO₂ respiration, described as the "Birch effect" (Barnard et al., 2020; Birch, 1958; Fraser et al., 2016; Jarvis et al., 2007; Lado-Monserrat et al., 2014). More broadly, the "pulse-reserve paradigm" describes respiration pulses in terms of soil re-wetting regimes, where the magnitude of a pulse is at least partially determined by the interval between re-wetting events (Collins et al., 2014; Lado-Monserrat et al., 2014; Patel et al., 2021). When re-wetting is frequent, microbial biomass and access to substrates is more consistent through time and pulse behavior is correspondingly muted; however, when re-wetting is infrequent and soils dry completely, substrates accumulate as labile reserves that are metabolized rapidly and released following the next re-wetting event (Evans et al., 2016). Although soil re-wetting can be considered a trigger for a CO₂ pulse, additional soil conditions such as temperature and substrate availability can influence the timing, magnitude, and duration of these phenomena post-wetting (Eberwein et al., 2017; Eberwein et al., 2015; Sihi et al., 2020). CO₂ pulses have been consistently observed in desert soils (Eberwein et al., 2015; Harms & Grimm, 2012; Huxman et al., 2004; Sponseller, 2007; Talmon et al., 2011), but the mechanisms that determine the size of a

pulse, and therefore the overall soil CO₂ emissions from deserts, remain unclear (Hursh et al., 2017).

There is considerable evidence that CO₂ respiration is limited by temperature and C availability (Davidson & Janssens, 2006; Davidson et al., 2012; Eberwein et al., 2015); however, CO₂ emissions derived from interactions between temperature, C, and re-wetting have not been well-quantified in desert soils. Temperature is positively correlated to kinetic energy and reaction rate of reactants that produce CO₂ (Lloyd & Taylor, 1994); therefore, I hypothesize that higher temperatures result in higher rates of instantaneous CO₂ flux (Richardson et al., 2012), and higher magnitudes of CO₂ pulses, that typically follow an Arrhenius function. Similarly, higher concentrations of substrates for CO₂ production result in more frequent enzymatic reactions following re-wetting, characterized by Michaelis-Menten kinetics (Eberwein et al., 2015; Evans et al., 2016); I hypothesize that the magnitudes of CO₂ pulses are similarly limited by the availability of C substrates post-wetting. Together, high-temperature, unlimited-C conditions provide an optimal environment for enzymatic reactions and therefore I expect these two mechanisms to synergistically increase CO₂ pulse responses to soil rewetting. However, soil rewetting may not induce optimal moisture conditions for respiration (Skopp et al., 1990) and may ultimately regulate temperature-substrate interactions. The 3-way interaction between moisture, temperature, and C limitation has not been well-quantified at sufficient resolution to establish clear relationships for desert soils, but I hypothesize that soil conditions at the time of re-wetting predict the trajectory and overall strength of the pulse response.

Although C drives CO₂ respiration directly, other resources including nitrogen (N) can contribute indirectly to CO₂ pulses by boosting or reducing microbial metabolic activities. Coupled C and N availability has been shown to interactively regulate CO₂ fluxes in forest and agricultural soils (Eberwein et al., 2017; Liang et al., 2015), producing the highest flux rates under high C- high N conditions, indicating that N substrates are indirectly responsible for microbial respiration. Two contrasting hypotheses exist to explain the relationship between CO₂ flux and N availability. The first, similar to a Michaelis-Menten hypothesis, is that reducing N limitation will increase microbial biomass and metabolism with a consequential increase to microbial respiration (Eberwein et al., 2015); within a pulse framework, higher N availability should stimulate larger microbial re-activation than under limited N conditions (Liang et al., 2016; Liang et al., 2015). Alternatively, the nitrogen mining hypothesis (Craine et al., 2007) describes a decrease in CO₂ respiration with increasing soil N availability because microbes invest fewer metabolic resources to acquire N when it is readily accessible. These two hypotheses may be contextually-dependent on historical soil conditions and microbial community adaptations, explaining continued support in literature (Janssens et al., 2010). The respiration response to N availability may also be nonlinear (Peng et al., 2017); under very limited N conditions, reducing N limitation may support Michaelis-Menten increases until a certain threshold is reached that no longer supports additional microbial investment in acquiring N. However, interactive C-N-temperature contributions to CO₂ rewetting pulses have not been extensively studied in the context of desert field conditions.

In a series of field experiments, I ask: How do soil temperature, C availability, and N availability modulate CO₂ pulses from re-wetted desert soils? I utilized a custom array of automated soil chambers, probes, and analyzers to quantify trace gas fluxes and corresponding soil conditions, *in situ* and at 30-minute resolution, in a set of re-wetting experiments targeting temperature, C, and/or N perturbations. I predicted that CO₂ pulse size would be positively correlated with temperature; if temperature and moisture interactively drive pulses, temperature at time of re-wetting would also be the strongest predictor of CO₂ pulse size. Second, I predicted that reducing C limitation during re-wetting would increase CO₂ pulse size. Third, I predicted that reducing N limitation during re-wetting of N-limited soils would increase CO₂ pulse size; however, reducing N limitation in soils where background N deposition rates are high would decrease CO₂ pulses. Finally, I predicted that temperature and C and N resources would have interactive, non-additive relationships to CO₂ pulses; I expected the strongest pulse responses to re-wetting to be in high-temperature soils where C and N availability were least limited.

Methods

Study sites and focal species

My data were synthesized from field campaigns conducted at multiple desert sites in southern California. The majority of data were collected from Boyd Deep Canyon Desert Research Center, a Colorado Desert constituent of the University of California Natural Reserve System located near Palm Desert, CA, USA (33.6480° N, 116.3765° W, 290 m elevation). I also used four desert sites located within a 50-km radius of Boyd

Deep Canyon to test additional nitrogen mechanisms of CO₂ pulses: Pinto Basin (33.8314° N, 115.7571° W, 746 m elevation); Wide Canyon (33.9430° N, 116.3943° W, 501 m elevation); Oasis (33.8957° N, 116.6894° W, 405 m elevation); and Morongo (33.9218° N, 116.7572° W, 510 m elevation). The climate in this region is characterized by hot summers and mild winters; although precipitation occurs more frequently in the winter, accounting for up to 85% annual water inputs in some years (WRCC 2021), summers can be marked by a few large rain events similar to monsoonal rains. Average monthly temperatures in this region range from 12 C (January-February) to 35 C (July-August) with average diel temperature ranges of 10-15 C (WRCC 2021). These sites lie in a N deposition gradient: ordered from lowest to highest, throughfall N deposition rates are estimated to be 2.2 kg ha⁻¹ yr⁻¹ at Boyd Deep Canyon (Eberwein et al., 2020), 2.6 kg ha⁻¹ yr⁻¹ at Pinto Basin, 3.2 kg ha⁻¹ yr⁻¹ at Wide Canyon, 5.6 kg ha⁻¹ yr⁻¹ at Oasis, and >5.6 kg ha⁻¹ yr⁻¹ at Morongo. Soils at Boyd Deep Canyon and surrounding sites are classified as hyperthermic Typic Torriorthents mapped within the Carrizo series, containing stony sands with high drainage. The dominant shrub at my sites and focal species of my experiments is creosote bush (*Larrea tridentata*); these shrubs facilitate "islands" of herbaceous annuals and organic matter, surrounded by barren interspaces. Because *L. tridentata* generates observable "islands" of biotic activity, I anticipated these shrubs to contribute substantially to carbon cycling in deserts and consequently to have large pulse responses to soil re-wetting.

Field campaigns at Boyd Deep Canyon

Data presented here were selected from five field campaigns conducted at Boyd Deep Canyon; all experiments were conducted at plots within a single watershed in the southernmost portion of the canyon. Prior to each campaign, pairs of polyvinyl chloride (PVC) soil collars measuring 20-cm in diameter were installed to 5-cm depth and adjacent to each other within a plot. One collar per pair was used for trace gas measurements and the other was used for soil climate measurements and was sampled for ancillary soil analyses; both collars in each pair received identical re-wetting treatments. For each experiment, soils were re-wetted by hand to simulate a 2-cm rain event, representing a medium-sized event for the reserve. Following re-wetting, soil climate (temperature, moisture) and fluxes of CO₂ were measured over 24-45 hours.

Four campaigns (Winter 2018, Summer 2018, Summer 2020, Winter 2021) experimentally manipulated availability of C, N, and/or both following re-wetting in different seasonal contexts. All re-wetting experiments were initiated during mid-morning hours (8:30-10:00) and used 3-4 focal shrubs (and corresponding interspaces) as replicates. C and N were added as aqueous dextrose (30 g/L) and ammonium-nitrate (13 g/L) solutions, respectively, as 2-cm simulated re-wetting events that matched those of unamended collars. These additions are unnaturally large and represent an endpoint of C and N limitation that allowed us to quantify the potential capacity for soil respiration in soils where substrates are naturally limited but which may experience increases with global change.

One campaign (Summer 2019) experimentally manipulated the time of day at which soils were re-wetted, as a proxy for soil temperature at time of wetting; collars were installed in cardinal directions around 8 focal *L. tridentata* shrubs for this experiment, where 2 shrubs constituted a treatment replicate. Within each replicate, collars were re-wetted at 3-hour intervals (0:00, 3:00, 6:00, 9:00, 12:00, 15:00, 18:00, 21:00), one collar per timepoint, as a proxy for diel variability in soil temperature that could drive CO₂ pulse dynamics. No nutrient amendments were added during this campaign.

Campaign period	Season	Nutrient manipulation	Post-wetting duration
Winter 2018	Wet	Wet, wet+N	45 hours
Summer 2018	Dry	Wet, wet+C+N	45 hours
Summer 2019	Dry	Wet only	24 hours
Summer 2020	Dry	Wet, wet+C, wet+N, wet+C+N	45 hours
Winter 2021	Wet	Wet, wet+C, wet+N, wet+C+N	45 hours

Field campaigns along a N deposition gradient

Two experimental campaigns were conducted in Summer 2019 and Summer 2020 which experimentally manipulated availability of NH₄⁺ or NO₃⁻ to soils under *L. tridentata* shrubs at sites along a desert N deposition gradient. Prior to each campaign, two pairs of polyvinyl chloride (PVC) soil collars measuring 20-cm in diameter were installed to 5-cm depth under shrubs. One collar per pair was used for trace gas measurements and the other was used for soil climate measurements and was sampled for ancillary soil analyses; both collars in each pair received identical re-wetting treatments,

and both pairs per shrub received matching NH_4^+ and NO_3^- treatment amounts. N treatments were added as aqueous solutions that spanned 0, 10, 20, 30, 40, 50, 60, and 70 kg ha^{-1} added NH_4^+ or NO_3^- . All re-wetting experiments were initiated during mid-morning hours (8:30-10:00); soils were re-wetted by hand to simulate a 2-cm rain event, representing a medium-sized event. An identical field campaign was conducted in Summer 2018 at Boyd Deep Canyon but using a smaller range of N addition treatments that spanned 0, 2, 4, 6, 8, 10, 12, and 15 kg ha^{-1} NH_4^+ or NO_3^- added. Following re-wetting, soil climate (temperature, moisture) and fluxes of CO_2 were measured over 24 hours.

Soil climate and trace gas measurements

To measure instantaneous soil temperature, moisture, and trace gas fluxes, I used an automated chamber array and sampling procedure outlined in Chapter 2. Briefly, eight automated long-term chambers (LI-8100-104; LI-COR Bioscience, Lincoln, NE, USA) with soil temperature (LI-8150-203 thermistor probe; LI-COR Bioscience, Lincoln, NE, USA) and moisture (LI-GS1 probe; LI-COR Bioscience, Lincoln, NE, USA) probe attachments were installed on soil PVC collars; probes were inserted to 5-cm soil depth. Each chamber collected measurements on a 30-minute interval. Air collected from an actively-measuring chamber was passed through a multiplexer (LI-8150; LI-COR Bioscience, Lincoln, NE, USA) followed by, in sequence: 1) a $\text{N}_2\text{O}/\text{CO}$ cavity-ringdown infrared analyzer (Los Gatos Research, San Jose, CA, USA); 2) a CO_2 infrared gas analyzer system (LI-8100A; LI-COR Bioscience, Lincoln, NE, USA); and 3) a coupled nitrogen dioxide (NO_2) converter and NO monitor (Model 401/410, 2B Technologies,

Boulder, CO, USA). The multiplexer, N₂O/CO analyzer, and the CO₂ system formed a closed loop, and a portion of air was siphoned from the sample loop through a one-way check valve and passed through the open-system NO monitor. Each chamber measurement sequence included a 30-second pre-measurement purge, a 2.5-minute active measurement period of trace gas concentrations and soil climate status, and a 30-second post-measurement purge.

Data processing and statistical methods

I batch processed instantaneous flux and climate data for each emissions collection campaign using methods adapted from Andrews & Jenerette (2020) and Krichels et al. (*in review*). Briefly, instantaneous fluxes of CO₂, N₂O, and NO were calculated as the regression coefficient of linear increase in gas concentration data during the 2.5-minute active chamber measurement period, corrected for soil collar dimensions and atmospheric parameters following the Ideal Gas Law ([Eric A. Davidson et al., 2000](#)). Instantaneous fluxes of each gas were compiled and integrated with instantaneous soil temperature and moisture measurements using a publicly-accessible R script (Andrews & Krichels 2021). My final dataset contained simultaneous measurements of CO₂, N₂O, NO, soil temperature, and soil moisture for each chamber at 30-minute resolution. These high-resolution measurements allowed for a more comprehensive characterization of the emissions for multiple trace gasses.

In addition to instantaneous measures, I constructed 24-hour time series for each chamber following re-wetting and extracted the magnitude and timing of each peak instantaneous flux and climate parameter as well as a 24-hour cumulative flux. Peak

fluxes were calculated as the maximum instantaneous flux recorded during a 24-hour measurement period; cumulative fluxes were calculated as the integrated area under each time series curve using linear trapezoidal method.

For data collected at Boyd Canyon, I assessed temperature and moisture dependence of CO₂ peak and 24-hour total fluxes by fitting regression curves to each one-way relationship and testing statistical significance using analysis of variance (ANOVA). To compare categorical effects of C and N amendments across seasons at my focal site, I constructed a general linear model (GLM) for 24-hour total CO₂ fluxes that contained nutrient treatment, season, and nutrient*season interaction factors. I tested statistical significance of each of these factors using 2-way ANOVA and post-hoc Tukey's tests to separate individual treatment groups. In my time-of-day study, I conducted an additional t-test to compare daytime to nighttime peak and 24-hour total CO₂ fluxes. For data collected in N addition experiments at Boyd Deep Canyon and sites along the N deposition gradient, I assessed N dependence of CO₂ peak and 24-hour total fluxes at each site and N form (NH₄⁺ vs. NO₃⁻) individually by fitting regression curves to each one-way relationship and testing significance using ANOVA. I also conducted these tests on pooled site data for the four sites in the N deposition gradient (Pinto Basin, Wide Canyon, Oasis, Morongo).

Results

CO₂ Birch effect trajectory following re-wetting

Across all field campaigns and treatments, instantaneous CO₂ fluxes ranged near-zero to 299.5 μmol m⁻² s⁻¹ (Figure 3.1). From wetting alone (no amendments),

instantaneous CO₂ fluxes ranged near-zero to 69.1 μmol m⁻² s⁻¹. In 80% of wet-only treatments, CO₂ fluxes peaked within the first 1-2 hours of wetting, followed by exponential decrease over the next 6-24 hours. For campaigns that measured longer than 24 hours, I observed smaller secondary pulses between 24 and 36 hours post-wetting. CO₂ fluxes did not return to pre-wet levels by the end of measurement periods, but I did not observe appreciable differences after 40 hours post-wetting.

In substrate-amended treatments, 32% of pulses peaked within the first 2 hours of wetting, primarily in wet+N treatment; 64% of pulses peaked between 2 and 18 hours post-wetting, with wet+C treatments generally peaking at 4-5 hours and wet+C+N treatments at 8-9 hours. For campaigns that measured longer than 24 hours, I observed smaller secondary pulses between 24 and 40 hours post-wetting; although these pulses were smaller than initial pulses, they were in many cases still larger than initial pulses in wet-only treatments. In almost all amended plots, CO₂ fluxes remained elevated above pre-wet levels after 48 hours.

CO₂ instantaneous flux and 24-hour pulse responses to soil temperature and moisture

I examined individual temperature and moisture dependence of CO₂ pulses using re-wetting scenarios without substrate amendments (Table 3.2, Figure 3.2). Instantaneous CO₂ fluxes increased with soil temperature up to ~45 °C, with the highest fluxes occurring between 30 and 45 °C (Figure 3.2a). For the few measurements made above 45 °C, CO₂ fluxes decreased with further increases in temperature. Within 24-hour pulses, peak CO₂ fluxes increased exponentially with their corresponding soil temperatures (Figure 3.2c; $y=1.49*e^{0.073x}$, $R^2=0.30$, $p<0.001$); similarly, 24-hour total CO₂ fluxes

increased exponentially with 24-hour average soil temperatures (Figure 3.2e;

$y=0.040*e^{0.078x}$, $R^2=0.25$, $p=0.003$).

Instantaneous CO₂ fluxes increased with instantaneous soil moisture up to 20%, above which fluxes decreased; importantly, CO₂ flux responses to moisture showed apparent patterns of hysteresis that matched time post-wetting (Figure 3.2b). Within each pulse, peak CO₂ fluxes were not correlated with corresponding soil moisture (Figure 3.2d; $p=0.11$); 24-hour total CO₂ fluxes were negatively correlated with 24-hour average soil moisture but moisture was a weak explanatory variable for CO₂ pulse size (Figure 3.2f; $y=0.860-0.034x$, $R^2=0.13$, $p=0.004$).

In a study that manipulated the time of re-wetting (Table 3.2, Figure 3.3), and by proxy soil temperature at time of re-wetting, CO₂ pulses were twice as strong during daytime re-wetting than nighttime ($p<0.001$); average peak CO₂ fluxes were 37.03 (4.58) and 14.38 (1.88) $\mu\text{mol m}^{-2} \text{s}^{-1}$ and 24-hour total CO₂ fluxes were 0.933 (0.065) and 0.429 (0.045) $\text{mol CO}_2 \text{m}^{-2}$ for daytime and nighttime re-wetting, respectively. Soil temperature at time of wetting was a strong predictor of peak CO₂ flux ($y=-28.94+1.54x$, $R^2=0.25$, $p=0.004$) and 24-hour total CO₂ flux ($y=-0.243+0.026x$, $R^2=0.22$, $p=0.008$). In contrast, 24-hour average temperature was not significantly correlated to either peak ($R^2=0.04$, $p=0.28$) or 24-hour total ($R^2=0.01$, $p=0.58$) CO₂ flux. 12-hour total CO₂ fluxes were lower than 24-hour totals but maintained similar responses to time of wetting, indicating the predictability of CO₂ pulse behavior even at shorter timescales.

24-hour CO₂ pulse responses to C and N amendments at Boyd Deep Canyon

In two field campaigns at my focal site that compared C and N amendments in a fully-factorial design (Table 3.1, Figure 3.4), average 24-hour total CO₂ pulses were 2.39 (0.34) mol CO₂ m⁻² in wet-only treatments. Wet+N plots did not significantly differ from wet-only treatments (p=0.99) but averaged slightly higher at 3.67 (0.66) mol CO₂ m⁻². Wet+C plots produced marginally stronger pulses than wet-only treatments (p=0.07), averaging 9.67 (1.26) mol CO₂ m⁻²; and wet+C+N plots produced the largest pulses (p<0.001), averaging 19.68 (3.97) mol CO₂ m⁻². CO₂ pulses were overall stronger in the dry season than in the wet season (p<0.001), and season magnified the effects of nutrient amendments. Although wet-only plots only increased from 2.02 (0.45) to 2.67 (0.48) mol CO₂ m⁻² from wet to dry season, wet+C plots increased from 8.24 (2.39) to 10.74 (1.31) mol CO₂ m⁻². In larger seasonal differences still, wet+N plots tripled in pulse strength from 1.59 (0.36) to 5.24 (0.72) mol CO₂ m⁻², and wet+C+N plots doubled from 12.51 (3.50) to 25.06 (5.91) mol CO₂ m⁻². Nutrient amendment effects on CO₂ pulses did not differ between shrub and interspace plots (p=0.83). In a separate field experiment comparing nutrient amendment effects across different intervals of re-wetting, wet+C+N amendments always produced stronger CO₂ pulses (p<0.001) but the effect of re-wetting interval on pulse size was negligible.

When I tested the effects of N amendments alone, out of C amendment contexts, wet+N treatments produced statistically larger 24-hour total CO₂ pulses than wet-only treatments (p=0.004), particularly during the dry season (Treatment*season p=0.01). In a complimentary study at Boyd Deep Canyon that tested CO₂ pulse responses to smaller N

amendments (Table 3.2, Figure 3.5a,b), added N was positively correlated to both peak and 24-hour total CO₂ fluxes and was marginally significant when amendments were as NO₃⁻ (peak: $y=4.16+1.16x$, $R^2=0.40$, $p=0.09$; 24-hour: $y=0.126+0.030x$, $R^2=0.38$, $p=0.10$) compared to nonsignificant increases under NH₄⁺ amendments.

24-hour CO₂ pulse responses to N amendments across an N deposition gradient

Across a 4-site N deposition gradient (Table 3.3, Figure 3.5c-f), NH₄⁺ amendments did not have clear effects on CO₂ pulses ($p=0.79$) when compared to unamended treatments; however, average 24-hour total CO₂ fluxes were 0.55 (0.03) and 0.71 (0.09) mol CO₂ m⁻² in all amended and unamended plots, respectively. Within sites, the only significantly negative correlation between amount of added NH₄⁺ and both peak CO₂ flux (Figure 3.5c; $y=49.62-0.43x$, $R^2=0.35$, $p=0.02$) and 24-hour total flux (Figure 3.5e; $y=0.793-0.007x$, $R^2=0.30$, $p=0.03$) was at Wide Canyon, the site with the second-lowest annual N deposition along my gradient (3.2 kg ha⁻¹ yr⁻¹). Contrastingly, NH₄⁺ increased 24-hour total CO₂ fluxes at Morongo, the most polluted site ($y=0.343-0.004x$, $R^2=0.25$, $p=0.05$). NO₃⁻ amendments were negatively correlated with 24-hour total CO₂ flux across all sites (Figure 3.5f; $y=0.702-0.004x$, $R^2=0.16$, $p=0.01$); within sites, Wide Canyon showed particularly strong negative correlations between NO₃⁻ amendments and both peak (Figure 3.5d; $y=52.64-0.56x$, $R^2=0.59$, $p<0.001$) and 24-hour total (Figure 3.5f; $y=0.675-0.007x$, $R^2=0.46$, $p=0.004$) CO₂ fluxes. However, Pinto Basin, the site receiving the lowest annual N deposition in my gradient (2.6 kg ha⁻¹ yr⁻¹), demonstrated positive correlation between NO₃⁻ amount and peak CO₂ fluxes (Figure 3.5d; $y=20.21+0.41x$, $R^2=0.62$, $p=0.02$).

Modulation of CO₂ temperature and moisture dependence by coupled C and N addition

I examined substrate modulation of temperature and moisture dependence for CO₂ pulses by comparing re-wetting scenarios with C and N substrate amendments to unamended scenarios (Table 3.2, Figure 3.6). Individual C and N amendments did not substantially alter temperature or moisture dependence of CO₂ fluxes compared to wetting alone; I combined these three treatments and compared this "substrate-limited" group to the "substrate-unlimited" wet+C+N group. Coupled C and N amendments revealed hysteresis patterns with soil temperature that were not as distinct under limited conditions. C+N amendments also increased the exponentiality of temperature dependence of peak CO₂ fluxes compared to substrate-limited groups (Figure 3.6c; wet+C+N: $y=2.36*e^{0.102x}$, $R^2=0.28$, $p=0.043$; limited group: $y=2.23*e^{0.063x}$, $R^2=0.30$, $p<0.001$); at 40 °C, peak CO₂ fluxes were up to six times larger in amended conditions compared to limited ones. Temperature dependence of 24-hour total CO₂ fluxes was best described using linear functions when I included substrate amendments, and coupled C and N amendments increased temperature dependence of pulses compared to my substrate-limited group by a factor of 10 (Figure 3.6e; wet+C+N: $y=0.294x-5.212$, $R^2=0.25$, $p=0.005$; limited group: $y=0.023x-0.206$, $R^2=0.23$, $p<0.001$).

Soil moisture was highly variable across treatment groups and effects of C and N amendments on moisture dependence were less clear than for temperature. Peak CO₂ fluxes declined linearly with their corresponding soil moisture values in substrate-limited conditions (Figure 3.6d; $y=-40.26x+23.49$, $R^2=0.04$, $p=0.04$), but this relationship explained very little variance in my data. The rate of decline was ten times stronger in

C+N amended plots but was only marginally significant ($y=-458.7x+148.1$, $R^2=0.12$, $p=0.09$). Coupled C and N amendments increased the negative moisture dependence of 24-hour total CO₂ fluxes by 5 times and produced a more predictable CO₂ response compared to substrate-limited conditions (Figure 3.6f; wet+C+N: $y=-0.533x+28.03$, $R^2=0.34$, $p=0.008$; limited group: $y=-0.018x+0.699$, $R^2=0.05$, $p=0.03$).

Discussion

Soil respiration is increasingly recognized as a response to multiple interacting soil mechanisms (Meredith et al., 2020); however, I know of no studies that explicitly explore temperature, moisture, C, and N dependence of CO₂ fluxes simultaneously in field conditions. My results provide new field evidence that CO₂ pulses in re-wetted desert soils are limited not only by climatic temperature and C but are also modulated by fine-scale temperature regimes and N availability. I report a large capacity of desert soil for CO₂ respiration; my observations of instantaneous CO₂ flux in saturated C and N conditions are nearly six times higher than the maximum emissions reported in literature (Table 3.2). However, lag in microbial recovery and/or access to C and N was still a rate-limiting mechanism of respiration following re-wetting, indicated by delayed peaks in CO₂ pulses under wet+C+N conditions compared to immediate peaks in wet-only conditions. As expected, I observed exponential increases in CO₂ pulses in response to temperature, even above 30 °C, and temperature dependence of CO₂ respiration was stronger when C and N limitation were reduced together. Finally, I find compelling evidence of a switch in effects of N limitation on CO₂ pulses that is dependent on long-term N deposition patterns; these mechanisms demand further research.

Bimodal CO₂ pulse response to experimental re-wetting

Consistent with my pulse hypothesis, soil re-wetting induced CO₂ pulses; however, I observed two modes of pulse behavior contingent upon C limitation (Figure 3.1) that I have not seen reported in literature. In treatments where C was limiting (wet-only, wet+N), CO₂ fluxes peaked quickly followed by exponential decay over the course of 24 hours, consistent with other observations from rewetted dry soils (Brangarí et al., 2020). Conversely, in C-saturated conditions (wet+C, wet+C+N), CO₂ fluxes increased more slowly to peak at higher magnitudes; decay of fluxes was also slower and produced secondary pulses ~24 hours post-wetting, following diel temperature patterns. These two modes of pulse behavior suggest that, following a re-wetting "trigger," C limitation determines the magnitude, duration, and shape of CO₂ pulses (Evans et al., 2016). In limited conditions, C is mobilized and then quickly depleted; however, in saturated conditions, C depletion may be limited by microbial biomass and/or enzymes which have lagged recovery rates post-wetting (Brangarí et al., 2020; Evans et al., 2016; Fraser et al., 2016). Diel increases in temperature 24 hours after initial wetting generated smaller, secondary pulses that I observed in 45-hour campaigns; these pulses were small in C-limited treatments, but continued C availability in saturated conditions produced larger secondary pulses as well. N availability did not induce a specific mode of behavior in CO₂ pulses but did alter the magnitude of CO₂ fluxes and the magnitude and duration of CO₂ pulses, suggesting that N substrates have an indirect role in soil respiration.

Carbon and temperature limitation constrain CO₂ pulse responses to rewetting

Consistent with my resource limitation hypothesis, saturation of C substrates in soils resulted in larger peak and 24-hour total CO₂ fluxes (Table 3.1, Figure 3.4), particularly during the dry season. I expected amendments of C to produce stronger CO₂ pulses in response to wetting (Barnard et al., 2020; Birch, 1958), given that C is the primary energetic component of respiration. Conversely, CO₂ pulses had a weak negative soil moisture dependence that I ascribe to seasonal differences in ambient soil moisture and substrate reserve size prior to wetting (Shen et al., 2016).

CO₂ pulse size increased exponentially with temperature in unamended resource conditions (Figure 3.2), supporting my temperature dependence hypothesis. Many biogeochemical models do not make predictions for temperature dependence of C processes above 35 °C (Davidson et al., 2012; Parton et al., 1998); I show that CO₂ pulses continue to increase with temperature above this threshold. I note that instantaneous CO₂ fluxes showed a non-linear response to temperature, with optimum fluxes occurring between 35 and 40 °C; this finding is consistent with previous work that quantified temperature sensitivity of soil respiration along an elevation gradient in California (Richardson et al., 2012). Peak CO₂ fluxes generally occurred within two hours post-wetting; the consistent peak and total flux relationships to temperature suggest that CO₂ pulse size is predominantly determined by the respiration response to temperature within the first hours following re-wetting when soils are wettest, and that temperature may be less important as soils dry. When I tested the relationships between temperature and the CO₂ rewetting response more explicitly by manipulating the time of day at which soils were re-wetted (Figure 3.5), I found strong differences between daytime and

nighttime re-wetting even when soils experienced the same range of temperatures over the course of 24 hours. Temperature at time of wetting was a strong positive predictor of 24-hour total CO₂ fluxes; since peak CO₂ fluxes were temperature-dependent, higher temperatures at time of wetting likely triggered higher peak respiration rates followed by more consistent rates of decline across all treatments.

Background N deposition alters the relationship between N addition and CO₂ pulses

N saturation at my focal site increased CO₂ pulses, particularly in the dry season, although these effects were weaker than for C saturation (Table 3.1, Figure 3.4). To complement the results at my focal site indicating N limitation of CO₂ pulses, I conducted additional field campaigns which quantified CO₂ pulse responses along two axes of N availability: background N deposition rates and experimental N addition. I found that experimental N amendments indirectly contributed to CO₂ pulse size, particularly when N was added as NO₃⁻ rather than NH₄⁺; however, the strength and direction of this relationship differed along a gradient of background N deposition, supporting both my N limitation and N mining hypotheses. The stronger respiration response to NO₃⁻ addition is interesting because it implies a microbial preference for nitrate over ammonium. Preference for specific forms of N by soil microbes continues to be unclear in literature based on studies that show relatively higher immobilization of NH₄⁺ (Recous et al., 1990), NO₃⁻ (Rochester et al., 1992), other forms of N such as urea (Wei et al., 2017), or no preference (Harrison et al., 2007). Evidence from plants suggests that temperature might mediate this response (Warren, 2009), where higher temperatures favor NO₃⁻ uptake, and a similar mechanism may be occurring in desert soils. Given

increasing susceptibility of desert systems to N deposition containing nitrogen oxides (NO_x) and ammonia (NH_3) (Sabo et al., 2019), my results provide a compelling argument to link CO_2 respiration to specific forms of N inputs.

At sites receiving lower N deposition, and at my focal site in particular, CO_2 pulses were positively correlated to amount of added N; I attribute this response to severe N limitation that, when it was reduced, increased N allocation to belowground (plant and/or microbial) biomass and correspondingly higher rates of respiration (Eberwein et al., 2015). However, this relationship switched in sites with high rates of background N deposition, suggesting that above some threshold N is highly-accessible to microbes and metabolic investment toward N acquisition decreases, reducing respiration rates and decreasing CO_2 pulse responses to re-wetting (Craine et al., 2007; Peng et al., 2017).

Interactive carbon, nitrogen, temperature, and moisture constraints on CO_2 respiration pulses

Consistent with my resource limitation hypothesis, simultaneous saturation of C and N produced CO_2 pulses that were larger than the response of either amendment individually or the additive response of both individual treatments (Figure 3.4,3.6), suggesting that respiration is subject to C and N co-limitation. While C constraints on respiration are well-documented, the relationship between N availability and CO_2 production is indirect and less clear from previous work (Peng et al., 2017). I suggest that simultaneous C and N saturation accelerates microbial biomass growth and activates

additional microbial activities (e.g. mineralization, nitrification, denitrification) following rewetting (Castellano et al., 2012), all of which increase respiratory requirements.

As expected (Liang et al., 2016), I observed the strongest CO₂ pulse responses in high-temperature, high-substrate conditions with the highest potential for enzymatic reactions. Interestingly, C and N amendments individually did not substantially alter temperature dependence of CO₂ fluxes; temperature dependence only increased in response to coupled C and N additions, suggesting not only substrate availability but also C:N stoichiometry contribute to temperature dependence of CO₂ pulses (Billings & Ballantyne, 2013). At seasonal timescales, CO₂ pulses were substantially larger following soil re-wetting in the dry season than in the wet season; since desert seasons differ in temperature and precipitation frequency, larger CO₂ pulses in the dry season are likely from a combination of higher temperatures and longer accumulation of substrate reserves in between infrequent rains (Collins et al., 2008; Reynolds et al., 2004). The dry season also magnified the CO₂ pulse response to substrate amendments, particularly those including N; these findings further support severe N limitation at my focal site that was allocated to metabolic infrastructure when limitation was reduced.

Synthesis

Based on my field results, I compiled a conceptual diagram to explain inter-related predictors of CO₂ pulse responses to rewetting, organized into proximate and longer-term climate and substrate controls (Figure 3.7). An advantage of this diagram is that it separates variables by temporal scale; for example, N deposition and instantaneous N limitation are both nitrogenous components that affect CO₂ pulses, but my results

indicate that these two mechanisms contribute to pulse size in different ways.

Additionally, my figure attempts to bridge results from lab studies, which tend to focus on proximate climate and substrate mechanistic interactions (Eberwein et al., 2015; Liang et al., 2015), and field studies, which tend to focus on patterns of CO₂ respiration in response to higher-order interactions (Huxman et al., 2004; Talmon et al., 2011).

Importantly, I show that studies quantifying desert soil respiration in terms of C and temperature dependence are missing important contributions by soil moisture and N limitation. Increasing acknowledgment of the complexity of respiration demands more integrative research that considers multiple mechanisms and their interactions; these results refine our understanding of interacting controls over desert CO₂ respiration using a robust field-based approach.

References

- Andrews, H.M., & Krichels, A. (2021). TraceGasArray: Calculation and integration of trace gas fluxes and soil climate data for high-resolution *in situ* chamber array. GitHub repository: <https://github.com/handr003/TraceGasArray>.
- Barnard, R. L., Blazewicz, S. J., & Firestone, M. K. (2020). Rewetting of soil: revisiting the origin of soil CO₂ emissions. *Soil Biology & Biochemistry*, 107819.
- Billings, S. A., & Ballantyne, F., 4th. (2013). How interactions between microbial resource demands, soil organic matter stoichiometry, and substrate reactivity determine the direction and magnitude of soil respiratory responses to warming. *Global Change Biology*, 19(1), 90–102.
- Birch, H. F. (1958). The effect of soil drying on humus decomposition and nitrogen availability. *Plant and Soil*, 10(1), 9–31.
- Brangarí, A. C., Manzoni, S., & Rousk, J. (2020). A soil microbial model to analyze decoupled microbial growth and respiration during soil drying and rewetting. *Soil Biology & Biochemistry*, 148, 107871.
- Cable, J. M., Ogle, K., Lucas, R. W., Huxman, T. E., Loik, M. E., Smith, S. D., Tissue, D. T., Ewers, B. E., Pendall, E., Welker, J. M., Charlet, T. N., Cleary, M., Griffith, A., Nowak, R. S., Rogers, M., Steltzer, H., Sullivan, P. F., & van Gestel, N. C. (2011). The temperature responses of soil respiration in deserts: a seven desert synthesis. *Biogeochemistry*, 103(1), 71–90.
- Castellano, M. J., Kaye, J. P., Lin, H., & Schmidt, J. P. (2012). Linking Carbon Saturation Concepts to Nitrogen Saturation and Retention. *Ecosystems*, 15(2), 175–187.
- Collins, S. L., Belnap, J., Grimm, N. B., Rudgers, J. A., Dahm, C. N., D'Odorico, P., Litvak, M., Natvig, D. O., Peters, D. C., Pockman, W. T., Sinsabaugh, R. L., & Wolf, B. O. (2014). A Multiscale, Hierarchical Model of Pulse Dynamics in Arid-Land Ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, 45(1), 397–419.
- Collins, S. L., Sinsabaugh, R. L., Crenshaw, C., Green, L., Porras-Alfaro, A., Stursova, M., & Zeglin, L. H. (2008). Pulse dynamics and microbial processes in aridland ecosystems. *The Journal of Ecology*, 96(3), 413–420.
- Craine, J. M., Morrow, C., & Fierer, N. (2007). Microbial nitrogen limitation increases decomposition. *Ecology*, 88(8), 2105–2113.

- Davidson, E. A., & Janssens, I. A. (2006). Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature*, *440*(March), 165–173.
- Davidson, E. A., Keller, M., Erickson, H. E., Verchot, L. V., & Veldkamp, E. (2000). Testing a conceptual model of soil emissions of nitrous and nitric oxides: using two functions based on soil nitrogen availability and soil water content, the hole-in-the-pipe model characterizes a large fraction of the observed variation of nitric oxide and nitrous oxide emissions from soils. *AIBS Bulletin*, *50*(8), 667–680.
- Davidson, E. A., Samanta, S., Caramori, S. S., & Savage, K. (2012). The Dual Arrhenius and Michaelis-Menten kinetics model for decomposition of soil organic matter at hourly to seasonal time scales. *Global Change Biology*, *18*(1), 371–384.
- Eberwein, J. R., Homyak, P. M., Carey, C. J., Aronson, E. L., & Jenerette, G. D. (2020). Large nitrogen oxide emission pulses from desert soils and associated microbiomes. *Biogeochemistry*, *149*(3), 239–250.
- Eberwein, J. R., Oikawa, P. Y., Allsman, L. A., & Jenerette, G. D. (2015). Carbon availability regulates soil respiration response to nitrogen and temperature. *Soil Biology & Biochemistry*, *88*(June), 158–164.
- Eberwein, J., Shen, W., & Jenerette, G. D. (2017). Michaelis-Menten kinetics of soil respiration feedbacks to nitrogen deposition and climate change in subtropical forests. *Scientific Reports*, *7*(1), 1752.
- Evans, S., Dieckmann, U., Franklin, O., & Kaiser, C. (2016). Synergistic effects of diffusion and microbial physiology reproduce the Birch effect in a micro-scale model. *Soil Biology & Biochemistry*, *93*, 28–37.
- Fan, Z., Neff, J. C., & Hanan, N. P. (2015). Modeling pulsed soil respiration in an African savanna ecosystem. *Agricultural and Forest Meteorology*, *200*, 282–292.
- Fraser, F. C., Corstanje, R., Deeks, L. K., Harris, J. A., Pawlett, M., Todman, L. C., Whitmore, A. P., & Ritz, K. (2016). On the origin of carbon dioxide released from rewetted soils. *Soil Biology & Biochemistry*, *101*, 1–5.
- Harms, T. K., & Grimm, N. B. (2012). Responses of trace gases to hydrologic pulses in desert floodplains: Trace gas fluxes from desert floodplains. *Journal of Geophysical Research*, *117*(G1), 221.
- Harrison, K. A., Bol, R., & Bardgett, R. D. (2007). Preferences for different nitrogen forms by coexisting plant species and soil microbes. *Ecology*, *88*(4), 989–999.

- Hursh, A., Ballantyne, A., Cooper, L., Maneta, M., Kimball, J., & Watts, J. (2017). The sensitivity of soil respiration to soil temperature, moisture, and carbon supply at the global scale. *Global Change Biology*, 23(5), 2090–2103.
- Huxman, T. E., Snyder, K. A., Tissue, D., Leffler, A. J., Ogle, K., Pockman, W. T., Sandquist, D. R., Potts, D. L., & Schwinning, S. (2004). Precipitation pulses and carbon fluxes in semiarid and arid ecosystems. *Oecologia*, 141(2), 254–268.
- Janssens, I. A., Dieleman, W., Luyssaert, S., Subke, J.-A., Reichstein, M., Ceulemans, R., Ciais, P., Dolman, A. J., Grace, J., Matteucci, G., Papale, D., Piao, S. L., Schulze, E.-D., Tang, J., & Law, B. E. (2010). Reduction of forest soil respiration in response to nitrogen deposition. *Nature Geoscience*, 3(5), 315–322.
- Jarvis, P., Rey, A., Petsikos, C., Wingate, L., Rayment, M., Pereira, J., Banza, J., David, J., Miglietta, F., Borghetti, M., Manca, G., & Valentini, R. (2007). Drying and wetting of Mediterranean soils stimulates decomposition and carbon dioxide emission: the “Birch effect.” *Tree Physiology*, 27(7), 929–940.
- Jenerette, G. D., & Chatterjee, A. (2012). Soil metabolic pulses: water, substrate, and biological regulation. *Ecology*, 93(5), 959–966.
- Krichels, A., Homyak, P., Aronson, E., Sickman, J., Botthoff, J., Shulman, H., Piper, S., Andrews, H., & Jenerette, G.D. (*in review*). Rapid nitrate reduction produces pulsed NO and N₂O emissions following wetting of dryland soils. *Biogeosciences*.
- Lado-Monserrat, L., Lull, C., Bautista, I., Lidón, A., & Herrera, R. (2014). Soil moisture increment as a controlling variable of the “Birch effect”. Interactions with the pre-wetting soil moisture and litter addition. *Plant and Soil*, 379(1), 21–34.
- Liang, L. L., Eberwein, J. R., Allsman, L. A., Grantz, D. A., & Jenerette, G. D. (2015). Regulation of CO₂ and N₂O fluxes by coupled carbon and nitrogen availability. *Environmental Research Letters: ERL [Web Site]*, 10(3), 034008.
- Liang, L. L., Grantz, D. A., & Jenerette, G. D. (2016). Multivariate regulation of soil CO₂ and N₂O pulse emissions from agricultural soils. *Global Change Biology*, 22(3), 1286–1298.
- Lloyd, J., & Taylor, J. A. (1994). On the temperature dependence of soil respiration. *Functional Ecology*, 8, 315–323.
- Marcé, R., Obrador, B., Gómez-Gener, L., Catalán, N., Koschorreck, M., Arce, M. I., Singer, G., & von Schiller, D. (2019). Emissions from dry inland waters are a blind spot in the global carbon cycle. *Earth-Science Reviews*, 188, 240–248.

- Meredith, L. K., Boye, K., Savage, K., & Vargas, R. (2020). Formation and Fluxes of Soil Trace Gases. *Soil Systems*, 4(2), 22.
- Miller, A. E., Schimel, J. P., Meixner, T., Sickman, J. O., & Melack, J. M. (2005). Episodic rewetting enhances carbon and nitrogen release from chaparral soils. *Soil Biology & Biochemistry*, 37(12), 2195–2204.
- Parton, W. J., Hartman, M., Ojima, D., & Schimel, D. (1998). DAYCENT and its land surface submodel: description and testing. *Global and Planetary Change*, 19(1-4), 35–48.
- Patel, K. F., Myers-Pigg, A., Bond-Lamberty, B., Fansler, S. J., Norris, C. G., McKeever, S. A., Zheng, J., Rod, K. A., & Bailey, V. L. (2021). Soil carbon dynamics during drying vs. rewetting: Importance of antecedent moisture conditions. *Soil Biology & Biochemistry*, 156, 108165.
- Peng, Y., Li, F., Zhou, G., Fang, K., Zhang, D., Li, C., Yang, G., Wang, G., Wang, J., Mohammad, A., & Yang, Y. (2017). Nonlinear response of soil respiration to increasing nitrogen additions in a Tibetan alpine steppe. *Environmental Research Letters*, 12(024018).
- Recous, S., Mary, B., & Faurie, G. (1990). Microbial immobilization of ammonium and nitrate in cultivated soils. In *Soil Biology and Biochemistry* (Vol. 22, Issue 7, pp. 913–922). [https://doi.org/10.1016/0038-0717\(90\)90129-n](https://doi.org/10.1016/0038-0717(90)90129-n)
- Reynolds, J. F., Kemp, P. R., Ogle, K., & Fernández, R. J. (2004). Modifying the “pulse-reserve” paradigm for deserts of North America: precipitation pulses, soil water, and plant responses. *Oecologia*, 141(2), 194–210.
- Richardson, J., Chatterjee, A., & Darrel Jenerette, G. (2012). Optimum temperatures for soil respiration along a semi-arid elevation gradient in southern California. *Soil Biology & Biochemistry*, 46, 89–95.
- Rochester, I. J., Constable, G. A., & MacLeod, D. A. (1992). Preferential Nitrate Immobilization in Alkaline Soils. *Australian Journal of Soil Research*, 30, 737–749.
- Sabo, R. D., Clark, C. M., Bash, J., Sobota, D., Cooter, E., Dobrowolski, J. P., Houlton, B. Z., Rea, A., Schwede, D., Morford, S. L., & Compton, J. E. (2019). Decadal shift in nitrogen inputs and fluxes across the contiguous United States: 2002-2012. *Journal of Geophysical Research: Biogeosciences*. <https://doi.org/10.1029/2019JG005110>

- Schimel, J. P. (2018). Life in Dry Soils: Effects of Drought on Soil Microbial Communities and Processes. *Annual Review of Ecology, Evolution, and Systematics*, 49(1), 409–432.
- Shen, W., Jenerette, G. D., Hui, D., & Scott, R. L. (2016). Precipitation legacy effects on dryland ecosystem carbon fluxes: direction, magnitude and biogeochemical carryovers. *Biogeosciences*, 13(2), 425–439.
- Sihi, D., Davidson, E. A., Savage, K. E., & Liang, D. (2020). Simultaneous numerical representation of soil microsite production and consumption of carbon dioxide, methane, and nitrous oxide using probability distribution functions. *Global Change Biology*, 26(1), 200–218.
- Skopp, J., Jawson, M. D., & Doran, J. W. (1990). Steady-state aerobic microbial activity as a function of soil water content. *Soil Science Society of America Journal. Soil Science Society of America*, 54(6), 1619–1625.
- Sponseller, R. A. (2007). Precipitation pulses and soil CO₂ flux in a Sonoran Desert ecosystem. *Global Change Biology*, 13(2), 426–436.
- Talmon, Y., Sternberg, M., & GrÜnzweig, J. M. (2011). Impact of rainfall manipulations and biotic controls on soil respiration in Mediterranean and desert ecosystems along an aridity gradient. *Global Change Biology*, 17(2), 1108–1118.
- Vargas, R. (2012). How a hurricane disturbance influences extreme CO₂ fluxes and variance in a tropical forest. *Environmental Research Letters: ERL [Web Site]*, 7(3), 035704.
- Vargas, R., Sánchez-Cañete P., E., Serrano-Ortiz, P., Curiel Yuste, J., Domingo, F., López-Ballesteros, A., & Oyonarte, C. (2018). Hot-Moments of Soil CO₂ Efflux in a Water-Limited Grassland. *Soil Systems*, 2(3), 47.
- Warren, C. R. (2009). Why does temperature affect relative uptake rates of nitrate, ammonium and glycine: A test with *Eucalyptus pauciflora*. *Soil Biology & Biochemistry*, 41(4), 778–784.
- Wei, H., Chen, X., He, J., Zhang, J., & Shen, W. (2017). Exogenous Nitrogen Addition Reduced the Temperature Sensitivity of Microbial Respiration without Altering the Microbial Community Composition. *Frontiers in Microbiology*, 8, 2382.
- Western Regional Climate Center (2021) Boyd Deep Canyon Reserve, California Weather Data. Retrieved from <https://wrcc.dri.edu/weather/ucde.html>

Tables

Table 3.1 Experimental predictors of CO₂ 24-hour total flux from rewetted desert soils. Only treatment sets testing a full nutrient addition suite (wet, wet+C, wet+N, wet+C+N) were used (n=2 field campaigns). Variance in CO₂ flux was explained using a reduced general linear model (GLM) with the lowest Akaike Information Criterion (AICc). Statistical significance of each independent variable in the best model was tested using analysis of variance (ANOVA) at 95% confidence, and separation of individual treatment groups was identified using post-hoc t-tests or Tukey's tests. Results describe boxplots displayed in Figure 3.4.

Model	AICc	Model parameter	p-value	Post-hoc test (decreasing order)
Nutrient addition * Season	1418.87	Season	<0.001	A = dry; B = wet
		Nutrient addition	<0.001	A = wet+C+N; B = wet+C; BC = wet+N; C = wet
		Season*Nutrient addition	0.021	A = dry wet+C+N; B = all others

Table 3.2 Temperature, moisture, and nitrogen dependence of CO₂ peak and 24-hour total flux from rewetted desert soils in amended and saturated nutrient conditions. Statistical significance of each independent variable was tested using analysis of variance (ANOVA) at 95% confidence.

Experiment set	Dependent variable	Independent variable	DF	F	p-value ($\alpha = 0.05$)
Unamended wetting experiments (Figure 3.2)	Peak CO ₂ flux ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	Temperature at peak CO ₂ flux (°C)	1	26.484	<0.001
		Moisture at peak CO ₂ flux (%)	1	2.603	0.112
	24-hour total CO ₂ flux ($\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	24-hour mean temperature (°C)	1	22.117	0.003
		24-hour mean moisture (%)	1	8.694	0.004
Time-of-day experiments (Figure 3.3)	Peak CO ₂ flux ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	Temperature at time of wetting (°C)	1	9.764	0.004
		24-hour average temperature (°C)	1	1.207	0.281
	24-hour total CO ₂ flux ($\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	Temperature at time of wetting (°C)	1	7.988	0.008
		24-hour average temperature (°C)	1	0.310	0.582
C & N amendment comparisons (Figure 3.6)	Peak CO ₂ flux ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	Temperature at peak CO ₂ (°C, C+N scenario)	1	7.632	0.043
		Temperature at peak CO ₂ (°C, limited scenarios)	1	23.678	<0.001
		Moisture at peak CO ₂ flux (% , C+N scenario)	1	2.742	0.090
		Moisture at peak CO ₂ flux (% , limited scenarios)	1	4.028	0.048
	24-hour total CO ₂ flux ($\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	24-hour mean temperature (°C, C+N scenario)	1	7.821	0.005
		24-hour mean temperature (°C, limited scenarios)	1	31.209	<0.001
		24-hour mean moisture (% , C+N scenario)	1	11.259	0.008
		24-hour mean moisture (% , limited scenarios)	1	4.713	0.033
N addition experiment (Figure 3.5)	Peak CO ₂ flux ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	NH ₄ ⁺ addition (kg ha^{-1})	1	0.905	0.378
		NO ₃ ⁻ addition (kg ha^{-1})	1	4.044	0.091
	24-hour total CO ₂ flux ($\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	NH ₄ ⁺ addition (kg ha^{-1})	1	1.957	0.211
		NO ₃ ⁻ addition (kg ha^{-1})	1	3.745	0.101

Table 3.3 Nitrogen dependence of CO₂ peak and 24-hour total flux from rewetted desert soils along a N deposition gradient. Statistical significance of each independent variable was tested using analysis of variance (ANOVA) at 95% confidence.

Dependent variable	N addition (kg ha ⁻¹)	Site	DF	F-ratio	p-value ($\alpha = 0.05$)
Peak CO ₂ flux (μmol CO ₂ m ⁻² s ⁻¹)	NH ₄ ⁺	All sites	1	0.023	0.884
		Pinto Basin	1	0.313	0.596
		Wide Canyon	1	7.503	0.016
		Oasis	1	3.051	0.131
		Morongongo	1	0.674	0.426
	NO ₃ ⁻	All sites	1	0.722	0.400
		Pinto Basin	1	9.985	0.020
		Wide Canyon	1	19.94	<0.001
		Oasis	1	0.171	0.694
		Morongongo	1	0.273	0.610
24-hour total CO ₂ flux (mol CO ₂ m ⁻² s ⁻¹)	NH ₄ ⁺	All sites	1	0.799	0.379
		Pinto Basin	1	0.556	0.484
		Wide Canyon	1	6.095	0.027
		Oasis	1	0.155	0.708
		Morongongo	1	4.625	0.050
	NO ₃ ⁻	All sites	1	7.016	0.012
		Pinto Basin	1	<0.001	0.992
		Wide Canyon	1	11.76	0.004
		Oasis	1	1.816	0.226
		Morongongo	1	0.488	0.511

Table 3.4 High CO₂ fluxes reported for various ecosystem types, primarily in drylands.

Source	Ecosystem type	Peak CO₂ flux ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)
Vargas, 2012	Tropical forest (post-hurricane)	21.5
Eberwein et al., 2017	Subtropical forest (C-saturated)	40
Jenerette & Chatterjee, 2012	Dryland transect (C-amended)	12.6
Fan et al., 2015	African savanna (unamended)	37
Sponseller, 2007	Sonoran desert (unamended)	50.9
Marcé et al., 2019	Intermittent re-wetted streams (unamended)	18
Cable et al., 2011	Deserts (unamended)	13.4
Vargas et al., 2018	Grassland (unamended)	20

Figures

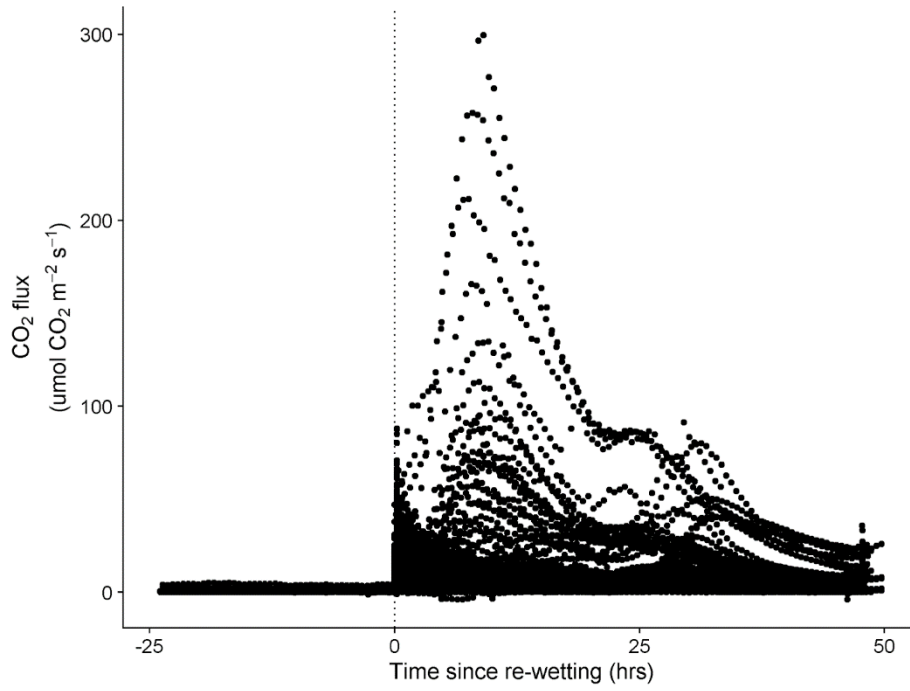


Figure 3.1 CO₂ pulse behavior following soil rewetting for all field campaigns (n=8). The dotted line at x=0 indicates the soil rewetting event; each point indicates an instantaneous CO₂ flux measurement.

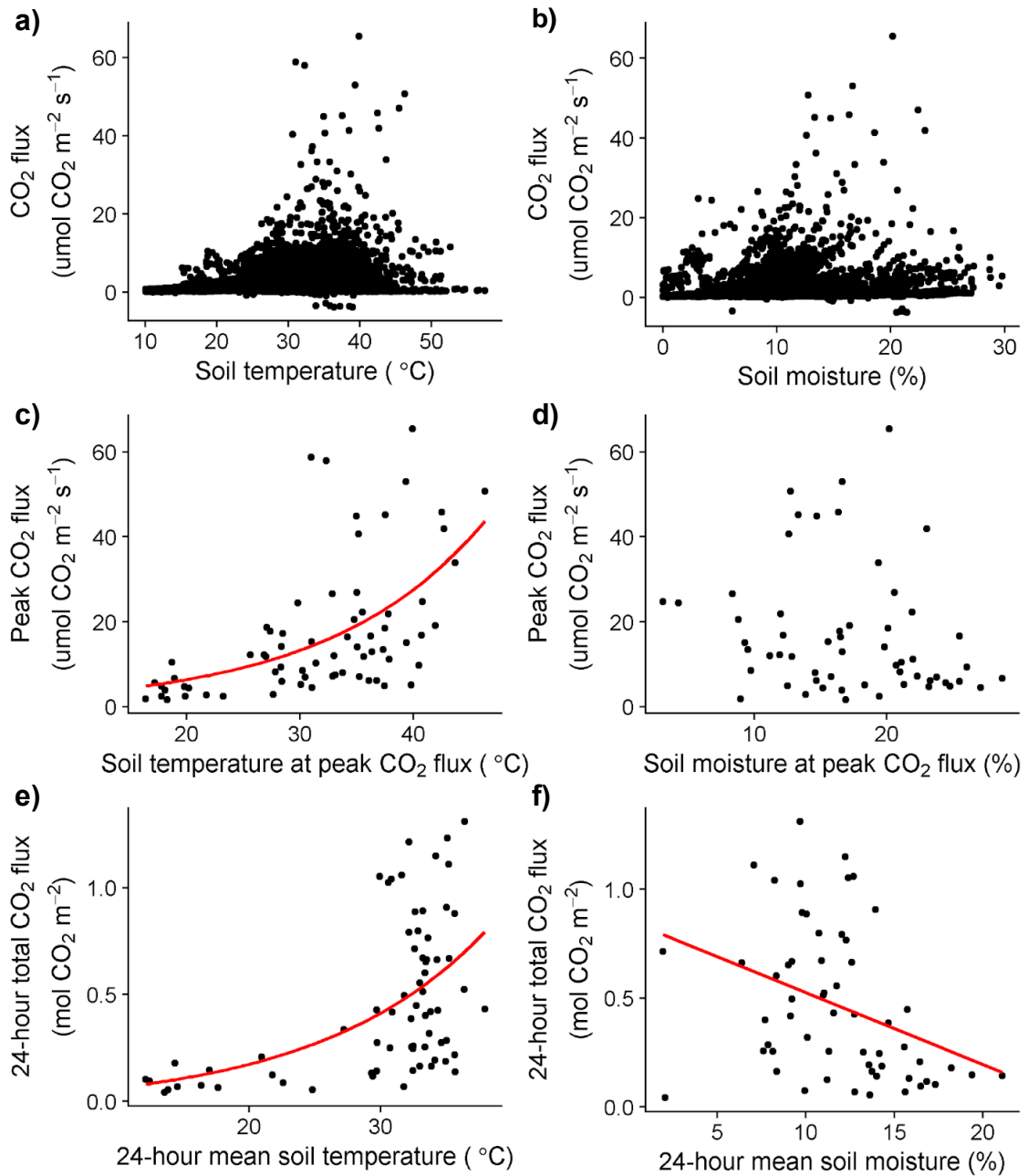


Figure 3.2 CO₂-temperature (a,c,e) and CO₂-moisture (b,d,f) relationships under rewetting only (no nutrient amendment) conditions. Instantaneous CO₂ flux plotted against instantaneous soil climate (a,b) were not tested for statistical significance. Peak instantaneous CO₂ flux for each pulse were compared to corresponding soil temperature (c) and moisture (d). 24-hour total CO₂ fluxes for each pulse, calculated using area-under-the-curve integration, were also compared to 24-hour average soil temperature (e) and moisture (f). Statistically significant ($p < 0.05$) regression curves are indicated in red; temperature correlations were generally exponential (c,e) compared to linear correlations to moisture (f).

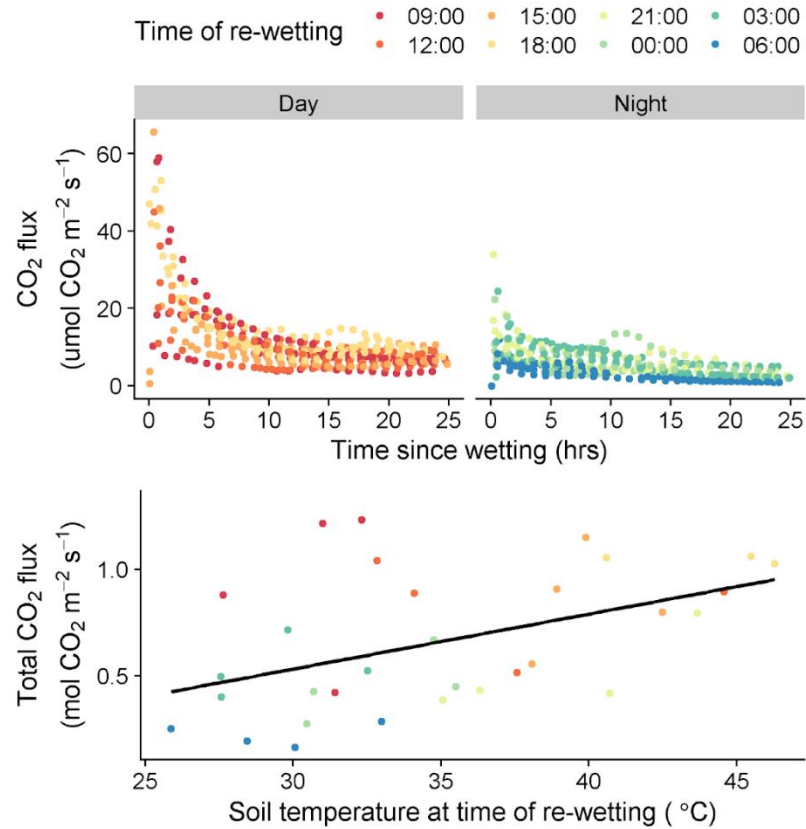


Figure 3.3 CO₂ pulse-temperature relationships under rewetting (no nutrient amendment) conditions for Summer 2019 campaign, in which temperature at time of wetting was most explicitly manipulated. **Top:** Instantaneous CO₂ fluxes at time post-wetting. Points are colored by time of day at which soils were rewetted and figure panels are separated by daytime and nighttime hours. **Bottom:** 24-hour total CO₂ flux as explained by soil temperature at time of rewetting; points are colored to match top panels. The statistically significant ($p < 0.05$) regression line is indicated in black.

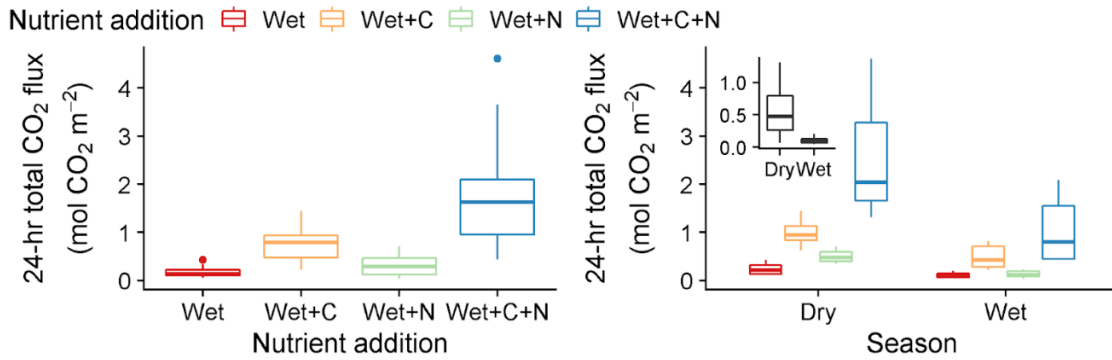


Figure 3.4 24-hour total CO₂ flux responses to experimental carbon and nitrogen amendments (left) and seasonal magnification of those amendments (right). Field campaigns were only included if they manipulated C and N in a fully-factorial suite (n=2 field campaigns); inlaid boxplot indicates differences in 24-hour total CO₂ fluxes in wet-only conditions (no amendments) between wet and dry seasons (n=5 field campaigns). Colors separate nutrient amendment treatments; statistical significance of season*amendment interactions are displayed in Table 3.1.

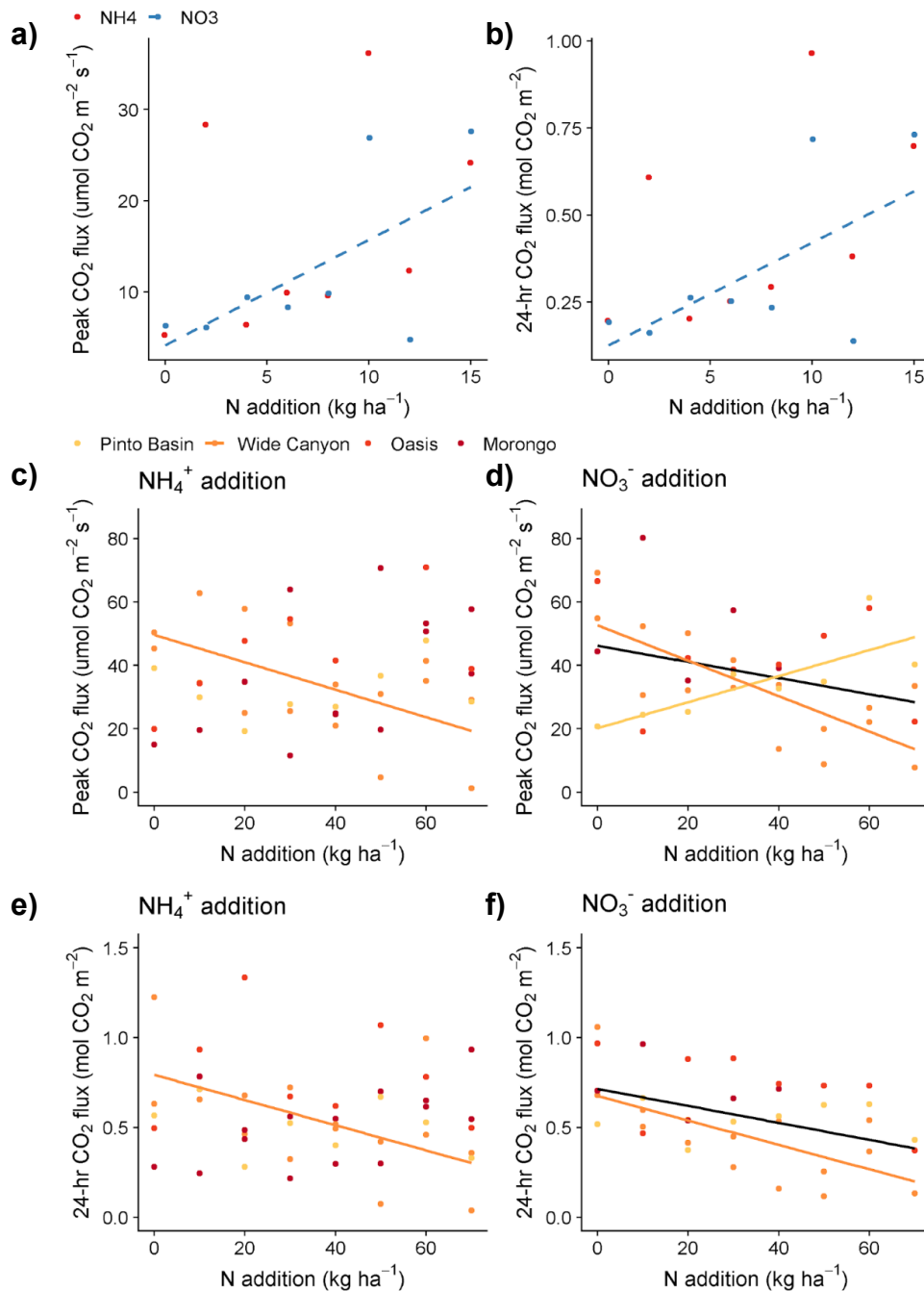


Figure 3.5 Peak (a,c,d) and 24-hour total (b,e,f) CO₂ flux responses to experimental nitrogen amendments at Boyd Deep Canyon (a,b) and in desert sites spanning a nitrogen deposition gradient (c-f). Solid lines indicate significant correlations and dashed lines indicate marginal significance at 95% confidence; colored lines represent site- or N type-specific relationships while black lines indicate significant relationships when all data are pooled. At Boyd Deep Canyon (a,b), colors indicate type of N amendment; in other plots (c-f), sites in the N deposition gradient are colored to indicate low (yellow) to high (red) throughfall N deposition.

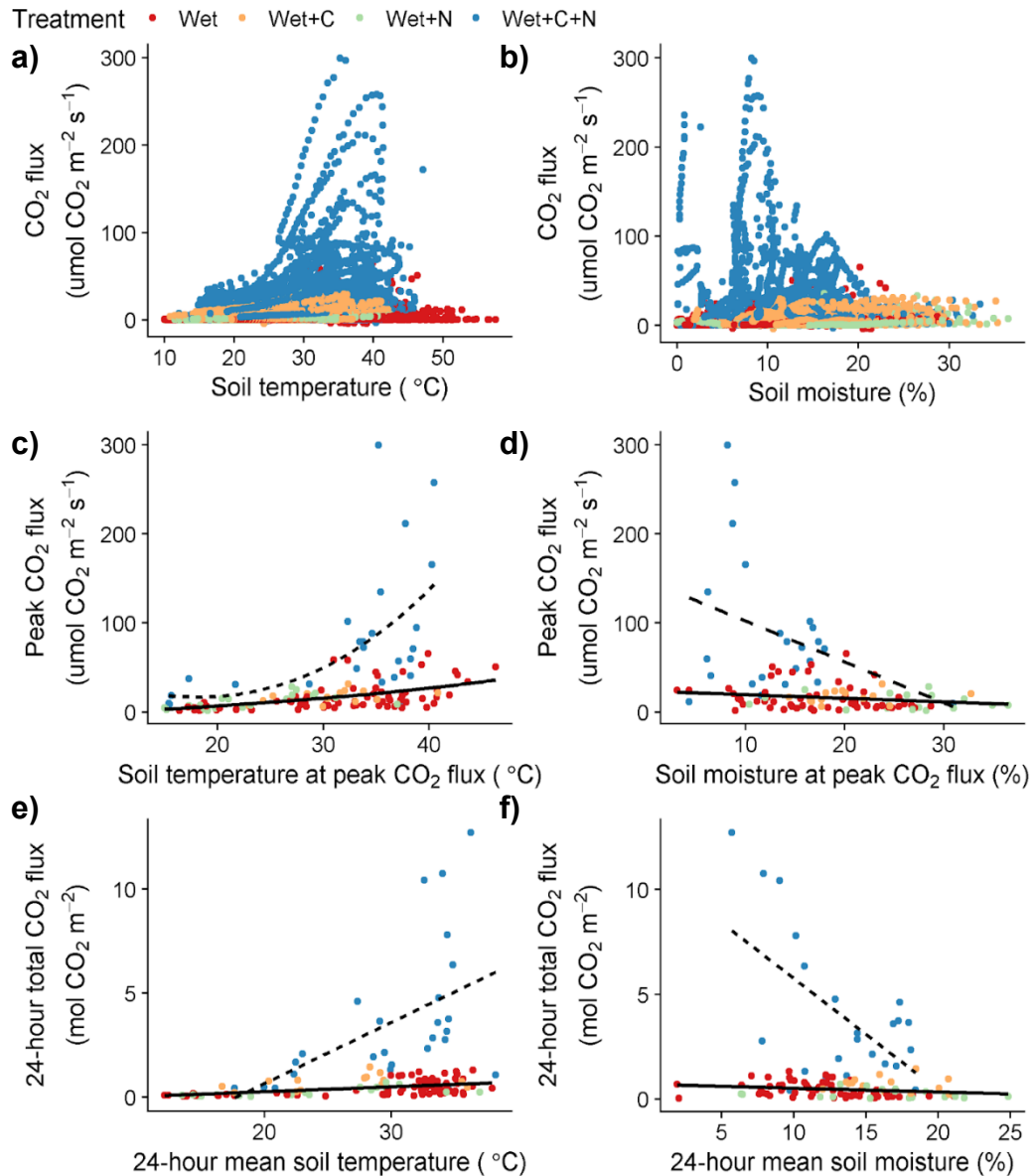


Figure 3.6 Co-limitation in CO₂ flux-temperature relationship (a,c,e) and contrasting flux-moisture interactions (b,d,f) introduced under nutrient amendments. Points are colored by experimental nutrient addition treatments. Instantaneous CO₂ flux plotted against instantaneous soil climate (a,b) were not tested for statistical significance. Peak instantaneous CO₂ flux for each pulse were compared to corresponding soil temperature (c) and moisture (d). 24-hour total CO₂ fluxes for each pulse, calculated using area-under-the-curve integration, were also compared to 24-hour average soil temperature (e) and moisture (f). For subsequent analyses, the “limited” wet-only, wet+C, and wet+N treatments were pooled and compared to the “unlimited” wet+C+N conditions. Statistically significant ($p < 0.05$) regression curves are indicated as solid lines (“limited” group) and dashed (“unlimited” group); correlations were generally linear (d,e,f) except for when comparing peak CO₂ flux to corresponding temperature (c).

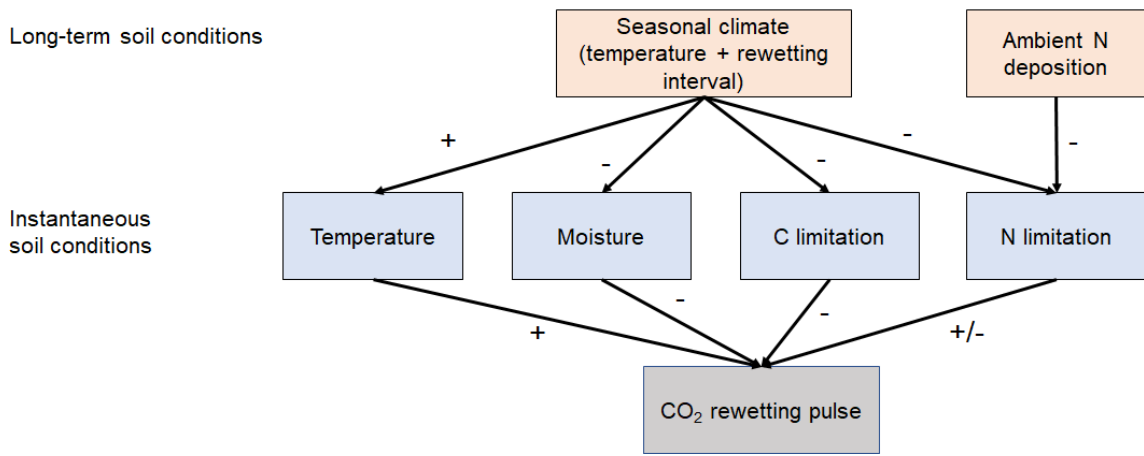


Figure 3.7 Conceptual diagram linking soil conditions at time of rewetting (blue) and longer-term soil conditions (red) to the CO₂ pulse response to rewetting that were tested in this study. I do not make predictions about the relative sizes of effects contributing to CO₂ pulses but indicate the direction of effect with arrows and +/- signs.

Synthesis and Future Directions

This dissertation expands current knowledge of biogeochemical cycling in dryland systems by identifying patterns of trace gas pulse responses to soil rewetting and quantifying individual and interactive relationships among pulses, soil temperature, moisture and rewetting history, and direct and indirect sources of carbon and nitrogen substrates. Across my chapters, I observed responses of CO₂, N₂O, and NO fluxes to soil rewetting; however, the type of response differed among ecosystem types. Birch effect CO₂ pulses occurred in sandy soils where water inputs were unmanaged (shrubland, desert), but irrigation inputs in clay agricultural soils initially suppressed CO₂ emissions. N₂O and NO produced consistent pulse responses to rewetting when measured (Chapters 1 and 2), and the timing of N₂O pulses was generally earlier post-wetting than NO. A consistent effect across all studies was seasonality of pulses; the magnitude of CO₂, N₂O, and NO pulses was considerably larger in the Mediterranean hot dry season compared to cool wet season and was a dominant explanatory variable for all field studies. This finding supports my hypothesis that pulses are interactively driven by seasonal differences in temperature, interval between rewetting events, and accumulation of C and N reserves in soil microsites, and that these mechanisms together are positively correlated to pulse size.

In invaded coastal sage scrub (Chapter 1), I provided new evidence that exotic grass litter enhanced pulses of CO₂ and N₂O, and that a shift from shrub to grass cover reduced CO₂ pulses without altering N pulses. In a high-temperature agricultural system (Chapter 2), I provided field-based evidence that subsurface drip irrigation increased

yield of both alfalfa and sudangrass and simultaneously reduced per-yield water use and per-yield soil emissions of CO₂, N₂O, and NO. The benefits of drip irrigation for reducing nitrogenous soil pulses were particularly strong for sudangrass, a crop requiring fertigation N inputs, and in summer harvests, when average soil temperature and moisture were also high. In a collection of desert sites (Chapter 3), I showed that soils had a large capacity for CO₂ respiration that had not been previously quantified in literature, and that CO₂ pulses in re-wetted desert soils were limited not only by climatic temperature and soil C but were also modulated by fine-scale temperature regimes and N limitation. I also found compelling evidence of a switch in the relationship between N availability and CO₂ pulse size that was dependent on long-term regional N deposition patterns. Together, these findings support my hypothesis that rewetting triggers pulses (or suppression) of trace gases from dryland soils, and that pulses are directly impacted by temperature, moisture, substrate availability. Plant and atmospheric controls over C and/or N substrate availability can also indirectly influence trace gas pulses. High-substrate, high-temperature, large-rewetting- interval conditions were generally predictors of large pulsed emissions of CO₂, N₂O, and NO; however, prolonged soil moisture limited CO₂ respiration in desert and agricultural soils.

Future Directions

While this dissertation quantifies multiple, interacting biogeochemical drivers of trace gas pulses, it can only hint at metabolic pathways that are producing CO₂, N₂O, and NO. A fundamental question in nitrogen cycling continues to be the proportions of N₂O

and NO formed via nitrification and denitrification and under what soil conditions these processes dominate (Butterbach-Bahl et al., 2013). Similarly, I have not attempted to separate microbial CO₂ respiration from plant root respiration; my data were collected under plant canopies, where I expected biological capacity for metabolism to be largest (Schlesinger et al., 1996), but I can only speculate on the relative proportions of different sources of respiration. Finally, I do not make quantitative connections to soil microbial community structures or activities that are a key component of soil metabolism and trace gas production but are not well understood (Rocca et al., 2015). Next-generation sequencing tools are increasingly being used to connect specific microbial taxa and transcripts to metabolic processes (Banerjee et al., 2016); similarly, stable isotope methods provide a promising method of distinguishing gases produced via different biochemical pathways (Park et al., 2011). The findings reported here can be expanded by linking microbial identities, community structures, and active metabolic processes that change in response to soil rewetting to production of trace gases in dryland ecosystems.

References

- Banerjee, S., Helgason, B., Wang, L., Winsley, T., Ferrari, B. C., & Siciliano, S. D. (2016). Legacy effects of soil moisture on microbial community structure and N₂O emissions. *Soil Biology & Biochemistry*, *95*, 40–50.
- Butterbach-Bahl, K., Baggs, E. M., Dannenmann, M., Kiese, R., & Zechmeister-Boltenstern, S. (2013). Nitrous oxide emissions from soils: how well do we understand the processes and their controls? *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *368*(1621), 20130122.
- Park, S., Pérez, T., Boering, K. A., Trumbore, S. E., Gil, J., Marquina, S., & Tyler, S. C. (2011). Can N 2 O stable isotopes and isotopomers be useful tools to characterize sources and microbial pathways of N₂O production and consumption in tropical soils?: Tropical soils N₂O Stable Isotopes. *Global Biogeochemical Cycles*, *25*(1). <https://doi.org/10.1029/2009GB003615>
- Rocca, J. D., Hall, E. K., Lennon, J. T., Evans, S. E., Waldrop, M. P., Cotner, J. B., Nemergut, D. R., Graham, E. B., & Wallenstein, M. D. (2015). Relationships between protein-encoding gene abundance and corresponding process are commonly assumed yet rarely observed. *The ISME Journal*, *9*(8), 1693–1699.
- Schlesinger, W. H., Raikes, J. A., Hartley, A. E., & Cross, A. F. (1996). On the Spatial Pattern of Soil Nutrients in Desert Ecosystems. *Ecology*, *77*(2), 364–374.