

Precipitation drives interannual variation in summer soil respiration in a Mediterranean-climate, mixed-conifer forest

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Abstract Predictions of future climate change rely on models of how both environmental conditions and disturbance impact carbon cycling at various temporal and spatial scales. Few multi-year studies, however, have examined how carbon efflux is affected by the interaction of disturbance and interannual climate variation. We measured daytime soil respiration (R_s) over five summers (June–September) in a Sierra Nevada mixed-conifer forest on undisturbed plots and plots manipulated with thinning, burning and their combination. We compared mean summer R_s by year with seasonal precipitation. On undisturbed plots we found that winter precipitation (PPT_w) explained between 77–96% of interannual variability in summer R_s . In contrast, spring and summer precipitation had no significant effect on summer R_s . PPT_w is an important influence on summer R_s in the Sierra Nevada because over 80% of annual precipitation falls as snow between October and April, thus greatly influencing the soil water conditions during the following growing season. Thinning and burning disrupted the relationship between PPT_w and R_s , possibly because of significant increases in soil moisture and temperature as tree density and canopy

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cover decreased. Our findings suggest that R_s in some moisture-limited ecosystems may be significantly influenced by annual snowpack and that management practices which reduce tree densities and soil moisture stress may offset, at least temporarily, the effect of predicted decreases in Sierran snowpack on R_s .

1 Introduction

The accumulation of atmospheric CO_2 is affected by annual fluctuations in efflux, and this variation appears to be heavily influenced by effects of changing temperature and precipitation patterns on terrestrial ecosystems (Houghton 2000). Quantifying how terrestrial carbon sequestration varies with land use change, disturbance, and climatic patterns would allow better predictions of future atmospheric CO_2 levels. However, a better understanding of carbon cycling over greater spatial and temporal scales and under different disturbance regimes is needed (Steffen et al. 1998). Multi-year measurements capturing soil respiration (R_s) variation can provide insight into variation in terrestrial carbon sequestration because R_s comprises a large portion of terrestrial carbon flux (Raich and Schlesinger 1992). R_s can vary greatly from year to year, even exceeding the variation of net ecosystem exchange, therefore potentially having a large effect on changes in ecosystem carbon uptake (Savage and Davidson 2001). While seasonal and daily patterns in R_s (reviewed by Singh and Gupta 1977) and short term disturbance effects on R_s (Algren and Algren 1965; Gordon et al. 1987; Ma et al. 2004; Tang et al. 2005b) have been well documented in many locations, multi-year studies are rare.

R_s is composed mainly of autotrophic respiration from roots and heterotrophic respiration from microbes (reviewed by Singh and Gupta 1977). Changes in the biophysical environment (e.g., temperature, soil moisture) that could influence plant or soil microbial physiological processes will likely affect R_s . Seasonal and diurnal variation in R_s is described using soil temperature alone, or with the addition of soil moisture in some ecosystems (Wildung et al. 1975; Schlentner and Van Cleve 1985; Raich and Schlesinger 1992; Euskirchen et al. 2003). On a global scale, spatial R_s variation is associated with annual precipitation and air temperature (Raich and Schlesinger 1992), and annual R_s variation is associated with temperature (Raich et al. 2002). On an ecosystem scale, however, much evidence suggests that temporal R_s variation would also be affected by seasonal precipitation (Walker et al. 1995; Galen and Stanton 1999; Hattenschwiler and Smith 1999; Weatherly et al. 2003; Ma et al. 2005; Monson et al. 2005; Smart and Penuelas 2005; Wahren et al. 2005). In dry environments, it has been reported that individual precipitation events temporarily increase respiration rates (Ma et al. 2005; Smart and Penuelas 2005), and precipitation is associated with interannual R_s variation in savannas, bushlands, and deserts (Raich et al. 2002).

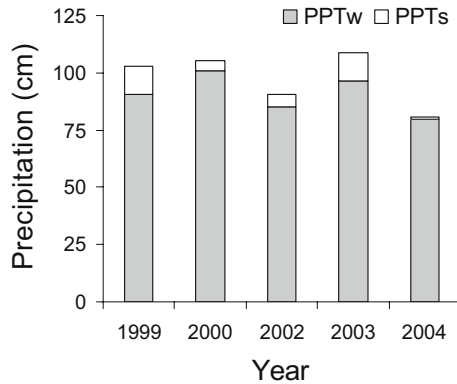
Precipitation frequency and intensity are predicted to change on both regional and global scales over the next century (Gordon and Famiglietti 2004; IPCC 2007). In fact, throughout the North American mountain west declines in snowpack have already occurred over the last half century, and they appear to be coupled with temperature increases (Mote et al. 2005). As precipitation varies interannually, year-to-year variation in R_s may be altered because the timing and magnitude of

precipitation events control many variables important to plants and microbes (e.g., snowpack, soil moisture, groundwater levels, and the length of a wet or dry season). Precipitation patterns are likely to have a particularly important role in regulating R_s in moisture-limited ecosystems, although the extent of the influence will vary by ecosystem type (Raich et al. 2002). The effect of precipitation on R_s may also vary based on disturbance and land use change. Indeed, it is clear from past work at our site and others that disturbance and land management can alter R_s (e.g., Algren and Algren 1965; Gordon et al. 1987; Ma et al. 2004; Tang et al. 2005b), but previous studies have not examined the interaction of disturbance and interannual climate on R_s over multiple years. We were interested in understanding this interaction in Sierra Nevada mixed-conifer forests, where changes in both precipitation patterns and land management are predicted (e.g., Hayhoe et al. 2004; SNFPA 2004).

Mixed-conifer forests of the Sierra experience a typical Mediterranean climate, with cold, wet winters and hot, dry summers, producing a strong seasonal water limitation that significantly affects vegetation composition and ecosystem functioning (Royce and Barbour 2001a, b). Climate change models for the area suggest more precipitation is expected to fall as rain instead of snow, resulting in a decrease in total and late winter snowpack of 30–90% (Hayhoe et al. 2004) and 50% (Miller et al. 2003), respectively. At our site, declines in snowfall may affect R_s dramatically since both heterotrophic and autotrophic respiration probably depend on water supply from snowmelt during the dry Sierran summer. However, predicting response to future declines in snowfall requires a better understanding of how precipitation levels and patterns affect year-to-year variation in R_s . In addition to experiencing altered precipitation patterns, these forests are currently being extensively treated with mechanical thinning and prescribed fire treatments to reduce fuel loads after a century of fire suppression (SNFPA 2004). At our study site, the last widespread fire occurred more than 140 years ago (North et al. 2005), while historically fall season surface fires burned every 12–17 years (McKelvey et al. 1996). In past research, we found that these treatments altered relationships between R_s , soil temperature, and soil moisture within one season (Concilio et al. 2005). In this study, we sought to determine whether larger-scale R_s drivers were also altered after burning and thinning. We measured daytime R_s over five summers (from 1999 to 2004) in burned, thinned, and undisturbed mixed-conifer to determine how changes in snowfall and land management will affect R_s during the dry Sierran summer.

The objectives of this study were to: (1) determine the effect of seasonal precipitation on interannual fluctuations in summer R_s in Sierran mixed-conifer forest, and (2) compare the influence of precipitation on summer R_s with and without burning and thinning treatments. We hypothesized that snowpack would influence summer (June–August) respiration processes and that the relationship between summer R_s and precipitation would be altered after disturbance. Since snow constitutes more than 80% of annual precipitation (Fig. 1) and plants probably depend on water from snowmelt during the dry summer season, we expected to find a positive relationship between total winter precipitation (which falls primarily as snow) and summer R_s . We expected that larger scale temporal drivers (i.e. interannual differences in precipitation) would be altered after treatments since these same treatments altered relationships between R_s , soil temperature, and soil moisture within one season (Concilio et al. 2005).

Fig. 1 Interannual precipitation patterns in Sierra Nevada mixed-conifer, including total precipitation from October of the previous year to September of the year of interest with stacked contributions of winter (Oct–April; PPT_w) and growing season (May–August; PPT_s) precipitation



2 Materials and methods

This study was conducted in the Teakettle Experimental Forest (TEF), located within the Sierra National Forest on the western slope of the Sierra Nevada mountain range of California (36° 58' N, 119° 2' W). Elevation at TEF ranges from 1,880 to 2,485 m (North et al. 2002). Site description including species composition, topography, soils and climate has been described previously (North et al. 2002). Plots were treated with three levels of thinning (none, understory, and overstory) crossed with two levels of burning (none and prescribed fire). The understory thinning removed all trees between 25 and 76 cm (10 and 30") diameter at breast height (dbh) while retaining at least 40% canopy cover. The overstory thinning removed all trees >25 cm dbh leaving only 22 regularly spaced, large diameter trees per hectare. The thinnings were applied in late fall of 2000 (thin and burn plots) and early spring of 2001 (thin-only plots). Trees were limbed and topped where they fell. The prescribed fire was applied by the Sierra National Forest following their standard operating procedures. Fuels from the thinning operations were left to dry for 1 year, and the prescribed fires were lit in fall of 2001 a week after the first substantial (2 cm) rainfall. All plots were burned within a 1 week period and the fire was extinguished by snow a week later.

Within the plot system of TEF, nine points a minimum of 25 m apart were randomly selected for sampling within each of the six treatment types, including three replicates of each of the three vegetation patch types: closed canopy (CC), ceanothus shrub (CECO), and open canopy (OC; $n = 24$ in 1999; $n = 54$ in other years). We stratified our sampling by these patch types because previous research found significant R_s differences between them (Ma et al. 2005). Measurements of soil respiration (R_s) were taken biweekly from June to August at each sampling point in the control plot in 1999, 2000, 2002, 2003, and 2004 with portable infrared gas analyzers (EGM-2 and EGM-4 Environmental Gas Monitor, PP Systems, UK) and attached SRC-1 Soil Respiration Chambers (PP Systems, UK). The treated plots were sampled from 2000 to 2004 (except for 2001, the year that treatments were applied).

Sampling points were the same for all years except 1999, during which time different points were sampled using the same representative vegetation patch types within the same plot system. R_s measurements were made on 4" diameter PVC

collars, which were inserted at least 1 week before measurements were taken to allow for settling. The EGM was calibrated weekly with standard 700-ppm CO₂ gas under ambient air pressure, and barometric pressure readings were taken at the time of sampling to correct for differences in pressure. All R_s measurements were corrected for machine error (Ma et al. 2005). We averaged R_s data by patch, month, and year for comparison with precipitation.

Precipitation data was obtained from the Pacific Gas and Electric Wishon Dam site, located 1.2 km northeast of the study site at latitude 37.003° N, longitude 118.986° W, and 2,000 m above sea level. Most precipitation at TEF occurs as snowfall between November and May (Fig. 1), but we have observed snowfall beginning as early as October. Peak stream flow rates occur with snowmelt during May, June, and early July (North et al. 2002). The growing season typically lasts from May through the end of September (Baker 1944). For this study, winter snowfall was identified as any precipitation occurring between October of the previous year and April of the year of interest (PPT_w); precipitation falling between May and August was considered growing season precipitation (PPT_s); and total annual precipitation was the combination of the two (PPT_a). Less than 0.05 cm of precipitation fell in September during the study and it was not included in the analysis. Snowfall levels during the study were within the normal range of variation for the region over the last century based on data from Cliff Camp, the nearest long-term snow survey station located 4 km northeast of TEF and at a similar elevation (1,920 m; North et al. 2002).

We used linear regression analysis to model the relationship between R_s and annual precipitation, winter precipitation, and growing season precipitation, for each of the three vegetative patch types within each of the treatment types (UN: undisturbed, UC: unburned, understory thinned, US: unburned, overstory thinned, BN: burned, unthinned, BC: burned, understory thinned and BS: burned, overstory thinned; $n = 5$ in UN and $n = 4$ in all other treatments). Residuals were graphed for all analyses and checked for regular distribution. Slopes of the linear regression lines for each patch type within the undisturbed forest were compared using dummy variable regression analysis. Slopes were considered significantly homogeneous if the calculated F value was less than the critical F value (by degrees of freedom and an alpha value of 0.05). All analyses were conducted using SAS software (V9.1, SAS Institute Inc., Cary, NC, USA) and a p -value of 0.1 was used to determine statistical significance.

3 Results

We found that total annual precipitation (PPT_a) was significantly correlated with summer R_s in undisturbed forest in each of the dominant vegetation patch types: closed canopy (CC: $p = 0.0076$, $R^2 = 0.70$) ceanothus shrub (CECO: $p = 0.0035$, $R^2 = 0.96$) and open canopy (OC: $p = 0.0693$, $R^2 = 0.72$). However, PPT_a did not explain more R_s variation than winter precipitation (PPT_w) alone, which was also significantly correlated with summer R_s in each of the vegetation patch types: (CC: $p = 0.0505$, CECO: $p = 0.0043$, OC: $p = 0.0041$; Fig. 2a). R_s increased as a function of PPT_w to the same degree in all three vegetation patch types, as evidenced by the parallel regression lines in Fig. 2a (slopes not significantly different [$F = 0.0769$, critical $F = 4.26$; dummy variable regression]). Precipitation during the growing

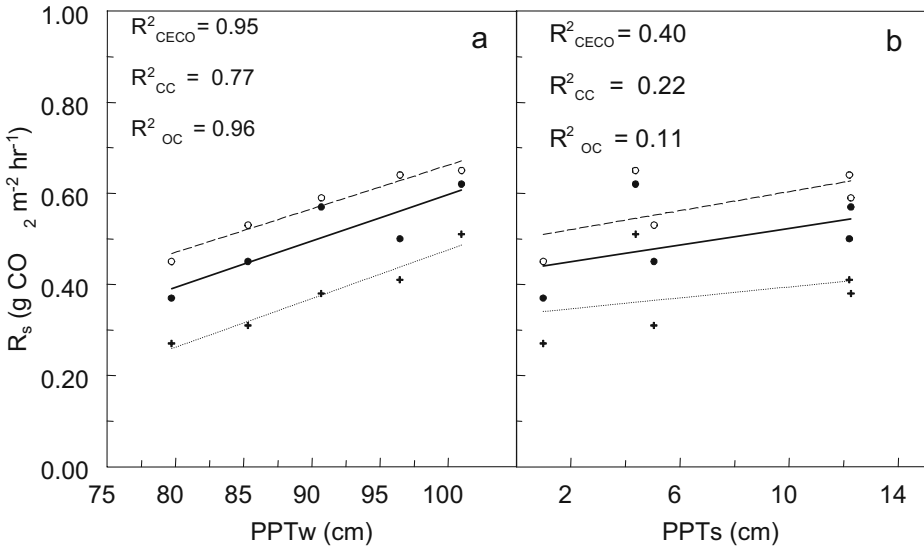


Fig. 2 Changes in soil respiration with precipitation in undisturbed forest. **a** Mean annual growing season soil respiration (R_s) by vegetative patch type versus winter precipitation (PPT_w), and **b** growing season precipitation (PPT_s). Patch types are closed canopy (CC; filled circles, solid line), ceanothus shrub (CECO; empty circles, dashed line), and open canopy (OC; crosses, dotted line). Results of linear regression analysis were used to draw the best-fit curve

season (PPT_s), between May and September, did not significantly affect R_s in any vegetation patch type (Fig. 2b).

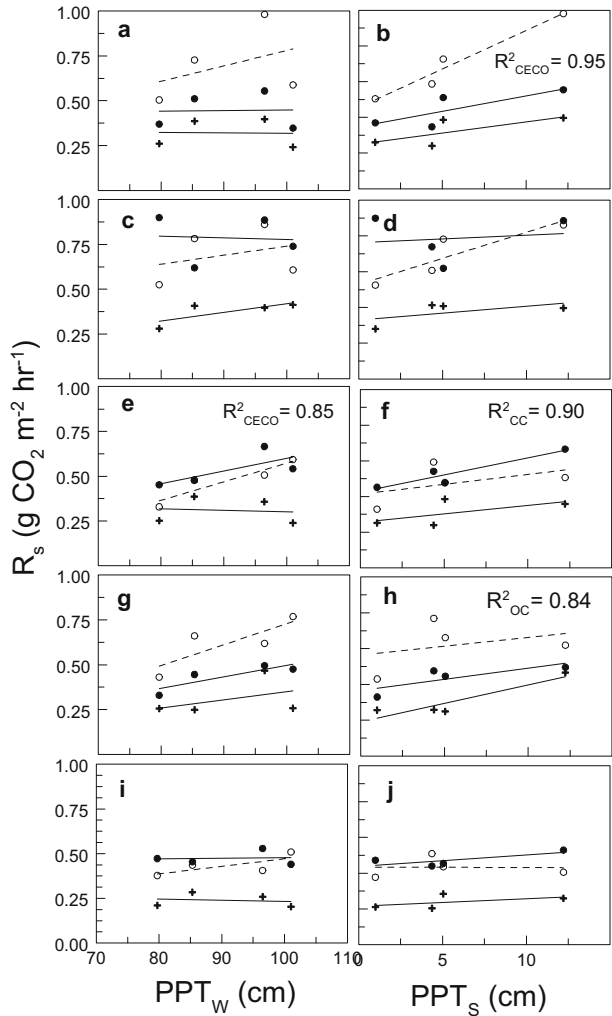
After experimental treatments, there were few significant relationships between R_s and winter or spring precipitation, although there were some exceptions (listed in Fig. 3). No clear relationship existed between R_s and PPT_w after thinning treatments (Fig. 3a, c), or thinning followed by burning (Fig. 3g, i). The only significant relationship between R_s and PPT_w in treated plots occurred in the ceanothus patches that were burned but not thinned ($p = 0.0776$; Fig. 3e), which was the least intensive treatment. In contrast, R_s was positively related to PPT_s in ceanothus patches after understory thinning alone ($p = 0.0236$; Fig. 3b), in closed canopy patches after burning alone ($p = 0.0514$; Fig. 3f), and in open canopy patches after burning following understory thinning ($p = 0.0847$, Fig. 3h). In general, even when the relationship was not significant, R_s appeared to be positively related to PPT_s in all three vegetation patch types after all but the most intensive treatment (Fig. 3b, d, f, h). In that treatment, the overstory thin-prescribed burn, there was no longer any relationship between R_s and PPT in any of the three vegetation patch types (Fig. 3i, j).

4 Discussion

4.1 Precipitation effects on R_s in undisturbed forest

Annual precipitation, coupled with air temperature, is associated with spatial R_s variation on a global scale (Raich and Schlesinger 1992). We found that within a

Fig. 3 Changes in soil respiration rate (R_s) with winter (PPT_w) and growing season precipitation (PPT_s) in burned and thinned treatments. Treatments include: **a, b** understory thinned, **c, d** overstory thinned, **e, f** burned-understony thinned, and **g, h** burned-overstony thinned treatments. Patch types are closed canopy (CC ; filled circles, solid line), ceanothus shrub ($CECO$; empty circles, dashed line), and open canopy (OC ; crosses, dotted line). Results of linear regression analysis were used to draw the best-fit curve. R^2 values are given for those relationships that were significant ($p < 0.10$)



Sierran old-growth mixed-conifer forest, annual precipitation is also an important influence on mean summer R_s . However, timing of precipitation appears to be as important as magnitude (Xu and Baldocchi 2004). At our site, previous winter’s precipitation (PPT_w) has a great effect on summer R_s —even more so than spring and summer rain (PPT_s). In the Sierra Nevada, PPT_w may be more important in explaining summer R_s than PPT_s because it constitutes more than 80% of annual precipitation (Fig. 1). Furthermore, PPT_w occurs mostly as snow, and several past studies have documented the importance of snowpack on ecosystem processes. For example, annual differences in precipitation and snowpack depth can have a significant effect on seedling occurrence and establishment (Hattenschwiler and Smith 1999), decomposition (Weatherly et al. 2003), and understory plant phenology, growth and composition (Walker et al. 1995; Wahren et al. 2005; Hurteau and North 2008). Changes in these processes would influence root growth and soil microbial activities, which determine autotrophic and heterotrophic respiration, respectively.

In addition, timing of snowmelt is an important driver of interannual variation in total annual net ecosystem exchange of coniferous forests (Monson et al. 2005).

Snowpack probably becomes an especially important influence on R_s in Mediterranean ecosystems like the Sierra Nevada that experience a strong seasonal drought (Fig. 4). Tree physiological processes and microbial decomposition depend on sufficient soil moisture levels during the growing season (Royce and Barbour 2001a, b). Soils are at field capacity shortly after snowmelt in late April when the forest generally exhibits the highest R_s of the growing season (Ma et al. 2005). Soil moisture decreases throughout the summer, from May through October, as drought sets in, and then rises again with the onset of fall rains in November (Fig. 4). Respiration rates drop throughout the summer as soil water becomes increasingly scarce (Fig. 4). Throughout most of the winter, snow covers the ground and both autotrophic and heterotrophic respiration may be limited due to constraints on photosynthesis (e.g., Lloyd et al. 2002; Monson et al. 2002) and subsequent limitations in labile carbon substrates for decomposers (e.g., Brooks et al. 2004, Mission et al. 2006). Thus, although temperature may limit respiration processes in the winter, it is clear from this and previous studies at our site (e.g., Ma et al. 2005) that moisture-availability is a greater influence on R_s throughout the growing season in this Sierran mixed-conifer forest (Fig. 4). This seasonal pattern is different than some other forests where R_s more closely matches soil temperature.

Although summer precipitation can elevate R_s temporarily (Ma et al. 2005) or cause respiration pulses (Xu and Baldocchi 2004), storms are usually ephemeral and available water is quickly evapotranspired or drained from the sandy, decomposed granitic soils typical of much of the Sierra Nevada (North et al. 2002; Gray et al. 2005). Indeed, one study conducted in the southern range of the Sierran

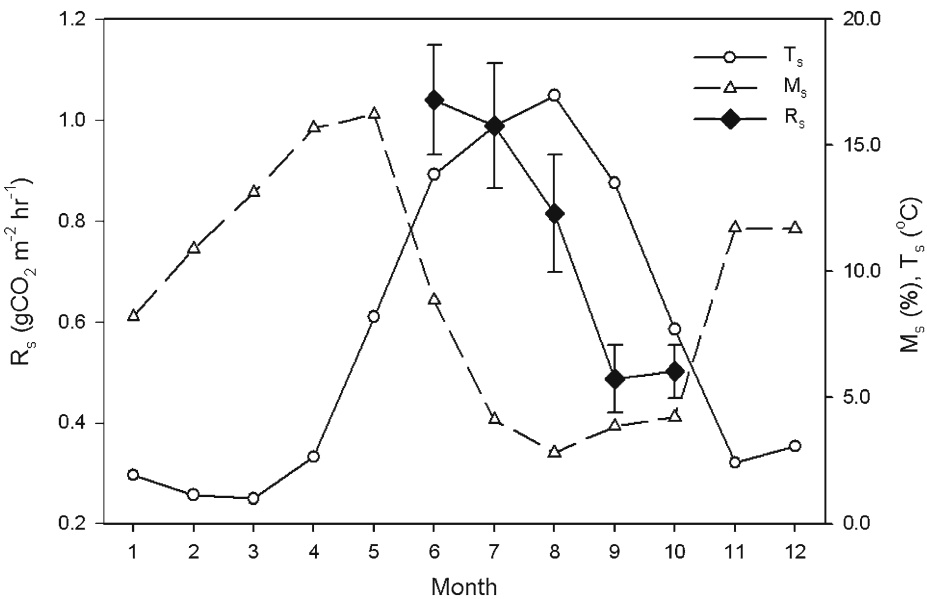


Fig. 4 Mean monthly soil respiration rate (R_s ; $\text{g CO}_2 \text{ h}^{-1} \text{ m}^{-2}$), soil temperature (T_s , $^{\circ}\text{C}$), and soil moisture (M_s , %) in 2000 in undisturbed forest. Bars represent one standard error from the mean

mixed-conifer found that watersheds under extreme water deficits lose about 70% of water from precipitation to evapotranspiration from the surface soil, about 15% transpired from deep roots, with the remaining 15% available for streamflow (Franco-Vizcaino et al. 2002). Water from snowmelt, rather than rain, is needed to sustain plant physiological processes in the Sierra Nevada (Tang et al. 2005a). Soil moisture only remains elevated in surface layers early in the season (Fig. 4), while groundwater is accessible far longer. At our site, stable isotopic analysis (Agneta Plamboeck) and dendrochronology research (Hurteau et al. 2007) suggest larger trees may access snowmelt supplied groundwater into July and early August after near-surface soil moisture levels become low. Our results show that R_s may remain elevated even after surface moisture conditions have already dropped markedly (i.e. in July and August; Fig. 4). Because Sierran trees can tap into groundwater (Arkley 1981; Anderson et al. 1995; Hubbert et al. 2001), high rates of photosynthesis may continue when surface soil moisture is extremely low. Photosynthesis can then drive both autotrophic and heterotrophic respiration by directly fueling roots with carbon for maintenance and growth and by indirectly fueling microbes with root exudates (Hanson et al. 2000, Brooks et al. 2004, Mission et al. 2006). With deeper snowpack, groundwater levels may remain elevated longer into the growing season. Soil moisture levels may also remain above the permanent wilting point longer, extending the onset of summer drought. Thus, with more snow, we would expect the active growing season to be expanded, and respiration to remain elevated longer into the summer.

In this study, we measured R_s in summer alone, but believe that our results may provide insight into total interannual R_s variation. Because of the well-documented importance of the spring and summer seasons for growth and productivity in the Sierra Nevada (Royce and Barbour 2001a, b), it is likely that the most dramatic interannual variations in R_s occur during this time period. Year-round data from another Sierran site shows a peak in R_s in the spring and summer and very little activity over winter, when the ground is covered with snow (Mission et al. 2006). Our last measurements in October indicate low R_s rates, when soils are dry and temperatures are low (Ma et al. 2005). Our site's montane, Mediterranean climate has a rapid shift from summer to winter, typically during October, after which snow covered soils have low moisture levels even though temperatures remain above freezing (North et al. 2002; Ma 2003). Once the ground is snow covered, we suspect soil conditions influencing respiration vary little year to year. We, however, were unable to make winter measurements due to deep snow pack conditions (typically >2 m), relative inaccessibility, and, at the time, developing but uncertain field methods. We encourage future research on year-round R_s variation, for a more comprehensive understanding of precipitation and disturbance effects.

Linking historical snow records in the Sierra with our results suggests high year-to-year variability in summer soil carbon efflux, and perhaps soil carbon sequestration. Sierran snowpack has high variability due to periodic El Niño and La Niña events. For example, at Fred Meadow, 15 km northwest of and at the same elevation as our study site, April snow depth between 1930 and 2005 ranged from 0 to 351.5 cm (mean = 126 cm; <http://cdec.water.ca.gov/cgi-progs/snowQuery>). During our sampling period, 2000 to 2004, winter precipitation only varied from 79.7 to 101.0 cm. Yet within this period of relatively low variability, mean daytime summer R_s was significantly different by year (Concilio et al. 2006). We calculated the total R_s from June to August for the forest based on a weighted summation of the area of

each patch type within mixed conifer and found that it ranged from 191 ± 53 g C per square meter during the driest year (2004) to 314 ± 44 g C per square meter during the wettest year (2000). Changes in future precipitation patterns, which are predicted to be much larger than the range in annual totals during this study, are likely to have significant effects on forest carbon sequestration.

Although R_s is significantly different among the three dominant vegetation patch types at TEF (Ma et al. 2005), we found that all three patch types had a similar response to changes in precipitation. This suggests a common soil respiration response can be predicted in spite of localized differences in vegetation patch type. Moreover, the differences in summer R_s between patch types within the same year (ranging from about 20–40%) were less than the differences within each patch type between a wet year and a dry year (68%, 41%, and 85% in CC, CECO, and OC, respectively). This higher annual variability suggests future changes in snowfall may be equally or more influential over summer R_s than changes in patch composition.

4.2 Precipitation effects on R_s after thinning and burning

Thinning and burning treatments disturbed the forest through removal of understory and overstory canopy, partial elimination of the forest organic horizon, and darkening of the forest floor. Disturbed areas were often exposed to open canopy and bare ground, which are two major factors for defining one of the three dominant vegetation patch types—open canopy (OC). Thus, we expected that the relationship between R_s and precipitation after treatments would be similar to that found in open canopy patches (OC). All burning and thinning treatments, however, appeared to have decreased the dependence of mean summer R_s on PPT_w in this mixed-conifer Sierran forest, suggesting that thinning and burning treatments profoundly impact R_s by changing stand conditions associated with R_s such as canopy cover, root occupation, soil organic matter distribution, soil microbial biomass and activities, and soil properties. Among these factors, canopy removal may be particularly important because of the influence of photosynthesis on soil respiration (Högberg et al. 2001). Further process-based studies will improve our understanding of the impacts of thinning and burning on R_s and the role of ecosystem functioning in carbon sequestration.

Variations did exist in the degree to which each treatment and vegetation patch type combination affected relationships between R_s and precipitation. This result was expected based on past research at the same site which found that: (a) interannual patterns in daytime summer R_s differed after disturbance (Concilio et al. 2006), (b) thinning and burning affected the soil environment differently (Ma et al. 2004; Concilio et al. 2005), and (c) seasonal and spatial drivers varied by patch type post-disturbance (Ma et al. 2004; Concilio et al. 2005). The degree of decoupling may serve as a good indication of the degree to which each disturbance treatment impacted soil respiration. For example, the most intensive treatment, burning following overstory thinning, appeared to have the most serious impact on soil respiration since no relationship remained in any patch between R_s and PPT_a , PPT_w , or PPT_s .

All disturbance treatments appeared to have disrupted the relationship between summer R_s and PPT_w , possibly due to changes in temperature and soil moisture regimes, biological variables, and soil properties. For example thinning and burning can increase soil temperatures (Concilio et al. 2005) and surface wind speeds,

changing the timing and intensity of snowpack runoff (Storck et al. 1999). Disturbance caused a shift in seasonal and spatial drivers of R_s at our site (Ma et al. 2004; Concilio et al. 2005, 2006), suggesting interannual drivers would also be affected. The lack of a clear relationship between PPT_w and R_s in thinned treatments (with or without burning) may be due to a reduction in moisture constraint. Removal of trees likely led to an increase in soil water inputs due to decreased interception of precipitation by the canopy and a decrease in evapotranspiration and competition for water in the summer when moisture is limiting. In plots that were thinned but not burned, soil moisture did increase after treatment (Concilio et al. 2005), but no change in soil moisture was reported after burning treatments alone or after understory thinning (Ma et al. 2004; Concilio et al. 2005). Soil moisture was measured within the top 15 cm of the soil surface, which would not reflect moisture available in deeper profiles and in bedrock fissures. Sierran trees tap into deep water reserves in weathered bedrock during the summer drought (Jones and Graham 1993; Witty et al. 2003), which is recharged through snowmelt. At one Sierra Nevada site, 70% of the water used by Jeffrey pine during the growing season (mid-June to October) was from stores in weathered bedrock (Witty et al. 2003). At our site, these reserves may have remained replenished long into the growing season after thinning and burning, even in years with less snowfall. Although increased litter from logging slash might also conserve soil moisture by acting as a protective mulch, we found no significant difference between litter depth in control or thinned plots during past research at our site (Concilio et al. 2005). We, therefore, believe that most of the moisture retention may be due to a decrease in evapotranspiration in the thinned sites.

Because of a small sample size and limited statistical power, some post-disturbance relationships between R_s and precipitation may not have been captured. For example, a shift from R_s dependence on PPT_w to PPT_s may have occurred after disturbances due to changes in microclimate or in the partitioning of autotrophic and heterotrophic respiration. It is also unclear from our data how long treatment-induced disruptions will last. Longer-term monitoring of R_s at our study site will serve to elucidate some of these patterns and responses.

4.3 Study implications

Our study may have a wide application to snow-dependent, moisture-limited forests, such as those in the Mediterranean climate zone. Although other studies on interannual variation in R_s exist, we are not aware of any that have been conducted in a Mediterranean-climate forest, nor any that have reported such a strong dependence on precipitation patterns. One study found that mean annual R_s was influenced predominantly by temperature and secondarily by precipitation across many sites (Raich and Schlesinger 1992); whereas, another reported that mean annual ecosystem respiration was influenced by the combination of temperature, deep snow, and summer drought in a deciduous forest (Goulden et al. 1996). In contrast, our models appeared relatively robust with winter precipitation alone. Further studies are needed in other ecosystems where seasonal moisture is severely limited to determine if seasonal precipitation is consistently an important influence on R_s .

This study indicated that interannual changes in summer R_s in old-growth mixed-conifer forest were determined by winter precipitation, which mainly falls as snow in this Mediterranean climate. If snowpack in the Sierra Nevada declines over the

next century and snowmelt begins earlier, as predicted by the general circulation models (Miller et al. 2003; Hayhoe et al. 2004), summer R_s will likely decrease throughout the region as microbial and plant respiratory processes are constrained by limited soil moisture. Future mechanistic models of ecosystem productivity and carbon sequestration will have to consider the effects of climate-induced changes in photosynthesis and respiration (Hui et al. 2003), and long-term empirical studies can contribute to making these models more robust. This study provides baseline data to compare R_s dependence on snowfall in above and below average snowfall years and during reoccurring climatic events such as El Niño and La Niña in old-growth forest and after experimental treatments.

We found that disturbance treatments can disrupt the relationship between R_s and PPT_w , suggesting models describing carbon flux should incorporate disturbance history and effects. After a century of fire suppression, fuels management practices are common throughout the western US forests. Models that fail to account for management effects on drivers of R_s may have large inaccuracies. Longer-term monitoring of disturbed sites is needed to better quantify the degree to which precipitation affects R_s in seasonally dry forests. Our results, however, suggest that widely used management practices may initially reduce summer moisture stress and decouple the tight relation between snowpack and soil respiration.

5 Conclusions

We report three main findings: (1) winter precipitation drives daytime summer soil respiration (R_s) in an old-growth, mixed-conifer Sierra Nevada forest, (2) although vegetative patches have significantly different R_s (Ma et al. 2005) they have a similar positive response to precipitation, and (3) disturbances disrupted the relationship between precipitation and R_s . In general, our findings, in conjunction with past research at TEF, strongly suggest that R_s in some moisture-limited ecosystems may be significantly influenced by changes in annual snowpack conditions. Management practices, however, that reduce tree densities and soil moisture stress may offset, at least temporarily, the effect of predicted decreases in Sierran snowpack on R_s .

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