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LETTER

Interannual precipitation controls on soil CO₂ fluxes in high elevation conifer and aspen forests

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Abstract

Long-term soil CO₂ emission measurements are necessary for detecting trends and interannual variability in the terrestrial carbon cycle. Such records are becoming increasingly valuable as ecosystems experience altered environmental conditions associated with climate change. From 2013 to 2021, we continuously measured soil CO₂ concentrations in the two dominant high elevation forest types, mixed conifer and aspen, in the upper Colorado River basin. We quantified the soil CO₂ flux during the summer months, and found that the mean and total CO₂ flux in both forests was related to the prior winter's snowfall and current summer's rainfall, with greater sensitivity to rainfall. We observed a decline in surface soil CO₂ production, which we attributed to warming and a decrease in amount and frequency of summer rains. Our results demonstrate strong precipitation control on the soil CO₂ flux in mountainous regions, a finding which has important implications for carbon cycling under future environmental change.

1. Introduction

Changes in the CO₂ emitted from soils (soil CO₂ flux or soil respiration) have the potential to affect atmospheric CO₂ concentrations and thus global climate. Temperature and moisture are the primary environmental drivers of the soil CO₂ flux (Raich *et al* 2002). While increasing temperatures have been observed across most of Earth in the last few decades, precipitation changes are more uncertain (Dore 2005).

In cold mountainous regions of the western United States, snow is the major moisture input, accounting for ~70% of annual precipitation (Serreze *et al* 1999). Winter precipitation in the western United States is interannually variable due to strong control by the North Pacific jet stream location as influenced by the El Niño Southern Oscillation (ENSO) and the Pacific decadal oscillation (Cheng *et al* 2021). Winter precipitation extremes, like atmospheric rivers, which

can produce large amounts of precipitation in short periods of time, are also influenced by the seasonality of the Madden–Julian Oscillation (Wang *et al* 2023). Some of these mountainous ecosystems also experience warm season precipitation inputs, in the form of the North American monsoon rains, which typically begin in early July and last through September. There are climatological linkages between winter snow and summer rainfall in the mountain west, as the same atmospheric conditions present with the warm phase of ENSO, El Niño, can produce above average snowfall as well as inhibit or delay the conditions that lead to the establishment of the monsoon rains the following summer (Adams and Comrie 1997). Thus, winter snowfall and summer rainfall are not always independent moisture inputs (Gutzler and Preston 1997).

Both snow and rain inputs have the potential to influence the soil CO₂ flux through two biologically different sources, plant root respiration and

microbial decomposition. Snowpack affects soil temperature and moisture, and thus influences vegetation and soil microbes throughout the year (Maurer and Bowling 2014, Sorenson *et al* 2020). Water derived from snowmelt has been shown to be the dominant water source for forest trees (Hu *et al* 2010). And because snow is an insulator, it protects the soils from extreme winter cold, allowing for active microbial decomposition year-round (Monson *et al* 2006). Despite snow's obvious importance as a water source to trees, there is evidence that forest photosynthetic activity and the amount of monsoon rain are positively related (Berkelhammer *et al* 2017). Yet, such warm season water pulses have been shown to stimulate microbial activity much more than plant activity in forested ecosystems (Carbone *et al* 2011) because these rains often do not penetrate deep enough in the soil profile to reach active plant roots. Moreover, the amount of summer rain trees can use may be connected to winter snowpack amounts, as trees with greater surface soil moisture are better able to use summer rains (Martin *et al* 2018, Berkelhammer *et al* 2020), likely because the surface roots are still active when those rains fall.

Climate change is altering the timing and magnitude of these snow and rain inputs. Most of the montane western US is seeing earlier snowmelt, and in some regions, snowpack decline (Mote *et al* 2018). The monsoon rains are also becoming more sporadic, and arriving later in the summer, than in previous decades (Grantz *et al* 2007). Each of these changes alone—and more importantly, when combined—decreases ecosystem water availability during the summer months, leading to increased observed (Gangopadhyay *et al* 2022) and predicted (Talsma *et al* 2022) summer drought, with potentially large implications for the soil CO₂ flux and the carbon cycle (Wieder *et al* 2022).

Given these environmental changes, we investigated the relationship between precipitation and soil CO₂ fluxes over interannual timescales. To do this, we conducted a long-term study in adjacent forest stands representative of the dominant coniferous and deciduous forest communities, mixed conifer and aspen. We show how interannual variability in snowpack and summer rain inputs differentially influence growing season soil CO₂ flux patterns and magnitudes, and we discuss these results in the context of future environmental change.

2. Methods

2.1. Field site and instrumentation

In August of 2009, two instrumented soil pits were established in adjacent stands of mixed conifer (*Abies lasiocarpa* and *Picea engelmannii*) and deciduous aspen (*Populus tremuloides*) forests at the Rocky Mountain Biological Laboratory in Gothic, Colorado (38.9592° N, longitude: 106.9898° W and elevation

of 2880 m; see figure S1 for schematic). Soils at the site are well-drained sandy loam superactive Ustic Haplocryolls. Mean annual temperature is 0.1 °C and mean annual precipitation is 626 mm, with historically ~80% of annual precipitation falling as snow (Carroll *et al* 2020).

In each forest type, a soil pit was excavated to 50 cm. At depths of 50, 15, and 5 cm below the surface, soil moisture and temperature probes (Decagon Devices 5TE, Pullman WA, USA) were inserted horizontally in the pit sidewall. After augering holes to 50, 15, 5, and 0.5 cm depths, 2.5 cm (1") polyvinyl chloride (PVC) pipes were inserted vertically in the litter/soil next to each pit. One solid state CO₂ concentration probe (Vaisala GMP222/GMP221, Vantaa Finland) and temperature thermistor (thermometrics EC95H303W) were placed in each of the PVC pipes, as well as on a metal *t*-post 1.5 m above the soil surface to measure above-surface conditions. Placement of probes at the very surface of the litter layer enabled quantification of soil plus litter CO₂ fluxes. Free space in each PVC pipe was filled with closed cell foam and sealed with putty. Each instrumented pit was connected to a satellite box with power and a multiplexer (Campbell Scientific AM16, Logan, UT USA) and satellite boxes were connected to a common datalogger (Campbell Scientific CR1000X) powered by solar panels and a battery. Soil temperature, moisture, and CO₂ concentrations were recorded each hour. To eliminate heating of the soil by the CO₂ probes, each hour the probes were powered on for 7 min to warm-up and stabilize, then sampled every second for the next two minutes, with the average of 120 measurements recorded on the datalogger (R. Jassal, pers. comm.). Soil temperatures measured by the thermistors in the PVC pipes before and after powering the CO₂ probes confirmed heating did not occur. Sensor data are published in Figshare (Carbone 2019) and mirrored in ESS-DIVE (Carbone 2023).

Supporting precipitation characteristic data including snowfall, water content in snow, and rainfall were collected nearby (550 m away) at the Rocky Mountain Biological Laboratory billy barr weather station in Gothic (www.gothicwx.org). Rainfall prior to 2000 was recorded at the site by the Gothic EPA station (GTH161).

2.2. Soil CO₂ flux calculations and analyses

Soil CO₂ flux was calculated during the snowpack-free periods of the study with the soil CO₂ concentration measurements using a gradient approach (Davidson and Trumbore 1995, Tang *et al* 2003, Vargas and Allen 2008, Maier-Kirschner 2014; see text S1 for details). We report daily mean fluxes, and because snowmelt varied from April to June across years, we conduct our analyses on standardized mean summertime (July–August–September, JAS) fluxes. Uncertainty was calculated as the standard deviation across time points. One large gap in CO₂

data collection occurred in 2017–2018 due to sensor removal for factory calibration. This gap did not affect 2017 nor 2018 JAS sums and means. However, the 5 cm probe in the aspen stand failed shortly after reinstallation, and thus we do not report JAS data for the aspen in 2018.

2.3. Tree and soil measurements

Within a 10 m radius of each soil pit, all stems greater than 2 cm were measured for diameter at breast height (DBH) and tree height (m). Height was measured with a laser rangefinder (Laser Technology Inc. TruPulse 200L, Cenntenial CO, USA). Litter layer and upper 10 cm of mineral soil ($n = 6$) samples were taken at each site in August 2013 with a 5 cm diameter corer. Cores were transferred to the laboratory and processed within 48 h. Soil carbon (C) and nitrogen (N) concentration was measured using an oxidation/reduction elemental analyzer (LECO Tru-Spec CN analyzer, Leco Corp. St. Joseph, MI, USA). Water extract pools, extractable organic carbon (EOC) and total extractable nitrogen (TEN) were prepared as 1:10, soil weight:extraction volume; and to solubilize microbial biomass, soils were extracted with 1% CHCl_3 (1:10 soil weight:extraction volume). EOC was measured using a total organic carbon (TOC) analyzer with an N measuring unit (Shimadzu TOC- VCPN; Shimadzu Scientific Instruments, Wood Dale, IL, USA). The microbial biomass carbon and nitrogen (MBC, MBN) were calculated as the difference between 1% chloroform slurry carbon and the EOC or TEN concentrations respectively, and were not corrected for extraction efficiency.

3. Results and discussion

3.1. Stand characteristics

While directly adjacent to each other with similar aspect, slope and underlying soil type, the two forest stands differ greatly in tree size and density. Aspen trees averaged 13.2 ± 8.5 cm DBH, (mean \pm 1SD), 7.6 ± 4.6 m tall, with a density of 0.2 trees m^{-2} . Conifer trees averaged 37.1 ± 21.4 cm DBH, 22.3 ± 7.6 m tall, with a density of $0.07 \text{ trees m}^{-2}$. These size (and likely age) differences measured in aboveground biomass were also present in belowground in soil C and N content. Soil C in the top 10 cm was lower in the aspen ($17.0 \pm 2.2\%$) than the conifer ($42.0 \pm 1.7\%$, mean \pm 1SE). Soil N was also lower in the aspen ($1.1 \pm 0.1\%$) than the conifer ($1.7 \pm 0.02\%$) leading to C:N ratios of ~ 16 in aspen versus ~ 25 in conifer forest. Similar patterns were observed in water extractable and microbial biomass C and N. EOC was lower in aspen ($0.70 \pm 0.1 \text{ mg C g}^{-1}$ dry soil) than conifer ($2.2 \pm 0.4 \text{ mg C g}^{-1}$ dry soil); TEN was below detection for aspen and in conifer was $0.09 \pm 0.04 \text{ mg N g}^{-1}$ dry soil. MBC was lower for aspen ($0.9 \pm 0.1 \text{ mg C g}^{-1}$ dry soil) than conifer ($2.7 \pm 0.5 \text{ mg C g}^{-1}$ dry soil) than conifer ($2.7 \pm 0.5 \text{ mg C g}^{-1}$ dry soil).

g $^{-1}$ dry soil) and MBN was also lower in aspen ($0.07 \pm 0.01 \text{ mg N g}^{-1}$ dry soil) than conifer ($0.20 \pm 0.03 \text{ mg N g}^{-1}$ dry soil). The C:N ratio in the extractable pool for aspen could not be determined because of the below detection N pool, but for the conifer was ~ 34 . The C:N ratio of microbial biomass were similar with aspen ~ 12 and conifer at ~ 14 .

3.2. Precipitation inputs

From 2013 to 2021, water year (WY, 1 October–30 September) precipitation ranged from 586 to 1100 mm, while the snowpack-free period ranged from 153 to 184 d (table S1). Both winter (1SD = 175 mm) and summer (1SD = 84 mm) precipitation inputs displayed large interannual variation, with a higher coefficient of variation in rainfall (43%) compared to snowfall (27%). Our study period years trend toward drier, in both snowfall and rainfall in comparison to the last three decades (figure 1). WY 2017–18, 2019–20, and 2020–21 were extremely dry years. WY 2013–14 and 2014–15, were back-to-back wet years, particularly with regards to summer rainfall.

3.3. Soil CO₂ concentrations

Soil CO₂ concentrations varied from ~ 400 ppm to more than 12 000 ppm over the course of each year, and varied with depth (figure 2). A strong bimodal pattern of increasing CO₂ concentrations in the late spring and again in the late summer months is apparent across the profiles. The spring increase is attributed to snowpack and soil moisture inhibiting CO₂ diffusion to the atmosphere, with greatest concentrations in heavy snow years (2014, 2017, 2019). The summer increase is due to increased soil CO₂ production. In between these peaks, there is a noticeable rapid decline of CO₂ concentration across the profile depths in spring or early summer each year that co-occurs with the snowmelt pulse in both stands (noted with arrows on x-axis figure 2). This measured decline in CO₂ concentration could be the result of displacement of CO₂ gas by meltwater and/or the dissolution of CO₂ (as dissolved inorganic C) in meltwater (Wen *et al* 2022).

3.4. Soil temperature and moisture

Soil temperature, volumetric water content, and snow-free CO₂ fluxes varied between stands and across years (figure 3). The aspen soil was generally warmer in the summer and cooler in the winter in comparison to the conifer (figure 3(b)) due to a more open canopy structure. There was an increasing summer temperature trend observed in the conifer forest over time in JAS, resulting in mean daily temperatures measured in the surface soil (0 and 5 cm) and air (1.5 m) under the canopy (trend line $r^2 = 0.7$, $p < 0.001$) being $\sim 1^\circ\text{C}$ and $\sim 1.5^\circ\text{C}$ warmer respectively in JAS of 2021 compared to JAS of 2014.

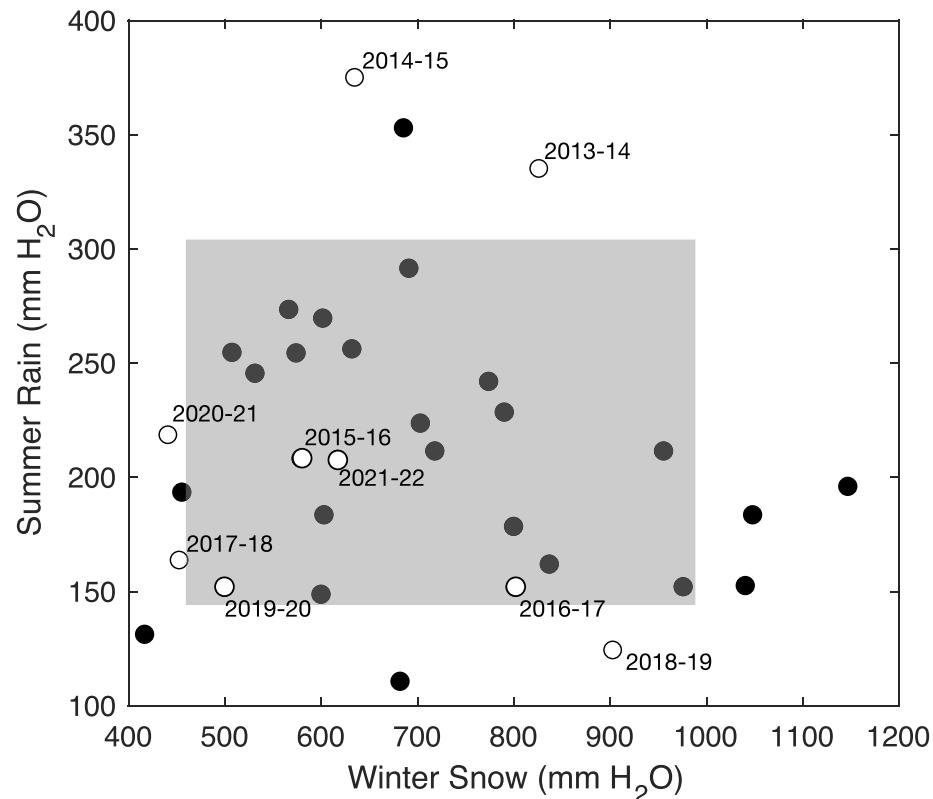


Figure 1. Winter snow (mm H₂O) and summer rain (mm H₂O) collected at the Rocky Mountain Biological Laboratory in Gothic, CO from 1989 to 2022. Gray box indicates the 10th and 90th percentiles for snowfall and rainfall. Study years shown in open circles with WY annotated, prior years in closed circles.

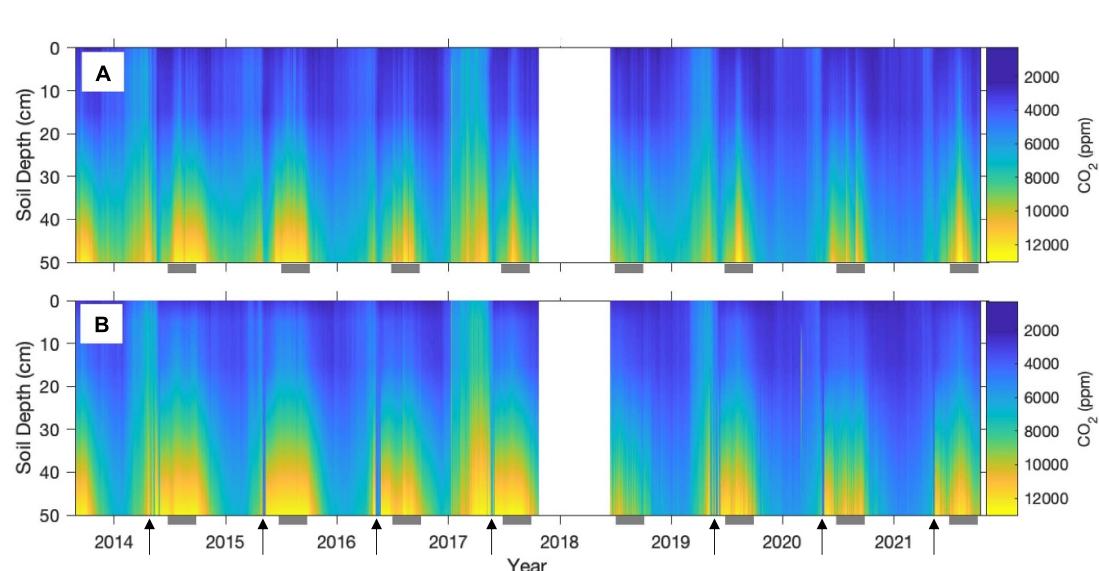


Figure 2. Soil CO₂ concentration (ppm) profiles from 2013 to 2021 in aspen (a) and conifer (b) stands. Values are linearly interpolated between different measurement depths (0, 5, 15, and 50 cm). Arrows identify the end of snowmelt pulse flush of CO₂ out of the measured profile. Grey bars identify July–August–September (JAS) time period.

Soil moisture across the profile (arithmetic mean of 3 depths; figure 3(c)) showed a peak following snowmelt in the spring and summer, with smaller episodic peaks following summer rain events. Soil moisture was lower in the aspen soil than in the conifer soil across most time periods. Exceptions to this

were in response to monsoon inputs in the summer, where rains more easily reached the soil surface due to a more open canopy structure. Soil moisture was also higher after aspen leaves senesced in fall, where we observed a rebound in soil moisture (most prominent in 2014, 2015, 2017, 2018). We hypothesize this

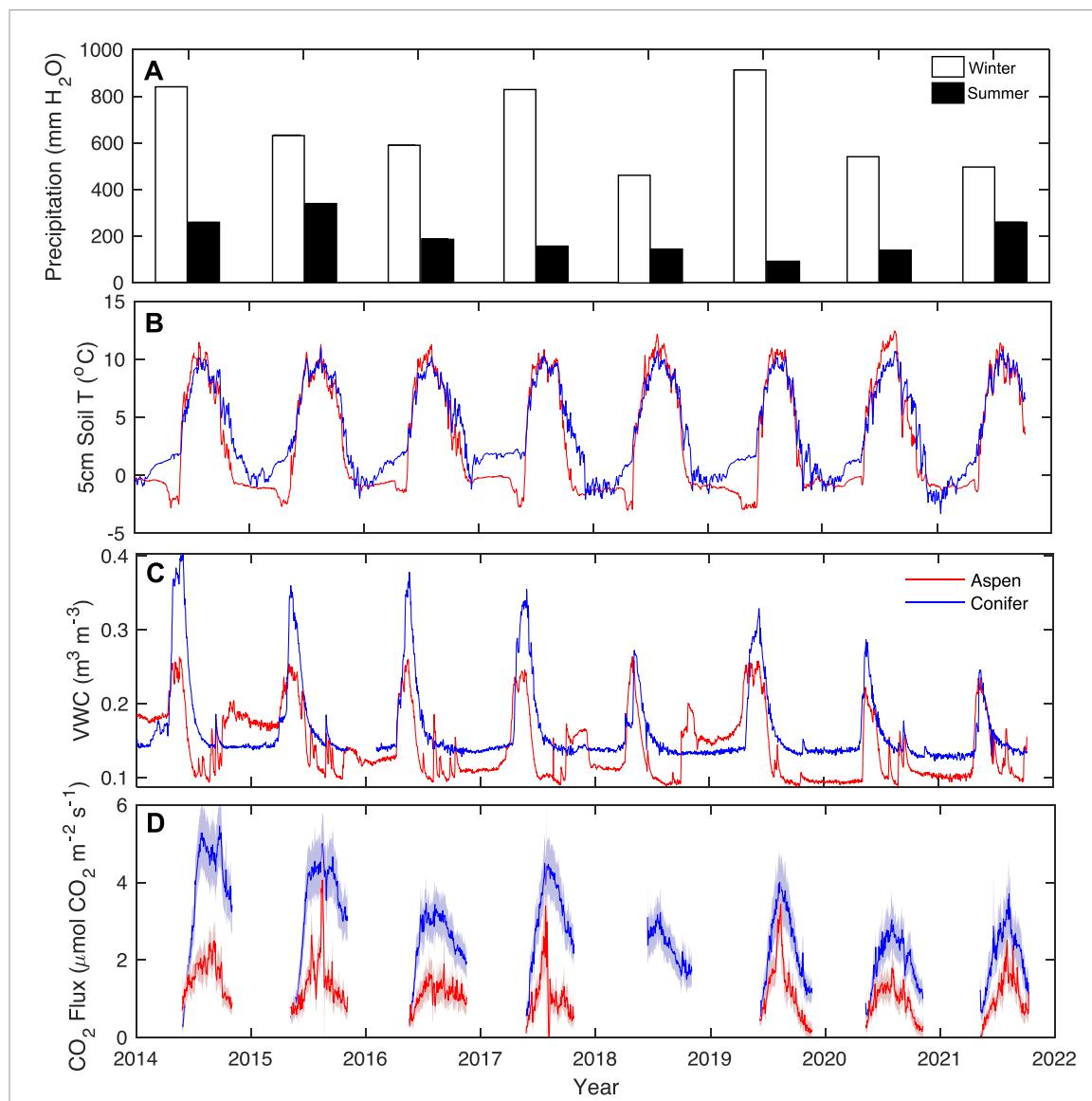


Figure 3. (a) Water year precipitation inputs winter (white bars) and summer (black bars), (b) soil temperature at 5 cm depth ($^{\circ}C$), (c) mean volumetric water content ($m^3 m^{-3}$) across all depths and (d) soil CO_2 fluxes ($\mu\text{mol CO}_2 m^{-2} s^{-1}$) from 2014 to 2021 in aspen (red) and conifer (blue) stands. We did not calculate aspen soil CO_2 fluxes in 2018 due to 5 cm probe failure.

is due to decreasing demand for water by aspen after leaf fall.

There was a general trend of decreasing surface (5 and 15 cm depths) soil moisture in the conifer stand over time ($r^2 = 0.7, p < 0.001$) when averaged over the summer months of JAS. We hypothesize this trend could be due to greater cool season water use by conifers (longer growing seasons) with warming temperatures. There was no moisture trend observed in the aspen stand at any depth, nor at 50 cm depth in the conifer stand ($\text{all } p > 0.1$).

3.5. Soil CO_2 fluxes

Across all years, the aspen had lower mean and cumulative soil CO_2 fluxes than the conifer (figure 3(d)). The difference between the two forests declined over time, primarily due to larger decreases in the conifer soil CO_2 fluxes. Across years, both forests experienced nearly twofold variations in fluxes with

lowest mean JAS fluxes in 2020 and the greatest in 2014 and 2015. In the aspen stand, fluxes ranged between 1.2 ± 0.3 and $1.9 \pm 0.3 \mu\text{mol CO}_2 m^{-2} s^{-1}$ (mean $\pm 1\text{SD}$), compared to 2.4 ± 0.3 – $4.7 \pm 0.5 \mu\text{mol CO}_2 m^{-2} s^{-1}$ in the conifer stand. Seasonally, the aspen CO_2 fluxes peaked earlier than conifer, but both were generally greatest in August when air and soil temperatures were at their annual maxima. In both stands, the largest fluxes occurred during 2014 and 2015, which were both wet monsoon summers; the smallest fluxes occurred during 2020, which was a comparatively dry monsoon (figures 1 and 3(a)). Cumulative summer CO_2 flux ranged from 106 ± 12 – $175 \pm 36 \text{ g C m}^{-2}$ in the aspen stand, compared with 224 ± 15 – $436 \pm 26 \text{ g C m}^{-2}$ in the conifer stand.

3.6. Precipitation inputs and soil CO_2 fluxes

The correspondence of the largest and smallest soil CO_2 fluxes to heavy and weak monsoon years suggests

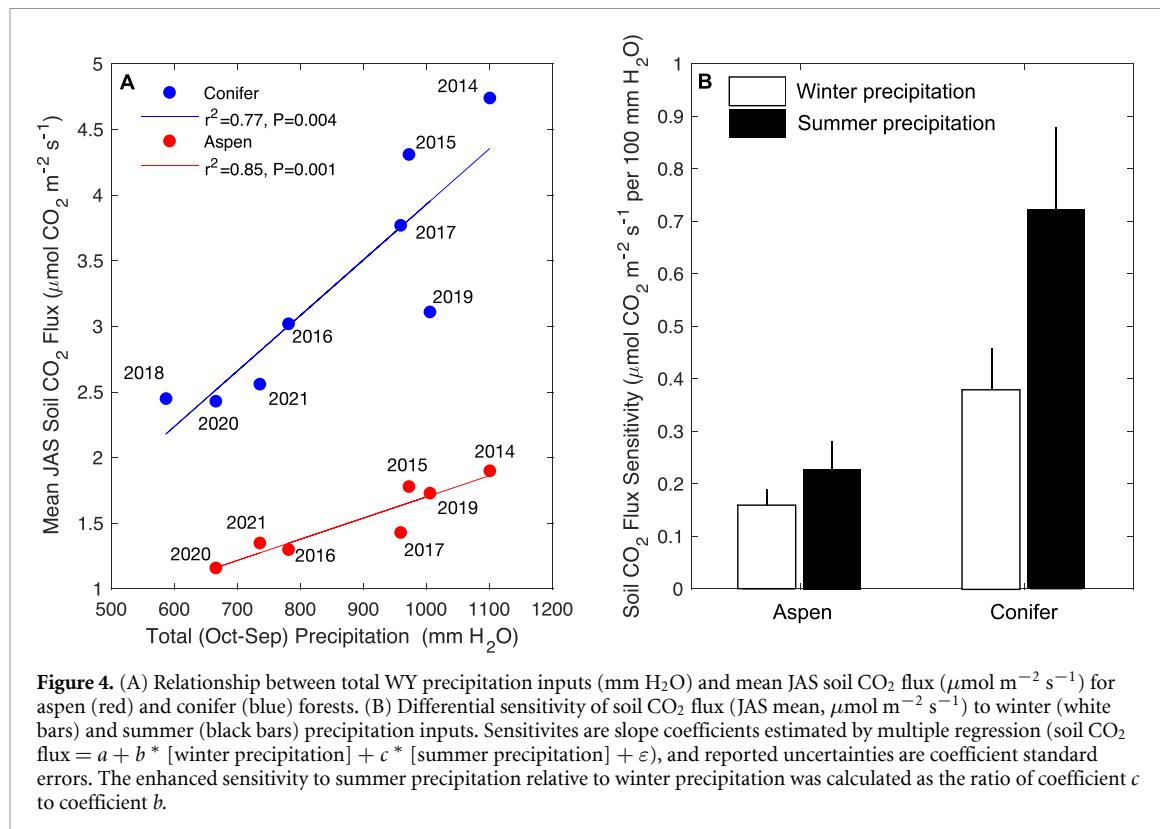


Figure 4. (A) Relationship between total WY precipitation inputs (mm H₂O) and mean JAS soil CO₂ flux (μmol m⁻² s⁻¹) for aspen (red) and conifer (blue) forests. (B) Differential sensitivity of soil CO₂ flux (JAS mean, μmol m⁻² s⁻¹) to winter (white bars) and summer (black bars) precipitation inputs. Sensitivities are slope coefficients estimated by multiple regression (soil CO₂ flux = $a + b * [\text{winter precipitation}] + c * [\text{summer precipitation}] + \varepsilon$), and reported uncertainties are coefficient standard errors. The enhanced sensitivity to summer precipitation relative to winter precipitation was calculated as the ratio of coefficient c to coefficient b .

a strong role for summer water inputs as a driver of interannual variability in soil CO₂ production. In both stands there is a strong correlation of total WY precipitation with mean summer soil CO₂ flux (figure 4(a)) over the study. In the aspen forest ($r^2 = 0.85$), the mean soil CO₂ flux increased at a rate of $0.161 \pm 0.029 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for every 100 mm increase in WY precipitation. In the conifer forest ($r^2 = 0.77$), the mean soil CO₂ flux increased at almost a three-fold faster rate ($0.423 \pm 0.094 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for every 100 mm increases in WY precipitation; difference between stands significant at $p < 0.001$). However, further analysis reveals a much higher sensitivity of the soil CO₂ flux to monsoon precipitation than to winter precipitation (figure 4(b), text S2). This pattern was sustained in both stands, but the enhanced sensitivity to summer precipitation was stronger in the conifer stand (summer sensitivity = $1.9 \times$ winter sensitivity) than the aspen (summer sensitivity = $1.5 \times$ winter sensitivity) stand. Consistent with the analysis using total WY precipitation, the sensitivity of soil CO₂ flux to precipitation inputs was higher in the conifer than the aspen stand in both winter and summer, likely due to larger tree biomass and soil C content and thus higher potential maximum rates of belowground metabolism. After accounting for precipitation inputs, the inclusion of other environmental factors (volumetric water content, soil temperature, and air temperature) did not improve the

explanatory power of our models (no factors significant at $p \leq 0.10$). We note that the soil CO₂ flux sensitivity to winter precipitation may be stronger if we were able to quantify winter soil CO₂ fluxes, however, winter fluxes are likely much smaller in comparison to summer fluxes given the cold temperatures and minimal plant activity.

We applied these CO₂ flux-precipitation relationships developed in the aspen and conifer (text S2) forests to hindcast the previous ~ 30 years of soil CO₂ fluxes. For that period, the mean estimated aspen JAS CO₂ flux was $144 \pm 28 \text{ g C m}^{-2}$ and ranged $87\text{--}204 \text{ g C m}^{-2}$. The mean estimated conifer JAS CO₂ flux was $331 \pm 73 \text{ g C m}^{-2}$ and ranged $180\text{--}473 \text{ g C m}^{-2}$. For both forest types, the maximum and minimum estimates coincided with maximum (WY 1994–95) and minimum (WY 2001–02) winter precipitation inputs, and the hindcast range in predicted fluxes is larger than observed during our period of study.

Precipitation inputs were better predictors of mean JAS soil CO₂ fluxes in both stands than temperature and soil moisture. Relationships between the mean JAS soil CO₂ flux and mean JAS temperature were not observed in either forest. Relationships between the mean JAS soil CO₂ flux and mean JAS soil volumetric water content were only significant in the conifer stand shallow soils (trend line $r^2 = 0.7$, $p < 0.005$) for both 5 and 15 cm soil depths.

3.7. Production of soil CO₂ in shallow and deep layers

Over all years, we found ~63% (57%–68%) of JAS soil CO₂ flux was produced in the conifer shallow soil layer (upper 10 cm) compared to ~44% (25%–52%) in the aspen shallow soil layer, with the remainder produced in the deeper layers (below 10 cm; see table S2). On interannual timescales, JAS shallow soil CO₂ production was more than three times as variable in the conifer stand ($1\text{SD} = 64 \text{ g C m}^{-2}$) than in the aspen stand ($1\text{SD} = 23 \text{ g C m}^{-2}$), and deep soil CO₂ production was more than twice as variable in the conifer stand ($1\text{SD} = 18 \text{ g C m}^{-2}$) than the aspen stand ($1\text{SD} = 9 \text{ g C m}^{-2}$). The total JAS soil CO₂ flux declined over the study period in both shallow and deep soil in both forests. But, the majority of the change was observed in the shallow soil in both forests. In 2021, only 50% of the JAS soil CO₂ flux was produced in the conifer shallow soil in comparison to 2014, and similarly in the aspen soil, only 40% of what it was in 2014. In the conifer deep soil, JAS production declined to 76% of 2014 amounts, and there was little or no change in the aspen deep soil production over time. Because the majority of the soil CO₂ was produced in the shallow soil layers, there was a similarly strong correlation between total precipitation inputs and JAS shallow soil CO₂ production in the aspen forest ($r^2 = 0.96$) and conifer forest ($r^2 = 0.76$) shown in figure 4(a).

3.8. Importance of warm season rains

We hypothesize most of the shallow soil CO₂ production change can be attributed directly to changes in monsoon rains, driving changes in shallow soil moisture (figure 3(c)) that impact fine root activity (Winnick *et al* 2020) and microbial decomposition occurring in organic-rich surface horizons. Following anomalously strong monsoons in the summers of both 2014 and 2015, weak monsoons persisted from 2016 to 2020, before returning to average in 2021. These warm season rains, which often do not penetrate beyond 15 cm soil depth, make up only 9%–35% of the total water inputs in a given WY (table S1), but they appear to be disproportionately important for stimulating soil CO₂ fluxes because of their timing and location of relevance. Analysis of shallow soil CO₂ production in relation to winter vs summer precipitation inputs shows (1) aspen shallow CO₂ production was one-third more sensitive to summer inputs than winter inputs, whereas aspen deep CO₂ production was not significantly correlated to either summer inputs or winter inputs; and (2) in the conifer stand, both shallow and deep CO₂ production were twice as sensitive to summer inputs compared to winter inputs, but shallow CO₂ production was three times more sensitive to precipitation inputs as was deep CO₂ production. These results suggest

surface processes, like litter decomposition and fine root activity, will be more sensitive to changing summer precipitation than more deeper soil processes.

4. Conclusion

Large uncertainties remain as to how precipitation will change in the future, particularly in the western US. Recent decades have recorded declining winter snowfall and delayed and more sporadic summer rains in the mountainous regions. Our study uniquely documented interannual variation in temperature, moisture, and soil CO₂ fluxes in two dominant montane forest types, and captured a wide range of hydroclimatic space. Our findings would not have been possible without long-term records of soil CO₂ fluxes, which are uncommon. Furthermore, there is a dearth of published soil CO₂ records in snow-dominated mountainous forested ecosystems, in particular aspen forests.

In the aspen and conifer forests we observed, summer soil CO₂ flux means and total sums varied two-fold over the study period, which experienced highly variable precipitation inputs in the context of the ~30 year record. We show that both winter snow and summer rain are major drivers of the soil CO₂ flux in both forest types, but that the sensitivity to summer rain is higher than it is to winter snow. Our long-term measurements elucidate the response of soil CO₂ flux to interannual and seasonal variability in precipitation inputs, and potentially large feedbacks to the terrestrial carbon cycle.

Data availability statement

The data that support the findings of this study are openly available at the following URL/DOI: <https://doi.org/10.6084/m9.figshare.7834406.v2>.

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