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Shallow snowpack inhibits soil respiration in sagebrush steppe through multiple biotic and abiotic mechanisms

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Abstract. In sagebrush steppe, snowpack may govern soil respiration through its effect on multiple abiotic and biotic factors. Across the Intermountain West of the United States, snowpack has been declining for decades and is projected to decline further over the next century, making the response of soil respiration to snowpack a potentially important factor in the ecosystem carbon cycle. In this study, we evaluated the direct and indirect roles of the snowpack in driving soil respiration in sagebrush steppe ecosystems by taking advantage of highway snowfences in Wyoming to manipulate snowpack. An important contribution of this study is the use of Bayesian modeling to quantify the effects of soil moisture and temperature on soil respiration across a wide range of conditions from frozen to hot and dry, while simultaneously accounting for biotic factors (e.g., vegetation cover, root density, and microbial biomass and substrate-use diversity) affected by snowpack. Elevated snow depth increased soil temperature (in the winter) and moisture (winter and spring), and was associated with reduced vegetation cover and microbial biomass carbon. Soil respiration showed an exponential increase with temperature, with a temperature sensitivity that decreased with increasing seasonal temperature (Q_{10} = 4.3 [winter], 2.3 [spring], and 1.7 [summer]); frozen soils were associated with unrealistic $Q_{10} \approx 7989$ due to the liquid-to-ice transition of soil water. Soil respiration was sensitive to soil water content; predicted respiration under very dry conditions was less than 10% of respiration under moist conditions. While higher vegetation cover increased soil respiration, this was not due to increased root density, and may reflect differences in litter inputs. Microbial substrate-use diversity was negatively related to reference respiration (i.e., respiration rate at a reference temperature and optimal soil moisture), although the mechanism remains unclear. This study indicates that soil respiration is inhibited by shallow snowpack through multiple mechanisms; thus, future decreases in snowpack across the sagebrush steppe have the potential to reduce losses of soil C, potentially affecting regional carbon balance.

Key words: Bayesian modeling; microbial biomass; microbial substrate use; root respiration; sagebrush steppe; snowpack; soil moisture; soil respiration; temperature sensitivity; vegetation.

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Introduction

In the Intermountain West of the United States, climate change is driving a decrease in the amount and duration of winter snowpack (Groisman et al. 2004, Pierce et al. 2008), and models project further declines over the coming century (Weare and Blossier 2012). Future snowpack reductions in mid-latitude sagebrush ecosystems may significantly alter hydrology and vegetation (Schlaepfer et al. 2012a), and thereby most other ecosystem processes. Snowpack may be a critical determinant of soil respiration (R_{soil}) (Aanderud et al. 2013) because it affects both abiotic (i.e., soil temperature and moisture) and biotic drivers (i.e., vegetation and the microbial community) (Groffman et al. 2006, Buckeridge and Grogan 2008, Muhr et al. 2009). There is substantial interest in the role of R_{soil} in regulating atmospheric [CO_2] in response to a changing climate (Cox et al. 2000, Schlesinger and Andrews 2000, Karhu et al. 2014). Thus, exploring the role of snowpack dynamics in driving changes in R_{soil} provides important insight into feedbacks between climate change and the terrestrial C cycle.

Snow is the dominant precipitation input in sagebrush steppe ecosystems in the Intermountain West (Knight et al. 2014). In this landscape, patchily distributed shrubs act as natural "snowfences" (Tedesche 2010), forming mounds of snow within and just downwind of shrub canopies, interspersed with shallower snow in interspaces. Soils in sagebrush steppe ecosystems are warm and dry during the mid- and late-growing season, cool and moist during the early growing season, and often sub-freezing during the winter (Gilmanov et al. 2004, Schlaepfer et al. 2012b). In the growing season, snow melt water from the previous winter may elevate soil moisture. In the winter, snowpack insulates the soil, reducing or eliminating freezing damage to roots and soil microbes (Hardy et al. 2001, Tierney et al. 2001, Groffman et al. 2006) and increasing liquid water content (Muhr et al. 2009). Areas where snow accumulates earlier in the winter or melts later in the spring may have a shorter effective growing season for soil organisms or vegetation (Loik et al. 2013). Deeper snowpack may thus alleviate plant and microbial water stress both by increasing soil water content, and reducing the snow-free period when evapotranspiration may exceed water inputs. Over time, the snowpack structures the vegetation and soil community within an ecosystem (Loik et al. 2013), influencing R_{soil} through direct effects on the soil environment as well as indirect effects mediated through vegetation. The interaction between changing snowpack and shrubland biogeochemistry may have important implications in the context of changing regional snowpack, as well as for ecosystem C balance in response to woody plant encroachment in cold drylands globally (Reynold et al. 1999, Naito and Cairns 2011).

Soil water is a critical abiotic control on R_{soil} (Moyano et al. 2012). In dry soils, water limitation directly inhibits activity of soil organisms (both plants and microbes), and also reduces diffusion of substrates and nutrients (Davidson et al. 2012). In saturated soils, anoxic conditions limit both aerobic respiration (Davidson et al. 2012) and the diffusion of CO_2 from the soil pore space to the atmosphere (Fang and Moncrieff 1999). Below 0°C, the amount of liquid water in soils is very sensitive to small changes in temperature (Romanovsky and Osterkamp 2000, Tilston et al. 2010, Tucker 2014) so that R_{soil} is likely to have a very high apparent temperature sensitivity around the freezing point (Tilston et al. 2010, Tucker 2014). In mid-summer, drought is often paralleled by high temperatures, which may cause R_{soil} to exhibit apparent negative temperature sensitivity (e.g., Borken et al. 2006).

Along with abiotic factors, biotic factors such as vegetation and microbes are important in determining R_{soil}. There is growing evidence that microbial community composition (Bradford and Fierer 2012, Nie et al. 2013), community-level responses of soil microbes, and changes in microbial biomass affect the apparent temperature sensitivity of R_{soil} (Bradford et al. 2008, Tucker et al. 2013, Karhu et al. 2014). Additionally, the total quantity, diameter, and activity of roots in the soil are highly variable and may account for substantial diurnal and seasonal variation in R_{soil} within a site (e.g., Mitra et al. 2014). Aside from direct respiration from roots, the composition and abundance of the vegetation in an ecosystem may have a range of effects on R_{soil} via litter inputs (Fierer et al. 2005, Cable et al. 2009), priming effects (Zhu and Cheng 2011), and plant influences on soil nutrient status, temperature, and moisture (Burke 1987).

In this study, our main objective was to understand how variable snowpack affects R_{soil} in a sagebrush steppe ecosystem. We evaluated the following hypotheses regarding abiotic affects: elevated snowpack will result in: (1) increased R_{soil} in the winter because of its insulating effect on the soil and resulting warmer soils and higher liquid water availability; (2) reduced R_{soil} in the early growing season due to later snow-free date; and (3) elevated R_{soil} in the summer by alleviating soil moisture limitation. At the same time, we expected that elevated snowpack will affect biotic components of the system thereby affecting R_{soil} such that elevated snowpack will: (4) increase microbial biomass C (*MBC*) via insulation and soil moisture affects as outlined above (in effect, *MBC* and R_{soil} are increased by the same abiotic factors), thereby indirectly increasing R_{soil}; (5) affect microbial substrate respiration diversity (H'); and (6) reduce the vegetation biomass and root abundance by inhibiting shrub growth, thereby reducing R_{soil} by reducing C inputs and root respiration.

To test these hypotheses, we analyzed data on R_{soil} under ambient (shallow) and elevated snowpack, at three field sites with long-term snowfences in Wyoming, in the context of a soil respiration model that incorporated functions for the effects of soil moisture, soil temperature, vegetation and microbial biomass, and substrate use. We used Bayesian methods to parameterize this model, to estimate the importance of biotic and abiotic factors, and to quantify uncertainty in parameter estimates and resulting predictions of R_{soil}. A novel aspect of this analysis was the incorporation of a multimodel comparison framework to test different ecological concepts of R_{soil} related to the hypotheses described in the preceding paragraph, thus we compare ten models of R_{soil} that are parameterized based on field and lab data as described below.

Materials and Methods

Site information

This study was conducted at three rural highway snowfence sites in southeast Wyoming: "Jelm" (located near the town of Jelm, WY) at 2452 m elevation (41.0313, −105.9961), "Pole Mountain" at 2652 m elevation (41.2518, −105.4350), and "Centennial" (located near Centennial, WY) at 2543 m elevation (41.3068, −106.1524). Snowfences were constructed at distances of 110–500 m from rural highways approximately 60 yr ago (the exact records for individual snowfences are not available) to prevent blowing snow from creating whiteout conditions. Deep snow (1–2 m) accumulates between 2 and 15 m downwind from each fence (Fig. 1). Beyond 15 m, the snowpack is generally shallow (< 40 cm).

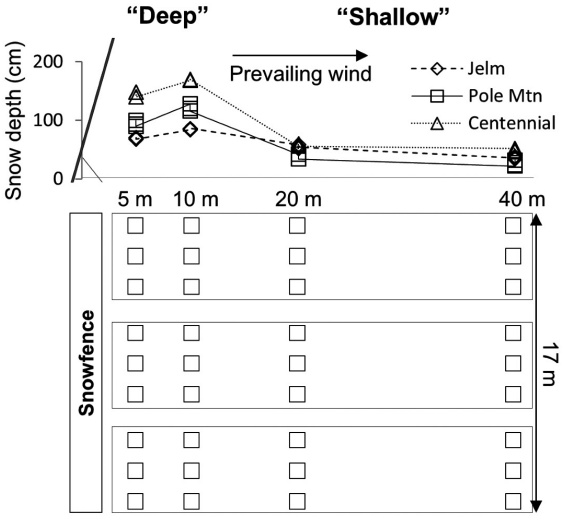

Fig. 1. Experimental design diagram with February 2012 snow depth (cm). At each of the three snowfence sites, 36 plots (0.5 × 0.5 m each) were established at four distances from the snowfence, in three blocks. The plots at 5 and 10 m downwind from the fence were considered the deep snow treatment, and plots at 20 and 40 m distance were the shallow snow control.

Each site was located in a montane *Artemisia tridentata* ssp. *vaseyana* (sagebrush) dominated ecosystem. At each site, we established 36 plots (0.5 m by 0.5 m), arranged in three blocks of 12 plots; nine plots (three plots per block) were established at each of 5, 10, 20, and 40 m downwind from the snowfence (Fig. 1). The 5 and 10 m plots were in elevated snow depth zones, and were combined to define the "deep snow" treatment, and the 20 and 40 m plots were combined to define the "shallow snow" treatment. Plots were established in August 2011, at which time we measured the cover of shrubs, grasses, forbs, and bare ground at each plot using a point-intercept approach with a 0.25 m × 0.25 m quadrat with 64 (8 × 8) individual points (Goodall 1953).

Field measurements

Field sampling was conducted in winter (6-Feb, 13-Feb, 20-Feb), spring (23-April, 8-May, 30-April), and summer (10-July, 26-June, 6-July) of 2012; each site was sampled once during each season (dates are for Jelm, Centennial, and Pole Mtn, respectively). Originally, we intended to capture periods when the entire site was snow covered (Feb.), when only the deep snow treatment was still snow covered (April/May), and when all plots were snow-free (late June-July). Preliminary site visits in 2010 and 2011 indicated that in late April or May, deep snow would persist in the elevated snow depth zones, whereas the shallow zones would be snow-free. However, 2012 was an unusually low snow year with a snowpack only 50–69% of the long-term average as of April 1, 2012 (NOAA NCDC 2012 Snow and Ice Report), and all three sites experienced earlier and more rapid snowmelt than anticipated. Thus, the April/May sampling occurred when snow was almost entirely melted, and snow was very patchy and shallow (<5 cm) where it persisted. On each date, we sampled all 12 plots within one block, such that the blocks do not represent true replicates. We chose this sampling strategy because mid-winter sampling required labor-intensive removal of snow from the plots, which we considered destructive sampling.

Soil respiration (R_{soil}, mg CO_2 m^{-2} h^{-1}) was measured at each plot using a PPSystems EGM-4 infrared gas analyzer with an SRC-1 R_{soil} chamber (PP-Systems, Amesbury, Massachusetts, USA). During the winter (February), R_{soil} was measured once at each of the 12 plots in the winter block, approximately 1 h after the snowpack was removed. We waited 1 h to allow the soil surface flux of CO_2 to equilibrate after snowpack removal. We did not conduct repeated measurements throughout the day during winter because long exposure to air was likely to induce soil freezing, and challenging winter work conditions made repeated measurements prohibitively time consuming. During spring and summer, R_{soil} was measured at each of the 12 plots within the seasonal block, 3–5 times throughout the day.

Thermochron I-button (Sunnyvale, California, USA) temperature sensors recorded soil temperature at 5 and 10 cm depth in 3 h intervals (January 1, 2012 until Jan 1, 2013) at the middle plot at each site and sampling distance (i.e., there were four pairs of I-buttons at each site). Additionally, during the spring and summer, soil temperature was measured at 5 cm depth at each plot concurrent with each R_{soil} measurement using an Omega soil temperature probe (Stamford, Connecticut, USA). These measurements could not be made during the winter because a frozen layer at the surface of the soil impeded probe insertion. On each date, after measuring R_{soil}, one soil sample at each plot was collected to 15 cm depth for lab analysis (below). During the winter, soil samples were collected using a steel chisel because the frozen, rocky soils could not be sampled using a soil corer. During the spring and summer, soil samples were collected using a 5 cm diameter soil corer.

Laboratory measurements

All soil samples were stored in a cooler with ice for transport to the lab, where they were stored overnight at 4°C. The following morning, soil samples were weighed and sieved to separate litter, roots, rock fragments > 2 mm diameter, and fresh soil. A subsample of roots and root-free soil was weighed and dried at 65°C for at least 48 h to determine dry mass, dry bulk density (*BD*, g dry soil cm^{-3}), and gravimetric water content (*GWC*, g H_2O g^{-1} dry soil).

GWC of thawed soils is not likely to represent the actual liquid water content of frozen soils, thus we implemented a literature-derived (Romanovsky and Osterkamp 2000, Tilston et al. 2010) correction factor for liquid water content (GWC_{liq}) below 0°C such that $GWC_{liq} = GWC \times 0.18 \times |T_{soil}|^{-0.45}$, where T_{soil} is the mean soil temperature (°C) across the 5 and 10 cm depths; note that GWC_{liq} = GWC for T_{soil} > 0°C. We test the importance of this assumption by comparing models for R_{soil} with and without this correction for ice formation (models ≤ 9, and 10, respectively, Appendix S1) (see Tucker 2014). Volumetric water content (θ, cm^3 H_2O cm^{-3} soil volume) was determined as $\theta_{liq} = GWC_{liq} \cdot BD$ (Hillel 2003). A subset of soil samples was stored until January 2013, at which time particle size analysis (PSA) was conducted via the hydrometer method (Day 1950) to determine soil texture.

Microbial biomass carbon and nitrogen (MBC and MBN) were measured for each soil sample using the chloroform fumigation-extraction method (Vance et al. 1987), with a standard extraction-efficiency correction factor of $k_{ec} = 0.45$. Extracted organic C and total N were measured on a Shimadzu VCSH TOC/N Analyzer (Kyoto, Japan).

Microbial substrate-use diversity (H') was determined using the MicroResp™ method (Campbell et al. 2003). After soil samples were preincubated in 96 deep well plates at ~50% water holding capacity and room temperature for 3 d in a chamber containing soda lime to remove CO_2 produced by soil respiration, one of 16 different substrates was added to each well with four replicates per substrate. Substrates included sugars (galactose, glucose, fructose, trehalose, arabinose), amino acids (aspartic acid, glutamic acid, alanine, arginine, glycine, phenylalanine), and carboxylic acids (citric, malic, oxalic, succinic, and dihydroxy benzoic acid). Plates were then sealed with a detection plate and incubated for 6 h at 24°C. The absorbance of detection plates was measured at 570 nm wavelength before ($t = 0$) and after 6 h ($t = 6$) of incubation using a PowerWave™ (BioTek, Winooski, Vermont, USA) microplate spectrophotometer. To correct for potential inter-plate differences, absorbance values of the DI water wells were subtracted from absorbance values for each of the substrate + soil wells. The substrate-use diversity (H') was calculated via the Shannon–Weaver index as: $H' = -\sum P_i \bullet \ln(P_i)$, where P_i is the relative activity of substrate i, obtained by dividing the actual activity of substrate i by the sum of activities for all substrates in that plate (Berg and Steinberger 2008).

Quantifying soil respiration responses to biotic and abiotic drivers

We analyzed our field and lab data in the context of a process-based model of soil respiration, and we implemented several alternative formulations of the model components to evaluate the importance of different biotic and abiotic drives of R_{soil}. Below we describe the general structure of the process model, then we outline the alternative formulations. Each model formulation can be described as a nonlinear or linear mixed effects model involving different combinations of the abiotic and/or biotic covariates.

The general model is motivated by the Lloyd and Taylor (1994) temperature response function, where the predicted soil respiration rate (R_{soil}) is given by the following equation:

$$R_{soil} = R_{ref} \cdot f_\theta(\theta) \cdot f_T(T_{soil}) \quad (1)$$

Where R_{ref} is the reference soil respiration when $f_\theta = f_T = 1$; f_θ is a function that rescales R_{ref} according to soil water availability (θ), and f_T is a function that rescales R_{ref} based on the soil temperature (T_{soil}).

In all models, R_{ref} is given by a linear mixed effects model:

$$R_{ref} = \alpha_0 + \alpha_1 \cdot \overline{T}_{soil} + \alpha_2 \cdot R + \alpha_3 \cdot M^* + \alpha_4 \cdot Veg + \varepsilon_s \quad (2)$$

Where ε_s is a site random effect (three levels), and the α's are coefficients describing the effects of the covariates: (1) $\overline{T}_{soil}$ (°C), the average soil temperature of the month preceding the sampling date; (2) R (g dry roots g^{-1} soil), root density; (3) M^*, an index of microbial activity [depending on the model, M^* is either MBC (mg C g^{-1} dry soil) or H' (unitless)]; and (4) Veg, percent cover of vegetation (the total cover of shrubs, forbs, and grasses). All models include the intercept (α_0) and the random effect (ε_s), but they differ with respect to the covariates and coefficients used in each model. Model 11 does not include soil moisture or soil temperature scaling functions (i.e., $f_\theta = f_T = 1$ for all θ and T_{soil}) such that R_{soil} is simply given by Eq. 2.

Following Davidson et al. (2012), models 1–10 include the soil moisture sensitivity function such that:

$$f_\theta(\theta) = D^{\left(\theta_{opt} - \theta\right)^2} \quad (3)$$

where θ_{opt} (cm^3 H_2O cm^{-3} soil) is the estimated optimal volumetric soil moisture, and D is an estimated parameter. Thus, R_{ref} in Eq. 2 is interpreted as the respiration rate at the optimal soil moisture level (θ_{opt}). Models 1–9 use $\theta = \theta_{liq} = GWC_{liq} \times BD$, whereas model 10 uses $\theta = GWC \times BD$ (i.e., not corrected for freezing).

Models 1–10 include a soil temperature sensitivity function that follows from Lloyd and Taylor (1994):

$$f_T(T_{\text{soil}}) = \exp\left[E_o \cdot \left(\frac{1}{T_{\text{ref}} - T_o} - \frac{1}{T_{\text{soil}} - T_o}\right)\right] \quad (4)$$

where T_{soil} (Kelvin) is soil temperature, Tref = 283.15 K is the reference temperature, E_o (Kelvin) is analogous to an activation energy term, and T_o (Kelvin) is an estimated parameter. Together, E_o and T_o determine the apparent temperature sensitivity of R_{soil} (e.g., Kirschbaum 2013).

We also computed the Q_{10} of R_{soil} because it is a commonly employed index of apparent temperature sensitivity. Here, Q_{10} describes the multiplicative change in R_{soil} in response to a 10°C increase in T_{soil}, and Q_{10} can be derived from Eq. 4 (Cable et al. 2011):

$$Q_{10} = \exp\left[E_o \cdot \left(\frac{1}{T_{\text{soil}} - 5 - T_o} - \frac{1}{T_{\text{soil}} + 5 - T_o}\right)\right] \quad (5)$$

Note that this derivation results in Q_{10} being a function of T_{soil}, and the parameters E_o and T_o, the latter of which are estimated at a season level (see Statistical model section). We computed three different indices of Q_{10}. The first two were calculated by evaluating Eq. 5 at specific values of T_{soil}. First, we computed season-specific Q_{10}'s using the season level E_o and T_o estimates, but set $T_{\text{soil}} = T_{\text{ref}}$ for all three seasons, to determine Q_{10} at the reference temperature across seasons. Second, we computed Q_{10} given the season-specific E_o and T_o estimates, and an index of the season-specific temperature by setting T_{soil} equal to the mean temperature of the month preceding sampling ($\overline{T}_{\text{soil}}$). Third, we computed Q_{10} during winter as a combined function of both liquid–solid transition of soil water and the winter-specific estimates of E_o and T_o; this was accomplished by estimating R_{soil} from Eq. 1 between −2 and −0.1°C, and calculating temperature sensitivity as $Q_{10} = (R_2/R_1)^{10/(T_2 - T_1)}$. The first Q_{10} index allows us to compare differences in "potential" temperature sensitivity across seasons (given the same T_{soil}); the second allows us to compare "actual" temperature sensitivity (given the seasonal-specific temperature conditions); the third allows us to evaluate the "apparent" temperature sensitivity given the combined effects of temperature and soil freezing (Tucker 2014).

Model comparison

A novel aspect of this analysis is the incorporation of a multimodel comparison framework to evaluate different drivers of R_{soil} (see Appendix S1 for details). The models we tested included different formulations and combinations of these drivers, and generally increased in model complexity from model 11, wherein R_{soil} is modeled as a linear function of R, MBC, Veg, $\overline{T}_{\text{soil}}$ (i.e., Eq. 2); to the full model 1, wherein R_{soil} is modeled as a function of both current and previous month average soil temperature (T_{soil} and $\overline{T}_{\text{soil}}$, respectively), soil liquid water content with the inclusion of freezing effects on the liquid–solid phase transition (θ_{liq}), and all biotic factors (i.e., Eqs 1–4). Model comparison criteria are described below.

Statistical model

A rigorous approach to data-model integration and uncertainty propagation was critical for estimating the parameters (and associated uncertainty) in the above model(s) (Eqs 1–4). To this end, we used a hierarchical Bayesian statistical framework for our data analysis (Clark et al. 2005, Ogle 2009). The Bayesian procedure yields the posterior distribution of the parameters, which is proportional to the likelihood of the data times the prior distribution of each parameter. We assumed a normal distribution to describe the likelihood of the measured (observed) soil respiration (R_{obs}) such that for each observation, $R_{\text{obs}} \sim N(R_{\text{soil}}, \sigma^2)$, where the predicted (or mean) R_{soil} is defined in Eq. 1, and σ^2 is the observation variance.

Where feasible and justified, model parameters were assigned semi-informative priors; for example, based on Lloyd and Taylor (1994), we assigned the following priors for the temperature sensitivity parameters: $E_o \sim N(308,10)$ and $T_o \sim N(227.1,10)$. Davidson et al. (2012), suggested that θ_{opt} should be near the maximum value measured in the field; thus, based on our soil moisture data, we assigned the following prior $\theta_{\text{opt}} \sim N(\theta_{\text{max}}, 0.1)$; the normal distributions are parameterized in terms of the mean and standard deviation. All other parameters were assigned relatively noninformative priors based on either wide uniform or vague normal distributions. The

model code with the specific priors is given in Appendix S2.

Each model was implemented in OpenBUGS (Lunn et al. 2009), which employs Markov chain Monte Carlo (MCMC) sampling methods to sample from the posterior distribution of the model parameters. Three parallel MCMC chains were run for 30 000 iterations for each model. Convergence was determined via the built-in Brooks–Gelman–Rubin (BGR) diagnostic tool (Brooks and Gelman 1998). MCMC samples prior to convergence were discarded as a burn-in period. Using the post burn-in MCMC samples, we computed the posterior mean and 95% credible interval (CI) for each parameter, which is defined by the 2.5th and 97.5th percentiles of each parameter's marginal posterior distribution; when 95% CIs do not overlap the posterior mean of another treatment group, parameters are deemed significantly different.

Inter-model comparisons were done using two metrics: the deviance information criterion (DIC) (Spiegelhalter et al. 2002) and posterior predictive loss (D∞) (Gelfand and Ghosh 1998). DIC is similar to the Akaike Information Criterion (AIC) in that it describes model fit, but it also penalizes for model complexity (Spiegelhalter et al. 2002). Similarly, D∞ is composed of a model fit component and also penalizes for model complexity (Gelfand and Ghosh 1998), but it tends to be less sensitive to model structure compared to DIC (Carlin et al. 2006). In both cases, a lower DIC or D∞ value indicates a "better" model.

Results

Variation in abiotic drivers among snow depth treatments

February snow depth was significantly greater in the deep than the shallow snow treatment [$P < 0.001$, deep: shallow = 1.71 (Jelm), 3.44 (Pole Mtn), 2.91 (Centennial)] (Fig. 1). Soil temperature (T_{soil}) increased from January to July/August, and decreased thereafter (Appendix S4 Fig. S1). From early January until mid-March (weeks 1–12), T_{soil} was lower under the shallow snow than the deep snow treatment (Table 1, Appendix S4 Fig. S1). During the snowmelt period, from March 20 to April 30, 2012 (weeks 13–18), T_{soil} were generally higher under the shallow snow treatment (Table 1). During the snow-free growing season, from May 1 to September 1, 2012 (weeks 18–36), T_{soil} were somewhat higher under the deep snow compared to the shallow snow treatment at Pole Mtn and Centennial, but not Jelm.

Soil liquid volumetric water content (θ_{liq}) was generally higher under the deep than the shallow snow treatment in winter and spring (Fig. 2). During winter, there was no difference between snow depth treatments with respect to total water content (i.e., liquid water + ice, results not shown), such that higher θ_{liq} was a function of warmer soils under the deeper snow. θ_{liq} was not different between snow depth treatments across all sites during the summer, when the soils were dry. Differences in θ_{liq} among sites (Fig. 2) could partly be explained by differences in water

Table 1. Mean soil temperatures (°C) for each snow depth level and associated *P*-value from a Student's t-test (done in the "R" statistical software package) that compares the two levels. Soil temperatures at 5 cm depth were averaged between the 5 and 10 m (Deep snow) and 20 and 40 m (Shallow snow) plots during winter (Jan 1–Mar 19), the snowmelt period (Mar 20–Apr 30), and the approximate snow-free growing season (May 1–Sept 1).

		Mean soil temperature (°C)		
Site	Level	Winter	Snowmelt	Growing season
Jelm	Shallow	−2.50	6.65	18.70
	Deep	−0.90	3.04	18.50
	P-value	<0.001	<0.001	0.65
Pole Mtn	Shallow	−1.98	5.20	17.40
	Deep	−0.04	4.10	19.0
	P-value	<0.001	0.006	<0.001
Centennial	Shallow	−0.97	3.64	14.30
	Deep	−0.40	3.33	17.30
	P-value	<0.001	0.363	<0.001

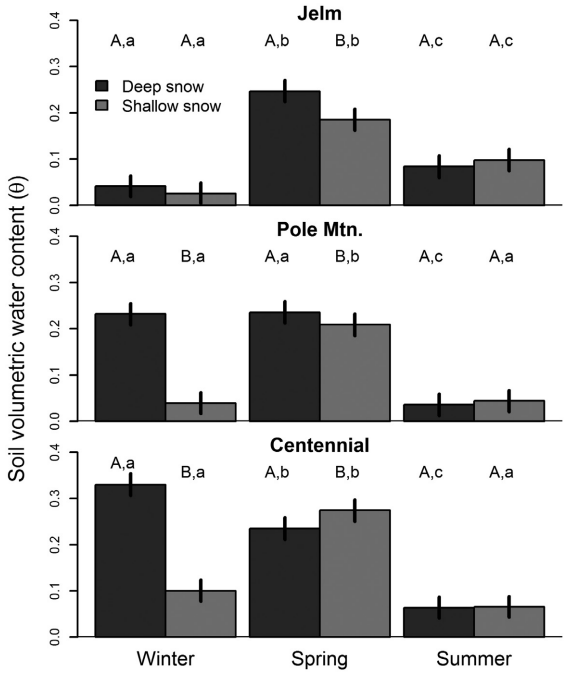

Fig. 2. Soil volumetric liquid water content (θ_{liq}) under the deep and shallow snow depth treatments across the three seasons. The capital letters indicate significant differences between the deep and shallow treatments within a given site and season; the lower case letters indicate significant differences between seasons within a given site and snow depth treatment. The error bars represent 95% credible intervals.

holding capacity due to differences in soil texture. For example, the Jelm site supported sandy soils (88% sand, 8% silt, 4% clay), the Pole Mtn soils were sandy loam (73% sand, 21% silt, 6% clay), and the Centennial soils were loamy (52% sand, 37% silt, 11% clay).

Variation in biotic drivers among snow depth treatments

The average percent cover of total vegetation across snow treatments was 50.3% (Jelm), 69.4% (Pole Mtn), and 80.5% (Centennial); see Appendix S4 Fig. S2a for percent cover of each vegetation type in deep and shallow snow. Across sites, the average percent cover differences (as deep minus shallow snow treatment) of the different vegetation cover classes were −5.26% for total vegetation, +18.9% for forbs, +3.6% for grasses, and −27.8% for shrubs. Within each site, the deep snow treatment was associated with a higher percent cover of forbs and a lower percent cover of shrubs, although, these differences were not significant at the Jelm site (Appendix S4 Fig. S2b). Grass cover increased with elevated snowpack at the Pole Mtn site but was not different at the other sites.

Microbial biomass carbon (MBC) tended to be greater under the shallow than deep snow treatment (significant in 5 of 9 (3 seasons × 3 sites) comparisons), as well as lower in the summer than in the winter and spring (significant in 4 of 6 (2 depths × 3 sites) comparisons) (Fig. 3). Microbial biomass nitrogen (MBN) showed a very similar pattern to MBC (Fig. 3); MBN was higher under the shallow snow treatment, and lower in the summer than in the winter and spring. Thus, we only used MBC for the modeling analysis, because MBC and MBN were positively correlated ($r = 0.59$), and are expected to reflect similar information about the microbial population.

The Shannon–Weaver Index of microbial substrate-use diversity (H′) was greater under the deep than shallow snow treatments during the winter at the Pole Mtn ($P < 0.01$) and Centennial sites ($P < 0.01$), and during the spring at the Centennial site ($P < 0.001$), and decreased from winter to summer at all sites and snowdepths ($P < 0.001$) (Table 2). Overall the differences in H′ across seasons was much greater than that between snow depths within a given season. H′ was significantly positively correlated with MBC across all sites in winter ($r = 0.53$, $P < 0.01$), spring ($r = 0.47$, $P < 0.01$), and summer ($r = 0.53$, $P < 0.001$). A detailed analysis of the microbial community-level physiological profiles is beyond the scope of this study, and is presented in Tamang et al. (unpublished manuscript).

Qualitative evaluation of soil respiration

Across seasons, measured R_{soil} generally increased with temperature, although a number of points deviated systematically from this trend, especially during the summer (lower right, Fig. 4a) at the Pole Mtn and Centennial sites when soils were very dry, and in the winter when T_{soil} dropped below 0°C (lower left, Fig. 4a), indicating that liquid water was limiting. Within a season, R_{soil} increased with increasing soil liquid volumetric water content (θ_{liq}; Fig. 4b). The sensitivity of R_{soil} to increasing

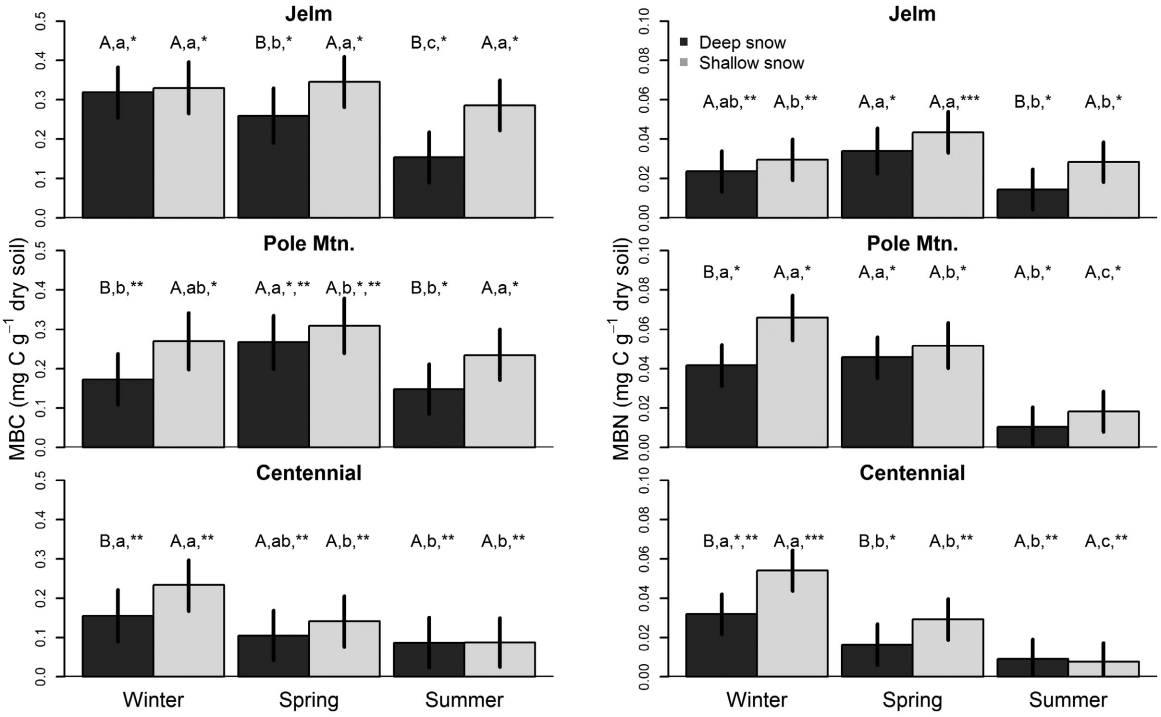

Fig. 3. Microbial biomass carbon (MBC) under the deep and shallow snow depth treatments across three seasons. The capital letters indicate significant differences between the deep and shallow snow depth treatments within a given site and season; the lower case letters indicate significant differences among seasons within a given sites and snow treatment. Asterisks indicate significant differences across sites, within a given season and snow treatment. The error bars represent 95% credible intervals.

Table 2. H′ values of substrate-use diversity based on Microresp analysis. Bold values indicate significant differences between deep and shallow snow levels at a particular site within a particular season. H′ decreases significantly from winter to spring to summer except at Pole Mtn from winter to spring, where the values are not statistically different.

	Jelm		Pole Mtn		Centennial	
Season	Deep	Shallow	Deep	Shallow	Deep	Shallow
Winter	2.766	2.748	**2.606**	**2.680**	**2.410**	**2.724**
Spring	2.598	2.586	2.647	2.661	**2.329**	**2.613**
Summer	2.250	2.396	2.189	2.298	0.979	1.145

θ_{liq} (as determined by the slope of the linear fit in Fig. 4b) was highest in the summer, when soils were warm and dry, and much lower in the winter and spring when soils were cold and moist. Across seasons, there was an apparent negative effect (*not shown)* of θ_{liq} on R_{soil}, driven by the co-occurrence of low θ_{liq} and high T_{soil} during the growing season, and high θ_{liq} with low T_{soil} during the spring and winter (above 0°C).

Model evaluation

We implemented 11 different models (Eqs 1–4) to identify the best model, which was evaluated using DIC and D∞ (Table 3), and thus to determine the most important drivers of R_{soil}. The simplest model (model 11) assumed that the reference respiration rate (R_{ref}) was governed by root density, MBC, and vegetation cover; this model performed the worst based on both D∞ and DIC. The model that assumed that R_{ref}

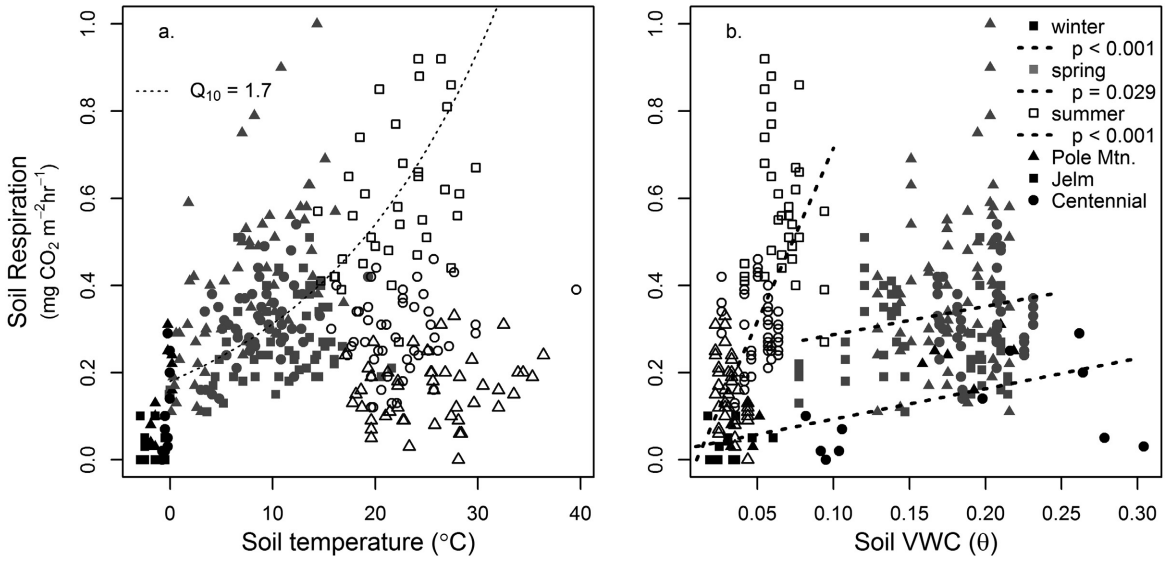

Fig. 4. Soil respiration versus (a) soil temperature at the three sites in 2012 (the dotted curve represents predicted R_{soil} based on Q_{10} = 1.7), and (b) soil volumetric liquid water content (θ_{liq}). Sites are indicated as: ▲ = Pole Mtn., ■ = Jelm, ● = Centennial; and seasonal as winter (black symbols), spring (gray symbols), and summer (open symbols). The *P*-values from a linear regression of R_{soil} on θ_{liq} for each season are given in the legend.

Table 3. Multimodel comparison drivers of soil respiration (R_s). D∞ is the posterior predicted loss based on the summed squared difference of the observed and predicted respiration rates; lower D∞ indicates a better model (better fit and/or lower complexity). Deviance information criteria (DIC) also accounts for model fit and penalizes for model complexity; as for D∞, lower DIC indicates a better model. The model (2) incorporating microbial CLPP (via H′), vegetation cover, and physical effects (including seasonal community-level thermal response and soil freezing effects) was the best model. Model (11), modeling R_{ref} as a linear function on microbial biomass, root density, and vegetation cover and seasonal average temperature was clearly the worst. Models are ordered top-to-bottom from greatest to least complexity based on the actual number of parameters. Model rank is determined by DIC (which in all cases in equal to the ranking based on D∞); when the DIC are very close (i.e., ΔDIC < 5) the models are considered equally good.

Model no.	Factors included in model							Model comparison statistics		
	$f_\theta(\theta)$	$f_T(T_{soil})$	$\overline{T}_{soil}$	Roots	Veg. cover	MBC	H′	Model rank	D∞	DIC
1	*	*	*	*	*		*	4	8.491	−492.8
2	*	*	*		*		*	1 (best)	8.114	−528.6
3	*	*	*	*	*			4	8.438	−493.8
4	*	*	*				*	2	8.322	−520.5
5	*	*	*			*		3	8.427	−513.3
6	*	*	*		*			3	8.391	−515.8
7	*	*	*	*				5	8.624	−489.9
8	*	*	*					6	9.973	−454.8
9	*	*						7	11.580	−415.4
10	*	*						8	15.240	−325.6
11			*	*	*	*		9 (worst)	21.930	−181.70

Table 4. Posterior results (means and 2.5 and 97.5th percentiles defining the 95% CIs) for parameters from Model 2 (Table 3). E_o and T_o are related to the temperature sensitivity of R_{soil} (Eq. 4), and letters in the "Comparisons" column indicate significant differences among seasons. The α parameters correspond to Eq. (3), and the symbols under Comparison indicate either a significant positive (+) or negative (−) effect. ε is the site random effect (Eq. 4), and θ_{opt} is the optimum soil water content (Eq. 2), $\log_{10}|\psi|_{opt}$ is optimum water content converted to water potential (ψ)(kPa) using the SPAW soil hydrology software package (Saxton and Rawl 2006); letters under Comparison indicate significant differences among sites.

Parameter	Mean	2.5%	97.5%	Comparisons
E_o winter	309.1	302.6	314.7	a
E_o spring	305.8	301	310	a
E_o summer	310.5	301.7	321.3	a
T_o winter	225.4	221.6	229.3	b
T_o spring	215.2	215.1	219.3	a
T_o summer	216.2	216	219.9	a
α_1 ($\bar{T}_{soil}$)	0.00380	6.50E-06	0.00828	+
α_3 (H′)	−0.135	−0.2221	−0.0321	−
α_4 (Veg)	0.1678	0.065	0.2749	+
ε_s (Jelm)	−0.2572	−0.3428	−0.1848	a
ε_s (Pole Mtn)	0.1678	0.2987	0.5563	c
ε_s (Centennial)	−0.135	−0.2315	−0.08901	b
θ_{opt} (Jelm)	0.2161	0.1796	0.2539	a
θ_{opt} (Pole Mtn)	0.4241	0.3857	0.4661	c
θ_{opt} (Centennial)	0.3648	0.3311	0.3978	b
$\log_{10}\lvert\psi\rvert_{opt}$ (J)	1.342	1.279	1.415	b
$\log_{10}\lvert\psi\rvert_{opt}$ (P)	0.845	0.477	1.041	a
$\log_{10}\lvert\psi\rvert_{opt}$ (C)	1.301	1.204	1.380	b

was rescaled by soil moisture (θ) and temperature to yield R_{soil} (model 10) was much better, and incorporating θ_{liq} via the freezing correction function (model 9) resulted in even greater model improvement. The inclusion of seasonally adjusted temperature sensitivity (model 8) improved the model modestly (i.e., lower DIC but nearly indistinguishable D∞). The models incorporating abiotic controls and either vegetation (model 6), microbial biomass (model 5), or microbial substrate-use diversity via H′ (model 4) performed equally well and better than the aforementioned models. The best model incorporated both microbial H′ and vegetation cover (model 2). Incorporating root density (models 1, 3, and 7) did not improve the model significantly, and actually resulted in lower DIC when comparing model 1 and model 2.

The predicted R_{soil} from the best model (model 2) fit the observed R_{soil} data well (R^2 = 0.65, Appendix S4 Fig. S3). The model slightly underpredicts high values of R_{soil}, which is common to many soil respiration models. All subsequent results are presented with reference to model 2, and estimated parameter values are presented in Table 4.

Response of soil respiration to abiotic and biotic drivers

In general, based on model 2, both temperature and moisture were important predictors of R_{soil}. The overall effect of soil moisture (f_θ, Eq. 2) increased with increasing θ_{liq}, up to the optimal water content (θ_{opt}, Fig. 5). θ_{opt} was lower for the Jelm site than the Pole Mtn and Centennial sites (Table 4). Because f_θ is a multiplicative scalar on R_{ref} in Eq. 1, a change in f_θ results in a directly proportional change in R_{soil}. Thus, under dry conditions (i.e., $\theta_{liq} < 0.05$), R_{soil} will be 5–20% of the rate under optimal soil moisture.

Soil temperature (T_{soil}) affected R_{soil} via several ways. T_o was higher (greater sensitivity to T_{soil}) in winter than in spring or summer (Table 4). The reference respiration rate (R_{ref}) was positively correlated with average T_{soil} of the month leading up to the measurement date ($\bar{T}_{soil}$) (i.e., $\alpha_1 > 0$,

Table 4). The temperature sensitivity of R_{soil}, as determined by the Q_{10} (Eq. 4) predicted at $\overline{T}_{soil}$, was highest in winter, intermediate in spring, and lowest in summer (Table 5). This effect has two components. First, Q_{10} at 10°C (T_{ref}) is higher for R_{soil} in winter than in spring or summer (Table 5), indicating higher temperature sensitivity of R_{soil} during the winter. Second, field temperature sensitivity (i.e., set $T_{ref} = \overline{T}_{soil}$) is a declining function of T_{soil}, such that the cold winter and cool spring soils should be associated with higher Q_{10} than hot summer soils. The Q_{10} of R_{soil} just below 0°C was much higher; incorporating the modeled effects of freezing water resulted in a Q_{10} of 7989 (95% CI = [3316, 18 400]) between −2 and −0.1°C during the winter.

Regarding the biotic drivers, R_{ref} was positively correlated with the percent cover of all vegetation ($\alpha_4 > 0$, Table 4), and it was negatively correlated with microbial substrate-use diversity (H′; $\alpha_3 < 0$). In the other model sets, root density and MBC were nonsignificant drivers of R_{ref} (Appendix S3). The site random effect (ε_{site}) was different among sites, indicating existence of potential important, but unmeasured, site-specific drivers of R_{soil}.

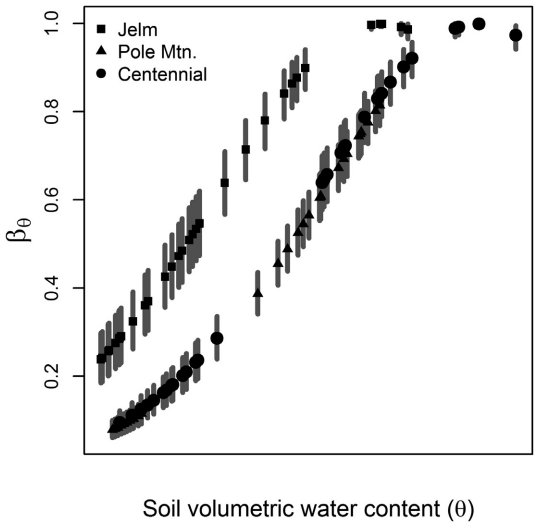

Fig. 5. Fitted multiplicative soil water effect (f_θ) versus soil volumetric liquid water content (θ_{liq}) for the three study sites; note that the Pole Mtn and Centennial predictions are indistinguishable. The gray bars represent the 95% credible intervals.

Discussion

Main findings

In our sagebrush steppe study system, changing snowpack depth substantially affects R_{soil} via multiple mechanisms (Fig. 6), which our approach to data modeling allowed us to quantify despite the noisy relationships apparent in bivariate plots of the data (Fig. 3a and b). The effect of snowpack on R_{soil} is unsurprisingly strongest in the winter when snow is present, but persist into the growing season. Our analysis demonstrates that R_{soil} in this ecosystem is most strongly controlled by soil moisture. Furthermore, the *interaction* between soil moisture and temperature is important both in the winter, when slight increases in temperature lead to large increases in liquid soil water, and in the growing season when drought conditions inhibit R_{soil}, even at warm temperatures. Shallow snowpack allows soil freezing in the winter, and provides only limited soil moisture in the early growing season, thus inhibiting R_{soil} via multiple mechanisms. Below we discuss the abiotic and biotic mechanisms underlying these

Table 5. Temperature sensitivity (Q_{10} = multiplicative increase in soil respiration in response to a 10°C increase in soil temperature; Eq. 4) at the average temperature of the month leading up to the measurement date ($\overline{T}_{soil}$), and at the reference temperature (T_{ref} = 10°C). Superscript letters indicate significant differences in Q_{10} across seasons. The Q_{10} of R_{soil} near freezing is the apparent temperature sensitivity that reflects the effect of the liquid–solid water transition between −2 and −0.1°C, and is presented in the winter only with its 95% credible interval.

Season	$\overline{T}_{soil}$	Q_{10} at $\overline{T}_{soil}$	Q_{10} at T_{ref}	Q_{10} near freezing (winter only)
Winter	−1.5	4.32^c	2.53^b	13 860 (5383, 33 580)
Spring	5.5	2.26^c	2.03^a	
Summer	19.6	1.74^a	2.08^a	

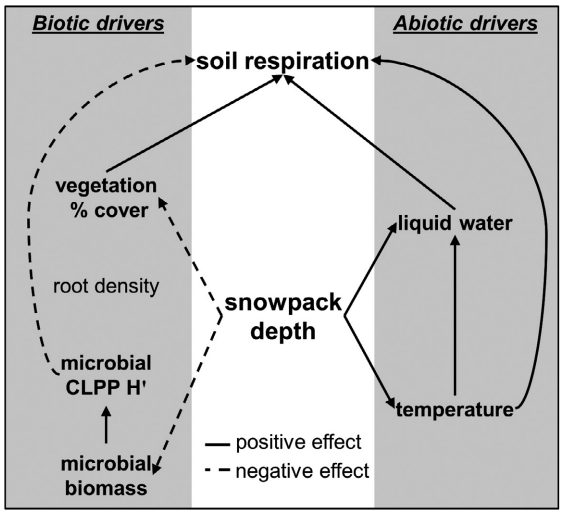

Fig. 6. Summary of the effects of snowpack depth on soil respiration as mediated through biotic and abiotic drivers. The solid lines indicate a positive effect, and the dashed lines indicate a negative effect. The absence of a line indicates the lack of an effect.

effects, and explore potential consequences of a changing snowpack for ecosystem carbon balance.

Snowpack mediated effects on soil respiration: Abiotic drivers

Increased snowpack depth significantly changed the soil environment in ways that increased R_{soil} in the winter and early growing season; the underlying biotic and abiotic drivers are summarized in Fig. 6. While the winter soil temperatures under the deep snow treatment were at most 4°C higher, and on average only about 1–2°C higher than those under the shallow snow treatment, these differences resulted in large increases of R_{soil} in the winter (Fig. 4a lower left corner), resulting in estimated Q_{10} of ~7989. This high apparent temperature sensitivity of R_{soil} during the winter, when soils are often below freezing, agrees with other studies that estimated Q_{10} values of winter R_{soil} in the range 60–200 (Mikan et al. 2002) to 6.65×10^5 (Monson et al. 2006). One explanation for this response is that the biotic temperature sensitivity of R_{soil} to field temperatures during winter is much higher than during spring or summer (Tucker et al. 2013), which may reflect differences in the decomposer community across seasons as was seen by Lipson et al. (2009) in a subalpine forest.

Under the theory of thermal acclimation of respiration (Luo et al. 2001, Atkin and Tjoelker 2003), the temperature sensitivity of plant or soil respiration should decrease as the average, growing temperature increases. This is supported by our Q_{10} values, which are highest in the winter and lowest in the summer (Table 5). However, this result is contrasted by the positive effect of average soil temperatures of the preceding month ($\overline{T}_{soil}$) on reference respiration (R_{ref}), which may reflect a thermal stimulation via community-level responses (Hartley et al. 2008, Nie et al. 2013, Karhu et al. 2014) of R_{soil}. Alternatively, this apparent stimulation may reflect seasonal phenological patterns of vegetation (such as green-up or root flush) or the soil microbial community. This result is consistent with Tucker et al. (2013), who used soils from the Pole Mtn. site to demonstrate seasonal thermal acclimation of R_{soil} temperature sensitivity, but stimulation of reference respiration rate in response to increasing laboratory incubation temperature.

A second, more important reason that the small warming effect of elevated snow depth has a disproportionately large effect on winter R_{soil} is that the fraction of soil water present as liquid versus ice is very sensitive to soil temperature in the critical range between −1°C and 0°C (Romanovsky and Osterkamp 2000, Tilston et al. 2010). It is worth noting that soil temperatures at the study sites may spend a significant fraction of the year [~17–35% (Appendix S4 Fig. S1)] in this critical range, making it ecologically relevant. Our results suggest that R_{soil} is very sensitive to soil moisture within this temperature range; a 0.25°C temperature change in this critical range can be associated with a 50–99% decrease in soil moisture (Romanovsky and Osterkamp 2000, Tilston et al. 2010). As ice forms in soil, the remaining liquid water forms isolated thin layers (Rivkina et al. 2000) where substrate availability may be rapidly depleted, and the substrate for microbial respiration may be restricted to recycling of microbial biomass and products (Ostroumov and Siegert 1996) Thus, the sensitivity of soil microbes to diminishing liquid water availability may be magnified by diminishing substrate availability and diffusion in soil microsites during freezing events (Tucker 2014, Davidson et al. 2014).

Along with reducing soil ice formation, deeper snowpack directly affects soil moisture during the early growing season because melting snow represents the major source of soil water in sagebrush steppe (Knight et al. 2014). Because R_{soil} in sagebrush steppe is low under dry conditions (Figs. 4b and 5) (Cable et al. 2011), water inputs due to snowmelt increase early growing season R_{soil}. During the summer, we did not observe any difference in soil water between the deep and shallow snow treatment plots. We emphasize, however, that we only measured soil water content in the upper 15 cm of the soil profile. Melting snow in sagebrush ecosystems is critical for recharging deep soil water storage (Kwon et al. 2008), and deeply rooted shrubs and forbs in these systems rely on deep soil water during the growing season. It is therefore likely that water derived from a deep snowpack may influence R_{soil} into the growing season via increased autotrophic respiration. However, the role of deep soil moisture in regulating R_{soil} via root activity remains unexplored (Mitra et al. unpublished manuscript).

Soil moisture during summer was highest at the Jelm site because a significant rain event occurred 2 d before sampling, whereas an extended period of drought preceded sampling at the other two sites. Correspondingly, R_{soil} was higher during the summer at Jelm than the other two sites (Fig. 4a). Therefore, it appears that during mid-summer water from recent rainfall is a more important driver of R_{soil} than snowmelt water, based on the strong temperature response of R_{soil} at the Jelm after a summer rain event (Fig. 4a open squares) compared to the other two sites. The large response to increased θ at Jelm may have been magnified by differences in soil texture. The Jelm soils were sandy, while the Pole Mtn. and Centennial soils had significantly higher content of both clay and silt. This difference resulted in lower optimum water content (θ_{opt}) for R_{soil} at the Jelm site, and thus a larger response to increased soil water under dry conditions, similar to observations at a nearby, sandy site (Mitra et al. unpublished manuscript). The effect of soil physical properties on the response of R_{soil} to soil water content has been demonstrated in other studies (Moyano et al. 2012) and is analyzed in detail by Moyano et al. (2013): a higher proportion of fine particles should result in higher θ_{opt}. Optimum water potential ($\log_{10}|\psi|_{opt}$) (Table 4) calculated from θ_{opt} and other soil physical characteristics using the SPAW Soil Water Characteristics software package (Saxton and Rawl 2006) indicated convergence of the optimum water potential values between the Jelm and Centennial sites, but $\log_{10}|\psi|_{opt}$ was lower at the Pole Mtn. site. For comparison, these values (ranging on average from 0.845 to 1.34 $\log_{10}$ kPa) were higher (that is, drier) than the value of 0.5 $\log_{10}$ kPa reported by Moyano et al. (2013).

Snowpack mediated effects on soil respiration: Biotic drivers

As expected, R_{soil} was positively correlated with vegetation percent cover, but this is unlikely due to the effects of root respiration since we saw no significant effect of root density on R_{soil}, similar to Mitra et al. (2014). Our estimates of root density are limited to spring and summer, and root density and its physiological activity may change significantly with seasonal plant phenology. Although Cleary et al. (2010) found no interannual trend in fine root biomass over 40 yr since burning in sagebrush steppe, further study should be conducted to explore the seasonal relationships between R_{soil} and fine root activity.

A surprising result from this study was the observed negative correlation of reference soil respiration rate with microbial substrate-use diversity (H′). Because H′ is a measure of the ability of the whole soil microbial community to respire a range of substrates one might expect high H′ to result in elevated reference respiration (R_{ref}), opposite of our finding that high H′ correlated with reduced R_{ref}. The observed pattern may be related to seasonal differences in the bioavailability of substrates in soils (e.g., Sherman and Steinberger 2012), or reflect a change in microbial community composition. H′ was positively correlated with soil microbial biomass, which tended to decrease from winter to spring and summer, suggesting a wider range of substrates present in cold than warm soils. Higher soil microbial biomass during winter might be explained by higher microbial carbon-use efficiency (CUE) at low than at high temperatures (Steinweg et al. 2008, Tucker et al. 2013) and we suggest that higher CUE might be possible with a larger range of available substrates (higher H′), which might explain the

relation between microbial biomass and H′. This mechanism may also explain the lack of a significant effect of microbial biomass on total R_{soil}: the effects on R_{soil} of higher microbial biomass and higher carbon-use efficiency at cold temperatures may in fact cancel each other out, resulting in no detectable effect of microbial biomass. Additionally, repeated freeze–thaw cycles in soil may reduce microbial biomass (e.g., Schimel and Clein 1996) and affect community composition, which may have affected the deep and shallow soil areas differently in our study, potentially explaining the observed differences in function.

Caveats and uncertainties and future directions

The use of highway snowfences installed for purposes other than research is associated with certain benefits and pitfalls. The ~60 yr duration of the snowfence treatments reduces the possibility that we are capturing transient effects of changing snowpack depths, and the large number of snowfences present across Wyoming allowed for a wide potential site selection. However, we cannot definitively exclude disturbances that occurred during snowfence installation as drivers of the results presented here. Additionally, the heterogeneity of the shrubland landscape (i.e., resource islands beneath shrubs separated by less fertile interspaces; Schlesinger and Pilmanis 1998) may not have been adequately accounted for by our sampling approach. However, R_{soil} was not strongly correlated with islands of fertility in a nearby sagebrush study area (Mitra et al. 2014), possibly because at these upper-elevation sagebrush steppe sites, vegetation cover is higher and root distribution more uniform than reported in drier desert shrubland sites (Knight et al. 2014).

Moreover, the model presented here underpredicts the highest rates of R_{soil}, a feature common to most R_{soil} models. This common model bias may reflect conditions not included in the model formulations, such as the effects of physical pumping of CO_2 from the soil (Fang and Moncrieff 1999), pulses of resource availability associated with microbial turnover (Schimel et al. 2007), root exudation and growth (Zhu and Cheng 2011), or a delay in the response of surface R_{soil} to soil profile conditions (Phillips et al. 2011). Our attempt to incorporate the effects of root biomass was unsuccessful, but more detailed measurements of rhizosphere activity throughout the season and between treatments would be very useful for addressing this question (e.g., Finzi et al. 2014).

A final caveat is that because our study occurred during an anomalously low snow year, it is possible that the ecosystem under average ambient snow conditions may behave somewhat more like the deep snow than the shallow snow plots. However, because future climate predictions are for shallower, more transient snowpack, we consider this both a caveat and a potential strength of the study.

Our parameterization of soil freezing resulted in a better model fit, yet a more rigorous approach to the quantification of soil ice formation and distribution would likely result in a clearer understanding of cold season R_{soil}. In the future, the role of soil water in determining R_{soil} should consider diffusion of substrates in the water-filled pore space (Davidson et al. 2014) as well as the microbial-scale hydraulic connectivity of the soil matrix (Manzoni and Katul 2014), although the different responses of root and microbial respiration make these more mechanistic models difficult to implement.

Changing snowpack in sagebrush ecosystems: how will soil respiration respond?

We demonstrate here that winter and early growing season R_{soil} are closely coupled to the depth of winter snowpack. We suggest that as snowpack continues to diminish throughout the Intermountain West (Groisman et al. 2004, Pierce et al. 2008), total R_{soil} will diminish as well. It remains to be determined if this decrease in R_{soil} would be offset by projected increasing temperatures. Shallower snow inhibits mid-winter R_{soil} primarily by allowing soils to undergo freezing, and inhibits early growing season R_{soil} primarily via reduction in a critical water source. Furthermore, increased drought frequency, coupled with decreased snow water input may result in increased cover of bare ground, which this study suggests might reduce R_{soil}. Because the proportion of annual R_{soil} occurring in winter in these systems remains uncertain, further research should better quantify this flux through multiple years in the context of multiple climate and vegetation changes.

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