

A Shift in Seasonal Rainfall Reduces Soil Organic Carbon Storage in a Cold Desert

Zachary T. Aanderud,^{1*} James H. Richards,² Tony Svejcar,³
and Jeremy J. James³

¹Department of Plant and Wildlife Sciences, Brigham Young University, 489 WIDB, Provo, Utah 84602, USA; ²Department of Land, Air and Water Resources, University of California, Davis, California 95616, USA; ³United States Department of Agriculture-Agricultural Research Service, Burns, Oregon 97720, USA

ABSTRACT

Shifts in the seasonal timing of rainfall have the potential to substantially affect the immense terrestrial stores of soil organic carbon (C, SOC). It remains unclear, however, how changes in the timing of rainfall are influencing SOC storage. We hypothesized that a sustained shift in rainfall timing from winter to a spring-summer regime would reduce desert SOC stores by creating moist and warm soil conditions, thus promoting decomposition. To investigate this, we evaluated how an 11-year seasonal shift in rainfall (winter to spring-summer regime) affected SOC storage (that is, dissolved organic C, light SOC, and heavy SOC) in soils beneath dominant shrub and perennial grass species in a cold desert sagebrush-steppe ecosystem. We also measured the soil C to nitrogen (N) ratios, standing litter stocks, and root biomass C to help interpret the long-term changes in SOC stores. As predicted, a seasonal shift in rainfall caused heavy SOC to decline beneath *Artemisia tridentata* ssp. *wyomingensis* by 14%, from 3.1 to 2.7 kg C m⁻², and *Pseudoroegneria spicata* by 19%, from 3.0 to 2.4 kg C m⁻². Neither dissolved organic C, nor the

light fraction, responded to changes in rainfall. The C to N ratio of heavy SOC beneath *Artemisia* declined by at least 6% under the warmer and moister conditions of the spring-summer regime, suggesting that alterations in decomposition dynamics contributed to the loss of SOC. Unexpectedly, coarse litter and root C in *Artemisia* soils were lower under the spring-summer than winter rainfall regime, suggesting that a decline in litter inputs may also have contributed to the loss of SOC. The C to N ratio of heavy SOC, litter stores (that is, coarse litter and thatch), and root C in *Pseudoroegneria* soils demonstrated similar responses as in *Artemisia* soils, but these variables were at best only marginally significant. Our results suggest that a sustained seasonal shift in rainfall from winter to spring-summer will reduce heavy SOC across cold deserts, and that this reduction will stem from alterations in decomposition dynamics and net primary production by plants. Further, as global temperatures rise we may see more overlap of moist and warm soil conditions, especially in ecosystems with winter rainfall regimes (for example, Mediterranean-climate ecosystems and temperate forests), that may reduce SOC in the absence of rainfall changes.

Key words: *Artemisia tridentata* ssp. *wyomingensis*; climate change; Great Basin Desert; *Pseudoroegneria spicata*; shrub-steppe ecosystem; soil organic matter.

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*Corresponding author; e-mail: zachary_aanderud@byu.edu

INTRODUCTION

Soils hold approximately 2,344 Pg of organic carbon (C), which is more C than in the atmosphere as CO₂ (carbon dioxide, 750 Pg) and vegetation (560 Pg) combined (Schlesinger 1997; Jobbágy and Jackson 2000). Therefore, even slight alterations of C inputs or outputs from this large terrestrial reservoir may dramatically influence atmospheric CO₂ concentrations. Although most soil organic C (SOC) is generally stable with turnover rates that span multiple decades to thousands of years (Schlesinger 1977), climate change is influencing the amount of SOC being stored belowground (Mack and others 2004; Bellamy and others 2005; Fröberg and others 2008).

As the global climate warms, rainfall regimes are also being altered (Karl and others 1995; IPCC 2007; Zhang and others 2007). These changes include alterations in rainfall timing, magnitude, and variability. Shifts in rainfall timing, in particular, have the potential to influence SOC storage by modifying rates of input and turnover. Unfortunately, there is little empirical evidence identifying how seasonal shifts in rainfall may influence SOC storage, especially on the timescale pertinent to global climate change (for example, decades to centuries). Thus, it remains unclear how these alterations will influence the inputs and outputs of organic C that regulate terrestrial C storage in biomes or contribute to rising atmospheric CO₂.

The annual amount of organic C entering SOC stores is determined by the balance between gross primary production (GPP) and ecosystem respiration (Lovett and others 2006), both of which are influenced by temporal patterns of rainfall and soil moisture (Jenkinson and others 1991; Tian and others 1998; Bates and others 2006; Davidson and Janssens 2006). Therefore, if a shift in rainfall timing creates soil conditions that are both moist and warm, heterotrophic respiration may be enhanced and lead to an increase in the decomposition of plant litter and existing SOC. This organic C output, however, may be offset by organic C inputs from GPP. Under these same soil conditions, net primary production by plants may change and either negate or exacerbate respiration effects on SOC stores.

Ecosystems at climatic extremes offer a unique opportunity to clearly assess the effects of rainfall timing on SOC (Weltzin and others 2003). For example, in desert ecosystems, processes that control SOC (for example, plant productivity and heterotrophic respiration) are highly dependent

on the seasonal availability of soil moisture and clearly sensitive to rainfall (Noy-Meier 1973; Comstock and Ehleringer 1992; West and others 1994; Huxman and others 2004; Fernandez and others 2006). Cold deserts, in particular, receive low levels of rainfall and snow falling predominantly during the winter and early spring when soils are cold. This seasonal climate regime results in low rates of C cycling in winter and high rates of cycling in spring before soils become too dry in the summer (Caldwell 1985). Further, desert SOC stores are relatively low and localized in “plant- or shrub-islands of fertility” in contrast to barren plant interspaces (Charley and West 1975; Jobbágy and Jackson 2000; Aanderud and others 2008). The combination of highly moisture-sensitive C cycling and simplistic SOC characteristics of cold deserts offers an excellent opportunity to identify how long-term shifts in rainfall may alter SOC storage.

To investigate interactions between rainfall timing and soil C storage, we evaluated how a long-term seasonal shift in rainfall, from a winter to a spring-summer regime, affected SOC in a cold desert sagebrush-steppe ecosystem. We hypothesized that this sustained shift in rainfall would reduce desert SOC stores by creating moist and warm soil conditions, thus promoting decomposition. We quantified SOC stores (that is, dissolved organic C, light SOC, and heavy SOC) beneath the widespread and dominant shrub (*Artemisia tridentata* ssp. *wyomingensis*) and perennial grass species (*Pseudoroegneria spicata*) following an 11-year experimental shift in rainfall. To determine how changes in SOC stores occurred, we also measured seasonal soil conditions (that is, soil moisture and temperature) under the two regimes, and the C to nitrogen (N) ratios of SOC and litter to provide some insight into the decomposition status or the degree of heterotrophic respiration activity experienced by the various stores (Parton and others 1987; Stevenson 1994; Schlesinger 1997). We purposely did not include hypotheses related to primary plant productivity as previous research on this field experiment failed to find rainfall change effects on the annual aboveground biomass, percent cover, and the density of *Artemisia* or *Pseudoroegneria* (Bates and others 2006). Given this finding, we expect any treatment differences in SOC to mostly likely reflect changes in SOC processing and loss, rather than variation in plant inputs. To solidify this assumption, we measured other components of organic C inputs, such as standing litter stocks and root biomass C.

MATERIALS AND METHODS

Site Description, Rainfall Manipulations, and Experimental Design

We conducted this study at the Northern Great Basin Experimental Range located near Burns, Harney County, OR, USA (43°22' N, 118°22' W, 1300 m elevation). Mean annual precipitation is 205 mm with approximately 75% falling as rain ($n = 50$ years). Soils are Xeric Haplargids with a surface AB horizon (≈ 0 –15 cm) and a subsurface Bt horizon (≈ 15 –30 cm). Soil mean %C was 0.84, %N was 0.11, and pH(H₂O) was 7.7, and texture is a clay loam. This desert sagebrush-steppe ecosystem is a mosaic of shrub and perennial grass species (36% of total ground cover) and barren plant interspaces (64% of total ground cover). The dominant shrub species is *Artemisia tridentata* spp. *wyomingensis* Beetle & A. Young (11% of total ground cover or 31% of total plant cover), and one of the dominant perennial grass species is *Pseudoroegneria spicata* (Pursh) A. Löve (4% of total ground cover and 11% of total plant cover) based on percent cover estimates by Bates and others (2006).

Beginning in fall of 1994, we shifted rainfall timing from a winter to a spring-summer regime by simulating rain events on plots (10 m length \times 12 m width) under five permanent rainout shelters (30 m length \times 12 m width). Under the winter regime, that is the historical regime for this cold desert, rainfall events were concentrated in winter and early spring (% total rainfall per month: October–April = 10.8%, May–July = 6.6%, August–September = 2.5%). In the spring-summer regime, more than 75% of the long-term mean annual precipitation was concentrated in May–July (% total per month: October–April = 3%, May–July = 26.4%, August–September = 0%). Both winter and spring-summer regimes received the same amount of total rainfall (205 mm), which represented the 50-year, long-term average. Treatments were randomly assigned to one of three plots located beneath each of the five-rainout shelters ($n = 5$), and all plots contained a 2-m buffer strip between treatments. There were three treatments under each shelter in the original field experiment (Svejcar and others 2003; Bates and others 2006); however, we only used the two treatments that represented a seasonal shift in rainfall. Our winter and spring-summer regimes are referred to by Svejcar and others (2003) and Bates and others (2006) as current and spring, respectively. Shelters were built in the summer of 1994, open on all

sides, and covered with fiberglass roofs from 1994 to 1998, which was replaced with clear polycarbonate material for the remainder of the manipulation. The polycarbonate roofing reduced ambient levels of photosynthetically active radiation by approximately 25% (Svejcar and others 1999). Typically, treatments received 13–20 rainfall events each year (averaging between 10 and 15 mm per event but occasionally up to 25 mm) from sprinkler systems attached to the roof of the shelters. For more details on the shelters and rainfall manipulations, see Svejcar and others (1999) and Bates and others (2006).

To determine the effects of rainfall timing on SOC, we quantified the SOC content of soils beneath *Artemisia* and *Pseudoroegneria* in the summer of 2006 after the soils had completely dried out following the last full year of rainfall manipulations (that is, 2004–2005). We selected these species based on their ecological importance in the Great Basin Desert of North America and prevalence across the Intermountain West. Within each treatment plot, three replicate subsamples were taken beneath each species from two soil horizons, AB (0–15 cm) and Bt horizon (15–30 cm) for a total of 12 samples per plot. Soil sampling was replicated in a complete block design (2 plant species \times 3 subsamples \times 2 soil depths \times 5 blocked replicates beneath each rainout shelter \times 2 rainfall treatments = 120 soil samples). All samples were removed with a 10-cm diameter \times 8-cm deep PVC core. These soil cores covered most of the soil horizon and profile by sampling the AB horizon from 0 to 8 cm and the Bt horizon from 18 to 26 cm. The soil profile terminated in a duripan at approximately 30 cm. We analyzed all the subsamples separately, but results are expressed as the average of the three subsamples. To calculate stores of SOC, concentrations at each depth were converted to an area basis using bulk densities and horizon depths, and expressed as one value per replicate. An average bulk density for each horizon was calculated from 60 10-cm diameter \times 8-cm deep PVC cores that were sampled in tandem with SOC soil cores. Further, to help interpret the long-term changes in SOC stores, we measured the effects of the rainfall treatments on: seasonal soil moisture and temperature for two of the 11 years; annual percent cover of *Artemisia* and *Pseudoroegneria* (as total perennial grass cover) for 4 of the 11 years; and soil C to nitrogen N ratios and standing litter stores (that is, thatch, fine litter, coarse litter, and roots) at the end of the 11 years.

Soil Organic C

Measurements of SOC included three fractions: dissolved organic C (DOC) equal to water-soluble nonhumic and humic substances, light SOC equal to partially decayed unrecognizable plant and animal products smaller than 2 mm that floated on 1.30 g cm⁻³ sodium polytungstate solution (see below), and heavy SOC equal to high molecular weight, recalcitrant, humic substances that are generally mineral associated that sank in 1.30 g cm⁻³ sodium polytungstate (Stevenson 1994; Six and others 1998). We quantified DOC from sieved (2 mm) fresh soil (within 72 h after removal from the field site) with 1:2 soil/water extractions that were passed through a 0.20- μ m nylon filter and measured on a TOC analyzer (Shimadzu, Columbia, MD). Light and heavy SOC were determined on sieved (2 mm) air-dried soils that were separated via density flotation as outlined by Six and others (1998). We used 1.30 g cm⁻³ instead of the commonly used 1.85 g cm⁻³ sodium polytungstate solution for separating light and heavy SOC to prevent fine clays from floating in the liquid and being assessed as light SOC. Light and heavy SOC were dried, weighed, ground, and analyzed for %N and %C on a C and N analyzer (Fisons Instruments, Beverly, MA). All soils contained little to no inorganic C following a 48-h fumigation with 2-M HCl (Harris and others 2001); therefore, our SOC values represent only organic C forms.

Soil Moisture and Temperature

We measured soil temperature and moisture biweekly in 1998 and 1999, during the growing season (April–September), to identify how the rainfall treatments influenced soil conditions. Both soil moisture and temperature were measured in all replicates in interspace soils between plants to minimize disturbance to vegetation. We measured soil moisture gravimetrically in each plot at two depths (0–15, 15–30 cm) with a 2-cm diameter \times 15-cm deep soil probe. Soils were weighed, dried at 105 °C for 48 h, and re-weighed to determine water content. We measured soil temperature with ST100 thermistors (Campbell Scientific Inc., Logan, UT) at a depth of 5-cm depth. These data were logged every 20 min on a CR-10X datalogger (Campbell Scientific Inc., Logan, UT) to create daily averages that we further combined to represent bi-weekly averages.

Litter and Root C

Measurements of litter C included three fractions that were retained on sieves following sieving:

coarse (diameter > 2 mm, includes woody material), fine (diameter \leq 2 mm), and thatch (dead grass tillers). We evaluated litter C stocks from the same samples used to measure SOC. These fractions were separated by hand and then each fraction was dried, weighed, ground, and analyzed for %C and %N as described for SOC. In addition to litter, we also quantified the amount of C in root biomass (no distinction between live and dead) in all soil cores. Roots were hand-picked from both the coarse and the fine litter fractions and analyzed as described for litter.

Statistics

For each species, we compared differences in SOC, litter C, root C, and litter C to N ratios between rainfall timing treatments using one-way ANOVA. Alternatively, we used two-way ANOVA to determine changes in SOC C to N ratios between treatments and depth for both *Artemisia* and *Pseudoroegneria*. The C to N ratios of SOC often vary with depth. By including depth, we were able to determine if the treatment effects associated with SOC chemical composition were depth-specific. Assumptions of ANOVA were tested using a Shapiro–Wilk test for normality and Levene’s test for homogeneity of variance (SAS 2001). We tested for the effect of the treatments (winter versus spring-summer rainfall) on soil moisture and temperature with repeated measures ANOVA (SAS PROC MIXED) with covariance structures selected using Bayesian Information Criterion.

RESULTS

The rainfall treatments created distinct seasonal differences in soil moisture and temperature conditions (Figure 1). Results from repeated measures ANOVA revealed significant time \times treatment interactions for moisture at 0–15 cm (F value = 12.8, $P < 0.0001$, df 10, $n = 5$) and at 15–30 cm (F value = 6.17, $P < 0.0001$, df 10, $n = 5$), and temperature (F value = 4.73, $P < 0.0001$, df 10, $n = 5$). From early spring to the end of May, soil moisture was at least 10% higher in the winter than the spring-summer regime, regardless of soil depth. From the middle of June through August; however, soil moisture was 14–72% higher in shallow soils (0–15 cm) and 7–32% higher in deep soils (15–30 cm) under the spring-summer than the winter regime. Soil temperature steadily increased approximately 15–20 °C from early spring to summer in both treatments. During July

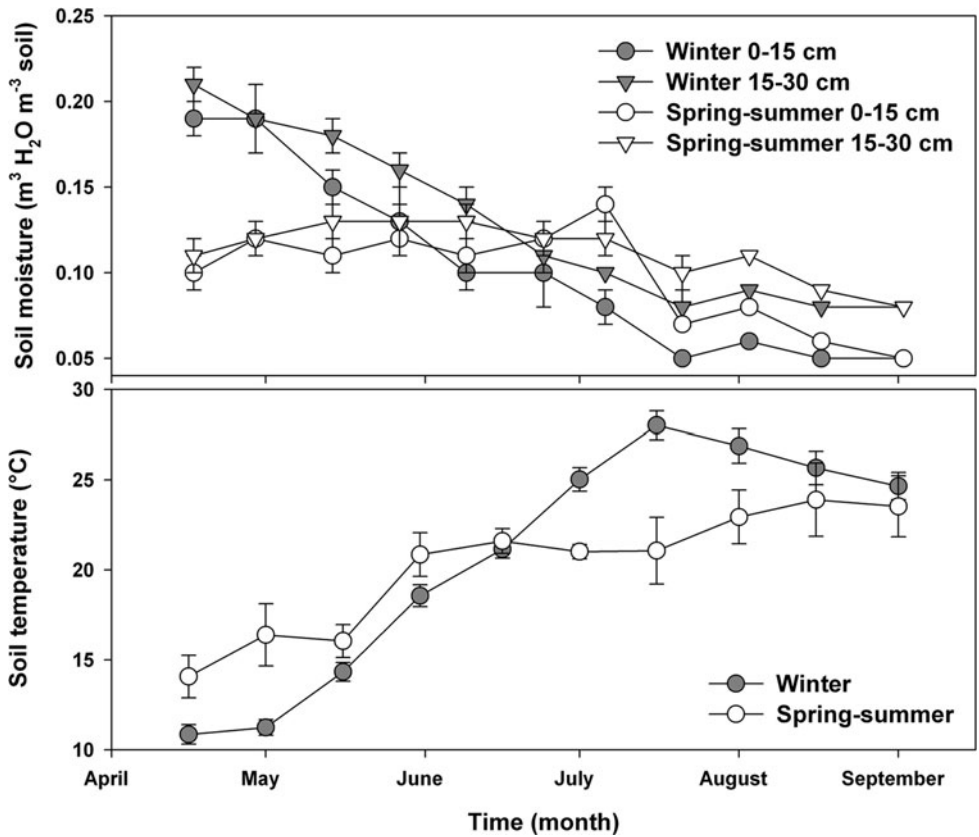


Figure 1. The effects of an experimental shift in rainfall timing on soil moisture and temperature in a cold desert sagebrush-steppe ecosystem. Rainfall regimes include winter and spring-summer treatments. Soil moisture was measured at two soil depths (0–15 and 15–30 cm), while temperature was measured at a depth of 5 cm. Values are biweekly means ± 1 SEM (*n* = 5).

and into August, soil temperatures were 2–7 °C higher under the winter than the spring-summer regime.

When rainfall shifted from a winter to a spring-summer regime, heavy SOC declined in *Artemisia* soils 14% from 3.1 to 2.7 kg C m⁻² (*F* value = 5.54, *P* = 0.05, *df* 1, *n* = 4–5) and in *Pseudoroegneria* soils 19% from 3.0 to 2.4 kg C m⁻² (*F* value = 9.60, *P* = 0.02, *df* 1, *n* = 4–5; Figure 2). This fraction was the most abundant store of C, constituting 85 and 81–87% of total SOC in *Artemisia* and *Pseudoroegneria* soils, respectively. There was no effect of changing rainfall timing on DOC or light SOC beneath either species (*F* value < 1.53, *P* > 0.25, *df* 1, *n* = 4–5). Values ranged for DOC from 0.03 to 0.04 kg C m⁻² and light SOC from 0.48 to 0.64 kg C m⁻².

A summer shift in rainfall reduced C to N ratios of SOC; however, these differences only occurred in heavy SOC in *Artemisia* soils. The C to N ratios of *Artemisia* heavy SOC varied by depth (*F* value = 33, *P* < 0.001, *df* 1, *n* = 9–10) and rainfall treatment (*F* value = 7.6, *P* < 0.01, *df* 1, *n* = 9–10), whereas the C to N ratios of *Pseudoroegneria* heavy SOC only varied by depth (*F* value = 32, *P* < 0.001, *df* 1, *n* = 10; Figure 3). *Artemisia* heavy SOC C to N ratios decreased by 7% in shallow and 6% in deep soils under the spring-summer when compared to the

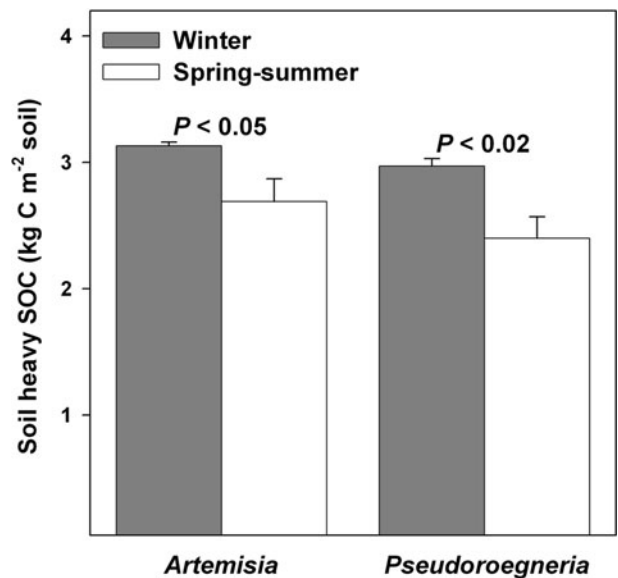


Figure 2. Reductions in heavy soil organic carbon (heavy SOC) fraction following an 11-year shift in rainfall timing from a winter to spring-summer regime. Values are means ± 1 SEM (*n* = 4–5) with associated *P* value.

winter regime. There were no differences in light SOC C to N ratios between the treatments with values ranging from 18 to 19.

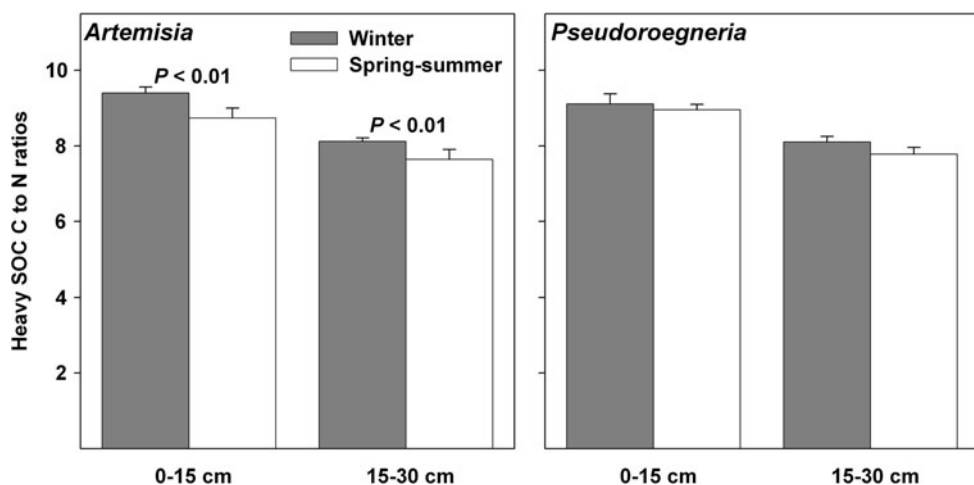


Figure 3. Changes to C to N ratios in heavy SOC by depth following a shift in rainfall timing. All values are means \pm 1 SEM ($n = 4-5$) with P values indicating significant differences between the overall rainfall treatment effect.

Stores of litter and root C declined in *Artemisia* soils and demonstrated a similar trend in *Pseudoroegneria* soils as rainfall shifted from winter to spring-summer (Figure 4). In soils beneath *Artemisia*, coarse litter C was 46% and root C was 71% lower under the spring-summer than the winter regime (F value > 4.96 , $P < 0.05$, $df 1$, $n = 4-5$). Thatch C demonstrated a marginally significant reduction in response to the rainfall treatments (F value = 3.59, $P > 0.09$, $df 1$, $n = 4-5$). In *Pseudoroegneria* soils, there was a tendency for thatch, coarse litter, and root C to be lower under the spring-summer than the winter regime. However, these reductions were only marginally significant (F value > 3.43 , $P = 0.05-0.10$, $df 1$, $n = 4-5$). There was no effect of the rainfall treatments on fine litter in soils beneath either species with values ranging from 0.05 to 0.14 kg C m⁻².

The C to N ratio of only one litter fraction, coarse litter, was influenced by the rainfall treatments. Coarse litter C to N ratios beneath *Pseudoroegneria* were 19% lower under the spring-summer than the winter regime (F value = 18, $P < 0.01$, $df 1$, $n = 4-5$). These ratios were 48 (± 2.0 SEM) and 39 (± 1.0 SEM) in the spring-summer and winter treatments, respectively. The C to N ratios of litter fractions ranged from thatch = 24 to 28, fine = 28 to 32, root = 38 to 54, and *Artemisia* coarse = 46 to 52.

DISCUSSION

As predicted, a sustained shift in rainfall timing from winter to a spring-summer regime reduced SOC stores, but only in one SOC fraction, heavy SOC. We found that our seasonal shift in rainfall

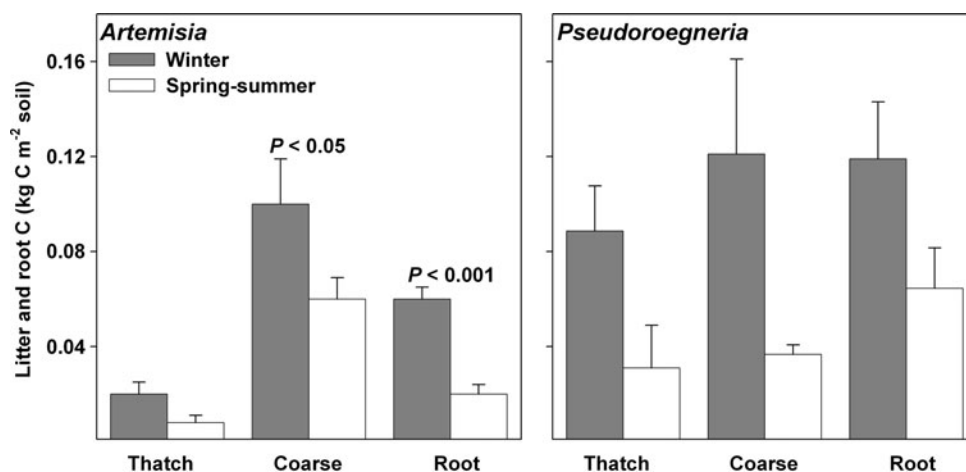


Figure 4. Reduction in litter and root C following a shift in rainfall timing. These fractions are defined as follows: coarse litter = woody and litter material with a diameter greater than 2 mm, thatch = standing and buried dead

grass tillers, and root = both live and dead roots of all sizes. All values are means \pm 1 SEM ($n = 4-5$) with associated P value if comparisons are significant.

consistently reduced the amount of organic C in heavy SOC beneath *Artemisia* and *Pseudoroegneria* by at least 14%. Heavy SOC is the most abundant and recalcitrant form of SOC, and the terminal fraction for SOC formation (Stevenson 1994; Neff and others 2002). In our cold desert soils, heavy SOC accounted for more than 81% of total SOC. Our results represent the first measured reduction in mineral SOC stores following a decadal change in rainfall. In the only other decadal-long rainfall manipulation that evaluated SOC stores, Fröberg and others (2008) found no treatment-induced changes in mineral soil C following a 33% increase or decrease in rainfall amount over 13 years in a deciduous forest. Thus, long-term rainfall change may equate to more striking consequences in xeric than mesic ecosystems, most likely due to desert's clear sensitivity and reliance on precipitation as a driver of soil C cycling.

Both DOC and light SOC are precursors to heavy SOC and a decrease in organic C inputs from these fractions may have contributed to the decline in heavy SOC. However, there was no difference in the amount of organic C in DOC or light SOC between rainfall treatments. The lack of responsiveness of DOC and light SOC may have resulted from an adequate supply of plant and animal residues that flowed into these fractions, regardless of the shift in rainfall, or a research design that failed to capture changes in these relatively more dynamic forms of SOC. Unfortunately, we only evaluated SOC at the end of the experiment and did not measure the flow of inorganic C or rates of transformation between SOC and litter. Therefore, we are unable to determine if the reduction in heavy SOC resulted from a decrease in the flow rate between other organic C fractions. We are able to address, however, how the reduction in heavy SOC occurred by evaluating our results in tandem with mechanisms that govern the input and output of SOC, specifically indices of heterotrophic respiration activity and primary plant production.

Multiple mechanisms mediate SOC storage such as soil edaphic characteristics (Schimel and others 1994), microbial metabolic efficiency (Allison and others 2005), and soil structure and aggregate formation (Blanco-Canqui and Lal 2004). But two mechanisms in particular are predominantly responsible for ecosystem SOC stores (Jenkinson and others 1991) and potentially contributed to our measured decline in heavy SOC. The first mechanism is a change in heterotrophic respiration that enhances SOC decomposition and leads to loss of heavy SOC as CO₂. The second mechanism is a decline in the net primary production by plants

that leads to lower inputs of C as litter and, ultimately, less C entering heavy SOC stores. The two seasonally distinct sets of soil conditions created by our rainfall may have produced the ideal environment for these mechanisms to influence heavy SOC. The winter treatment that mirrored the historical rainfall regime caused soils to be moist through spring when soil temperatures were relatively low and allowed soils to dry down during summer. Alternatively, the spring-summer manipulation caused soils to be moist throughout the summer months when soil temperatures were at a seasonal high. We did measure high soil temperatures during the summer under the winter regime, but these temperatures coincide with low soil moisture levels, and thus probably had little effect on C cycling. We will discuss each of these two dominant mechanisms in detail.

As predicted, a seasonal shift in rainfall, which coincided with warmer soil temperature, seemed to elevate the activity of microorganisms, stimulate heterotrophic respiration, and lead to a decline in heavy SOC. We found evidence for this in terms of changes in heavy SOC C to N ratios. Lower C to N ratios are indicative of more decomposed C substrates and provide some insight into the degree of heterotrophic respiration activity (Stevenson 1994; Parton and others 1987; Schlesinger 1997). Heavy SOC in shallow and deep soils beneath *Artemisia* had lower C to N ratios under the spring-summer than the winter regime. Therefore, the heavy SOC remaining after 11 years was more decomposed under the spring-summer than the winter regime. There was a tendency for *Pseudoroegneria* heavy SOC C to N ratios to decline under the spring-summer regime. For example, heavy SOC decreased by 2% in shallow and 4% in deep soils under the spring-summer regime. SOC stores worldwide are related to both rainfall and temperature, with SOC decreasing with increasing soil temperature for a given level of rainfall (Post and others 1982). In winter, low soil temperatures limit microbial-mediated processes, such as decomposition, even when moisture is available. We suggest that the rate of heavy SOC decomposition was possibly accelerated during spring-summer, due to soils being warmer when moisture was present. Also, the rate of heavy SOC decomposition may have remained the same between the rainfall regimes, but the period of time that was conducive for decomposition was lengthened under the spring-summer regime. Either of these alterations in decomposition dynamics may have occurred and contributed to the loss of SOC.

Contrary to our predictions that any difference in SOC would mainly result from changes in organic C outputs (not inputs), we found evidence that a decline in *Artemisia* net primary production possibly lead to lower inputs of C entering SOC. The shift to a summer regime potentially deterred *Artemisia* root allocation belowground with root C (dead and alive) declining by 71% under the spring-summer regime. This shrub species remains active into the summer and is known to respond to summer rainfall with increased reproductive shoot development (Evans and others 1991). Further, Padilla and others (2009) found that seven species of Mediterranean shrubs increased root allocation in response to drought without altering their aboveground growth rates. If the opposite is also true, the higher summer soil moisture availability under the spring-summer regime may have allowed *Artemisia* to decrease its root allocation while still capturing enough soil moisture to support similar amounts of aboveground biomass. Elevated rates of root decomposition may have decreased root C, but this seems unlikely because root C to N ratios were similar between rainfall treatments. Besides roots, coarse litter C beneath *Artemisia* declined and the litter C to N ratio indicated that this pool was more decomposed under the spring-summer regime. Root and litter C responses in *Pseudoroegneria* soils demonstrated similar tendencies, but the relatively higher growth rates of *Pseudoroegneria* relative to *Artemisia*, may have buffered the effects of lower litter inputs. For example, thatch and root C were at least two times higher in *Pseudoroegneria* than in *Artemisia* soils, regardless of rainfall treatment. To fully understand these root and litter effects, we need to improve our understanding of the factors controlling organic C turnover in water-limited ecosystems, such as identifying the relative importance of soil moisture, litter and root chemistry (for example, lignin to nitrogen ratios (Adair and others 2008)), and organic C pool size in regulating transformation rates between SOC pools, and the role of UV-related decomposition of surface litter (Brandt and others 2007) in these interactions.

For *Pseudoroegneria* and *Artemisia*, a shift away from the historical rainfall pattern did not influence aboveground production (Bates and others (2006)). During 6 of the 11 years of the manipulation, annual aboveground biomass, percent cover, and density for *Pseudoroegneria* and *Artemisia* were relatively constant. Plant species responses to rainfall change are often mixed and species-specific, and the magnitude of these responses may be driven by how far the rainfall change strays from the historical pattern (Grime and others 2000;

Knapp and others 2002; Fay and others 2003; Svejcar and others 2003; Grime and others 2008). For example, Bates and others (2006) failed to find differences in *Pseudoroegneria* or *Artemisia*, but a shallow-rooted early season perennial grass, *Poa secunda*, lost more than half of its aboveground biomass in response to the summer shift in rainfall. This decline was also mirrored in several other species causing total aboveground biomass of herbaceous plants to be approximately 50% lower under the spring-summer than the winter regime. Our shift in rainfall was dramatic; however, the deep-rooted systems of both the species considered here may have provided a buffer against inadequate levels of moisture in the early spring under the spring-summer regime. Further, *Artemisia* and *Pseudoroegneria* may have a greater capacity to alter their period of maximal growth, which is currently in late spring (mid April–mid June; Caldwell and others 1981; Caldwell 1985), to coincide with patterns of high resource availability and temperatures suitable for rapid growth. For example, the high phenotypic plasticity of *Pseudoroegneria* (Huber-Sannwald and others 1996) may have helped this species survive and benefit from the increased availability of summer moisture.

Precipitation in the winter often falls as snow on cold desert sagebrush-steppe ecosystems ($\approx 25\%$ of mean annual precipitation at our site), and we only simulated rainfall. For our precipitation manipulation, we were more interested in rainfall changes during the spring and summer and not necessarily what occurs over winter when snow dominates. As global temperatures rise, however, snow pack levels will continue to decrease (IPCC 2007, 2008). There remains much uncertainty concerning the ecohydrological effects of snow versus rainfall in cold deserts.

Desert ecosystems comprise 15% of the terrestrial global landscape and hold approximately 9% of total global stores of SOC (Jobbágy and Jackson 2000) and if rainfall shifts to a more summer-dominated regime these stores may be reduced. Further, cold deserts, in particular, comprise almost 10% of the terrestrial landscape of the United States, excluding Alaska (730,000 km², Holechek and others 2000). When scaled to the ecosystem level, accounting for the relative ground cover of *Artemisia* and perennial grasses (using *Pseudoroegneria* as a standard for all perennial grasses that had a total ground cover of 21%), the reduction of heavy SOC represented a disappearance of 173 Mg C km⁻² in only 11 years. The loss of C may actually be substantially higher because our results are a conservative estimate. We did not account for

changes in C stores in barren plant interspaces or in soils beneath other species, such as annual grasses and perennial forbs.

Our measured reduction in heavy SOC most likely constituted a positive feedback to atmospheric CO₂ concentrations; however, this loss of C will not necessarily alter the dynamics of the global climate system, given the relative stock of organic C in desert ecosystems. The real utility of our study is that it addresses how an ecosystem of widespread importance may change in the face of an altered climate regime. Although much of the earth's surface is experiencing change in rainfall, there remains substantial uncertainty regarding how rainfall will vary in the future (Weltzin and others 2003; IPCC 2008). Regardless of the uncertainty surrounding future predictions of rainfall change, our research begins to answer a fundamental and potentially universal question of how SOC stores will respond to rainfall change. We found that cold desert SOC stores will decline over the first decade if the shift in rainfall coincides with warmer soil temperatures. Both aboveground and belowground processes will create this decline as SOC decomposition is enhanced and net primary production by plants is reduced. This finding may not be unique to cold desert shrub-steppe ecosystems. As global temperatures rise we will see more overlap of moist and warm soil conditions, especially in ecosystems with winter rainfall regimes (for example, Mediterranean-climate ecosystems and temperate forests). Under these conditions, even in the absence of rainfall change, we predict that SOC will be lost as SOC decomposition rates are enhanced. Further, the western United States continues to suffer from severe multiyear droughts and this aridity may only worsen with rising global temperatures (Cook and others 2004). Under these dry and warm soil conditions, we predict that SOC decomposition will decline leading to a stabilization of SOC stores. The real unknown in both of these examples is how species-specific, above- and belowground responses to rainfall change will determine amounts of organic C entering SOC stores across ecosystems.

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