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REGULAR ARTICLE

Exotic grass litter modulates seasonal pulse dynamics of CO_2 and N_2O, but not NO, in Mediterranean-type coastal sage scrub at the wildland-urban interface

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Abstract
Aims Mediterranean shrublands adjacent to urbanization experience nitrogen deposition and exotic grass invasions which likely have downstream consequences for carbon and nitrogen emissions from soils. We tested a hypothesis that soil wetting produces trace gas pulses modified by seasonal wetting history, grass litter availability, and cover type in these systems.
Methods Over two seasons, we conducted 48-h wetting experiments and measured CO_2, N_2O, 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 (*Erioginum fasciculatum*).
Results CO_2 and N_2O pulses consistently appeared 15 min post-wetting and diminished within 12 h; NO peaked later and remained elevated at 24 h. All pulses were stronger in the dry season than wet season. Grass litter amendments increased CO_2 and dry-season N_2O pulses without significantly modifying NO pulses. Grass cover reduced CO_2 pulses compared to shrub cover.
Conclusions Our results support the hypothesis that shrubland soils produce stronger pulses of CO_2, N_2O, and NO during the dry season when wetting is less frequent. We show that invasive grass litter can provide a labile C source that stimulates CO_2 and N_2O, but not NO, emissions from shrubland soils.

Keywords Soil rewetting · Grass invasion · Coastal sage scrub · Trace gas pulse · Plant litter

Abbreviations

CSS	Coastal sage scrub
C	Carbon
N	Nitrogen
CO_2	Carbon dioxide
N_2O	Nitrous oxide
NO	Nitric oxide

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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 (CO_2) 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 (N_2O) 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, N_2O, like CO_2, 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 N_2O 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, CO_2 and N_2O emissions are both limited by C substrates (Liang et al. 2016), and the relative impact of C on N_2O 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 Castro 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 N_2O, 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 CO_2 and N_2O (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 CO_2, N_2O, 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, we 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 CO_2, N_2O, and NO soil emissions? We 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, we predicted that the magnitude of CO_2, N_2O, 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, we aimed to better understand the ecosystem consequences of grass invasion in Mediterranean shrublands at large.

Materials and methods

Study site

We conducted our 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*, *Erioginum 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, 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. We conducted our 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 we expected would produce maximum differences in pulses. Our study also coincided with California's return to historic normal rainfall following a multi-year, extreme drought (Griffin and Anchukaitis 2015).

Litter addition plot design

Throughout the reserve, we 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"). We 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, we 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, we 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 CO_2, N_2O, and NO fluxes following experimental wetting

We measured NO and N_2O fluxes from large collars and CO_2 fluxes from small collars; prior to sampling, we removed live standing biomass from collars to limit interference with instruments. We did not attempt to separate autotrophic and heterotrophic sources of respiration; because the fluxes we measured from dry soils were low, we assumed that CO_2 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. CO_2 measurements were made on small collars using a 10-cm diameter closed-chamber system (LI-8100A; LI-COR Bioscience, Lincoln, NE, USA; Fig. 1). To measure NO and N_2O, we constructed an open-chamber system (Fig. 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 N_2O/CO cavity ringdown infrared analyzer (Los Gatos Research, San Jose, CA, USA); and (3) a combined nitrogen dioxide (NO_2) converter/NO monitor system (Model 401/410, 2B Technologies, Boulder, CO, USA). To quantify each flux, we measured concentrations of CO_2, N_2O, and NO every 1, 1, and 10 s, respectively, for approximately 5 min inside the sealed chambers. NO_2 and NO concentrations were measured simultaneously, but NO_2 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-min measurement period, corrected for soil collar area and meteorological parameters using the Ideal Gas Law (Davidson et al. 2000). Our 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.

We quantified trace gas fluxes in our study following two experimental wetting campaigns: one during a dry season (August 2016) and one during a wet season (April 2017). Before wetting, we measured ambient, "pre-wet" fluxes of CO_2, N_2O, and NO. We 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. We took flux readings again at 15 min, 6 h, and 48 h post-wetting. Individual rain events in the Motte Reserve can range 0.18 to 6.17 cm (Western Regional Climate Center 2019), so our simulated rain was representative of a mid-size event. During the dry season, we made additional measurements at 1, 12, and 24 h post-wetting, but eliminated these timepoints during the wet season campaign because they did not alter calculations of peak and 45-h cumulative fluxes for any gas species. For each gas species in each wetting campaign, we constructed time series of observed fluxes, which were used for subsequent analysis. Concurrent to each trace gas measurement, we 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, we 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 and 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). We therefore assumed *S. barbatus* litter to be predominantly a source of organic C while contributing proportionally less N. To

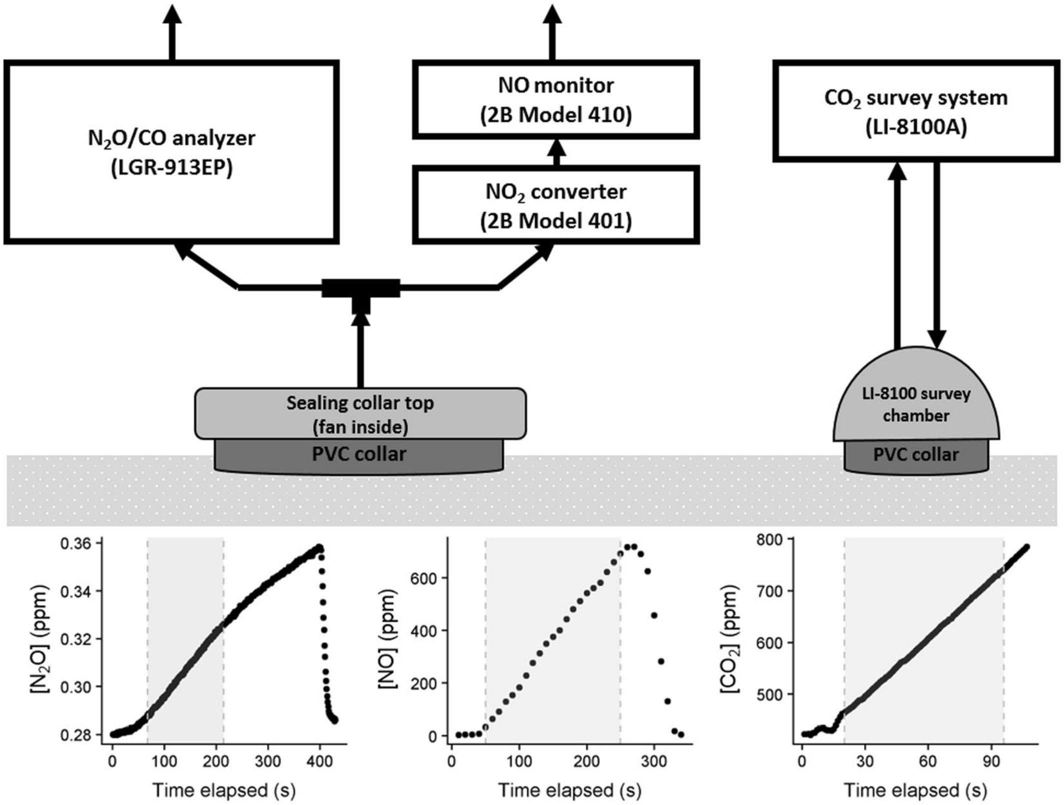

Fig. 1 Instrumentation diagram of our custom array of gas analyzers (top) and sample instrument output from which fluxes were calculated (bottom). Arrows indicate direction of airflow in this chamber system, which is closed for CO_2 and open for both N_2O and NO, and grey shaded regions of graphs indicate the area of linear increase that was used to calculate flux of each gas

investigate potential N sources for NO and N_2O, we quantified soil pools of extractable N (ammonium (NH_4^+) and nitrate (NO_3^-)) before and after wetting. During the wet season campaign, we collected soil cores 2.5 cm in diameter and 10 cm deep from small soil collars prior to 48 h post-wetting and transported cores on ice for subsequent processing in lab. Each core was homogenized and subsampled for pools of extractable NH_4^+ and NO_3^-. Briefly, a 2.5 mg subsample of homogenized soil was extracted with 25 mL of 2 M KCl, then quantified using a discrete analyzer (AQ2 Discrete Analyzer, SEAL Analytical, Mequon, WI, USA). We only measured extractable soil N pools during the wet season; however, changes in NH_4^+ and NO_3^- in response to wetting were used to assess mobilization of soil N.

Data analysis

From each time series of soil climate and gas flux, we extracted peak and cumulative fluxes over each 48-h measurement period. Peak fluxes were calculated as maximum emission across the 48-h time series. We calculated 48-h 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 h, 48 h) were used to calculate peak and cumulative fluxes to avoid measurement differences between seasons. We assessed effects of season, plant cover type, and litter amendments on time series by constructing a linear mixed model for each gas species (CO_2, N_2O, 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-h cumulative flux responses of each gas, we 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). We also used this method to compare peak and average soil temperature and moisture across all treatment combinations. Wet-season soil extractable N (NH_4^+ and NO_3^-) concentrations were compared using 3-way ANOVA across all combinations of cover type, litter treatment, and collection timepoint (pre-wet/48-h post-wet). We 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; $p = 0.113$). We 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

We 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 °C and 24.81 °C in the dry and wet season, respectively. However, peak temperatures, taken 6 h post-wetting and coinciding with midday, averaged 3 °C higher in the dry season (40.79 °C) compared to the wet season (37.72 °C; $p = 0.049$). Peak soil temperatures also averaged 3 °C higher in grass cover (40.91 °C) compared to shrub cover (37.60 °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%; $p < 0.001$) (Fig. 2a). As expected, soil moisture increased following experimental wetting but never

Table 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)

Measured variable	Plant community	Litter treatment	Pre-wet (sd)	48-h post-wet (sd)	Δ (sd)
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)

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-h post-wet). Bolded values indicate significant changes in variable conditions from pre-wet to 48-h post-wet with 95% confidence ($p < 0.05$). Note that while NO_3^- did not change by individual treatments, 48-h post-wet concentrations were significantly higher than pre-wet when all plots were combined ($p = 0.002$)

exceeded 30%. Although moisture decreased over 48 h, it did not return to pre-wet conditions (Fig. 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 (Fig. 2a; $p = 0.090$), particularly during the wet season.

CO_2 pulse following wetting

Pre-wet CO_2 fluxes did not differ across seasons ($p = 0.148$; Table 2) and averaged 4.2 μg CO_2 m^{-2} s^{-1}. Across all treatments, CO_2 fluxes following wetting responded with a pulse consistent with the Birch effect: fluxes peaked within 15 min of wetting, decreased over the next 6 h, and returned to almost pre-wet levels by 48 h post-wetting (Fig. 2b). CO_2 pulses were stronger and remained elevated for longer following wetting in the dry season than in the wet season (Fig. 2b): peak fluxes averaged twice as high (Fig. 3a; $p < 0.001$), and 48-h cumulative fluxes were up to 10 times greater (Fig. 3d; $p < 0.001$). Plant cover type modulated the seasonality of CO_2 pulse responses; the highest fluxes of CO_2 in the study were observed 15 min post-wetting in dry-season shrub plots, averaging 137.88 μg CO_2 m^{-2} s^{-1} (Fig. 2b). In both seasons, shrub cover also produced marginally higher CO_2 fluxes at 6 h post-wetting (Fig. 2b). Although peak CO_2 fluxes did not differ by cover type, shrub cover produced higher 48-h cumulative soil CO_2 fluxes compared to grass cover (Fig. 3a; Table 2; $p = 0.040$). Additional litter enhanced CO_2 pulses regardless of season or cover type (Fig. 2b). Litter-amended plots produced higher fluxes of CO_2 than did control plots at 15 min and 6 h post-wetting (Fig. 2b). 48 h after wetting, CO_2 fluxes from litter-amended plots also remained elevated above pre-wet levels but only during the dry season. Peak and cumulative CO_2 fluxes were marginally (Fig. 3a; Table 2; $p = 0.078$) and significantly (Fig. 3d; Table 2; $p = 0.016$) higher, respectively, from litter-amended plots compared to controls.

N_2O pulse following wetting

Pre-wet N_2O fluxes were consistent across seasons (Table 2; $p = 0.407$), averaging 0.17 ng N_2O-N m^{-2} s^{-1}. N_2O produced pulses following wetting: fluxes increased within the first 15 min of wetting and peaked between 15 min (wet season) and 6 h (dry season). Fluxes sharply declined following peak, in most cases returning to pre-wet conditions by 48 h (Fig. 2c). While seasonal effects on N_2O pulses appeared early post-wetting, litter effects appeared at 6 and 48 h (Fig. 2c), during which litter-amended, dry-season soils maintained high N_2O fluxes compared to declining trends in other treatments. N_2O pulses did not differ across plant cover types. Peak N_2O fluxes were significantly higher during the dry compared to wet season with average rates of 2.10 and 1.46 ng N_2O-N m^{-2} s^{-1}, respectively (Fig. 3b; Table 2; $p = 0.032$), and litter-amended conditions produced similarly high peak N_2O fluxes compared to controls (Table 2; $p < 0.050$). The dry season also contributed to greater 48-h cumulative fluxes of N_2O (Table 2; $p = 0.010$), and added litter marginally increased N_2O cumulative fluxes over controls (Table 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-h cumulative fluxes of N_2O were also influenced by a season*litter interaction (Fig. 3e; Table 2; $p = 0.010$), in which added litter enhanced 48-h 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 2; $p = 0.091$), averaging 10.30 ng NO-N m^{-2} 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 h post-wetting and at levels up to five times higher than pre-wet fluxes, averaging 147.69 ng NO-N m^{-2} s^{-1}; by 48 h post-wetting, fluxes declined but remained elevated above pre-wet conditions, particularly during dry months (Fig. 2e). Dry-season wetting produced larger NO pulses than did wet-season wetting; peak and 48-h cumulative fluxes both differed by as much as seven orders of magnitude between seasons (Fig. 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 (Fig. 2c), and in both seasons, litter

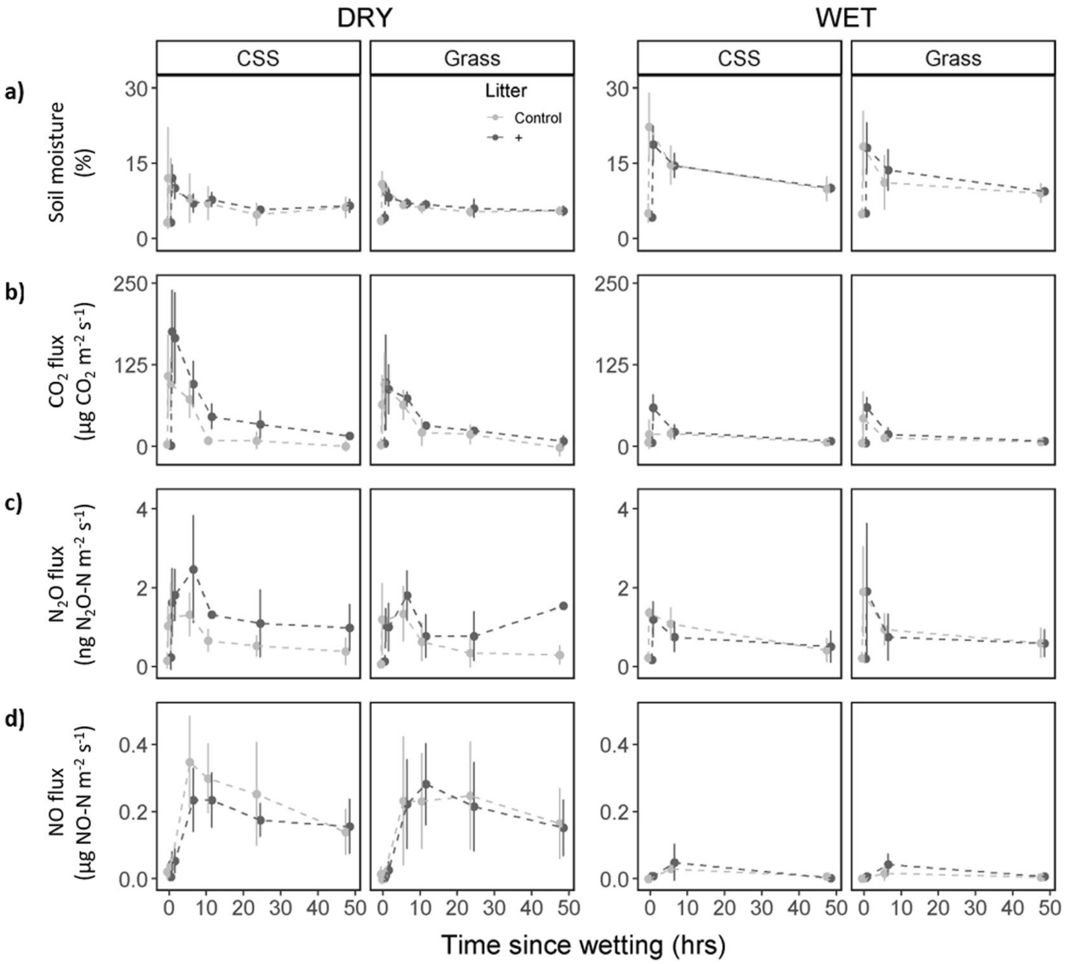

Fig. 2 Soil moisture (**a**) and trace gas pulse (**b**–**d**) responses to experimental wetting in CSS shrub (“CSS”) and exotic grass (“Grass”) plant cover types during a dry and wet season. Points and standard deviation bars indicate timepoint measurements and dotted lines indicate extrapolated time series curves. Colors indicate litter amendment treatments

amendments also produced strong immediate responses to wetting as indicated by higher fluxes at 15 min post-wetting. CSS shrub cover also produced larger NO fluxes than did grass cover 15 min post-wetting (Fig. 2c).

Discussion

Our results provide new evidence that CO_2, N_2O, and NO emissions from Mediterranean-type soils exhibit seasonally-distinct pulse responses to wetting, that exotic grass litter enhances pulses of CO_2 and N_2O, and that a shift from shrub to grass cover reduces CO_2 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 (Fig. 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, our 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 CO_2 and N_2O, 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;

Table 2 Drivers of peak and 48-h total fluxes of CO_2, N_2O, and NO

Dependent variable	Significant fixed effects	F-value	*p*-value
Peak CO_2 flux (μg CO_2 m^{-2} s^{-1})	Season	12.964	< 0.001*
	Litter	2.676	0.110
Peak N_2O flux (ng N_2O-N m^{-2} s^{-1})	Season	4.920	0.032*
	Litter	4.253	0.046*
	Season*Litter	3.344	0.075
Peak NO flux (μg NO-N m^{-2} s^{-1})	Season	63.959	< 0.001*
48-h CO_2 flux (μg CO_2 m^{-2} s^{-1})	Season	84.873	< 0.001*
	Litter	6.433	0.016*
	Community	4.567	0.040*
	Season*Community	2.590	0.117
48-h N_2O flux (ng N_2O-N m^{-2} s^{-1})	Season	5.891	0.021*
	Litter	2.247	0.144
	Season*Litter	7.439	0.010*
48-h NO flux (μg NO-N m^{-2} s^{-1})	Season	50.439	< 0.001*

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 <0.15. Statistically significant p values ($\alpha = 0.95$, $p < 0.05$) are indicated by *

Wolkovich et al. 2010). Although we hypothesized invasion-induced changes in plant cover would increase nutrient cycling in CSS, cover type was the weakest driver of pulse responses, only constraining CO_2 pulses in grass compared to shrub cover. Our 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 CO_2 and N_2O pulses, contrasted with lagging NO pulses, has not been previously observed in dryland experimental wetting studies. Although pulses of CO_2 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 N_2O pulses (Leitner et al. 2017), providing support that nitrification and denitrification are both water-limited processes, but our results suggest NO may not respond as quickly as N_2O in shrubland soils.

CO_2 and N_2O pulses peaked within 6 h of wetting and diminished to almost pre-wet levels after 12–24 h, indicating a quick recovery of biological respiration and enzyme activity in response to increases in soil moisture but subsequent reduction independent of moisture availability (Fig. 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 our site, abundant N and limited C could constrain the CO_2 and N_2O pulses we observed while promoting longer pulses of NO. Because soils were still moist after 24 h (Fig. 2a), CO_2 and N_2O 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 CO_2 and N_2O (Fig. 2d), particularly during the dry season, and may be explained by sustained soil moisture and N availability during the 48-h measurement period (Table 1; Fig. 2a). Although we did not directly quantify the sources of N_2O and NO, we suspect NO was predominantly formed through nitrification, a process which occurs independent of C availability and in larger magnitudes in most arid systems (Hartley and Schlesinger 2000). However, the much smaller and faster pulses of N_2O we observed may be attributed to denitrification in short-lived anoxic soil microsites (Galbally et al. 2008; Sexstone et al. 1985), as N_2O 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 CO_2, N_2O, and NO pulses was season, with larger pulses of all three trace gases occurring in the dry season compared to the wet season (Figs. 2 and 3). Our 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. Our site received a total of 9.9 mm and 198.4 mm rainfall in the 3 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.

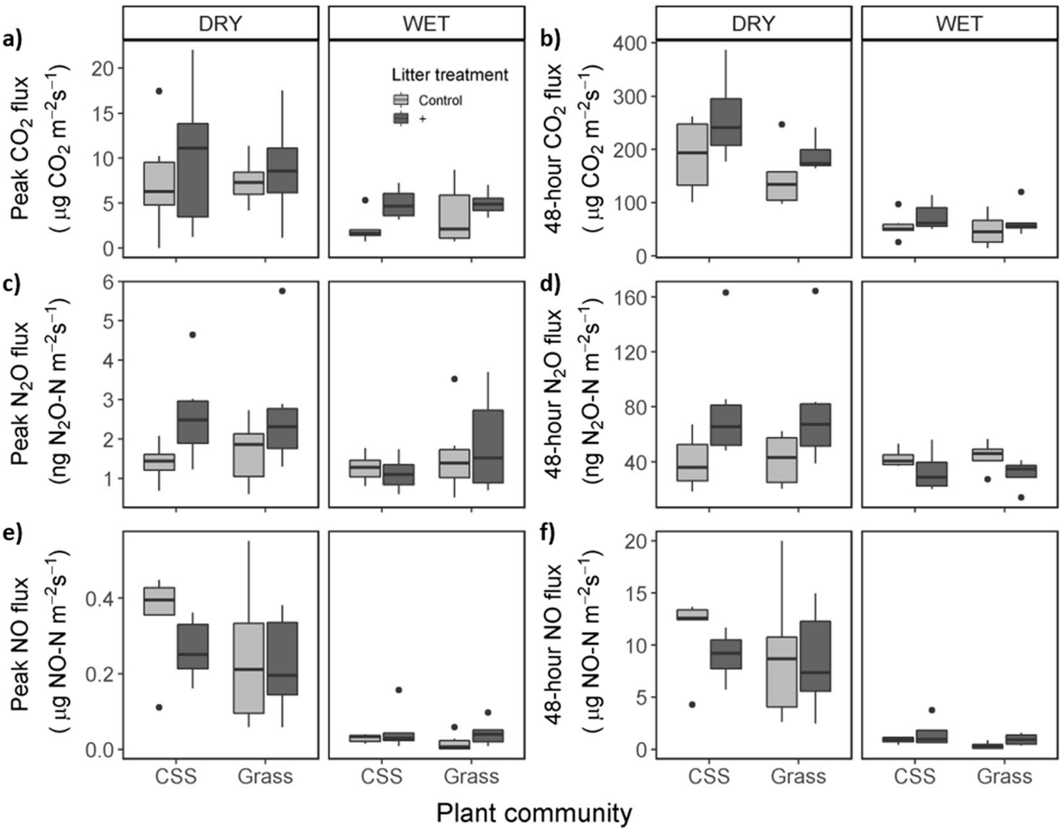

Fig. 3 48-h peak (**a**, **c**, **e**) and cumulative (**b**, **d**, **f**) fluxes following experimental wetting in CSS shrub ("CSS") and exotic grass ("Grass") plant cover types treated with grass litter amendments ("+") or not ("Control") during a dry and wet season. Peak fluxes were calculated as maximum fluxes during the 48-h measurement period and cumulative fluxes were interpolated using area-under-the-curve integration from each 48-h time series. Quantile outliers are notated as dots above or below boxes and whiskers; refer to Table 1 for statistical significance of relationships

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. Our 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.

We found strong dry-season and weak wet-season C and N gas pulses in CSS, despite non-significant seasonal differences in pre-wet fluxes (Fig. 2). Peak NO fluxes we 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, 1993; Hall et al. 2008; Homyak and Sickman 2014). Conversely, N_2O peaks we observed across both seasons were lower compared to other dryland studies, which have reported fluxes as high as 1.5 µg N_2O-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 we 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 our study. All other patterns we 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 our study period only differed by 3 °C at peak daytime temperature and by 2 °C at minimum measured temperature across seasons. Our spot measurements may underestimate the influence of temperature on trace gas pulses broadly; however we would still expect differences in temperature-gas flux relationships to be apparent in our timed sampling regimen. Therefore, we expect seasonal effects of temperature on pulses to be negligible within the context of this study, and we interpret differences in pulse magnitudes primarily as an effect of seasonal wetting history. The stronger dry-season N_2O pulses we observed contrast with DAYCENT estimations of stronger wet-season N emissions (Li et al. 2006), and our 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 CO_2 and N_2O, but not NO (Fig. 3). We expected *S. barbatus* litter to contribute substantial quantities of C based on its higher C:N ratio compared to *E. fasciculatum*; however, we expected that the high quantity of litter we 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 we expected NO pulses to respond to grass litter in a similar fashion to N_2O. At our site, grass litter did not significantly enhance already-high soil N availability (Table 1). We 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). We 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 CO_2 and N_2O 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 we suspect this mechanism applies to our study as well.

The strongest CO_2 and N_2O pulse responses to litter were during the dry season, when amendments were added and litter was freshest. Previous studies have shown that CO_2 emissions from substrate-amended soils tend to be strongest during the first wetting after litter is added, and that pulses diminish during subsequent rewettings, 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 CO_2 and N_2O responses to wetting in plots with added litter. We performed our dry-season experimental wetting 3 days after litter addition, so the pulses we 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 and Meyer 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 we still observed intact litter in plots during the wet season, we expect that it contained proportionally more recalcitrant than labile C, contributing less to alleviating C limitation and dampening CO_2 and N_2O 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 CO_2 pulses but did not significantly alter N trace gas pulses. We 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, we observed weaker CO_2 pulses from soils in exotic grass cover compared to shrub cover, and we detected no significant differences in N trace gas pulses between cover types (Fig. 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 ours (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 and Suding 2014) and decrease root respiration, producing the smaller CO_2 pulses we observed in grass cover.

The effects of plant cover on CO_2 pulses were particularly strong during the dry season, when grasses were senesced and shrubs were dormant (Fig. 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 CO_2 fluxes did not differ between cover types, shrub cover produced larger wetting-induced increases in CO_2 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 N_2O that we 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 N_2O fluxes that we 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 N_2O pulses may be suppressed here more than in other dryland systems. We suspect our study site is more invaded and polluted than other shrubland systems where pulses have been measured, additionally highlighting our study's importance for understanding N cycling at the wildland-urban interface.

Although only 25% of rain events occur during the dry season at our 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, we show that although a shift from shrub to grass cover reduces wetting-induced pulses of soil CO_2 respiration, inputs of labile grass litter at the onset of the dry season elevate CO_2 and N_2O 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 CO_2 or N_2O, 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, we 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.

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Data availability All raw and processed datasets generated during this study are publicly available via DRYAD Repository (https://doi.org/10.6086/D1K38D).

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