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Warming induced changes in soil carbon and nitrogen influence priming responses in four ecosystems

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ABSTRACT

Soil contains the largest terrestrial pool of carbon (C), but how this pool will be affected by global change remains unknown. Warmer temperatures generally increase soil respiration, while additional C inputs from plants to soil can increase or decrease soil C decomposition rates through a phenomenon known as priming. Priming occurs when soil organic matter (SOM) decomposition rates change in response to a fresh substrate, though the mechanisms underlying priming are poorly understood. Here, we measured priming in four ecosystems during a seven-week incubation with weekly glucose additions. Soil was collected from field warming experiments in the four ecosystems, so our experiment assessed the influence of long-term warming on priming. All treatments exhibited negative priming (reduced SOM decomposition) after the first substrate pulse. Subsequent substrate pulses elicited variable responses, and the effect of long-term warming on priming was ecosystem-dependent. Priming was correlated with changes in soil C and N in response to warming: ecosystems that lost soil C and N over nine years of experimental warming exhibited low rates of priming (decreased SOM decomposition), while ecosystems that gained soil C and N in response to warming had high priming. Consequently, priming may accelerate C losses in ecosystems that exhibit warming-induced C increases, and vice versa, thus partially buffering soil C content against change.

1. Introduction

Soils contain twice as much carbon (C) as the atmosphere and three times as much as all terrestrial vegetation (Ciais et al., 2013). Therefore, understanding how this C pool will respond to changes in temperature is vital for predicting how terrestrial ecosystems will feed back to future climate change. Increased atmospheric carbon dioxide (CO_2) concentration is causing higher global temperatures (Hartmann et al., 2013) and C fixation rates in plants (Curtis and Wang, 1998; De Graaff et al., 2006), but how these factors will interact together to affect terrestrial C-cycling remains uncertain.

Warming can increase soil C losses by stimulating respiration (Dalias et al., 2001; Rustad et al., 2001), though these short-term losses may be offset by long-term acclimatization of respiration (Luo et al., 2001; Oechel et al., 2000), decreased microbial biomass (Frey et al., 2008) and reduced soil moisture suppressing microbial activity (Allison and Treseder, 2008). A recent meta-analysis tested whether soil C loss in response to warming was proportional to soil C stocks, suggesting that ecosystems with high soil C pools (e.g., arctic and tundra) showing the largest soil C losses (Crowther et al., 2016). Warming can also influence soil C balance by altering plant productivity and community composition. Some studies report that warming can increase plant inputs (Cowles et al., 2016; Rustad et al., 2001; Wu et al., 2011a), though others have found that this response can diminish over time (Wu et al., 2012). Shifts in plant communities under warmer climates are also often reported (Wu et al., 2012; Xu et al., 2015; Zhou et al., 2011), and these changes can alter ecosystem C balance in a number of ways including altering the stoichiometry of organic inputs to the soil (Carrillo et al., 2017; Xu et al., 2015), nitrogen (N) cycling (Wu et al., 2012), and microbial community composition (Carrillo et al., 2017). Changes in the quantity and quality of C inputs to soil is known to alter C-cycling dynamics, a phenomenon known as 'priming.'

Priming is defined as a change in native soil organic matter (SOM) decomposition in response to fresh inputs (Kuzyakov, 2010). Despite the potentially large role priming can play in altering terrestrial C-cycling (Carney et al., 2007; Cheng, 2009), few studies have directly measured priming in response to warming (Ghee et al., 2013; Zhu and Cheng, 2011). Additionally, most studies assess priming effects after a single substrate pulse, an unlikely scenario in natural environments that receive continuous or pulsed inputs via root exudates and plant litter.

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Priming responses were affected by whether the same amount of substrate was added as a single pulse, repeated pulses, or continuous additions (Hamer and Marschner, 2005; Hoyle et al., 2008; Qiao et al., 2014). Therefore, to more accurately understand how ecosystems may respond to changing C inputs as a result of climate change, more repeated or continuous C pulse studies are required.

The focus of this study was to measure priming after repeated C amendments in four ecosystems, and to assess how long-term warming would influence those effects. The four ecosystems, situated along an elevation gradient in Northern Arizona, USA, included grass-dominated areas in mixed conifer and ponderosa pine forests, a pinyon-juniper woodland and a cool desert grassland. We predicted that warming would decrease C and N stocks, with greater losses in colder ecosystems (Crowther et al., 2016; Kirschbaum, 1995), and that priming would correlate negatively with these changes in soil nutrients. We reasoned that more labile compounds would be selectively degraded during the nine-year warming treatment, resulting in a pool of relatively more recalcitrant SOM in ecosystems with greater losses and that this more recalcitrant pool would be less susceptible to priming effects (Blagodatskaya et al., 2011a).

2. Materials and methods

2.1. Site description and warming treatment

Field sites were located in Northern Arizona, USA, along the C. Hart Merriam Elevation Gradient (http://www.mpcer.nau.edu/gradient; Table 1). Sites included four ecosystems: mixed conifer forest, ponderosa pine forest, pinyon-juniper woodland, and cool desert grassland. In 2002, intact plant-soil cores, 30 cm in diameter and 30 cm deep, were extracted from grass-dominated areas in each ecosystem, placed in PVC cylinders and either re-planted in the same ecosystem ("ambient" treatment) or transplanted to the next one lower in elevation as an ~3 °C warming treatment ("transplanted" treatment; Wu et al., 2011b). The warmed cores from the grassland ecosystem were transplanted to the Great Basin desert site. To compensate for lower precipitation in the transplanted mesocosms, rainfall collectors were used to add additional precipitation to simulate the rainfall of the native ecosystem. Rainfall collectors were located adjacent to the experimental plots, avoiding shading effects or other possible changes to the light environment. See Blankinship et al. (2011); Wu et al. (2011a, 2011b) for more complete site descriptions as well as a detailed description of the warming treatment design.

2.2. Soil C and N

In August 2011, soil (0–15 cm) from 6 to 7 replicate mesocosms of the ambient and transplanted treatments was collected and homogenized. Soils were sieved (2 mm mesh) and stored at 4 °C for less than a week prior to the start of the incubation (see details below). Subsamples (n = 3) of each homogenized soil sample were oven dried at 105 °C, ground with a mortar and pestle, and analyzed for total C and N using a Carlo Erba NC2100 elemental analyzer configured through a CONFLO III to a DELTA V Advantage mass spectrometer (Thermo Fisher Scientific, West Palm Beach, FL USA). Additional subsamples (n = 5) were extracted with a 0.1 M K_2SO_4 solution to measure extractable C and N. Briefly, 50 mL of 0.1 M K_2SO_4 was added to approximately 15 g dry weight soil, shaken for 1 h, and then filtered using a Whatman #1 filter. The filtered extracts were subsequently dried at 60 °C, ground and analyzed for C and N as described above.

At the end of the experiment, subsamples of soil from the incubations described below were analyzed for total C and N, as well as extracted with a 0.1 M K_2SO_4 solution to measure extractable C and N as described previously.

Table 1
Site characteristics of the five ecosystems along the C. Hart Merriam elevation gradient near Flagstaff, AZ, USA.

Ecosystem	Elevation (m)	MAT* (°C)	MAP* (mm)	Soil C (g m^{-2})	Soil N (g m^{-2})
Great Basin Desert	1556	12.8	127.3	–	–
High Desert Grassland	1760	12.6	169.6	2378.6	200.9
Pinyon-Juniper Woodland	2020	10.8	272.0	2041.7	184.4
Ponderosa Pine Forest	2344	8.9	392.8	2596.6	160.4
Mixed Conifer Forest	2620	6.6	543.3	6626.5	506.7

MAT, Mean Annual Temperature; MAP, Mean Annual Precipitation.
* Based on weather station data from 2002 to 2010 (http://perceval.bio.nau.edu/MPCER_OLD/gradient/).

2.3. Incubation experiment

Approximately 40 g dry weight soil was weighed into specimen cups. Water was added to bring the moisture content to 60% of field capacity, after which the cups with soil were placed in 470 mL airtight Mason jars. Half of the samples (n = 5) received 250 μg C g^{-1} soil once a week as 100 μL of a glucose solution (U-^{13}C glucose; $\delta^{13}C$ = 1369‰) for seven weeks, while the remaining samples received an equal amount of deionized water (non-amended controls). The quantity of amendment was chosen as it is approximately 1.5 times previously measured microbial biomass C of the ecosystems, which has been shown to induce priming responses (Blagodatskaya and Kuzyakov, 2008), and is within estimates of plant exudation rates (Cheng and Gershenson, 2007; Nguyen, 2003). After each glucose or water addition, soils were stirred to distribute the substrate. Jars were incubated at room temperature (~23 °C) in the dark.

Headspace samples were removed through a septum two and five days after each weekly glucose or water amendment and analyzed for $\delta^{13}CO_2$ using a Picarro G2101-i CO_2 cavity ring-down isotope spectroscope (Picarro Inc., Sunnyvale, California, USA). Immediately afterwards, jars were opened for approximately 30 min, re-sealed, and two additional gas samples were taken to determine CO_2 concentrations using a LI-COR 6262 CO_2/H_2O gas analyzer (LI-COR Biosciences Inc. Lincoln, NE, USA). One sample was taken at t = 0 (~30 min after closing the jars to allow soil and headspace atmosphere to re-equilibrate) and one approx. 2 h later. We calculated respiration from these measurements.

The use of isotopically labeled glucose allowed us to partition CO_2 released in the amended samples into glucose-derived CO_2 and native SOM-derived CO_2 using a mass balance equation:

$$C_{SOM} = C_{total}\,(\delta_{total} - \delta_{glucose})/(\delta_{SOM} - \delta_{glucose}) \quad (1)$$

where C_{SOM} is the respiration rate (μg C h^{-1} g^{-1} dry weight soil) of native SOM, C_{total} is the measured respiration rate (μg C h^{-1} g^{-1} dry weight soil) from glucose-amended samples, δ_{total} is the $\delta^{13}C$ signature of CO_2 from glucose-amended samples, $\delta_{glucose}$ is the $\delta^{13}C$ signature of the glucose solution (1369‰), and δ_{SOM} is the averaged $\delta^{13}C$ signature from the native SOM measured from the non-amended control samples. Percent priming was then calculated as:

$$\%\ \text{priming} = (\text{SOM-C}_{glucose} - \text{SOM-C}_{non\text{-}amended})/\text{SOM-C}_{non\text{-}amended} * 100 \quad (2)$$

where SOM-$C_{glucose}$ is the CO_2 production rate (μg C h^{-1} g^{-1} dry weight soil) from native SOM in glucose-amended samples and $SOM_{non\text{-}amended}$ is the CO_2 production rate (μg C h^{-1} g^{-1} dry weight soil) from SOM in non-amended control samples. Priming was expressed in terms of percentages to standardize measurements from ecosystems with

different rates of soil respiration. Percent priming from days 2 and 5 were averaged to characterize weekly priming dynamics, and are hereafter referred to as 'priming'.

2.4. Data analyses

To test for differences in total C and N, and extractable C and N between the ecosystems and treatments, we used analysis of variance (ANOVA), with post hoc Student's *t*-tests. A repeated measures ANOVA was used to test for differences in weekly priming rates across the seven-week incubation between the ecosystems and treatments. To test for transplant effects, *t*-tests were conducted within each ecosystem on % priming and total and extractable C and N measured in weeks 1 and 7. Student's *t*-tests were also used to test whether % cumulative priming was different from zero for each ecosystem and treatment. Regression analysis was used to investigate relationships between total and extractable soil C and N, and priming during weeks 1 and 7. All tests were conducted in JMP PRO 11 (SAS Institute Inc., Cary, NC, USA).

To test the relationship between nutrient accumulation and soil priming effects across all ecosystems, we used ordinary least-squares linear regression. Nutrient accumulation (or loss) for each ecosystem type was calculated as the difference in percent C (or percent N) between the transplanted and ambient treatments. Priming effects were calculated as the difference in % cumulative priming between the transplanted and ambient treatments. We used bootstrapping (1000 iterations) to estimate uncertainty in the slope and intercept parameters (Manly 2007). For each bootstrap iteration, we sampled with replacement of $n = 5$ from each ecosystem type and treatment, calculated nutrient accumulation (or loss) and soil priming effects for each iteration, and fit a linear regression model. We then calculated 95% confidence intervals for the resulting vectors of parameter estimates for the slope and intercept. Relationships were considered significant if the 95% confidence intervals of the slopes did not overlap zero.

3. Results

3.1. Effect of warming on soil carbon and nitrogen content

Soil from the four ecosystems contained different amounts of total C and N ($P < 0.0001$ for C and N; Fig. 1A and B), with the highest amount of C and N in the mixed conifer ecosystem and the lowest in ponderosa pine. Transplanting affected soil C and N content in ecosystem dependent ways ($P < 0.0001$ for C and N; Fig. 1), but did not always decrease soil C as predicted. For example, transplanting reduced total soil C and N in the mixed conifer ecosystem, but increased soil C in the grassland (Fig. 1A & B). The amount of extractable C and N was approximately an order of magnitude less than total C and N (Fig. 1C and D). Again, the transplant treatment had ecosystem-dependent effects ($P = 0.0152$ for extractable C; $P < 0.0001$ for extractable N). Transplanting significantly increased extractable C in the grassland ecosystem, but had no effects in the other three ecosystems (Fig. 1C). In contrast, transplanting significantly changed extractable N in all ecosystems, with transplanting increasing extractable N in the mixed conifer, pinyon-juniper and grassland ecosystems and decreasing it in ponderosa pine (Fig. 1D). These variable, ecosystem-dependent effects on soil nutrients in response to transplanting are in agreement with a short-term study (2 years) conducted at these sites that show transplanting (warming) had inconsistent, ecosystem-dependent effects on C-cycling (Wu et al., 2011b), and that the response of an ecosystem to warming is not a simplistic function of temperature, as we had hypothesized.

3.2. Soil organic matter priming

Priming significantly varied throughout the seven-week incubation (Table 2; Week x Ecosystem x Transplant $P < 0.0001$). All soils exhibited a negative priming response (i.e., a decline in SOM decomposition) after the first pulse of glucose (Fig. 2). However, there was a significant interaction between ecosystem and warming in week one ($P = 0.006$), with no effect of transplanting on priming in the mixed conifer, pinyon-juniper and grassland ecosystems, while transplanting made priming more negative in the ponderosa pine ecosystem (Fig. 2).

By week seven, there was no significant effect of transplanting on priming. Ecosystem was the dominant factor in determining priming rates ($P < 0.0001$), with the pinyon-juniper and grassland ecosystems exhibiting the highest priming (22.7% and 17.2%, respectively) while the mixed conifer and ponderosa pine ecosystems had the lowest (6.3% and −22.2%, respectively; Fig. 2).

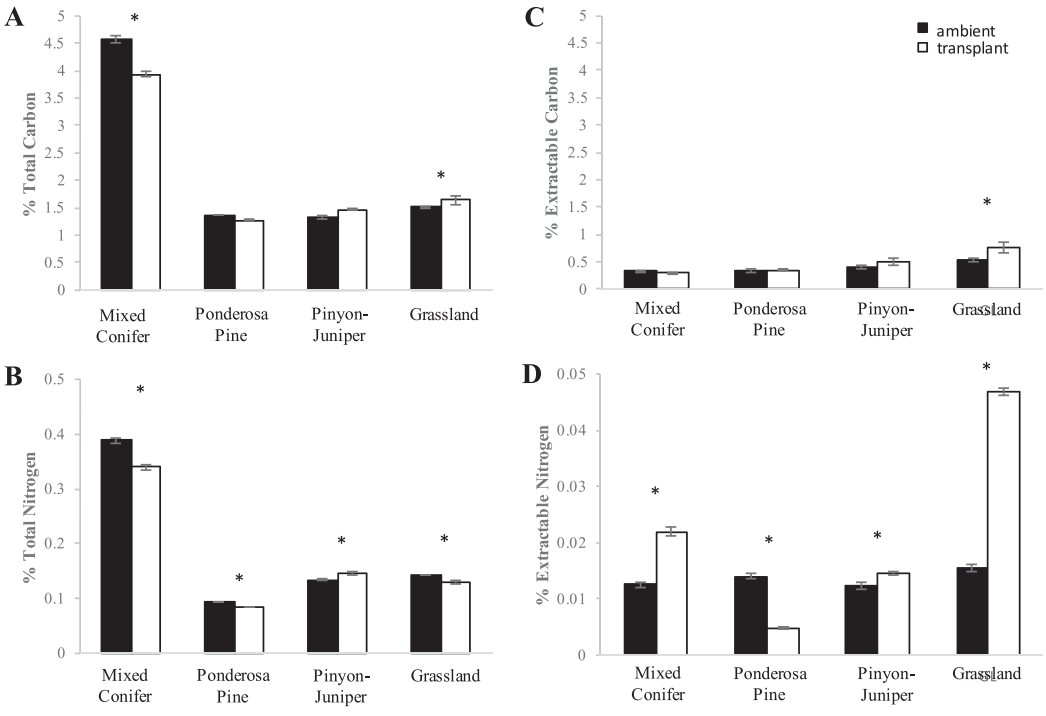

Fig. 1. Total soil carbon (A; $n = 3$) and nitrogen (B; $n = 3$), and K_2SO_4 extractable carbon (C; $n = 5$) and nitrogen (D; $n = 5$) in the ambient (solid bars) and transplanted (open bars) soils (± 1 SE) after nine years. Stars (*) show significant differences between the ambient and transplanted soil (*t*-test; $P < 0.05$). Note that the y-axis scales are different between the carbon and nitrogen graphs, and that the extractable nitrogen y-axis scale is an order of magnitude smaller than the total nitrogen y-axis scale.

Table 2
F ratios of effects of ecosystem, transplanting, and week on priming effects.

Factor	degrees of freedom	*F* ratios
Ecosystem	3	12.2***
Transplant	1	2.5
Ecosystem × Transplant	3	4.33*
Week	6	152.88***
Week × Ecosystem	18	15.05***
Week × Transplant	6	3.78**
Week × Ecosystem × Transplant	18	6.23***

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

When priming was summed over the seven-week incubation (cumulative priming), only one ambient ecosystem (grassland) showed significantly positive priming (13.0%; $P = 0.03$; Fig. 3). There was an interaction between transplanting and ecosystem ($P = 0.013$), where transplanting increased cumulative priming in the pinyon-juniper ecosystem, but had no significant effect in the mixed conifer, ponderosa pine or grassland ecosystems (Fig. 3).

3.3. Relationship between soil carbon and nitrogen content, and soil organic matter priming

There was a significant positive relationship between extractable C measured at the end of the experiment and week 7 % priming. There were no significant relationships between total soil C, total soil N, or extractable N measured in week 1 or 7 and week 1 and week 7 % priming effects, respectively (Table 3). There was, however, a positive relationship between the transplant-induced change in total soil C and change in % cumulative priming (slope = 14.1, bootstrapped 95% CI [4.4, 26.8]; Fig. 4A), and between the transplant-induced change in total soil N and change in % cumulative priming (slope = 314.6, bootstrapped 95% CI [149.5, 553.8]; Fig. 4B). In other words, ecosystems that lost C or N after transplanting showed a decrease in priming compared to the same soil under ambient conditions. There were no significant relationships between changes in extractable C or N and changes in priming (Fig. 4C and D).

4. Discussion

As increasing CO_2 concentrations are raising the global temperature (Hartmann et al., 2013) and increasing C-fixation rates of plants (Curtis and Wang, 1998), it is essential that we better understand how these factors will interact to influence the global C-cycle. Here we show that warming-induced changes in soil C and N concentrations were correlated with altered priming effects in four different ecosystems.

We found a positive relationship between transplant-induced changes in total soil C and N and the change in priming between the ambient and transplanted soils. Ecosystems that lost C and N after nine years of being transplanted to a warmer climate primed less SOM-C over the seven-week incubation than ecosystems that gained C and N, regardless of the amount of total soil C or N in that ecosystem. Newly formed SOM (< 12-years old) has been shown to be more susceptible to priming and is preferentially oxidized compared to older SOM (> 12-years old) (Blagodatskaya et al., 2011a, 2011b; Dijkstra and Cheng, 2007). This result suggests that priming may be a function of the 'decomposability' of SOM, as newly formed SOM would contain relatively more labile compounds than older SOM. Although we did not measure the age of the respired CO_2, our results were consistent with the hypothesis that the quality, or decomposability, of remaining SOM in ecosystems that lost C and N in response to warming may have been reduced, resulting in the observed lower priming rates. Conversely,

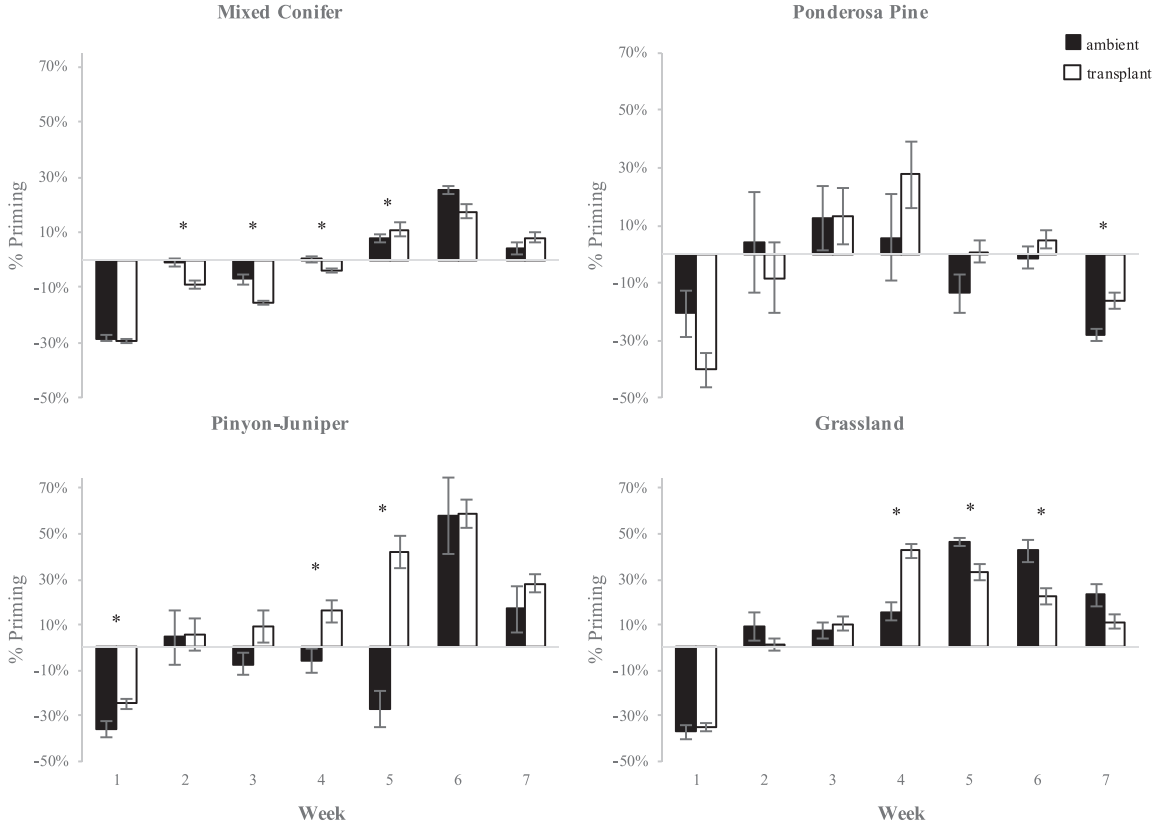

Fig. 2. Weekly % priming ($n = 5$) in the four ecosystems of the ambient (solid bars) and transplanted (open bars) soils (± 1 SE). Percent priming was calculated as the difference in soil organic matter C respiration rates in the glucose amended treatment and non-amended control divided by the respiration rate of the non-amended control (% priming = (SOM-$C_{glucose}$ − SOM-$C_{non\text{-}amended}$)/SOM-$C_{non\text{-}amended}$ * 100). Stars (*) represent significant differences ($P < 0.05$) between the ambient and transplanted treatment.

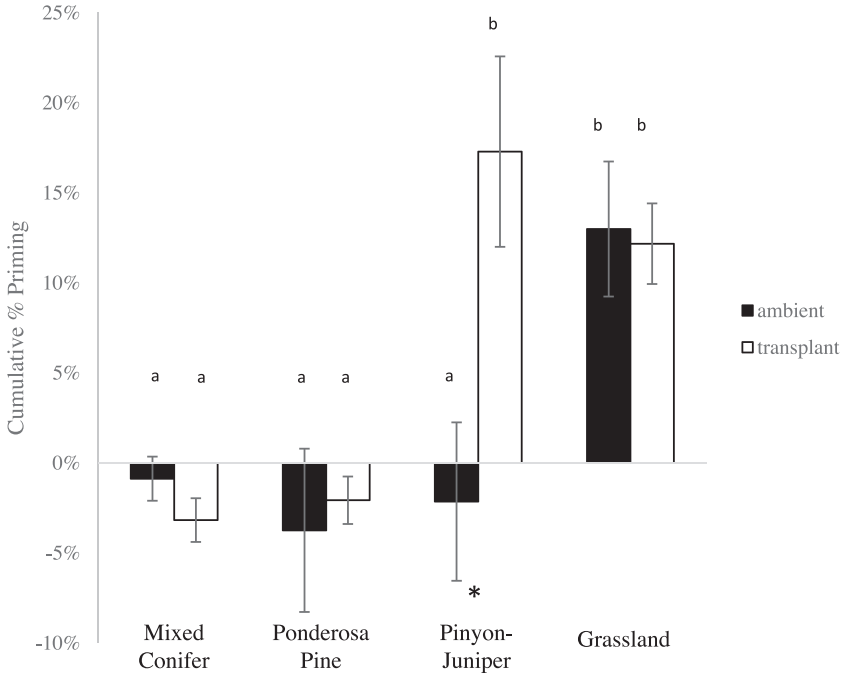

Fig. 3. Cumulative % priming (n = 5) over the seven-week incubation in four ecosystems of ambient (solid bars) and transplanted (open bars) soils (± 1 SE). Letters show significant differences between the soil and transplant treatments (ANOVA; $P < 0.05$), and stars (*) represent significant differences between the ambient and transplanted soil within an ecosystem (t-test; $P < 0.05$).

Table 3
Slopes and coefficients of determination (R^2) of the relationships between total and extractable C and N measured in week 1 and 7, and % priming measured in week 1 and 7.

Factor	week 1			week 7		
	slope	R^2	P-value	slope	R^2	P-value
Total C	0.01	0.06	0.24	0.009	0.003	0.76
Total N	0.14	0.06	0.26	0.39	0.04	0.26
Extractable C	−0.08	0.05	0.18	5.27	0.12	**0.03**
Extractable N	−0.17	0.001	0.84	−13.56	0.01	0.59

ecosystems that gained C and N may have contained more labile SOM compounds that were more vulnerable to decomposition, resulting in higher priming rates.

Though there were no significant correlations between total soil C or N and priming, or extractable N and priming in weeks 1 or 7, there was a positive relationship between extractable C and priming in week 7. As priming is defined as a change in SOM decomposition in response to a fresh substrate amendment, this positive correlation between priming and extractable C makes sense. Many studies show that extracellular enzyme activities increase during positive priming (Blagodatskaya and Kuzyakov, 2008; Zhu et al., 2014), thus facilitating the breakdown of complex organic molecules that make up SOM and increasing the pool of available C and N for microbial uptake.

Microbial mining for N is a commonly proposed mechanism to explain the strength of priming responses (Kuzyakov, 2010; Murphy et al., 2015; Zhu et al., 2014). It is thought that when fresh C is added to the soil, microbial demand for other nutrients (e.g., N) increases, stimulating the breakdown of recalcitrant SOM in order to liberate those nutrients (e.g., N). In this experiment, we hypothesized that priming would negatively correlate with soil N concentrations; however, there were no relationships between total soil N or extractable N concentrations and priming in the different ecosystems. We did find a positive relationship between the change in total soil N in response to transplanting and change in cumulative priming within an ecosystem, indicating that ecosystems that gained soil N primed more SOM. These patterns suggest that N plays a role in governing the strength of priming effects, but may be less important than other ecosystem properties, such as plant community composition (Carrillo et al., 2017), and the size and/or composition of the microbial community (Eilers et al., 2010; Garcia-Pausas and Paterson, 2011; Liu et al., 2017).

All soils showed a significant negative priming response after the first pulse of glucose, indicating that less native SOM was decomposed in the presence of glucose than in the non-amended control soil. Kuzyakov and Bol (2006) also found an initial negative priming response shortly after sugar addition (2–3 days), but the priming rate increased after longer incubation, leading them to propose priming as a chain of mechanisms based on the “utilizability” of available substrates. Even though soils contain vast amounts of C, microbes are thought to be C-limited (Alden et al., 2001; Fontaine et al., 2007) because of mineral protection and the recalcitrant nature of this C (Mikutta et al., 2006). Therefore, it is not surprising that SOM decomposition rates decreased in the presence of a labile C source as it is often energetically costly to break down these complex organic molecules. Mau et al. (2015) found a similar negative priming response using soil from the ponderosa pine site; however, other studies adding a similar amount of C report positive priming responses immediately after a labile C amendment (Eilers et al., 2010; Garcia-Pausas and Paterson, 2011). Some explanations for this difference could be that the time between amendment addition and priming measurements varies among the studies, or that the method used to measure CO_2 was not identical in all investigations. For example, Eilers et al. (2010) measured CO_2 accumulation at six times during a 24 h incubation, while Garcia-Pausas and Paterson (2011) measured CO_2 respiration rates six times over a nine-day incubation. In contrast, we focused on longer-term dynamics rather than the very short-term effects of the glucose amendment, measuring respiration rates twice over a seven-day period for seven weeks.

5. Conclusions

Global CO_2 concentrations and temperatures are increasing, which are altering plant growth dynamics and C inputs to soil. We need to better understand the interactive effects of these factors in order to accurately predict future C pools and fluxes. The potential for oxidizing SOM through priming is now recognized to be widespread and quantitatively important (Heimann and Reichstein, 2008), though the magnitude of priming is variable in response to repeated pulses of substrate, and remains difficult to predict. More long-term, repeated or continuous substrate input studies are needed to better understand the

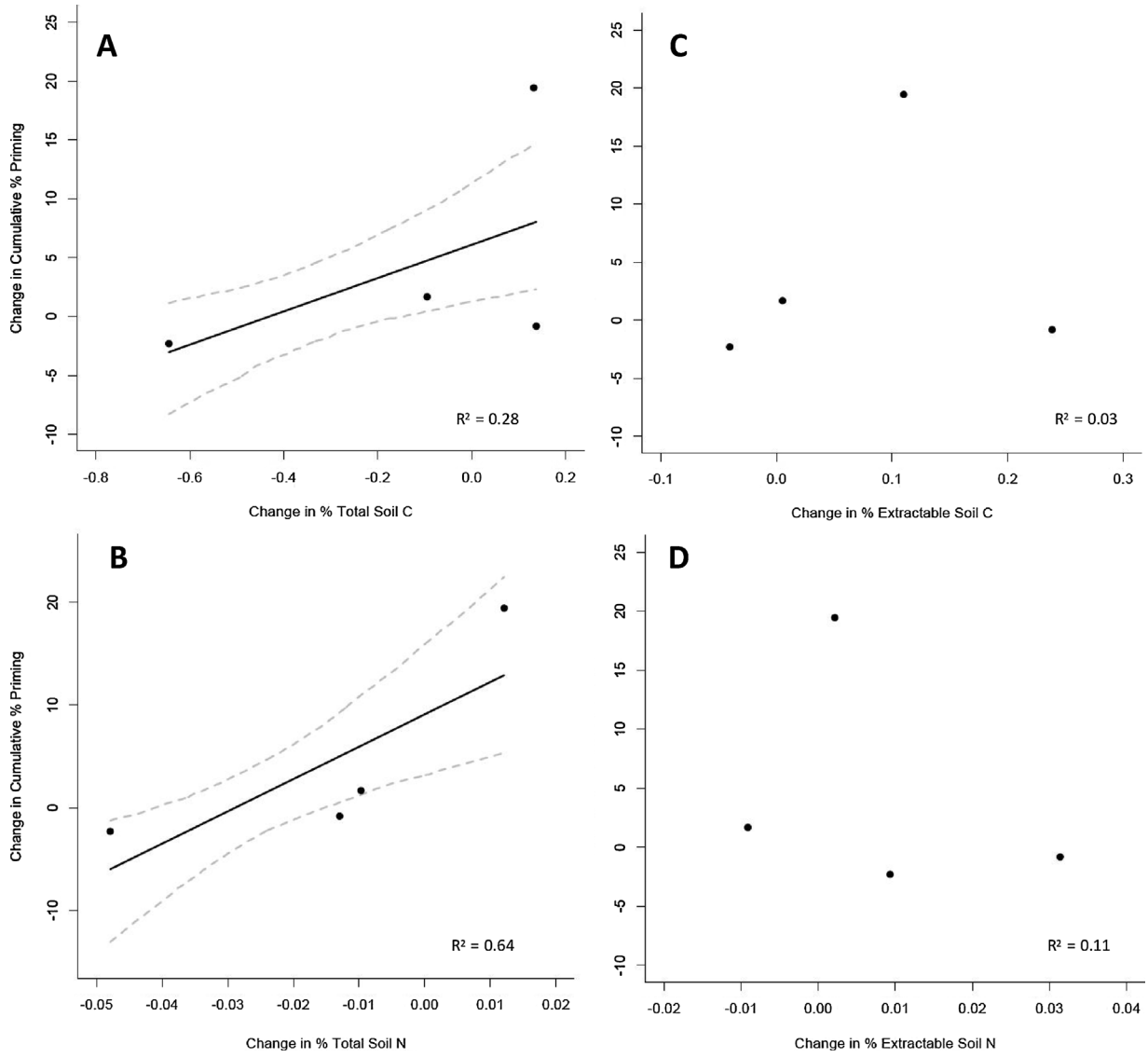

Fig. 4. Relationships between the difference in cumulative % priming between the transplanted and ambient ecosystems and the difference in % total soil C (A; slope = 14.1, bootstrapped 95% CI [4.4, 26.8]), % total soil N (B; slope = 314.6, bootstrapped 95% CI [149.5, 553.8]), % extractable C (C; slope = 13.9, bootstrapped 95% CI [−32.5, 103.5]), and % extractable N (D; slope = −191.6, bootstrapped 95% CI [−467.3, 78.0]) between the transplanted and ambient soils. Points show the mean differences after 1000 bootstrap iterations, and striped grey lines represent the bootstrapped 95% CIs of the slopes that did not overlap zero.

mechanisms driving these responses. Here we show that priming is variable in time and space in response to repeated pulses of a labile carbon substrate, and that long-term warming significantly altered priming in only one of the four ecosystems studied. We also demonstrate that changes in soil nutrient pools were correlated with altered priming effects, suggesting a potential buffering mechanism whereby warming induced SOM losses reduce priming and attenuate further C loss. In contrast, warming-induced increases in soil C and N enhance priming thus reducing potential C sequestration. These results are in agreement with a *meta*-analysis that found warming-induced increases in primary production were offset by increases in soil C-cycling (Lu et al., 2013), and suggest that one contributing mechanism to this offsetting may be buffering caused by changes in priming that are sensitive to changes in C stocks.

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