Effects of organic matter amendments on net primary productivity and greenhouse gas emissions in annual grasslands

REBECCA RYALS¹ AND WHENDEE L. SILVER

University of California, Berkeley, Department of Environmental Science, Policy, and Management, 130 Mulford Hall No. 3114, Berkeley, California 94720 USA

Abstract. Most of the world's grasslands are managed for livestock production. A critical component of the long-term sustainability and profitability of rangelands (e.g., grazed grassland ecosystems) is the maintenance of plant production. Amending grassland soils with organic waste has been proposed as a means to increase net primary productivity (NPP) and ecosystem carbon (C) storage, while mitigating greenhouse gas emissions from waste management. Few studies have evaluated the effects of amendments on the C balance and greenhouse gas dynamics of grasslands. We used field manipulations replicated within and across two rangelands (a valley grassland and a coastal grassland) to determine the effects of a single application of composted green waste amendments on NPP and greenhouse gas emissions over three years. Amendments elevated total soil respiration by $18\% \pm 4\%$ at both sites but had no effect on nitrous oxide or methane emissions. Carbon losses were significantly offset by greater and sustained plant production. Amendments stimulated both above- and belowground NPP by 2.1 ± 0.8 Mg C/ha to 4.7 ± 0.7 Mg C/ha (mean \pm SE) over the threeyear study period. Net ecosystem C storage increased by 25–70% without including the direct addition of compost C. The estimated magnitude of net ecosystem C storage was sensitive to estimates of heterotrophic soil respiration but was greater than controls in five out of six fields that received amendments. The sixth plot was the only one that exhibited lower soil moisture than the control, suggesting an important role of water limitation in these seasonally dry ecosystems. Treatment effects persisted over the course of the study, which were likely derived from increased water-holding capacity in most plots, and slow-release fertilization from compost decomposition. We conclude that a single application of composted organic matter can significantly increase grassland C storage, and that effects of a single application are likely to carry over in time.

Key words: annual grassland ecosystems; California grasslands, USA; mediterranean climate; methane; net primary productivity; nitrous oxide; soil respiration.

Introduction

Rangelands represent the largest land use area globally, covering more than one-quarter of the world's land surface and storing approximately one-third of the world's terrestrial C in soils and vegetation (White et al. 2000, Asner et al. 2004). The primary economic output of rangelands is livestock production, supplying meat, dairy products, leather, and wool (Herrero et al. 2009). The sustainability and profitability of rangelands is largely a function of forage quality and quantity (Briske et al. 2011). However, these ecosystems have, to varying degrees, experienced degradation of vegetation and soils due to overgrazing, plant invasions, and climate change (Asner et al. 2004, Schipper et al. 2007, Bai et al. 2008). Thus, management practices aimed at enhancing plant production may have considerable potential to restore or increase grassland C storage and feed back on the global C cycle (Schimel et al. 1990, Conant et al. 2001,

Manuscript received 17 April 2012; revised 9 July 2012; accepted 17 July 2012. Corresponding Editor: C. C. Cleveland.

¹ E-mail: rebecca_ryals@brown.edu

Follett 2001, Schuman et al. 2002, Derner and Schuman 2007).

Management practices can affect grassland C storage or loss by altering soil chemical or physical characteristics (Cambardella and Elliott 1992, Paustian et al. 1997, Janzen et al. 1998), plant morphology or growth, soil moisture, or rates of microbial activity (Stromberg and Griffin 1996, Steenwerth et al. 2002, Jones and Donnelly 2004). Amending soils with organic material generally increases nutrient availability, and thus is a common practice used in cropping systems to enhance NPP (Cassman et al. 2002, Blair et al. 2006) and in some land reclamation sites to facilitate soil amelioration and plant establishment (Larney and Angers 2012). Animal manure, crop residues, composted urban waste, and sewage sludge are common forms of organic matter amendment.

The application of organic matter to rangelands has been proposed as an approach for increasing plant productivity, as a waste management strategy, and for climate change mitigation (Hall and Sullivan 2001, Cabrera et al. 2009). Organic matter additions to

rangeland soils increase soil C pools directly and have the potential to indirectly increase ecosystem C storage by stimulating plant growth. Organic matter additions to rangelands can also provide a pathway to divert organic waste from landfills or for manure management from nearby dairies, thereby reducing greenhouse gas emissions from traditional waste management.

Carbon benefits of enhanced NPP due to organic matter amendments may be offset from a global warming perspective by the stimulation of soil greenhouse gas emissions. Organic matter amendments increase soil C and nitrogen (N) pools and may alter soil environmental conditions (e.g., moisture, temperature, and pH), thereby increasing the potential for carbon dioxide (CO₂), nitrous oxide (N₂O), and methane (CH₄) emissions (Gregorich et al. 2005). The extent of management effects on soil greenhouse gas emissions is a large source of uncertainty in grasslands (Soussana et al. 2004). Manure amendment can increase CO₂ and N₂O fluxes (Chadwick et al. 2000, Dalal et al. 2003, Mosier et al. 2004, Davidson 2009); composted animal waste and plant matter tends to result in lower greenhouse gas emissions relative to green manures or synthetic fertilizers (Vallejo et al. 2006, Alluvione et al. 2010). However, the effects of organic matter additions on greenhouse gas dynamics in rangelands are largely unstudied (Lynch et al. 2005, Cabrera et al. 2009).

The purpose of this study was to examine the immediate and residual effects of amendments of composted green waste on plant production and greenhouse gas emissions in annual grasslands. We hypothesized that the application of composted organic matter to rangeland soils would increase the above- and belowground net primary productivity (NPP) for at least one year, and that these increases in ecosystem C inputs would be partially or wholly offset by elevated rates of soil greenhouse gas emissions (CO₂, N₂O, and CH₄). We tested this hypothesis over three years using replicated field experiments in the two dominant annual grassland types in California. Unlike perennial grassland systems, annual grasses germinate, grow, and die over an annual cycle, allowing us to estimate net ecosystem C storage from the changes in plant and soil C pools and fluxes.

MATERIALS AND METHODS

Study sites

Rangelands are the dominant cover type in California, covering an estimated 17–23 million ha (FRAP 2003, Brown et al. 2004). Of this area, ~9 million ha are valley or coast range grasslands (Kuchler 1964). Valley grasslands extend along the central and southern parts of California and are composed largely of nonnative annual grass and forb species such as *Avena barbata*, *Bromus hordeaceus*, *Lolium multiflorum*, *Erodium* spp., and *Trifolium* spp. (Bartolome et al. 2007), as well as invasive species such as *Taeniatherum caput-medusae*. Coast range (hereafter coastal) grasslands experience a mesic coastal climate and are also dominated by a

similar mix of nonnative annual grasses. Native perennial grass species, such as *Danthonia californica* and *Stipa pulcra*, can also occur (Jackson and Bartolome 2002). The mediterranean climate of both valley and coastal grasslands of California is characterized by cool, wet winters and warm, dry summers. The growing season begins with the rains in September–November and ends with the onset of the dry season in April–June.

The field experiment was conducted on valley grasslands at the Sierra Foothill Research and Extension Center in Browns Valley, California (39.24° N, 121.30° W) and on coastal grasslands in Nicasio, California (38.06° N, 122.71° W). Annual precipitation averages 730 mm/yr (22-year mean) at the valley grassland and 950 mm/yr (38-year mean) at the coastal grassland. During the years of this experiment, the valley grasslands received 380, 641, and 843 mm/yr of precipitation, primarily as rainfall; mean air temperatures ranged from 2°C in January to 35°C in July. Soils are derived from Mesozoic and Franciscan volcanic rock and classified as xeric inceptisols and alfisols in the Auburn-Sobrante complex (Beaudette and O'Geen 2009) (available online).² The site has been grazed by cattle for at least 150 years (D. Flavell, personal communication). At the coastal grassland, annual precipitation during the study period was 771, 1050, and 1163 mm/yr, and mean air temperatures ranged from 6°C in January to 20°C in July. Soils are derived from Franciscan mélange and classified as mollisols in the Tocaloma-Saurin-Bonnydoon series (Beaudette and O'Geen 2009) (see footnote 2). The site has been grazed by cattle since at least 1900, with a brief period of exclusion from 2000 to 2005.

Experimental design

The field experiment was established in October 2008 and continued for three growing seasons, to August 2011. Treatments consisted of untreated controls and composted organic matter amendments. Plots were 25 × 60 m buffered by a >5-m strip arranged in three randomized complete blocks. Blocks were situated in different microwatersheds in each grassland type to capture some of the landscape-scale heterogeneity associated with vegetation communities, potential residual effects of field-scale land use history, and soil texture. An organic-rich soil amendment was produced by adding a single application of commercially available composted organic green waste (Feather River Organics, Marysville, California, USA) with a N concentration of 1.87% and a C:N ratio of 11. A thin surface dressing \sim 1.3 cm thick (equivalent to 1.42 kg C/m² and 129 g total N/m², or 7.0 kg of dry matter/m²) was applied in December 2008. All plots were grazed using a rotational regime typical of the region to achieve a residual dry matter level of $\sim 130 \text{ g/m}^2$. Sites were grazed during the

² http://casoilresource/lawr.ucdavis.edu/soilsurvey

spring and fall for up to four weeks, depending on the amount of available forage. During grazing, cattle were not isolated within plots, but instead allowed to graze the entire block.

Climate data, soil moisture, and soil temperature

Local daily rainfall and air temperature records were obtained from Browns Valley for the valley grassland site (data available online)³ and from the Marin Municipal Water District (J. Klein, personal communication) for the coastal grassland site. We define a water year as the period that encapsulates one rainy and one dry season, spanning from 1 September through 31 August of the following year (Chou et al. 2008).

In May 2009, automated TDR-based probes were installed at 0–30 cm depth to measure volumetric water content (Campbell Scientific CS616, n=3 per plot [Campbell Scientific, Logan, Utah, USA]). Automated soil temperature probes were installed at 0–5 cm depth (Campbell Scientific 108L, n=1 per plot). Soil moisture and temperature data output was averaged on hourly and daily timescales.

Soil greenhouse gas emissions

Soil respiration was measured weekly during the growing season and every other week during the summer over the first two water years. Soil CO2 fluxes are extremely low, with little temporal variability during the summer in annual grasslands (Nijs et al. 2000, Xu et al. 2004, Chou et al. 2008). We measured soil respiration monthly during the third water year. Soil CO2 fluxes were measured during daylight hours using a LI-8100 infrared gas analyzer (~2.5-minute flux periods [LI-COR Biosciences, Lincoln, Nebraska, USA]) fitted with an opaque soil efflux chamber. The chamber was used in a survey mode with polyvinyl chloride collars (n = 5 per plot). Collars were driven approximately 3 cm into the soil and left to equilibrate for at least 30 minutes before flux measurements were taken. Soil respiration measurements were started three (coastal) to six (valley) weeks prior to organic matter applications. As a first approximation of annual soil respiration rates we used linear interpolation between sampling time points and summed the resulting data as an estimate of the mass of C per unit area respired over the water year (Silver et al. 2005, Chou et al. 2008). Previous work at the valley grassland identified the importance of the fall wet-up event for estimating accurate annual soil respiration fluxes (Chou et al. 2008). In an attempt to capture the largest fluxes, we measured soil respiration no more than 48 hours before and after fall wet-up events.

Soil CH₄ and N₂O fluxes were measured every two weeks for the first six months, which was when we expected to see the largest fluxes (Chou et al. 2008), and monthly thereafter until September 2010. Vented static

flux chambers (Keller and Reiners 1994) were placed at four random locations within each plot during each sampling period. Gas samples (30 mL) were collected from the chamber headspace at 0, 5, 15, 25, and 40-minute time points, immediately transferred to evacuated glass vials, and analyzed within 72 hours (Chou et al. 2008). Methane concentrations were analyzed on a gas chromatograph using a flame ionization detector, and an electron capture detector was used to analyze N₂O concentrations. Fluxes were then calculated using an iterative exponential curve-fitting approach (Matthias et al. 1978).

Wet-up events can stimulate trace gas emissions, particularly in dry, organic-rich soils (Fierer and Schimel 2002, Chou et al. 2008). We conducted a laboratory incubation experiment to determine the potential trace gas emissions from amended and control soils during wet-up events. Soils from the valley grassland were collected from control and amended plots (n = 9 per plot) and composited by treatment. Approximately 200 g of soil were placed into 0.9-L (quart) mason jars and categorized as one of four incubation treatments (n = 5): control, control + wet-up, amended, and amended + wet-up, where control and amended treatments refer to ambient dry-season field moisture conditions (approximately 4% gravimetric soil moisture) and wet-up refers to the addition of 40 mL of deionized water representing an average first rainfall event in autumn. Jars were incubated in a dark growth chamber with daily air temperatures fluctuating from 20° to 35°C, a typical range experienced during wet-up events in the field. Soil CO2, N2O, and CH4 fluxes were measured daily until trace gas fluxes were not significantly different between treatment and controls (30 days). Cumulative fluxes were calculated as previously described. Positive soil greenhouse gas fluxes indicate net source to the atmosphere, whereas negative values indicate a terrestrial sink.

Aboveground and belowground net primary productivity

The vegetation communities at the study sites are strongly dominated by annual grass and forb species. These plants germinate at the onset of the fall rains and die at the end of the wet season. Aboveground biomass at the end of the wet season plus biomass removed during earlier grazing events is equivalent to aboveground net primary production (ANPP) (Harper et al. 2005). Aboveground biomass was determined by harvesting plants in a 200-cm² area (n = 9 per plot) at the time of peak biomass at the end of the growing season. All aboveground vegetation was clipped to the soil surface. Harvested plant material was dried at 65°C, weighed, and analyzed for C concentration on a Carlo Erba Elantech elemental analyzer (Milan, Italy). Carbon content of aboveground biomass was determined by multiplying C concentration by mass. Aboveground biomass was also measured using the approach described no more than 24 hours immediately before and

³ http://www.cimis.water.ca.gov/cimis/data.jsp

after grazing to determine biomass removed by cattle (Marshall et al. 1998). Aboveground NPP was determined by adding the biomass removed by cows to the biomass collected at peak standing biomass. Plots at the coastal grassland were grazed during or just before peak standing biomass due to site-specific management requirements; thus biomass measurements were made prior to grazing at this site and may slightly underestimate ANPP.

The root systems of annual grasses are concentrated in the soil surface layer, with <15% of root biomass occurring below 15 cm and a majority of root growth occurring before April (Jackson et al. 1988). Belowground net primary productivity (BNPP) was determined by measuring root biomass during late spring of water years 2 and 3 and adjusting values by a multiplication factor of 1.5 to account for intra-annual root turnover (Higgins et al. 2002). Eight 0-10 cm and four 10-20 cm quantitative soil cores (6 cm diameter) were sampled per plot. Roots from each core were extracted according to Metcalfe et al. (2007) with the following modifications based on methods testing with soils from these sites. Roots from each core were picked by hand for three 10-minute intervals, sieved at 2 mm to break up large aggregates, and picked by hand for five additional 10-minute intervals for a total of 80 minutes. Roots were then rinsed free of soil and dried at 65°C until reaching a constant dry mass. For each core, the pattern of cumulative extraction over time was used to predict total root biomass. Upon drying and weighing, roots were finely ground and analyzed for C concentration on a Carlo Erba Elantech elemental analyzer using acetanilide as a standard. Carbon content of belowground biomass was determined by multiplying C concentration by mass. All production data (ANPP, BNPP, and NPP) are expressed in units of mass of C per area using the biomass to C content conversions described previously. Expressing production terms using this convention allows us to explicitly compare C inputs and outputs.

Soil carbon content and bulk density

Soil bulk density (0–10 cm depth) was measured by digging pits (one per plot) and carefully excavating 9 cm diameter cores \sim 5 cm back from an undisturbed face of the pit. All bulk density measurements were rock corrected. Upon extraction from cores, dry rock masses and volumes were measured and subtracted from initial bulk density calculations.

Total soil organic C concentrations were measured prior to the application of organic matter amendment and at the ends of each subsequent growing season (May or June). Soils were collected using a 7 cm diameter corer to 10 cm depth (n=9 per plot). Large roots and identifiable compost fragments were removed by hand. Soils were then air dried and pulverized with a ball grinder (SPEX Sample Prep Mixer Mill 8000D, Metuchen, New Jersey, USA).

Carbon concentrations were measured using a Carlo Erba Elantech elemental analyzer using atropine as a standard and converted to content using bulk density values specific to each plot.

Modeling net change in ecosystem carbon storage

We modeled the annual net change in ecosystem C storage with and without compost additions using an approach modified from Hanson et al. (2000) and Chou et al. (2008) as follows:

Net C Storage = ANPP + BNPP -
$$R_h - R_{oa}$$
 - DOC

where R_h is heterotrophic respiration which includes the nonroot and nonrhizosphere component of soil respiration during the growing season, R_{oa} is CO_2 evolved from decomposition of the organic matter amendment, and DOC is dissolved organic C losses.

In annual grasslands, the sum of ANPP and BNPP represents total annual litter inputs, which turn over approximately annually (Heady et al. 1992). Partitioning soil respiration into its autotrophic and heterotrophic components is difficult in annual grasslands, and outside the scope of this study. Instead, we modeled net ecosystem C storage with a range of Rh values to represent a low (30%), medium (50%), and high (60%) level measured in similar ecosystems (Craine et al. 1999, Zhou et al. 2007, Chou et al. 2008). Carbon losses through $R_{\rm h}$ were constrained to the growing season, as no treatment differences in soil respiration were detected during the dry summer months. We assumed that the relative proportion of soil respiration components was equal across treatments as a first approximation. We used 0.05 yr⁻¹ as the decomposition rate of the compost (Lynch et al. 2005) to calculate annual losses of compost as CO₂, which is similar to the rate derived from a DayCent model simulation (R. Ryals, M. D. Hartman, M. S. DeLonge, W. J. Parton, and W. L. Silver, unpublished manuscript). We assumed that the compost mass reduction via decomposition was lost primarily as CO₂ to the atmosphere. Carbon losses through leaching of DOC are negligible in these ecosystems relative to soil CO₂ effluxes (Dahlgren and Singer 1994, Sanderman and Amundson 2009). Therefore, DOC is assumed to be zero for estimates of net C storage. In this experiment, treatment plots were amended only once, at the beginning of water year 1. Therefore, direct C inputs from compost addition are constrained to water year 1, but losses through decomposition carry over all three years. Belowground NPP was estimated for water year 1 using the plot-specific root: shoot ratios averaged for water years 2 and 3.

Statistical analysis

One-way analyses of variance (ANOVA) were used to identify statistically significant treatment effects on soil organic C, cumulative soil CO₂ flux, soil moisture, soil temperature, ANPP, BNPP, and net ecosystem C storage. Analyses included a blocking effect and were

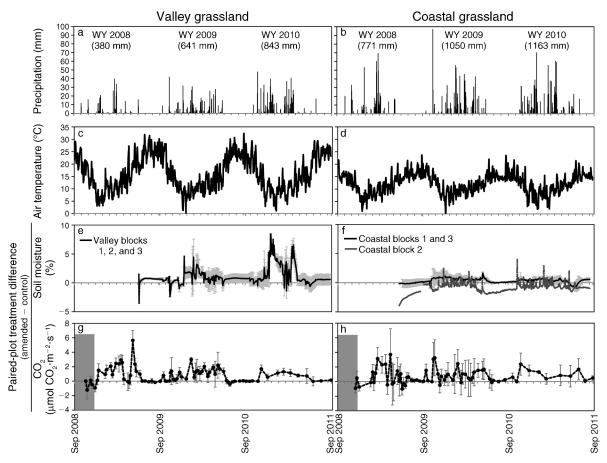


Fig. 1. (a, b) Daily precipitation data from September 2008 to August 2011 (water years [WY] 2008, 2009, 2010) measured at (a) the valley grassland and (b) the coastal grassland. (c, d) Air temperature data from (c) valley and (d) coastal grasslands. (e) Paired-plot treatment difference of volumetric soil water content (0-30 cm) at the valley grassland. Values above zero indicate greater soil moisture content in amended soils compared to control soils. The black line is the mean of all three blocks, and the gray area is \pm SE. (f) Paired-plot treatment difference in volumetric soil water content (0-30 cm) at the coastal grassland. The black line is the mean of blocks 1 and 3, and the light gray area is \pm SE. The dark gray line is the mean of coastal grassland block 2, indicating greater soil water content in the control plot. (g, h) Paired-plot treatment difference in soil respiration at (g) valley and (h) coastal grasslands. Error bars are \pm SE. The gray block on the left of the graphs indicates measurements taken prior to amendment. Values above zero indicate greater total soil respiration from amended soils compared to control soils. There were no treatment differences in soil temperature at either grassland (P > 0.10).

performed separately for valley and coastal sites. To assess changes over time within sites, we used repeated measures multivariate analysis of variance (MANOVA) with ANPP, BNPP, soil moisture, soil temperature, and soil CO₂, N₂O, and CH₄ fluxes as response variables. Each grassland type was analyzed separately with block, treatment, time, and interactions as MANOVA model effect factors. Correlations between net C storage, ecosystem C pools, soil moisture, and precipitation were explored using multiple linear regressions.

Statistical tests were performed using JMP 7.0.2 (SAS Institute 2007). Variables that were not normally distributed were log transformed to meet assumptions for ANOVA. Data are reported either as mean values or treatment differences followed by \pm SE. Statistical significance was determined as P < 0.10 unless otherwise noted.

RESULTS

Response of soil respiration and greenhouse gas emissions to organic matter amendment

Soil respiration (root plus microbial respiration) was significantly higher in amended soils than in control soils during the growing season (P < 0.0001 at both sites) (Fig. 1). There was approximately $18\% \pm 2\%$ and $19\% \pm 2\%$ more C respired from the amended soils relative to the controls from the valley (P = 0.06) and coastal (P = 0.10) sites cumulatively over the three years of the study (Fig. 2). Within sites soil CO₂ fluxes varied by as much as 30-50% among years, reflecting patterns in the timing and amount of rainfall. Soil respiration was positively correlated to soil moisture ($R^2 = 0.51$, P < 0.001 at valley and $R^2 = 0.65$, P < 0.001 at coastal sites), and treatment effects (amended–control) were positively

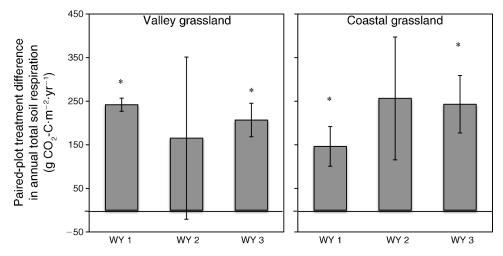


Fig. 2. Annual total soil respiration for three water years (WY) (see *Methods: Climate data, soil moisture, and soil temperature*) from the valley and coastal grassland experimental field sites. The bars are means of paired-plot treatment differences with \pm SE. Instantaneous fluxes (measured approximately weekly) were linearly interpolated and integrated to obtain mass of C per unit area per year. Values above zero indicate greater total soil respiration from amended soils compared to control soils. * P < 0.05.

correlated to annual precipitation ($R^2 = 0.47$, P < 0.05 for both sites). The highest cumulative soil respiration losses occurred during water year 2, which was characterized by late warm-season rains, and treatment differences in cumulative soil respiration were not statistically significant during this time period.

Approximately $88\% \pm 0.01\%$ and $73\% \pm 0.07\%$ of the cumulative annual soil CO_2 efflux occurred during the growing season at the valley and coastal grassland, respectively, with no statistically significant treatment effect on the seasonal distribution of soil respiration. Analysis of paired-plot treatment differences of growing season soil respiration revealed that amended soils at the valley grassland lost an additional 614 ± 191 g CO_2 -C/m² over the three-year study. Similar trends were observed at the coastal grassland, which experienced increased losses of 646 ± 162 g CO_2 -C/m² from the amended plots.

There were no significant treatment effects on CH₄ and N₂O fluxes, and no significant changes over time. At the valley grassland, mean CH₄ fluxes were -2.5 ± 0.6 g CH₄-·ha⁻¹·d⁻¹, and mean N₂O fluxes were 0.13 ± 0.13 g N₂O-N·ha⁻¹·d⁻¹. At the coastal grassland, mean CH₄ fluxes were -1.4 ± 0.7 g CH₄-·C·ha⁻¹·d⁻¹, while mean N₂O fluxes were 1.0 ± 0.4 g N₂O-N·ha⁻¹·d⁻¹.

Greenhouse gas emissions during wet-up events

We conducted a controlled laboratory experiment to estimate the potential greenhouse gas emissions associated with wet-up events. Wet-up led to a pulse of CO_2 from both amended and control soils, and soil respiration in amended soils remained elevated over controls for 22 days (P < 0.05). Nitrous oxide fluxes were also elevated from amended soils and lasted four days following wet-up (P < 0.01; Fig. 3). Methane fluxes were negligible and did not respond to the wet-up event.

Cumulative N_2O emissions accounted for just $0.49\% \pm 0.05\%$ and $0.83\% \pm 0.13\%$ of the total global warming potential during the wet-up event from control and amended soils, respectively. The vast majority of the greenhouse gas emissions from these soils was from CO_2 .

Response of net primary productivity and soil C to organic matter amendment

Organic matter amendments significantly enhanced plant growth at both the valley and coastal grassland sites (Appendix). During the first water year, amendments increased ANPP by 70% at the valley site and by 44% at the coastal site. The effects of the one-time application of organic matter carried over into the two subsequent growing seasons at a similar magnitude. Over all three study years, ANPP increased by a total of 436 ± 68 and 161 ± 78 g C/m² ($P \le 0.01$) at the valley and coastal grasslands, respectively (Fig. 4). Average annual increases in ANPP were 145 \pm 16 and 54 \pm 3 g C/m² at the valley grassland and coastal grassland, respectively (P < 0.05 for all years at both sites). Shootto-root ratios increased significantly with organic matter applications at the valley grassland from 3.75 ± 0.06 to 5.45 ± 0.09 (P = 0.08) and did not change significantly at the coastal grassland, where the shoot-to-root ratio was 3.00 ± 0.14 . Root biomass increased at both sites, particularly in the 0-10 cm depth (Fig. 4). At the valley grassland, root biomass increased by 33.6 \pm 11.7 g C/m² in amended plots at the 0-20 cm depth over three years (P < 0.05). Belowground NPP showed similar, but more variable trends with amendments at the coastal grassland. Organic matter amendments significantly increased total NPP by 2.0 ± 0.8 Mg C/ha at the coastal grassland (P = 0.10) and 4.7 ± 0.7 Mg C/ha at the valley

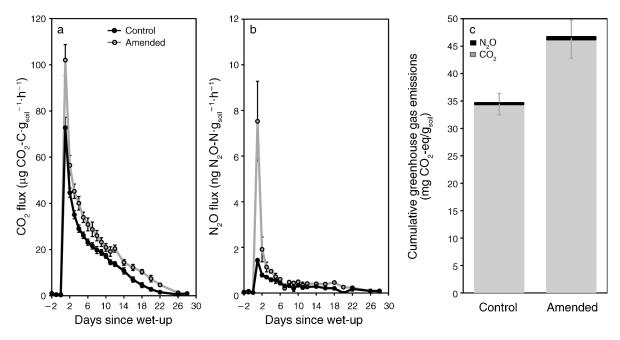


Fig. 3. Greenhouse gas emissions during a 30-day laboratory incubation of valley grassland control and amended soils. Soils were incubated in 0.9-L (quart) mason jars (\sim 200 g) in a growth chamber under typical late summer climate. A fall wet-up event was simulated by the addition of 40 mL of distilled water. (a, b) Fluxes of CO₂ and N₂O were significantly greater from amended soils compared to control soils for 22 (P=0.018) and 4 (P=0.009) days, respectively. Methane fluxes were not significantly different from zero in either treatment. Symbols are means \pm SE (n=5). (c) Cumulative N₂O emissions accounted for 0.5% of total emissions from control soils and 0.8% of total soil greenhouse gas emissions evolved during the 30-day experiment.

grassland (P < 0.01) over the three-year study period (Fig. 5).

By the end of the first water year, organic matter additions significantly increased the soil organic C pool by 24% in the 0–10 cm depth at the valley grassland site (P=0.06). Soil C stocks remained larger in water years 2 and 3 (P=0.01) (Fig. 6).

Changes to net ecosystem carbon storage

We assessed the net impact of organic matter amendments at the field scale through a mass balance of inputs and outputs. When including C added in compost, the amended plots showed an increase in net ecosystem C storage of 17.7 \pm 1.4 and 13.8 \pm 1.8 Mg C/ ha (P < 0.0001) at the valley and coastal grassland, respectively. A large portion (65–88%) of the additional ecosystem C was due to the direct addition of C from the compost amendment in water year 1, only 12% of which decomposed during the three-year study period.

Organic matter additions also altered ecosystem C fluxes. Above- and belowground NPP increased, as did C emissions via soil respiration. Modeled C storage from both control and amended plots was consistently negative across years and sites (Appendix Table A1), indicating that these annual grasslands were losing C, findings that have been observed in many grassland ecosystems (Ojima et al. 1994, Bellamy et al. 2005, Chou et al. 2008). The net balance of C fluxes (excluding compost amendments) was consistently more positive

for all amended plots compared to control plots at the valley grassland site and at two out of three paired plots at the coastal grassland (Fig. 7). The magnitude of the response was sensitive to assumptions about the contribution of heterotrophic respiration to total soil respiration. Assuming 50% $R_{\rm h}$, valley grasslands gained 198 ± 50 to 582 ± 43 g C/m² over three years following a single application of compost. Amended fields from two sets of paired plots at the coastal grassland showed similar gains of 192 ± 75 and 241 ± 96 g C/m². The third showed a decline in C storage by 281 ± 60 g C/m². For this pair of plots, soil volumetric water content was lower in the treatment than in the control, whereas the opposite trend was observed for all other fields (Fig. 1).

DISCUSSION

Patterns in soil respiration and greenhouse gas emissions

Organic matter amendments to surface soils increased soil respiration by an average of 18–19% over the three-year study. Soil respiration is the combination of heterotrophic and autotrophic respiration, and both could have been stimulated by compost additions. Adding composted organic material to the soil surface likely increased the decomposition rate of the compost, although compost, having already experienced intensive decomposition during formation, is generally considered more stable material than fresh litter (Bernal et al. 1998, Goyal et al. 2005). Approximately 12% of the added compost decomposed over the three-year study; this

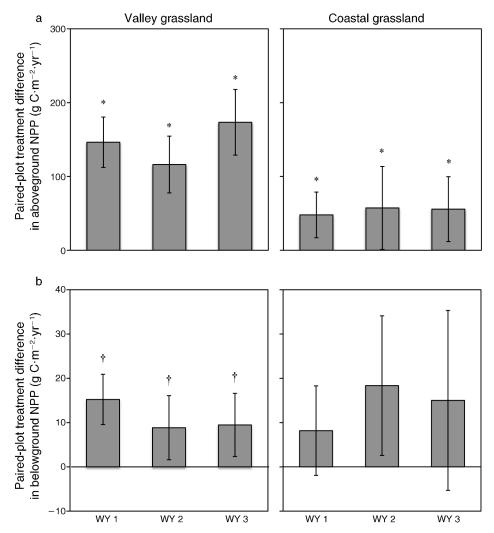


Fig. 4. (a) Aboveground net primary production from three water years (WYs) at the valley and coastal grassland experimental field sites. (b) Belowground net primary production (0–20 cm) from three water years (WYs) at the valley and coastal grassland experimental field sites. Root biomass was sampled at 0–10 and 10–20 cm depths. Values are provided in the Appendix: Table A1. Bars represent paired-plot treatment differences (mean \pm SE).

* P < 0.05; † P < 0.10.

resulted in the emission of 171 g CO_2 -C/m², or ~3.5% \pm 0.2% of the total C respired from amended soils over the study. Compost decomposition contributed $24\% \pm 6\%$ of the treatment differences in soil respiration. If we assume that autotrophic respiration accounted for 50% of the total soil respiration measured in both treatment and controls (Hanson et al. 2000), then the remaining heterotrophic respiration (not derived directly from compost) was only $\sim 6\% \pm 3\%$ greater in the amended treatment than in the control. This indicates that a priming effect by the compost on background soil C losses, if it occurred, was small (Kuzyakov et al. 2000, Kuzyakov 2010). It is important to note that soil respiration rates are temporally dynamic and respond rapidly to changes in soil moisture and temperature. Interpolation of measurements in time may miss important CO₂ fluxes.

Organic matter amendments could have altered the ratio of autotrophic to heterotrophic respiration in these soils. We provide evidence here that both autotrophic and heterotrophic respiration were likely to have increased as a result of the amendments. The tight coupling of root and microbial respiration in annual grassland soils may limit the degree to which their ratio can change. For example, the morphology and phenology of annual grasses results in little carbohydrate storage relative to perennial plants. Thus root respiration is likely to be directly proportional to plant activity at short temporal scales (Warembourg and Estelrich 2001, Tang and Baldocchi 2005). Plant activity increased as a result of compost additions, which likely increased autotrophic respiration. Similarly, the majority of heterotrophic respiration in soils comes from recently derived organic matter (Trumbore 2000, Giardina and

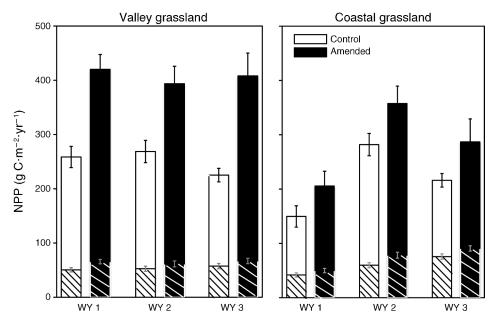


Fig. 5. Net primary production from three water years (WYs) at the valley and coastal grassland experimental field sites. The solid portion of the bars shows aboveground biomass, and the hatched portion shows belowground biomass in control (open) and amended (solid) plots. Data are shown as mean \pm SE.

Ryan 2002, Carbone and Trumbore 2007). During the growing season, most of this input occurs belowground in annual grasslands (Higgins et al. 2002). Therefore, rates of heterotrophic respiration were likely to have increased as a result of increased plant activity (i.e., the production of labile organic matter), and are likely to be relatively tightly coupled with NPP in annual grassland soils.

We predicted that compost additions would increase the production and emissions of N₂O and CH₄ from rangeland soils. Grasslands can be an important source of N_2O (Bouwman et al. 1993), and manure application to rangeland soils can significantly increase N_2O emissions (Rees et al. 2004, Jones et al. 2007). Organic matter amendments increase both the amount of mineral N in soils and water-holding capacity of soils, creating conditions favorable for N_2O production via nitrification and denitrification (Firestone and Davidson 1989). Similarly, we expected that organic matter amendments would increase CH_4 emissions or decrease the net rate of

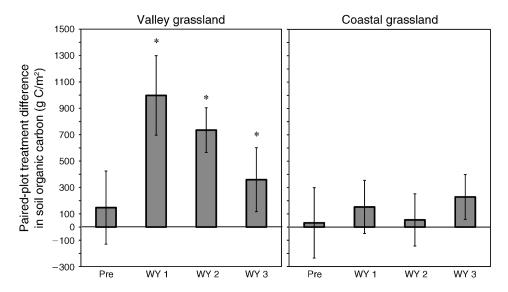


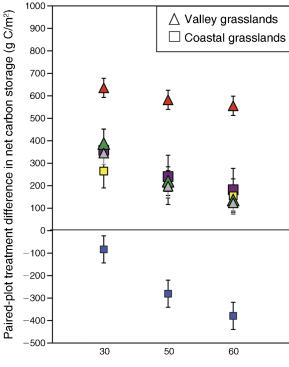
Fig. 6. Soil organic C content at 0–10 cm depth at the valley and grassland sites measured prior to the application (Pre) of composted organic matter and at the end of each water year (WY). Bars are means of paired-plot treatment differences \pm SE. * P < 0.05.

CH₄ uptake by soils (Le Mer and Roger 2001, Mosier et al. 2004). Although soil moisture was higher in amended fields, we saw no significant changes in N2O or CH4 fluxes in these soils. The lack of significant N2O emissions with compost additions could be due to the relatively slow decomposition of the organic matter, slow rate of N release from decomposition, and greater plant N uptake, as evident by increased biomass production. We expected the highest rates of N2O emissions to occur during wet-up events when temperatures were relatively high and plant-microbe competition for mineral N was low (Birch 1964, Franzluebbers et al. 2000, Grover et al. 2012). In our laboratory incubation, we were able to stimulate N₂O production for a short time period following soil wetting, but rates of N₂O emissions as a global warming potential were insignificant, particularly relative to the high CO2 emissions observed from both treatment and control soils. In contrast, soil N₂O emissions from temperate grasslands amended with a range of chemical fertilizers and manures were up to 4900 g $N_2O-N-C\cdot ha^{-1}\cdot d^{-1}$ compared with pre-amendment emissions of 4 g N₂O-N- $C \cdot ha^{-1} \cdot d^{-1}$ (Rees et al. 2004, Jones et al. 2007).

Effects on above- and belowground net primary production and soil carbon

We observed large increases in ANPP in both grassland types, and consistent trends over time despite a wide range in precipitation among water years. In annual grasslands, ANPP typically increases linearly with increasing precipitation (McCulley et al. 2005, Chou et al. 2008, Wu et al. 2011). We did not observe a significant linear increase in ANPP with rainfall during the study period. Aboveground NPP was greater in amended plots than in controls, findings that are consistent with studies measuring the response of crops to amendments (Edmeades 2003, Badgley et al. 2007) as well as studies of grassland response to N fertilization (Baer et al. 2003, LeBauer and Treseder 2008, Yahdjian et al. 2011). Aboveground NPP at the valley grassland showed a much stronger response than the coastal grassland, even when considering the slight differences in sampling times. Aboveground NPP at the valley site increased by $78\% \pm 13\%$ in the amended plots over the three years compared to $42\% \pm 14\%$ at the coastal site. This could be due to a greater impact of compost amendments on water and N availability at the former site compared to the more mesic coastal grassland (Harpole et al. 2007).

In rangelands, ANPP provides forage for livestock (Asner et al. 2004, Briske et al. 2011). Land management decisions in rangelands often focus on increasing the amount, quality, and sustainability of forage production. These decisions in turn affect the feasibility and sustainability of associated C sequestration or greenhouse gas offset programs. In annual grasslands, ANPP can often be predicted by the timing and magnitude of rainfall and the previous year's production (Hedrick



Contribution of heterotrophic respiration to total soil respiration (%)

Fig. 7. Paired-plot treatment difference in net C storage summed over three water years at the valley (triangles) and coastal (squares) grasslands sites calculated using low (30%), medium (50%), and high (60%) scenarios of the fraction of heterotrophic respiration to total soil respiration. Each paired plot (n=3 per grassland type) is shown in a unique color. Bars represent \pm SE. Values above zero indicate greater C storage in amended plots compared to control plots. Only one paired plot at the coastal grassland showed consistent C loss in the amended plot.

1948, Heady 1956, Bartolome et al. 1980, Chou et al. 2008). Organic matter additions and other management practices that increase the size of soil C pools are likely to have a positive impact on NPP through increased water-holding capacity and N availability. Compared to chemical fertilizers, which provide a short-term pulse of nutrients (Wight and Godfrey 1985, Fauci and Dick 1994), organic matter amendments act as a slow-release fertilizer during decomposition (Sommers 1977), and thus may provide longer-term or sustained increases in aboveground NPP (e.g., Gerzabek et al. 1997, Blair et al. 2006). These effects may last several years. The longlasting effects of a single application of compost could serve to buffer impacts of decreasing precipitation predicted for some regions with climate change (Stavast et al. 2005, Kowaljow et al. 2010).

Detecting changes in C storage in the bulk soil pool (i.e., without fractionation or other separation techniques) is difficult due to the large variability of the soil C pool in grasslands. In this study, recognizable compost fragments were removed prior to soil C

determination to avoid overestimating C pools from amended soils. Regardless, we were able to detect an increase in the bulk soil C pool at the valley site. The increase in soil C was likely derived from a combination of compost incorporation into soil and additions of newly fixed C from NPP. In a three-year study monitoring the effects of a one-time application of either inorganic or organic fertilizers in a degraded semiarid rangeland in Patagonia, Kowaljow et al. (2010) observed a similar pattern of increase in soil organic C and enhanced microbial activity. Soil organic C formation and stabilization is promoted by management practices or technologies that increase the quantity of C inputs (Gentile et al. 2011). In rangelands, soil organic content is strongly dependent on root biomass and turnover due to the high belowground allocation of grasses and forbs and longer residence time of rootderived C (Jobbagy and Jackson 2000, Kätterer et al. 2011). In our experiment, root biomass increased significantly in the valley grassland and followed the same trend in the coastal grassland. Application of composted organic material to the soil surface increased both above- and belowground productivity over the three growing seasons, leading to greater annual C inputs from vegetation. Thus, management techniques like composted organic matter additions that increase production have the potential to increase the size of the soil organic C pool over the long term.

Changes in net ecosystem carbon storage

The control plots from both sites appeared to be losing C. The ecosystem C balance of grasslands is typically highly variable over time and space (Novick et al. 2004, Xu et al. 2004, Klumpp et al. 2011), but several recent studies have reported C losses from rangeland soils (Bellamy et al. 2005, Schipper et al. 2007, Chou et al. 2008). Chou et al. (2008) reported significant losses of soil organic C for four consecutive years in a mediterranean annual grassland with and without experimental rainfall additions. The greatest losses occurred in a year with late-season (late spring-summer) rainfall. In annual grasslands, late, warm-season rainfall can stimulate heterotrophic respiration after plants have stopped growing or have senesced, resulting in ecosystem C losses. Carbon storage in grasslands is also sensitive to shifts in vegetation. Continual declines in ecosystem C storage may also be explained by a nonequilibrium status of California grasslands and ongoing gradual declines in soil C following annual grass invasion (Koteen et al. 2011).

Organic matter amendments decreased the rate of C loss in most plots. This was true even when not considering the C added via the amendments, and was due to the stimulation of NPP. Assuming that heterotrophic respiration was 50% of total soil respiration (see Fig. 7 for a range of R_h : R_a scenarios), rates of net ecosystem C storage increased by 25–70% with organic matter amendments, with a rate of C sequestration of 51

 \pm 77 to 333 \pm 52 g C/m² over the three-year study. This value increases to 1770 \pm 142 to 1383 \pm 188 g C/m² when considering the amendment C added at the field scale. A full life cycle assessment would be needed to determine the actual greenhouse costs or savings beyond the field scale, but if organic matter amendments are diverted from fates with high greenhouse gas emissions (i.e., landfills, manure slurry ponds) then considerable C offsets may be achieved through this management approach (M. S. DeLonge, R. Ryals, and W. L. Silver, unpublished manuscript).

Our results show that a single application of composted organic matter led to sustained increases in NPP for at least three years, with no sign of diminishing effects. Moreover, increases in plant production significantly offset elevated soil respiration from microbial activity in five out of six paired plots. The amended plot that had lower net C storage relative to its paired control plot also had lower soil volumetric water content, whereas the opposite trend was observed at the other fields (Fig. 2). This finding suggests that water limitation has the potential to alter the source–sink potential of annual grasslands (Harpole et al. 2007).

Conclusions

We found that a single application of composted organic matter shifted the C balance of annual grassland ecosystems and resulted in greater C storage. Increases in above- and belowground NPP were observed over three water years, with no obvious sign of a diminishing trend. Enhanced plant productivity was partially offset by elevated soil respiration, but we detected no statistically significant treatment effects on N_2O or CH_4 fluxes. We were able to detect an increase in soil C at the valley site, which was surprising given the large background pool size.

Our results have important implications for rangeland management in the context of climate change mitigation. Urban and agricultural green waste is often an important source of greenhouse gas emissions (IPCC 2001). Here we show that an alternative fate for that material can significantly increase NPP and slow rates of ecosystem C losses at the field scale. This approach provides important co-benefits to landowners, such as the sustained increase in forage production measured here. Multiyear field studies are critically needed to explore the potential of ecosystem management to contribute to climate change mitigation. These data are also needed to construct comprehensive and credible life cycle analyses that explicitly include ecosystem dynamics in C offset protocols.

ACKNOWLEDGMENTS

This research was supported by generous grants from the Marin Community Foundation, the Rathmann Family Foundation, and the Lia Fund, as well as a Conservation Innovation Grant from the USDA to the Environmental Defense Fund and a grant from the Kearney Foundation for Soil Science. We thank M. Almaraz, M. Beaton, W. Cea, J. Cosgrove, L. Curtis-

Whitchurch, C. Kyauk, L. Lintott, A. McDowell, A. Mendoza, J. Treffkorn, Z. Statman-Weil, J. Wedgeworth, M. Williams, and M. Wong for assisting with field data collection and/or laboratory analysis. Dustin Flavell and dedicated staff provided key assistance at SFREC. Special thanks go to John Wick, Peggy Rathmann, and Jeffrey Creque for their invaluable contributions at the coastal grassland. We also thank the Marin Agricultural Land Trust for its sponsorship, and N. Scolari, B. Berner, P. Hickey, D. Lewis, S. Larson, S. Carlsen, T. Estrada, C. Epifano, and Marin Organic for their partnership in the Marin Carbon Project. We thank M. Torn, T. Dawson, and two anonymous reviewers for thoughtful comments on the manuscript.

LITERATURE CITED

- Alluvione, F., C. Bertora, L. Zavattaro, and C. Grignani. 2010. Nitrous oxide and carbon dioxide emissions following green manure and compost fertilization in corn. Soil Science Society of America Journal 74:384–395.
- Asner, G. P., A. J. Elmore, L. P. Olander, R. E. Martin, and A. T. Harris. 2004. Grazing systems, ecosystem responses, and global change. Annual Review of Environment and Resources 29:261–299.
- Badgley, C., J. Moghtader, E. Quintero, E. Zakem, M. J. Chappell, K. Aviles-Vazquez, A. Samulon, and I. Perfecto. 2007. Organic agriculture and the global food supply. Renewable Agriculture and Food Systems 22:86–108.
- Baer, S. G., J. M. Blair, S. L. Collins, and A. K. Knapp. 2003. Soil resources regulate productivity and diversity in newly established tallgrass prairie. Ecology 84:724–735.
- Bai, Z. G., D. L. Dent, L. Olsson, and M. E. Schaepman. 2008.
 Global assessment of land degradation and improvement. 1.
 Identification by remote sensing. Report 2008/01. ISRIC: World Soil Information, Wageningen, The Netherlands.
- Bartolome, J. W., W. J. Barry, T. Griggs, and P. Hopkinson. 2007. Valley grassland. Pages 367–393 in M. R. Stromberg, J. D. Corbin, and C. M. D'Antonio, editors. California grasslands ecology and management. University of California Press, Berkeley, California, USA.
- Bartolome, J. W., M. C. Stroud, and H. F. Heady. 1980. Influence of natural mulch on forage production on differing California annual range sites. Journal of Range Management 33:4–8.
- Beaudette, D. E., and A. T. O'Geen. 2009. Soil-Web: an online soil survey for California, Arizona, and Nevada. Computers and Geosciences 35:2119–2128.
- Bellamy, P. H., P. J. Loveland, R. I. Bradley, R. M. Lark, and G. J. D. Kirk. 2005. Carbon losses from all soils across England and Wales 1978–2003. Nature 437:245–248.
- Bernal, M. P., M. A. Sanchez-Monedero, C. Paredes, and A. Roig. 1998. Carbon mineralization from organic wastes at different composting stages during their incubation with soil. Agriculture Ecosystems and Environment 69:175–189.
- Birch, H. F. 1964. Mineralisation of plant nitrogen following alternate wet and dry conditions. Plant and Soil 20:43–49.
- Blair, N., R. D. Faulkner, A. R. Till, and P. R. Poulton. 2006. Long-term management impacts on soil C, N and physical fertility. Part 1: Broadbalk experiment. Soil and Tillage Research 91:30–38.
- Bouwman, A. F., I. Fung, E. Matthews, and J. John. 1993. Global analysis of the potential for N₂O production in natural soils. Global Biogeochemical Cycles 7:557–597.
- Briske, D. D., J. D. Derner, D. G. Milchunas, and K. W. Tate. 2011. An evidence-based assessment of prescribed grazing practices. Pages 21–74 in D. D. Briske, editor. Conservation benefits of rangeland practices. USDA Natural Resource Conservation Service. Allen Press, Lawrence, Kansas, USA.
- Brown, S., A. Dushku, T. Pearson, D. Shoch, J. Winsten, S. Sweet, and J. Kadyszewski. 2004. Carbon supply from changes in management of forest, range, and agricultural lands of California. Winrock International, for the California

- Energy Commission, PIER Energy-Related Environmental Research, Sacramento, California, USA.
- Cabrera, V. E., L. J. Stavast, T. T. Baker, M. K. Wood, D. S. Cram, R. P. Flynn, and A. L. Ulery. 2009. Soil and runoff response to dairy manure application on New Mexico rangeland. Agriculture Ecosystems and Environment 131:255–262.
- Cambardella, C. A., and E. T. Elliott. 1992. Particulate soil organic-matter changes across a grassland cultivation sequence. Soil Science Society of America Journal 56:777–783
- Carbone, M. S., and S. E. Trumbore. 2007. Contribution of new photosynthetic assimilates to respiration by perennial grasses and shrubs: residence times and allocation patterns. New Phytologist 176:124–135.
- Cassman, K. G., A. Dobermann, and D. T. Walters. 2002. Agroecosystems, nitrogen-use efficiency, and nitrogen management. Ambio 31:132–140.
- Chadwick, D. R., B. F. Pain, and S. K. E. Brookman. 2000. Nitrous oxide and methane emissions following application of animal manures to grassland. Journal of Environmental Quality 29:277–287.
- Chou, W. W., W. L. Silver, R. D. Jackson, A. W. Thompson, and B. Allen-Diaz. 2008. The sensitivity of annual grassland carbon cycling to the quantity and timing of rainfall. Global Change Biology 14:1382–1394.
- Conant, R. T., K. Paustian, and E. T. Elliott. 2001. Grassland management and conversion into grassland: effects on soil carbon. Ecological Applications 11:343–355.
- Craine, J. M., D. A. Wedin, and F. S. Chapin. 1999. Predominance of ecophysiological controls on soil CO₂ flux in a Minnesota grassland. Plant and Soil 207:77–86.
- Dahlgren, R. A., and M. J. Singer. 1994. Nutrient cycling in managed and non-managed oak woodland-grass ecosystems. Final Report: Integrated Hardwood Range Management Program. Land, Air, and Water Resources Paper 100028, Davis, California, USA.
- Dalal, R. C., W. J. Wang, G. P. Robertson, and W. J. Parton. 2003. Nitrous oxide emission from Australian agricultural lands and mitigation options: a review. Australian Journal of Soil Research 41:165–195.
- Davidson, E. A. 2009. The contribution of manure and fertilizer nitrogen to atmospheric nitrous oxide since 1860. Nature Geoscience 2:659–662.
- Derner, J. D., and G. E. Schuman. 2007. Carbon sequestration and rangelands: a synthesis of land management and precipitation effects. Journal of Soil and Water Conservation 62:77–85.
- Edmeades, D. C. 2003. The long-term effects of manures and fertilisers on soil productivity and quality: a review. Nutrient Cycling in Agroecosystems 66:165–180.
- Fauci, M. F., and R. P. Dick. 1994. Soil microbial dynamics: short-term and long-term effects of inorganic and organic nitrogen. Soil Science Society of America Journal 58:801–806
- Fierer, N., and J. P. Schimel. 2002. Effects of drying-rewetting frequency on soil carbon and nitrogen transformations. Soil Biology and Biochemistry 34:777–787.
- Firestone, M. K., and E. A. Davidson. 1989. Microbiological basis of NO and N2O production and consumption in soil. Dahlem Workshop Reports, Berlin, Germany.
- Follett, R. F. 2001. Soil management concepts and carbon sequestration in cropland soils. Soil and Tillage Research 61:77–92.
- Franzluebbers, A. J., R. L. Haney, C. W. Honeycutt, H. H. Schomberg, and F. M. Hons. 2000. Flush of carbon dioxide following rewetting of dried soil relates to active organic pools. Soil Science Society of America Journal 64:613–623.
- FRAP. Fire and Resource Assessment Program. 2003. The changing California: 2003 forest and range assessment.

- California Department of Forestry and Fire Protection. The Resources Agency, Sacramento, California, USA.
- Gentile, R., B. Vanlauwe, and J. Six. 2011. Litter quality impacts short- but not long-term soil carbon dynamics in soil aggregate fractions. Ecological Applications 21:695–703.
- Gerzabek, M. H., F. Pichlmayer, H. Kirchmann, and G. Haberhauer. 1997. The response of soil organic matter to manure amendments in a long-term experiment at Ultuna, Sweden. European Journal of Soil Science 48:273–282.
- Giardina, C. P., and M. G. Ryan. 2002. Total belowground carbon allocation in a fast-growing Eucalyptus plantation estimated using a carbon balance approach. Ecosystems 5:487–499.
- Goyal, S., S. K. Dhull, and K. K. Kapoor. 2005. Chemical and biological changes during composting of different organic wastes and assessment of compost maturity. Bioresource Technology 96:1584–1591.
- Gregorich, E. G., P. Rochette, A. J. VandenBygaart, and D. A. Angers. 2005. Greenhouse gas contributions of agricultural soils and potential mitigation practices in Eastern Canada. Soil and Tillage Research 83:53–72.
- Grover, S. P. P., S. J. Livesley, L. B. Hutley, H. Jamali, B. Fest,
 J. Beringer, K. Butterbach-Bahl, and S. K. Arndt. 2012.
 Land use change and the impact on greenhouse gas exchange in north Australian savanna soils. Biogeosciences 9:423–437.
- Hall, B., and P. Sullivan. 2001. Alternative soil amendments. In USDA Rural Business Cooperative Service, editor. Horticulture Technical Note. National Center for Appropriate Technology, Washington, D.C., USA
- Hanson, P. J., N. T. Edwards, C. T. Garten, and J. A. Andrews. 2000. Separating root and soil microbial contributions to soil respiration: a review of methods and observations. Biogeochemistry 48:115–146.
- Harper, C. W., J. M. Blair, P. A. Fay, A. K. Knapp, and J. D. Carlisle. 2005. Increased rainfall variability and reduced rainfall amount decreases soil CO₂ flux in a grassland ecosystem. Global Change Biology 11:322–334.
- Harpole, W. S., D. L. Potts, and K. N. Suding. 2007. Ecosystem responses to water and nitrogen amendment in a California grassland. Global Change Biology 13:2341–2348.
- Heady, H. F. 1956. Changes in a California annual plant community induced by manipulation of natural mulch. Ecology 37:798–812.
- Heady, H. F., J. W. Bartolome, M. D. Pitt, G. D. Savelle, and
 M. C. Stroud. 1992. California prairie. Pages 313–332 in
 R. T. Coupland, editor. Natural grasslands. Elsevier, New York, New York, USA.
- Hedrick, D. W. 1948. The mulch layer of California annual ranges. Journal of Range Management 1:22–25.
- Herrero, M., P. K. Thornton, P. Gerber, and R. S. Reid. 2009. Livestock, livelihoods and the environment: understanding the trade-offs. Current Opinion in Environmental Sustainability 1:111–120.
- Higgins, P. A. T., R. B. Jackson, J. M. Des Rosiers, and C. B. Field. 2002. Root production and demography in a California annual grassland under elevated atmospheric carbon dioxide. Global Change Biology 8:841–850.
- IPCC. 2001. Climate Change 2001: Mitigation—contribution of Working Group III. *In* B. Metz, O. Davidson, R. Swart, and J. Pan, editors. Assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.
- Jackson, L. E., R. B. Strauss, M. K. Firestone, and J. W. Bartolome. 1988. Plant and soil-nitrogen dynamics in California annual grassland. Plant and Soil 110:9–17.
- Jackson, R. D., and J. W. Bartolome. 2002. A state-transition approach to understanding nonequilibrium plant community dynamics in California grasslands. Plant Ecology 162:49–65.
- Janzen, H. H., C. A. Campbell, R. C. Izaurralde, B. H. Ellert, N. Juma, W. B. McGill, and R. P. Zentner. 1998.

- Management effects on soil C storage on the Canadian prairies. Soil and Tillage Research 47:181–195.
- Jobbagy, E. G., and R. B. Jackson. 2000. The vertical distribution of soil organic carbon and its relation to climate and vegetation. Ecological Applications 10:423–436.
- Jones, M. B., and A. Donnelly. 2004. Carbon sequestration in temperate grassland ecosystems and the influence of management, climate and elevated CO₂. New Phytologist 164:423–439.
- Jones, S. K., R. M. Rees, U. M. Skiba, and B. C. Ball. 2007. Influence of organic and mineral N fertiliser on N_2O fluxes from a temperate grassland. Agriculture Ecosystems and Environment 121:74–83.
- Kätterer, T., M. A. Bolinder, O. Andren, H. Kirchmann, and L. Menichetti. 2011. Roots contribute more to refractory soil organic matter than above-ground crop residues, as revealed by a long-term field experiment. Agriculture Ecosystems and Environment 141:184–192.
- Keller, M., and W. A. Reiners. 1994. Soil atmosphere exchange of nitrous oxide, nitric oxide, and methane under secondary succession of pasture to forest in the Atlantic lowlands of Costa Rica. Global Biogeochemical Cycles 8:399–409.
- Klumpp, K., T. Tallec, N. Guix, and J. F. Soussana. 2011. Long-term impacts of agricultural practices and climatic variability on carbon storage in a permanent pasture. Global Change Biology 17:3534–3545.
- Koteen, L. E., D. D. Baldocchi, and J. Harte. 2011. Invasion of non-native grasses causes a drop in soil carbon storage in California grasslands. Environmental Research Letters 6.
- Kowaljow, E., M. Julia Mazzarino, P. Satti, and C. Jimenez-Rodriguez. 2010. Organic and inorganic fertilizer effects on a degraded Patagonian rangeland. Plant and Soil 332:135–145.
- Kuchler, A. W. 1964. Potential vegetation of the conterminous United States. Special Report No. 36. American Geographical Society, New York, New York, USA.
- Kuzyakov, Y. 2010. Priming effects: interactions between living and dead organic matter. Soil Biology and Biochemistry 42:1363–1371.
- Kuzyakov, Y., J. K. Friedel, and K. Stahr. 2000. Review of mechanisms and quantification of priming effects. Soil Biology and Biochemistry 32:1485–1498.
- Larney, F. J., and D. A. Angers. 2012. The role of organic amendments in soil reclamation: a review. Canadian Journal of Soil Science 92:19–38.
- LeBauer, D. S., and K. K. Treseder. 2008. Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. Ecology 89:371–379.
- Le Mer, J., and P. Roger. 2001. Production, oxidation, emission and consumption of methane by soils: a review. European Journal of Soil Biology 37:25–50.
- Lynch, D. H., R. P. Voroney, and P. R. Warman. 2005. Soil physical properties and organic matter fractions under forages receiving composts, manure or fertilizer. Compost Science and Utilization 13:252–261.
- Marshall, S. A., C. P. Campbell, and J. G. Buchanan-Smith. 1998. Herbage biomass and intake of beef cows with calves grazing a grass-legume pasture in southern Ontario. Canadian Journal of Animal Science 78:211–218.
- Matthias, A. D., D. N. Yarger, and R. S. Weinbeck. 1978. Numerical evaluation of chamber methods for determining gas fluxes. Geophysical Research Letters 5:765–768.
- McCulley, R. L., I. C. Burke, J. A. Nelson, W. K. Lauenroth, A. K. Knapp, and E. F. Kelly. 2005. Regional patterns in carbon cycling across the Great Plains of North America. Ecosystems 8:106–121.
- Metcalfe, D. B., M. Williams, L. Aragao, A. C. L. da Costa, S. S. de Almeida, A. P. Braga, P. H. L. Goncalves, and J. D. Silva. 2007. A method for extracting plant roots from soil which facilitates rapid sample processing without compromising measurement accuracy. New Phytologist 174:697–703.

- Mosier, A., R. Wassmann, L. Verchot, J. King, and C. Palm. 2004. Methane and nitrogen oxide fluxes in tropical agricultural soils: sources, sinks and mechanisms. Environment Development and Sustainability 6:11–49.
- Nijs, I., J. Roy, J. L. Salager, and J. Fabreguettes. 2000. Elevated CO₂ alters carbon fluxes in early successional Mediterranean ecosystems. Global Change Biology 6:981– 994.
- Novick, K. A., P. C. Stoy, G. G. Katul, D. S. Ellsworth, M. B. S. Siqueira, J. Juang, and R. Oren. 2004. Carbon dioxide and water vapor exchange in a warm temperate grassland. Oecologia 138:259–274.
- Ojima, D. S., K. A. Galvin, and B. L. Turner. 1994. The global impact of land-use change. BioScience 44:300–304.
- Paustian, K., O. Andren, H. H. Janzen, R. Lal, P. Smith, G. Tian, H. Tiessen, M. Van Noordwijk, and P. L. Woomer. 1997. Agricultural soils as a sink to mitigate CO₂ emissions. Soil Use and Management 13:230–244.
- Rees, R., S. Jones, R. E. Thorman, I. McTaggart, B. Ball, and U. Skiba. 2004. The effect of organic and mineral nitrogen fertilisers on emissions of NO, N₂O and CH₄ from cut grassland. Pages 268–276 in D. J. Hatch, D. R. Chadwick, S. C. Jarvis, and J. A. Roker, editors. Controlling nitrogen flows and losses. 12th Nitrogen Workshop. University of Exeter, Exeter, UK.
- Sanderman, J., and R. Amundson. 2009. A comparative study of dissolved organic carbon transport and stabilization in California forest and grassland soils. Biogeochemistry 92:41– 59.
- SAS Institute. 2007. JMP 7.0.2. SAS Institute, Cary, North Carolina, USA.
- Schimel, D. S., W. J. Parton, T. G. F. Kittel, D. S. Ojima, and C. V. Cole. 1990. Grassland biogeochemistry–links to atmospheric processes. Climatic Change 17:13–25.
- Schipper, L. A., W. T. Baisden, R. L. Parfitt, C. Ross, J. J. Claydon, and G. Arnold. 2007. Large losses of soil C and N from soil profiles under pasture in New Zealand during the past 20 years. Global Change Biology 13:1138–1144.
- Schuman, G. E., H. H. Janzen, and J. E. Herrick. 2002. Soil carbon dynamics and potential carbon sequestration by rangelands. Environmental Pollution 116:391–396.
- Silver, W. L., A. W. Thompson, M. E. McGroddy, R. K. Varner, J. D. Dias, H. Silva, P. M. Crill, and M. Keller. 2005. Fine root dynamics and trace gas fluxes in two lowland tropical forest soils. Global Change Biology 11:290–306.
- Sommers, L. E. 1977. Chemical composition of sewage sludges and analysis of their potential use as fertilizers. Journal of Environmental Quality 6:225–232.
- Soussana, J. F., P. Loiseau, N. Vuichard, E. Ceschia, J. Balesdent, T. Chevallier, and D. Arrouays. 2004. Carbon cycling and sequestration opportunities in temperate grasslands. Soil Use and Management 20:219–230.

- Stavast, L. J., T. T. Baker, A. L. Ulery, R. P. Flynn, M. K. Wood, and D. S. Cram. 2005. New Mexico blue grama rangeland response to dairy manure application. Rangeland Ecology and Management 58:423–429.
- Steenwerth, K. L., L. E. Jackson, F. J. Calderon, M. R. Stromberg, and K. M. Scow. 2002. Soil microbial community composition and land use history in cultivated and grassland ecosystems of coastal California. Soil Biology and Biochemistry 34:1599–1611.
- Stromberg, M. R., and J. R. Griffin. 1996. Long-term patterns in coastal California grasslands in relation to cultivation, gophers, and grazing. Ecological Applications 6:1189–1211.
- Tang, J. W., and D. D. Baldocchi. 2005. Spatial-temporal variation in soil respiration in an oak-grass savanna ecosystem in California and its partitioning into autotrophic and heterotrophic components. Biogeochemistry 73:183–207.
- Trumbore, S. 2000. Age of soil organic matter and soil respiration: radiocarbon constraints on belowground C dynamics. Ecological Applications 10:399–411.
- Vallejo, A., U. M. Skiba, L. Garcia-Torres, A. Arce, S. Lopez-Fernandez, and L. Sanchez-Martin. 2006. Nitrogen oxides emission from soils bearing a potato crop as influenced by fertilization with treated pig slurries and composts. Soil Biology and Biochemistry 38:2782–2793.
- Warembourg, F. R., and H. D. Estelrich. 2001. Plant phenology and soil fertility effects on below-ground carbon allocation for an annual (*Bromus madritensis*) and a perennial (*Bromus erectus*) grass species. Soil Biology and Biochemistry 33:1291–1303.
- White, R., S. Murray, and M. Rohweder. 2000. Grassland ecosystems. World Resources Institute, Washington, D.C., USA.
- Wight, J. R., and E. B. Godfrey. 1985. Predicting yield response to nitrogen fertilization on northern Great Plains rangelands. Journal of Range Management 38:238–241.
- Wu, Z. T., P. Dijkstra, G. W. Koch, J. Penuelas, and B. A. Hungate. 2011. Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. Global Change Biology 17:927–942
- Xu, L. K., D. D. Baldocchi, and J. W. Tang. 2004. How soil moisture, rain pulses, and growth alter the response of ecosystem respiration to temperature. Global Biogeochemical Cycles 18.
- Yahdjian, L., L. Gherardi, and O. E. Sala. 2011. Nitrogen limitation in arid-subhumid ecosystems: a meta-analysis of fertilization studies. Journal of Arid Environments 75:675–680
- Zhou, X., S. Q. Wan, and Y. Q. Luo. 2007. Source components and interannual variability of soil CO₂ efflux under experimental warming and clipping in a grassland ecosystem. Global Change Biology 13:761–775.

SUPPLEMENTAL MATERIAL

Appendix

Carbon pools and fluxes from control and organic matter amended plots for three water years at the valley and coastal grassland experimental sites (*Ecological Archives* A023-004-A1).