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Decreased carbon limitation of litter respiration in a mortality-affected piñon-juniper woodland

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Abstract

Microbial respiration depends on microclimatic variables and carbon (C) substrate availability, all of which are altered when ecosystems experience major disturbance. Widespread tree mortality, currently affecting piñon-juniper ecosystems in Southwestern North America, may affect C substrate availability in several ways; for example, via litterfall pulses and loss of root exudation. To determine piñon mortality effects on C and water limitation of microbial respiration, we applied field amendments (sucrose and water) to two piñon-juniper sites in central New Mexico, USA: one with a recent (< 1 yr), experimentally-induced mortality event and a nearby site with live canopy. We monitored the respiration response to water and sucrose applications to the litter surface and to the underlying mineral soil surface, testing the following hypotheses: (1) soil respiration in a piñon-juniper woodland is water- and labile C-limited in both the litter layer and mineral soil; (2) water and sucrose applications increase temperature sensitivity of respiration; (3) the mortality-affected site will show a reduction in C limitation in the litter; (4) the mortality-affected site will show an enhancement of C limitation in the mineral soil. Litter respiration at both sites responded to increased water availability, yet surprisingly, mineral soil respiration was not limited by water. Temperature sensitivity was enhanced by some of the sucrose and water treatments. Consistent with hypothesis 3, C limitation of litter respiration was lower at the recent mortality site compared to the intact canopy site. Results following applications to the mineral soil suggest the presence of abiotic effects of increasing water availability, precluding our ability to measure labile C limitation in soil. Widespread piñon mortality may decrease labile C limitation of litter respiration, at least during the first growing season following mortality.

1 Introduction

Arid and semi-arid ecosystem processes are dynamic over time, pulsing in response to rainfall events (Reynolds et al., 2004; Schwinning and Sala, 2004). Rain stimulates net ecosystem carbon dioxide (CO_2) exchange by affecting leaf-level gas exchange, ecosystem and soil respiration (Sala and Lauenroth, 1982; Potts et al., 2006; Jenerette et al., 2008). The response of soil respiration to small (< 5 mm) rain events is fueled by heterotrophs utilizing soil organic carbon (C) and thus could be an important mechanism for net C loss (Huxman et al., 2004; Carbone et al., 2011). Predicting future climate effects on soil C requires a better understanding of controls over, or limitations to, arid and semi-arid respiration.

Fundamentally, heterotrophic C mineralization is controlled by temperature, moisture, and substrate supply (Witkamp, 1966; Parton et al., 1994; Schimel and Weintraub, 2003). Temperature plays a minor role in very dry conditions and is more important at higher moisture levels (Conant et al., 2004; Curiel Yuste et al., 2007; Carbone et al., 2011). Increases in soil moisture enhance substrate availability for microorganisms, thus increasing respiration rates and enhancing temperature sensitivity of respiration (Davidson and Janssens, 2006; Borken and Matzner, 2009). Quality of substrate is important; labile C compounds, such as sugars, yield higher respiration rates than lower quality substrate, such as recalcitrant soil organic matter (Bosatta and Ågren, 1999). Thus, greatest respiration rates might occur under high temperatures, high moisture and high labile C supply. However, limitation to respiration has yet to be quantified for all these factors simultaneously in a semi-arid system.

The heterotrophic response to a rain pulse in dry systems consists of a large initial response that declines over time (Birch, 1958) and is referred to as a “Birch effect”. The decline of respiration following a post-rainfall pulse is often attributed to water limitation coincident with rapid surface drying (Cable and Huxman, 2004; Huxman et al., 2004). However, what appears to be a drying effect could instead result from rapid consumption and depletion of labile substrate. Previous research in a semi-arid shrubland soil suggests that labile C depletion occurs within two to three days of wetting (Saetre and Stark, 2005). This theory of labile substrate depletion could explain the finding that Sonoran desert soil respiration demonstrated a threshold response to artificial rain event size (Sponseller, 2007). Thus, the size of the Birch effect could depend on limitation by labile C availability in addition to water limitation.

The widespread piñon mortality that has occurred in the US southwest (Breshears et al., 2005) has likely altered key factors that regulate the Birch effect. Increases in soil temperature and drying of the litter surface may result from increased solar radiation penetration following canopy loss. Counteracting these effects, the loss of transpiring roots may increase water stored in soil. The fall of dead piñon needles would increase C supply in the litter; C supply to the rhizosphere would decline with the loss of live, exuding roots. The net effect of these changes on the Birch effect is difficult to predict without understanding limiting factors to respiration rates in semi-arid systems. We used field manipulations to assess water and labile C limitation of respiration in a piñon-girdling experiment in central New Mexico. To establish the repeatability of our approach, we first conducted two experiments in an intact piñon-juniper woodland. We then conducted a third set of experiments which compared the intact site to a site that experienced a mass piñon mortality event. Our main hypotheses were that:

1. soil respiration in a piñon-juniper woodland is water- and labile C-limited in both the litter layer and mineral soil,
2. water and sucrose applications increase temperature sensitivity of respiration,
3. the mortality-affected site will show a reduction in C limitation in the litter,
4. the mortality-affected site will show an enhancement of C limitation in the mineral soil.

2 Materials and methods

2.1 Site description

Our study site was located in a piñon-juniper woodland in central New Mexico, USA on an extended mesa at an elevation of 2100 m a.s.l. (Chupadera Mesa, 34.3585° N, −106.266° W). The climate is characterized by mild winters and hot, dry summers with sporadic heavy rains during the monsoon season, typically July through September. The woodland was comprised of two tree species, *Pinus edulis* and *Juniperus monosperma*, with a sparse understory of C_3 (*Oryzopsis hymenoides*) and C_4 grasses (*Bouteloua gracilis* (H.B.K.) Lag.). The soil is a lithic mollic calciorthid (Piñon Channery Loam, Soil Survey Staff, NRCS); soil pH ranged from 7.3 to 7.7 (D. Warnock, personal communication, 2012). Both sites were flat (∼ 0 % slope) and experienced similar weather conditions throughout the experiment. One site remained unaltered (Reference) and the other site (Girdled) experienced a girdling treatment to induce piñon mortality. In September 2009 during a four-day period at the Girdled site, all piñon trees above 7 cm diameter at breast height (dbh) within a 4-ha area were girdled using chainsaws and the cuts were sprayed with herbicide (glyphosate) to ensure mortality. Mortality of treated trees was confirmed in spring 2010. Based on allometric relationships, litterfall from girdled trees was equivalent to $0.22\,\mathrm{kg\,C\,m^{-2}}$. Replication of the girdling treatment was sacrificed so that a spatial scale large enough for the goals of the broader study could be achieved. Thus, site differences are specific to the girdling treatment applied and should not be extrapolated to generalize mortality effects in piñon-juniper ecosystems. To establish repeatability of our methods, we conducted two experiments in the Reference site starting 7 July ("Experiment 1") and 10 August ("Experiment 2") 2010. We conducted a comparison of the Girdled and Reference site limitations in a simultaneous dual-site experiment beginning 16 August 2010 ("Girdled-Reference comparison experiment").

2.2 Soil and litter properties

To compare soil C : N between the Girdled and Reference site, on 16 August 2010, soil and surface litter samples were collected from each site for analysis of organic C, inorganic C and nitrogen (N) content. Mineral soil cores (0–10 cm) and overlying litter were collected from five replicate locations underneath piñon canopies, sieved to remove coarse roots and rocks (2 mm) and dried at 60 °C. Samples were homogenized in a ball mill before being analyzed for total C and N content on an elemental analyzer at the EcoCore Laboratory at Colorado State University (TruSpec, LECO Corp., St. Joseph, MO). Total C was adjusted to organic C by subtracting inorganic C content (as $CaCO_3$), which was determined on subsamples by treating them with 6 N HCl in closed vials and monitoring the pressure of the headspace gas resulting from CO_2 generation (Sherrod et al., 2002).

Gravimetric moisture was determined by mass loss after oven drying (60 °C) for litter samples collected from both sites 16 and 25 August 2010, representing the start and end dates of the Girdled-Reference comparison experiment. Volumetric soil moisture content was monitored throughout the experimental period using CS616 sensors (Campbell Scientific, Logan, UT) placed at three depths (5 cm, 10 cm, and 30 cm below the mineral soil surface) underneath three different piñon canopies at each site.

2.3 Experimental treatments

We assessed water and labile C limitation of respiration at both sites by monitoring the response of respiration to water and sucrose solutions. Fifteen individual experimental areas (each 491 cm^2) were selected for proximity to piñon trees (30 cm from the stem) and presence of a piñon needle litter layer. Over twelve of the experimental areas, we applied treatment solutions evenly using a syringe and needle; three areas were retained as untreated controls (“untreated”). Treatments were applied to either the top of the surface litter or to the top of the mineral soil underneath the litter. After mineral soil applications, the litter layer was replaced. Four treatments were applied. Three areas received a pure distilled water application of 1222 ml m^{-2} (1.2 mm) to the litter surface ("litter water" treatment). Three areas received the same amount of distilled water to the mineral soil surface ("soil water" treatment), taking care to minimize disturbance to the litter when removing it or replacing it after treatment. Three areas received 1222 ml m^{-2} of a sucrose-distilled water solution (0.463 mol sucrose l^{-1}, commercial grade) applied to the litter surface ("litter sucrose" treatment), and three areas received 1222 ml m^{-2} of the sucrose solution to the mineral soil surface in the same fashion as the pure distilled water treatment ("soil sucrose" treatment). Sucrose applications were equivalent to 6.8 mol C m^{-2}. At a "typical" microbial respiration rate of 2 µmol C m^{-2} s^{-1}, this would have represented nearly 40 days' worth of substrate.

2.4 Respiration response

We monitored the response of respiration for five days following treatment application. Immediately after application, each treated area was covered with a PVC chamber connected to an Automated C Efflux System (ACES) (Butnor et al., 2003). The respiration system sequentially measured CO_2 concentration and flow rates to and from a series of 16 chambers each covering a surface area of 491 cm^2 (including one null chamber) and calculated respiration rates using an open-system approach. Chambers were covered in reflective insulation (Reflectix, Inc. Markleville, IN) to prevent heating. The system switched chambers once every ten minutes, completing one cycle every 160 min. When chambers were not being sampled, ambient air was circulated through the chambers at a rate of 1.5 l min^{-1} to minimize buildup of chamber [CO_2] and prevent disruption of the ambient soil-air [CO_2] gradient.

Thermocouples (Omega Engineering, Omaha, NE) in each chamber measured soil temperature at 5 cm and chamber air temperature at 5 cm above the surface. The treatments were timed to occur 20 min before each chamber was sampled for the first time. Similarly, "untreated" chambers were inserted over an untreated area 20 min prior to the first chamber measurement.

2.5 C and water limitation calculations

To calculate labile C and water limitation, we used an approach analogous to that used to determine the stomatal limitation of photosynthesis (Farquhar and Sharkey, 1982), which is calculated from the difference between ambient assimilation and assimilation at maximum CO_2 availability inside the leaf in the absence of stomatal restriction. We experimentally maximized water availability by adding enough water to thoroughly wet the surface without saturating the pores completely (which would restrict gas diffusion, an undesired effect). We maximized substrate availability by adding enough sucrose in a water solution to cause an immediate increase in respiration rate, determined by preliminary trials. We determined water limitation by comparing the respiration response from the water treatments to the background respiration. We determined C limitation by comparing the respiration response from the sucrose treatments to the response from the water-treatments because the same amount of water was also added in the sucrose treatment. Limitations were calculated for C and water in both the litter and mineral soil. Reduction of respiration due to water limitations in the litter (l_{LitterW}) was calculated for each chamber using:

$$l_{\mathrm{LitterW}} = \frac{(R_{\mathrm{LitterW}} - R_{\mathrm{U}})}{R_{\mathrm{LitterW}}} \tag{1}$$

where R_{LitterW} is the mean instantaneous respiration of the three litter water-treated chambers and R_{U} is the mean instantaneous respiration of the three untreated chambers. Reduction of respiration due to water limitation in the mineral soil (l_{SoilW}) was calculated similarly:

$$l_{\mathrm{SoilW}} = \frac{(R_{\mathrm{SoilW}} - R_{\mathrm{U}})}{R_{\mathrm{SoilW}}} \tag{2}$$

Reduction of respiration due to labile C limitation in the litter (l_{LitterC}) was calculated using:

$$l_{\mathrm{LitterC}} = \frac{(R_{\mathrm{LitterC}} - R_{\mathrm{LitterW}})}{R_{\mathrm{LitterC}}} \tag{3}$$

and labile C limitation in the mineral soil (l_{SoilC}) was calculated similarly:

$$l_{\mathrm{SoilC}} = \frac{(R_{\mathrm{SoilC}} - R_{\mathrm{SoilW}})}{R_{\mathrm{SoilC}}} \tag{4}$$

Note that the limitation factors so calculated would, at least theoretically, range between zero and one. We calculated limitations for two different time scales following application. First, we used the instantaneous flux rates from the Reference site only to obtain a time series of limitation factors for the duration of both experiments using synchronous respiration rates among treatments. Then, from these time series we determined an appropriate time window since application to calculate cumulative limitations, which were used to compare the Girdled site to the Reference site. Cumulative limitations were calculated from cumulative sums of respiration rates using linear interpolation between measurement time points.

2.6 Statistical analyses

We investigated differences among treatment effects using non-linear mixed-effects modeling. Initial assessment revealed that respiration decayed over time following treatment and also fluctuated consistently with diel variation in soil and air temperature. Thus, we fit our data to an exponential decay model (Eq. 5) that also included a temperature sensitivity parameter. Because respiration often increases exponentially with temperature (Lloyd and Taylor, 1994), we first included an exponential temperature function along with the decay function:

$$R = R_{\max} \exp(-kt) + \exp(\alpha T_{\mathrm{soil}}) + \beta \tag{5}$$

R is the respiration rate for each treatment and time step (μmol C m^{-2} s^{-1}), R_{max} is a fitted parameter representing the maximum respiration response to the treatment, k is a fitted parameter representing the decay of respiration over time, t is time following treatment application (days), α is a fitted parameter representing temperature sensitivity, T_{soil} is soil temperature at 5 cm (mineral soil and untreated) or chamber air temperature (litter), and β is an intercept which was allowed to vary randomly for each chamber. If model parameterization failed due to lack of convergence, we re-fit the data using a linear temperature function as shown in Eq. (6).

$$R = R_{max} \exp(-kt) + \alpha T_{soil} + \beta \tag{6}$$

We used PROC NLMIXED in SAS® to fit the fixed and random parameters for each treatment, analyzing data from each experiment date separately. Significant treatment effects were determined by fitting parameters defined as differences among treatments and testing their equivalence to zero. Water-treated respiration parameters were compared to the untreated respiration parameters. To detect if sucrose had an effect beyond that of water, parameters from the sucrose treatment were compared to the water treatment.

To determine the relative degree of C or water limitation, we determined if l for each location and treatment was significantly greater than zero using a t-test. We determined differences in C : N, percent N, and limitation factors between sites for each location (litter or mineral soil) and each limiting factor (C or water) using a t-test if normality and homoscedasticity assumptions were met; otherwise, the Mann–Whitney rank sum test was used. t-tests were conducted using R (R Development Core Team 2011); repeated-measures ANOVAs, multiple comparisons and nonlinear modeling were conducted using SAS® after confirming that data met assumptions of these tests. Unless otherwise indicated, $\alpha = 0.05$.

3 Results

Consistent with our hypotheses, respiration responded to both water and sucrose additions and results were similar for the repeated experiments conducted at the Reference site (Table 1; Fig. 1). Treating the litter yielded a stronger immediate respiration response than treating the mineral soil (Table 1; Fig. 1).

Nonlinear model parameters revealed treatment effects on the Birch effect and temperature sensitivity of respiration. Respiration rates were affected by temperature as indicated by the significant linear temperature coefficients (α; Eq. 6). Some sucrose and water treatments increased temperature sensitivity (Table 1). Comparing the respiration decay constants (k) among the treatments revealed two key findings. First, the reduced k in the sucrose applications compared to the water applications helped sustain a detectable sucrose effect over that of water (Fig. 1). Thus, labile C limitation peaked later than water limitation (Figs. 2 and 3). Second, the low k following treatments to the mineral soil indicated that the Birch effect was elevated over a longer time period compared to the litter treatment response.

As expected, temperature and moisture differed between the site with girdled piñons (Girdled site) and the undisturbed Reference site. Chamber temperatures were 1.6 °C warmer at the Girdled site than the Reference site in the soil (5 cm; $P < 0.0001$) and 2.7 °C warmer in the chamber air ($P < 0.0001$; Fig. 4). Litter moisture was greater at the Reference site than at the Girdled site on the day the treatments were applied (Table 2; $P = 0.006$). After the experiment ended, there was no difference in litter moisture between the two sites ($P = 0.25$). Soil moisture sensors showed declining water content over the course of the experiment; soil water content was similar between the two sites at 10 cm and 30 cm depth but soil at 5 cm was drier at the Reference Site, indicating increased soil water storage at the Girdled site ($n = 3$ per depth, Fig. 5). Neither C : N nor percent N varied among the two sites in surface soil ($P = 0.62$ and $P = 0.59$) and litter ($P = 0.70$ and $P = 0.18$) collected 16 August 2010 (Table 2).

Water and sucrose treatments to the litter affected respiration at the Girdled site differently than the Reference site (Fig. 6). The initial response (R_{max}) to sucrose was higher at the Reference site than the Girdled site, whereas responses to water applications were more similar (Table 1). Respiration pulses decayed faster at the Girdled site compared to the Reference site; this was true for both water and sucrose applications to the litter (Table 1).

Limitations calculated from the first 24 h of respiration data were used to compare the Reference site to the Girdled site (Fig. 7). Girdled site water limitation of litter respiration was not different from the Reference site ($P = 0.68$). In contrast, C limitation of litter respiration was higher at the Reference site than at the Girdled site ($P = 0.03$). Contrary to our hypotheses, respiration was not limited by water in the mineral soil ($P = 0.48$ at reference site and $P = 0.19$ at Girdled site). Respiration was limited by C in the mineral soil at the Girdled site ($P = 0.02$) but not at the Reference site ($P = 0.37$); the sites were not significantly different from each other ($P = 0.98$).

4 Discussion

The response of respiration to water and sucrose additions indicates that the Birch effect in this semi-arid woodland is limited by labile C availability after a small wetting event. Labile C limitation has been detected previously in mesic forests and deserts (Ekblad and Nordgren, 2002; Schaeffer et al., 2003; Ziegler and Billings, 2011); we provide the first evidence from a semi-arid ecosystem, challenging the notion that semi-arid systems are simply water-limited. Water additions stimulated respiration, yet respiration from sucrose-treated litter was higher than respiration from water-treated litter even while litter was presumably drying. Furthermore, labile C limitation peaked about one day later than water limitation. We conclude that the decline in respiration following litter wetting could have been partially due to labile C depletion. This idea is supported by previous evidence of labile C depletion in semi-arid soils post-wetting (Saetre and Stark, 2005).

Our results suggest that a piñon mortality event reduces limitation of respiration to labile C. Labile C availability in the litter layer may have increased as a result of the influx of dead needles, reducing the dependence of respiration on labile C. Or, decreased litter moisture driven by the loss of overstory could have increased the dependence of respiration on water inputs, thus reducing the response to labile C.

Supporting the latter argument, we found evidence that wetted litter dried faster at the Girdled site. Both water and sucrose applications to the litter yielded a respiration pulse that declined faster at the Girdled site than at the Reference site. Rapid decay at the Girdled site may have resulted from faster drying of the litter layer. Faster drying may have resulted from a more open canopy at the Girdled site and higher solar radiative flux warming the air in contact with the litter layer, thus increasing the litter-air vapor pressure gradient and drying the litter faster. Reduced litter moisture at the Girdled site at the start of the experiment is another line of evidence supporting this theory. However, water limitation for the first 24 h following application was no different between the two sites, suggesting that faster drying was compensated for by the higher initial response ($R_{\max}$) of respiration to water at the Girdled site (Table 1). The dynamic response of respiration to these treatments emphasizes the importance of time scales when calculating respiratory limitations from instantaneous rate measurements.

Nitrogen (N) availability is another variable potentially affecting our assessment of labile C limitations. Lower C : N of substrate can reduce microbial competition for available N and can enhance mineralization of labile C (Ziegler and Billings, 2011). Previous research has found reduced C : N of litter from trees killed by bark beetles (Morehouse et al., 2008; Griffin et al., 2011). Contrary to these findings, litter layer C : N was no different between the Girdled and Reference sites. Opening of the Girdled site canopy following needle drop may have increased abiotic gaseous N loss from the litter surface (McCalley and Sparks, 2009), counteracting a reduction in Girdled site litterfall C : N. We cannot conclude that differences in N availability explain the differences in labile C limitation between the two sites; post-mortality N limitation should be further examined.

Respiration was less responsive to applications to the mineral soil compared to applications to the litter. This was unexpected due to the dry conditions at the time of water application. Although we minimized physical deplacement of CO_2 by using a small water amount, another abiotic process may have been important following the mineral soil applications: soil carbonate dissolution and precipitation. Over short time scales, dissolution and precipitation of calcium carbonate depends on the activity of carbonic acid formed when CO_2 dissolves in water, as might occur in basic soils with high levels of biological CO_2 generation. The overall reactions can be summarized as (Plummer and Busenberg, 1982):

$$H_2O_{(aq)} + CO_{2\,(g)} + CaCO_{3\,(s)} \Leftrightarrow 2HCO^{-}_{3\,(aq)} + Ca^{2+}_{(aq)} \tag{7}$$

According to Eq. (7), carbonate dissolution is a sink for CO_2 and precipitation is a source for CO_2. Thus, soil respiration may be reduced after water additions if carbonate were dissolved. Upon soil drying, $CaCO_3$ would re-precipitate, increasing soil CO_2 evolution. These mechanisms could explain why applications to the mineral soil generated a damped soil respiration pattern in contrast to the distinct exponential response seen after the treatments to the litter layer. Calculation of limitation factors over a longer time period, including both wet and dry periods, could correct for this. Research has suggested that abiotic fluxes of CO_2 can be as large as biological fluxes in areas with carbonate bedrock (Serrano-Ortiz et al., 2010); this mechanism should be considered during interpretation of instantaneous respiration rates in arid- and semi-arid calcareous soils.

In addition to moisture and labile C, temperature was also important for respiration. The effect of temperature increased for some of the sucrose treatments, suggesting an interaction effect among temperature, moisture and labile C supply on soil respiration. Our results support the theory that temperature sensitivity is enhanced at high levels of both soil moisture and substrate availability (Davidson and Janssens, 2006). Our findings also suggest that a temperature-moisture interaction effect might be most apparent at high labile C, pointing to a possible mechanism for temperature and moisture interaction effects on soil respiration measured in the field (Suseela et al., 2011).

5 Conclusions

In this piñon-juniper ecosystem, the response of CO_2 efflux to future climate change will depend on changes in surface moisture, temperature and labile C availability. We propose that the Birch effect is maximized by high temperature and unlimited access to labile C and moisture, but that low levels of any variable would minimize the Birch effect. By girdling trees, we induced a disturbance that altered all three of these variables and found that a reduction in labile C limitation was the net result of these changes. Mass tree mortality events are currently affecting forests on a global scale and could increase in size and frequency with global warming (Mitton and Ferrenberg, 2012). The response of regional C cycling to such events could ultimately depend on labile C limitation.

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References

Birch, H. F.: The effect of soil drying on humus decomposition and nitrogen availability, Plant Soil, 10, 9–31, 1958. 14477

Borken, W. and Matzner, E.: Reappraisal of drying and wetting effects on C and N mineralization and fluxes in soils, Glob. Change Biol., 15, 808–824, 2009. 14477

Bosatta, E. and Ågren, G.: Soil organic matter quality interpreted thermodynamically, Soil Biol. Biochem., 31, 1889–1891, 1999. 14477

Butnor, J., Johnsen, K., Oren, R., and Katul, G.: Reduction of forest floor respiration by fertilization on both carbon dioxide-enriched and reference 17-year-old loblolly pine stands, Glob. Change Biol., 9, 849–861, 2003. 14481

Cable, J. and Huxman, T.: Precipitation pulse size effects on Sonoran Desert soil microbial crusts, Oecologia, 141, 317–324, 2004. 14477

Carbone, M., Still, C., Ambrose, A., Dawson, T., Williams, A., Boot, C., Schaeffer, S., and Schimel, J.: Seasonal and episodic moisture controls on plant and microbial contributions to soil respiration, Oecologia, 167, 265–278, 2011. 14477

Conant, R., Dalla-Betta, P., Klopatek, C., and Klopatek, J.: Controls on soil respiration in semi-arid soils, Soil Biol. Biochem., 36, 945–951, 2004. 14477

Curiel Yuste, J., Baldocchi, D., Gershenson, A., Goldstein, A., Misson, L., and Wong, S.: Microbial soil respiration and its dependency on carbon inputs, soil temperature and moisture, Glob. Change Biol., 13, 2018–2035, 2007. 14477

Davidson, E. and Janssens, I.: Temperature sensitivity of soil carbon decomposition and feedbacks to climate change, Nature, 440, 165–173, 2006. 14477, 14488

Ekblad, A. and Nordgren, A.: Is growth of soil microorganisms in boreal forests limited by carbon or nitrogen availability?, Plant Soil, 242, 115–122, 2002. 14486

Farquhar, G. and Sharkey, T.: Stomatal conductance and photosynthesis, Ann. Rev. Plant Physio., 33, 317–345, 1982. 14482

Griffin, J. M., Turner, M. G., and Simard, M.: Nitrogen cycling following mountain pine beetle disturbance in lodgepole pine forests of Greater Yellowstone, Forest Ecol. Manag., 261, 1077–1089, 2011. 14487

Huxman, T., Snyder, K., Tissue, D., Leffler, A., Ogle, K., Pockman, W., Sandquist, D., Potts, D., and Schwinning, S.: Precipitation pulses and carbon fluxes in semiarid and arid ecosystems, Oecologia, 141, 254–268, 2004. 14477

Jenerette, G. D., Scott, R. L., and Huxman, T. E.: Whole ecosystem metabolic pulses following precipitation events, Funct. Ecol., 22, 924–930, 2008. 14477

Lloyd, J. and Taylor, J.: On the temperature dependence of soil respiration, Funct. Ecol., 8, 315–323, 1994. 14483

McCalley, C. K. and Sparks, J. P.: Abiotic gas formation drives nitrogen loss from a desert ecosystem, Science, 326, 837–840, 2009. 14487

Mitton, J. B. and Ferrenberg, S. M.: Mountain pine beetle develops an unprecedented summer generation in response to climate warming, Am. Nat., 179, 163–171, 2012. 14489

Morehouse, K., Johns, T., Kaye, J., and Kaye, M.: Carbon and nitrogen cycling immediately following bark beetle outbreaks in southwestern ponderosa pine forests, Forest Ecol. Manag., 255, 2698–2708, 2008. 14487

Parton, W. J., Ojima, D., Cole, C., and Schimel, D.: A General Model for Soil Organic Matter Dynamics: Sensitivity to Litter Chemistry, Texture and Management, Soil Science Society of America, Madison, WI, 147–167, 1994. 14477

Plummer, L. and Busenberg, E.: The solubilities of calcite, aragonite and vaterite in CO_2-H_2O solutions between 0 and 90 °C, and an evaluation of the aqueous model for the system $CaCO_3-CO_2-H_2O$, Geochim. Cosmochim. Ac., 46, 1011–1040, 1982. 14488

Potts, D. L., Huxman, T. E., Cable, J. M., English, N. B., Ignace, D. D., Eilts, J. A., Mason, M. J., Weltzin, J. F., and Williams, D. G.: Antecedent moisture and seasonal precipitation influence the response of canopy-scale carbon and water exchange to rainfall pulses in a semi-arid grassland, New Phytol., 170, 849–860, 2006. 14477

Reynolds, J., Kemp, P., Ogle, K., and Fernández, R.: Modifying the "pulse-reserve" paradigm for deserts of North America: precipitation pulses, soil water, and plant responses, Oecologia, 141, 194–210, 2004. 14477

Saetre, P. and Stark, J.: Microbial dynamics and carbon and nitrogen cycling following rewetting of soil beneath two semi-arid plant species, Oecologia, 142, 247–260, 2005. 14478, 14486

Sala, O. E. and Lauenroth, W. K.: Small rainfall events: an ecological role in semiarid regions, Oecologia, 53, 301–304, 1982. 14477

Schaeffer, S., Billings, S., and Evans, R.: Responses of soil nitrogen dynamics in a Mojave Desert ecosystem to manipulations in soil carbon and nitrogen availability, Oecologia, 134, 547–553, 2003. 14486

Schimel, J. and Weintraub, M.: The implications of exoenzyme activity on microbial carbon and nitrogen limitation in soil: a theoretical model, Soil Biol. Biochem., 35, 549–563, 2003. 14477

Schwinning, S. and Sala, O.: Hierarchy of responses to resource pulses in arid and semi-arid ecosystems, Oecologia, 141, 211–220, 2004. 14477

Serrano-Ortiz, P., Roland, M., Sanchez-Moral, S., Janssens, I., Domingo, F., Goddéris, Y., and Kowalski, A.: Hidden, abiotic CO_2 flows and gaseous reservoirs in the terrestrial carbon cycle: review and perspectives, Agr. Forest Meteorol., 150, 321–329, 2010. 14488

Sherrod, L., Dunn, G., Perterson, G., and Kolberg, R.: Inorganic carbon analysis by modified pressure-calcimeter method, Soil Sci. Soc. Am. J., 66, 299–305, 2002. 14480

Sponseller, R.: Precipitation pulses and soil CO_2 flux in a Sonoran Desert ecosystem, Glob. Change Biol., 13, 426–436, 2007. 14478

Suseela, V., Conant, R., Wallenstein, M., and Dukes, J.: Effects of soil moisture on the temperature sensitivity of heterotrophic respiration vary seasonally in an old-field climate change experiment, Glob. Change Biol., 18, 336–348, 2011. 14489

Witkamp, M.: Decomposition of leaf litter in relation to environment, microflora, and microbial respiration, Ecology, 47, 194–201, 1966. 14477

Ziegler, S. E. and Billings, S. A.: Soil nitrogen status as a regulator of carbon substrate flows through microbial communities with elevated CO_2, J. Geophys. Res., 116, G01011, doi:10.1029/2010JG001434, 2011. 14486, 14487

Table 1. Results of non-linear mixed effects modeling of the temporal respiration response to treatments. Bold values indicate parameters which were significantly different from the untreated (for water treatments) or water-treated (for sucrose treatments) parameters ($\alpha = 0.05$). The litter treatments significantly pulsed respiration on both experiment dates. For the July experiment, each treatment response decayed at different rates. Temperature sensitivity was only affected by the soil sucrose treatment in July and the litter sucrose treatment in August.

Experiment start date	Site	Treatment	R_{max}	k	α
7 Jul	Reference	untreated	0.07	−0.24	−0.01
		soil water	**0.98**^{a}	**2.40**^{b}	−0.01
		soil sucrose	0.38	**0.44**^{a}	**0.06**^{b}
		litter water	**1.45**^{c}	**0.67**^{b}	0.01
		litter sucrose	**3.57**^{c}	**2.32**^{a}	−0.01
10 Aug		untreated	0.45	0.20	−0.014
		soil water	0.33	0.49	0.014
		soil sucrose	0.24	−0.047	0.022
		litter water	**2.28**^{c}	**0.85**^{a}	−0.0036
		litter sucrose	**6.83**^{c}	0.79	**0.018**^{b}
16 Aug	Reference	untreated	0.53	0.19	−0.015^{b}
		soil water	0.55	0.45	−0.01
		soil sucrose	**1.65**^{a}	0.11	−0.0045
		litter water	**2.43**^{c}	**0.826**^{a}	**0.012**^{b}
		litter sucrose	**6.86**^{c}	**0.50**^{b}	0.017
	Girdled	untreated	0.23	0.33	0.0040
		soil water	0.54	0.57	−0.0048
		soil sucrose	1.10	0.15	−0.0026
		litter water	**2.71**^{c}	**1.21**^{a}	**−0.0048**^{a}
		litter sucrose	**4.17**^{c}	1.04	**0.0096**^{b}

P values for significane of parameters: $^{a} \leq 0.05$; $^{b} \leq 0.01$; $^{c} \leq 0.001$.

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Table 2. Properties of soil samples collected underneath piñon canopies on 16 August 2010 from the 0 cm to 10 cm depth and litter layer samples collected just above the mineral soil surface at the same locations as the soil samples. BD = bulk density, IC = inorganic C, CCE = % $CaCO_3$ equivalent, SWC = soil water content, LWC = litter water content, OC : N = organic C to total nitrogen ratio. Values in parentheses are the SE of the mean ($n = 5$).

	Reference	Girdled
BD* ($g\,cm^{-3}$)	1.44	1.02
IC (CCE)	0.82 (0.31)	0.87 (0.54)
SWC ($g\,H_2O\,g^{-1}$ dry)	0.08 (0.02)	0.08 (0.03)
LWC ($g\,H_2O\,g^{-1}$ dry)	0.12 (0.01)	0.06 (0.01)
% N – soil	0.28 (0.06)	0.33 (0.05)
% N – litter layer	1.23 (0.06)	1.01 (0.14)
OC : N – soil	13.2 (0.33)	12.9 (0.43)
OC : N – litter layer	33.1 (2.2)	34.4 (2.5)

[*] Bulk density measurements were conducted one year prior to study and represent the average of two samples collected at 5 cm depth.

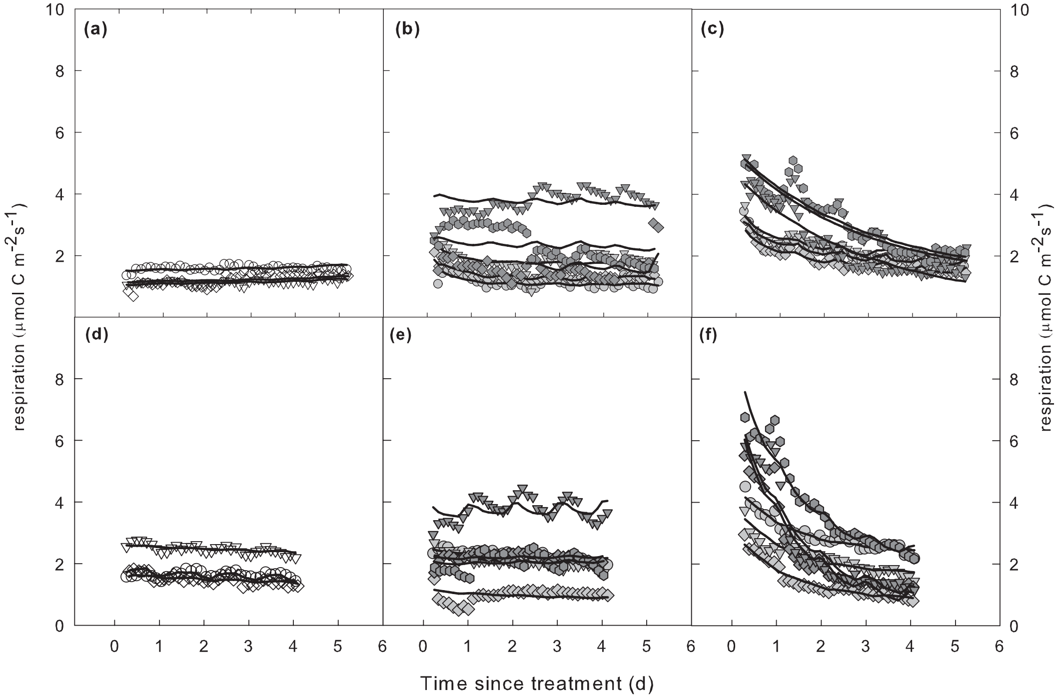

Fig. 1. Reference site Experiment 1 (top row) and Experiment 2 (bottom row) respiration in **(a, d)** control, **(b, e)** mineral soil, and **(c, f)** litter surface applications. Light grey symbols indicate water-only and dark grey symbols indicate sucrose + water treatments. Lines represent predictions from nonlinear mixed-effects models (see Table 1). Different symbols represent different respiration chambers.

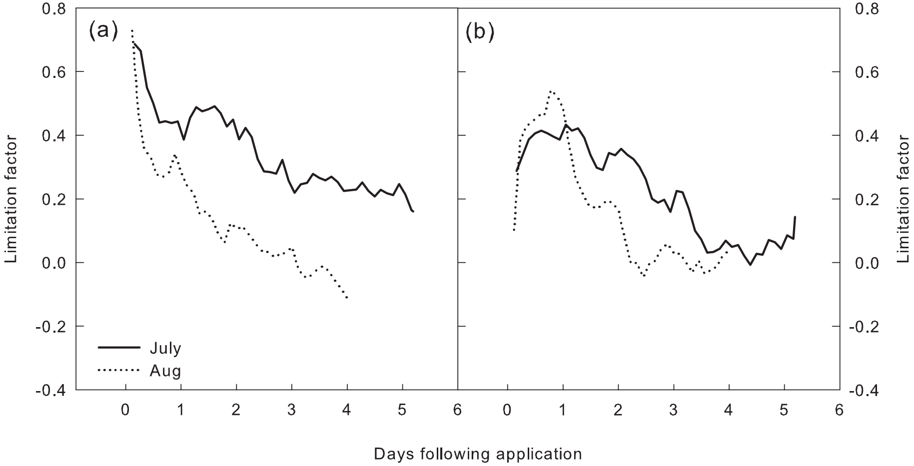

Fig. 2. Limitation of litter respiration to **(a)** water and **(b)** sucrose over time for Reference site Experiments 1 and 2. Limitation factors were calculated using Eqs. (1) and (3) from the text; they would theoretically range between zero and one.

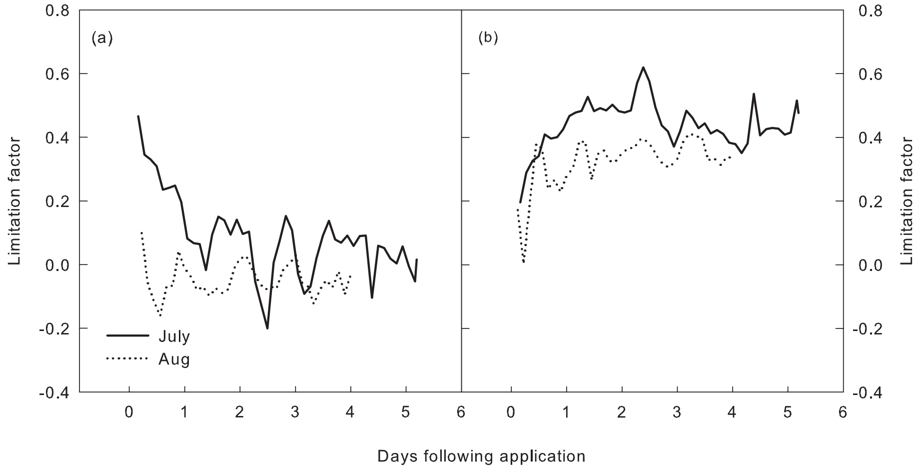

Fig. 3. Limitation of mineral soil respiration to **(a)** water and **(b)** sucrose over time for Reference site Experiments 1 and 2. Limitation factors were calculated using Eqs. (2) and (4) from the text; they would theoretically range between zero and one.

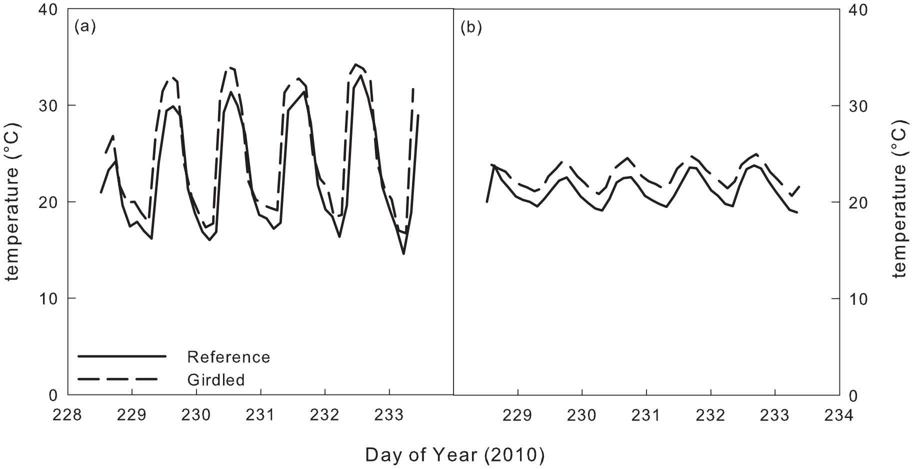

Fig. 4. Temperatures in the soil respiration chambers during the Girdled-Reference comparison experiment in the **(a)** air and **(b)** soil at 5 cm; the Reference site is indicated by the solid line and the Girdled site is indicated by the dotted line.

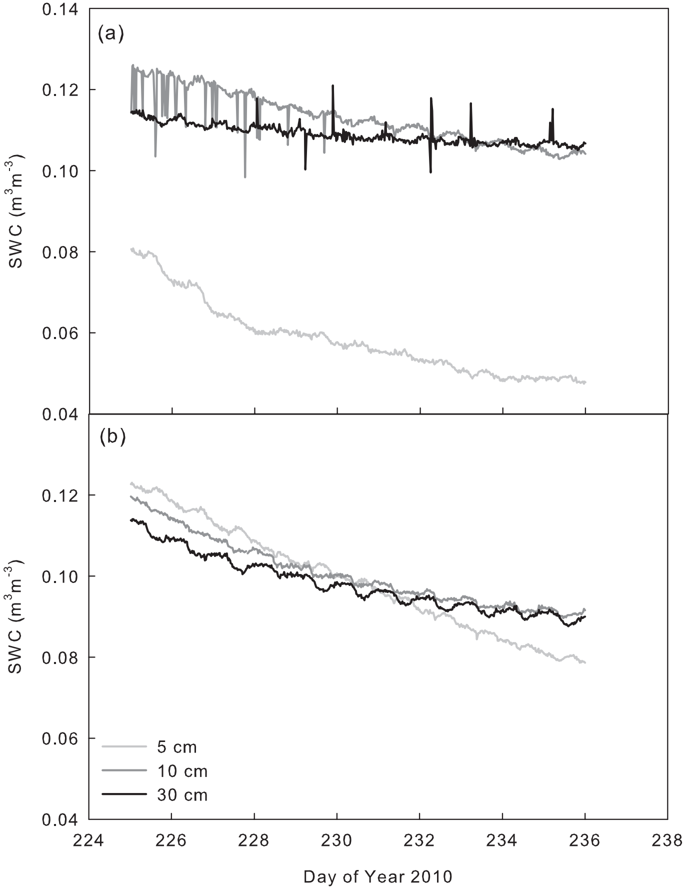

Fig. 5. Soil moisture at the **(a)** Reference and **(b)** Girdled sites ($n = 3$ for each depth) during the Girdled-Reference comparison experiment.

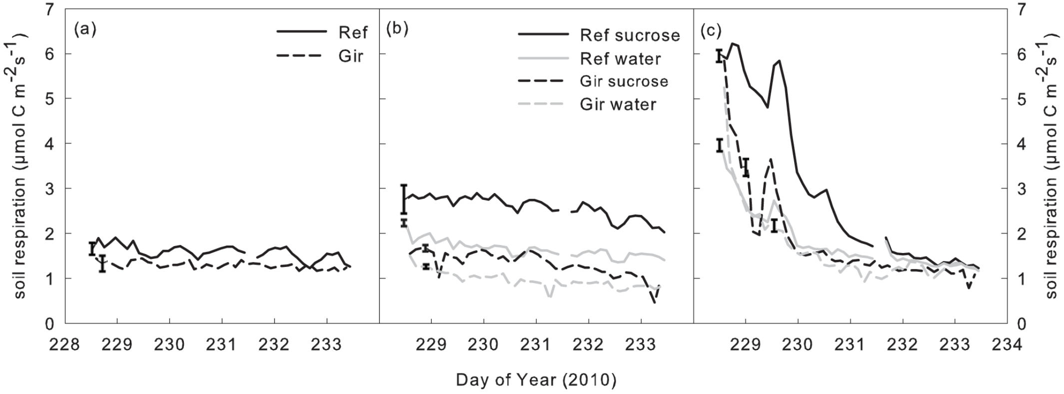

Fig. 6. Girdled-Reference comparison experiment respiration response for **(a)** untreated chambers, **(b)** mineral soil surface applications, and **(c)** litter surface application. Error bars represent ±SE (within-treatment mean over all sample timepoints).

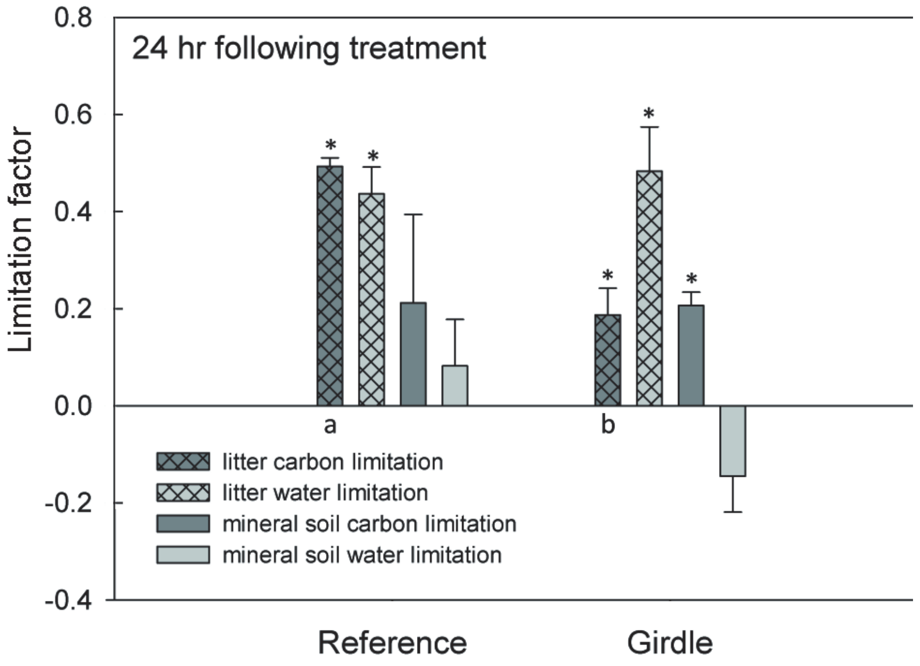

Fig. 7. C and water limitation of respiration at the Reference site compared to the Girdled site. Standard error bars are shown ($n = 3$). Proportional limitations were calculated from the first 24 h of respiration data using Eqs. (1–4) from text. Asterisks denote limitations significantly greater than zero (using a t-test) and different letters below the columns denote groups that are significantly different from each other (t-test, $\alpha = 0.05$). Negative proportion represents a treatment where the water addition yielded a higher respiration rate than the water plus sucrose treatment.