Agricultural and Forest Meteorology 214–215 (2015) 201–207

Contents lists available at ScienceDirect

Agricultural and Forest Meteorology

journal homepage: www.elsevier.com/locate/agrformet

Does soil respiration decline following bark beetle induced forest mortality? Evidence from a lodgepole pine forest

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ARTICLE INFO

Article history:
Received 19 November 2014
Received in revised form 22 July 2015
Accepted 17 August 2015

Keywords:
Soil CO_2 efflux
Soil respiration
Photosynthesis
Mountain pine beetle
Lodgepole pine

ABSTRACT

Lodgepole pine (*Pinus contorta* var. *latifolia*) forests across western North America have been undergoing a major mortality event owing to a mountain pine beetle (*Dendroctonus ponderosae*) infestation. We studied biotic and abiotic drivers of growing season soil respiration in four mature stands experiencing different levels of mortality between 2008 and 2012 in southeastern Wyoming, USA. Bark beetle infestation significantly altered forest structure during the 5-year study period. Live basal area (LBA) declined and mortality ranged from near zero to more than 80% in stands with the lowest and highest mortality, respectively. LBA explained 66% of the spatial variation in peak growing season soil respiration, which ranged from $1.4 \pm 0.1\ \mu mol\ m^{-2}\ s^{-1}$ in stands with lowest LBA to $3.1 \pm 0.2\ \mu mol\ m^{-2}\ s^{-1}$ with highest LBA. However, within stands, soil respiration did not change over the five-year study period, likely because pre-infestation LBA governed ecosystem-level differences. During peak growing season, soil respiration was significantly correlated with fine root biomass and mid-day photosynthetic photon flux density, providing strong evidence that autotrophic respiration dominated the forest soil respiration flux. Each factor predicted from 35% to 55% of seasonal soil respiration variability with the highest correlation coefficients in stands with the lowest mortality. However, we did not observe significant changes in the peak growing season soil respiration over time within stands undergoing beetle infestation, suggesting that remaining soil respiration activity in dead stands may be attributed to heterotrophic activity and surviving vegetation. Ecosystem modeling often does not adequately represent complex changes in stand structure following beetle infestation, but these dynamic processes should be included to better predict disturbance effects on carbon (C) cycling.

1. Introduction

Forests assimilate more carbon (C) in the form of carbon dioxide (CO_2) than they release into the atmosphere by ecosystem respiration (Randerson et al., 2002) unless an ecosystem disturbance releases a portion back to the atmosphere. Soil respiration (also referred to as “soil CO_2 efflux”) is a major component of the ecosystem C balance and consists of plant- and microbe-derived respiration (Luo and Zhou, 2006). Understanding both autotrophic and heterotrophic components is essential for predicting how soil respiration affects the global C cycle because they have different responses to seasonality, substrate availability, and other environmental factors including disturbances (Luo and Zhou, 2006).

Soil respiration is biologically driven and subject to similar environmental controls as photosynthesis. Respiratory processes of plant roots and mycorrhizal microorganisms, roughly half of the total soil respiration (Högberg et al., 2009), are highly dependent on recent photosynthates (Högberg et al., 2001). These activities are characterized by large seasonal fluctuations typically due to temperature, moisture and light shifts (Davidson et al., 1998; Luo and Zhou, 2006; Makita et al., 2014). Respiration by plant roots and mycorrhizal symbionts is considered to be more sensitive to changes in temperature, compared to respiration by soil without roots (Boone et al., 1998). The positive response of soil respiration to temperature explains on average 80% of the seasonal variation in CO_2 fluxes, but may be confounded by changes in soil moisture that can moderate temperature sensitivity (Bowden et al., 1998; Davidson et al., 1998).

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http://dx.doi.org/10.1016/j.agrformet.2015.08.258
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Following forest disturbance, recovery of the ecosystem C balance occurs over differing time scales that depend on the severity and type of disturbance (Odum, 1969). For instance, ground fire burns needles and twigs on trees and the O horizon of the forest floor (Romme et al., 2009), harvesting removes larger woody materials (Grand et al., 2014) and insect-induced disturbance kills trees and is accompanied by increased and then decreased needle fall over a few years (Norton et al., 2015). These differences influence post-disturbance soil respiration and the dynamics of decomposition on the forest floor. Photosynthesis and net ecosystem production are greatly diminished or lost altogether following insect-induced disturbance which varies depending on stand mortality levels (Brown et al., 2010). However, five or more years following insect-induced disturbance, the development of understory vegetation (Norton et al., 2015) and the release of surviving trees from competition (Hubbard et al., 2013) plays an important role in sequestering C, potentially compensating for the reduction in production due to insect-induced mortality (Brown et al., 2010; Moore et al., 2013).

Predicting the effects of forest disturbances on C balance is complicated by many factors. The overall effect of insect-induced disturbance on ecosystem respiration (including respiration from aboveground and belowground biomass) can be insignificant (Reed et al., 2014; Speckman et al., 2015), but the absolute response of each respiration component requires further examination (Speckman et al., 2015). Soil autotrophic respiration declines following tree mortality (Högberg et al., 2001), but heterotrophic respiration may increase for a short period of time (LundmarkThelin and Johansson, 1997; Bhupinderpal et al., 2003). On the other hand, the increased input of N-rich needles (Morehouse et al., 2008; Norton et al., 2015) may stimulate photosynthesis of surviving vegetation, increasing C storage while neither increasing nor decreasing heterotrophic respiration (Olsson et al., 2005). However, the underlying mechanisms of altered respiration processes have not been completely identified. This large uncertainty is mainly due to the lack of respiration component data at different insect-induced mortality levels.

In this study, we measured soil respiration for five years in a lodgepole pine (*Pinus contorta* var. *latifolia*) forest that was affected by a mountain pine beetle (*D. ponderosae*) infestation (hereafter "beetle infestation"). The objective of this study was to investigate how soil respiration responded to lodgepole pine forest mortality due to the beetle infestation. We quantified (1) temporal changes in soil respiration (seasonal and time since infestation) and how these changes were affected by stand-level mortality, and (2) abiotic and biotic factors responsible for variations observed in soil respiration during the post-disturbance years. We expected that soil respiration rates and relationships with environmental drivers would vary with beetle infestation status.

2. Materials and methods

2.1. Study area

This study was conducted in a lodgepole pine forest at 2745 m elevation in the Medicine Bow National Forest, southeastern Wyoming (41°3′ N, 106°7′ W; Fig. S1). The climate in the study area is cold in winter and moderate in summer with approximately 900 mm annual precipitation and −2.0 °C mean annual temperature (USDA, SNOTEL, Wyoming). Most of the annual precipitation falls as snow that accumulates from October to April and persists until June (Curtis and Grimes, 2004). During the study period, approximately 13% of the precipitation fell during July–September (hereafter "peak growing season"). Mean temperature for the peak growing seasons in 2008–2012 varied from 6.5 °C to 8.0 °C (Wyoming SNOTEL Site Cinnabar Park (1046) – NRCS National Water and Climate Center).

Supplementary material related to this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agrformet.2015.08.258.

2.2. Stand characteristics

In the spring and summer of 2009, four stands with known beetle infestation status were instrumented for monitoring: beetle infested in 2007 (hereafter BB07); beetle infested in 2008 (hereafter BB08); beetle infested in 2009 (hereafter BB09); and an uninfested stand (hereafter UN). The experimental stands were located on a glacial outwash plain with slopes less than two percent comprising a total area of 35 hectares (Fig. S1) and shared the same soil characteristics (Norton et al., 2015). The study area was located within the footprint of an 18-m tall eddy covariance tower (Reed et al., 2014). In 2009, all stands were dominated by lodgepole pine trees in the overstory with little to no understory present. Five plots per stand, approximately 150 m^2 each, were randomly located to represent the spatial variations in vegetation characteristics of the stand. Tree ages in all stands ranged between 66- and 90-years, and average (±se) tree diameter at breast height (DBH) was 23 ± 1.6 cm in BB07, 24 ± 0.4 cm in BB08, 14 ± 0.4 cm in BB09, and 10 ± 0.8 cm in UN. Trees with DBH $\leq$10 cm were not infested by beetles (UN) compared to trees with DBH >10 cm (BB07, BB08 and BB09) (Table 1).

2.3. Soil respiration and environmental measurements

Soil respiration was measured using an EGM4 CO_2 Gas Analyzer and a SRC1 Soil Respiration Chamber (PP Systems, Amesbury, MA) sealed onto three permanently inserted PVC collars, which were randomly located within each plot. A sampling day was 4 stands × 5 plots × 3 subplots, totaling 60 measurements. Soil respiration measurement times were chosen randomly between 9:00 AM and 6:00 PM. Any presence of lichen or moss in the collars was recorded and

Table 1
Total basal area (TBA), live basal area (LBA), and mortality rates in uninfested (UN) and infested by beetles in 2009 (BB09), 2008 (BB08) and 2007 (BB07) stands from 2008 to 2012. Numbers are mean ± se. TBA includes both live and dead tree basal areas. Lower case letters demonstrate statistical significance of differences within a column and year at $\alpha \leq 0.05$ based on ANOVA Tukey's HSD test (DF = 5). Inf. year – beetle infestation year.

Obs. year	Stand	Inf. year	TBA (m^2 ha^{-1})	LBA (m^2 ha^{-1})	Mortality (%)
2008[*]	UN	0	115 ± 8.6 a	107 ± 15 a	7
	BB09	0	40.6 ± 8.6 a	40.1 ± 2.1 a	1
	BB08	0	47.8 ± 8.6 a	45.6 ± 3.2 a	5
	BB07	1	29.3 ± 11 a	16.0 ± 5.0 a	45
2009[*]	UN	0	71.5 ± 14 a	71.5 ± 14 a	0
	BB09	0	42.0 ± 2.6 a	34.6 ± 1.1 b	18
	BB08	1	45.5 ± 1.7 a	29.7 ± 3.1 b	35
	BB07	2	41.3 ± 5.0 a	22.6 ± 7.3 b	54
2010	UN	0	78.5 ± 6.8 a	72.1 ± 9.1 a	8
	BB09	1	37.0 ± 2.4 b	33.5 ± 2.8 b	9
	BB08	2	40.9 ± 6.2 b	18.6 ± 4.5 b	55
	BB07	3	34.4 ± 4.4 b	7.8 ± 3.7 b	77
2011	UN	0	72.7 ± 6.1 a	66.6 ± 9.0 a	8
	BB09	2	37.4 ± 3.3 b	27.1 ± 3.7 b	28
	BB08	3	40.3 ± 4.6 b	9.1 ± 3.3 b	77
	BB07	4	35.7 ± 4.5 b	6.0 ± 3.2 b	83
2012	UN	0	66.4 ± 8.2 a	60.3 ± 8.4 a	9
	BB09	3	36.1 ± 1.7 b	25.5 ± 2.5 b	29
	BB08	4	44.3 ± 2.0 b	11.9 ± 4.0 b	73
	BB07	5	33.0 ± 5.1 b	5.9 ± 3.2 b	82

[*] Survey area was not set as permanent plots; Measurements in 2010–2012 are made in the permanent surveying area.

any vegetation growing inside a collar was clipped prior to measurements. The gas analyzer was calibrated once a month in the laboratory against a CO_2 standard (1020 ppm). The flux measurements were taken twice per month in 2009, 2010, and 2011, and once per month in 2008 and 2012 from the end of May to beginning of October. Next to each soil respiration collar, we removed the fresh litter and recorded temperature at 5 cm depth in soil and volumetric soil moisture content (VWC) using a Theta-Probe (Decagon Devices, Inc., Pullman, WA, USA) in the top 6 cm of mineral soil below the litter. Soil samples were regularly collected for gravimetric soil water content (SWC) (Gardner, 1986) and compared to the in situ VWC measurements for calibration. Photosynthetic photon flux density (PPFD; expressed in $\mu mol\ m^{-2}\ s^{-1}$) was measured using a LI-190SA (Quantum sensor, Li-Cor Inc.) mounted on the 18-m tower above the tree canopy.

2.4. Biomass indices

Species and DBH of trees were measured annually at each plot. Identification of beetle infestation was conducted visually by monitoring the presence or absence of exit holes, pitch tubes and sawdust. The uninfested stand consisted of live trees with no sign of the presence of the beetles. Live basal area (LBA) was calculated using DBH of live trees and total basal area (TBA) was summed for all trees (live plus dead) in the plots; insect-induced mortality was calculated as 1 – (LBA/TBA). The three largest trees were selected in each plot for plot-level tree age using an increment borer.

Mineral soil samples (0–10 cm) were collected from each plot at the end of August each year. Soils were sampled from a 100 cm^2 (10 cm × 10 cm) area and to 10 cm deep due to very rocky subsoil beneath this depth. Within 24 h after sampling, fresh soil samples were sieved with a 2 mm-sieve and roots were extracted. Extracted roots were categorized by size as fine (diameter < 2 mm) and coarse (diameter > 2 mm). Roots were washed, oven dried (65° C for 48 h), and weighed to determine root biomass per unit area.

2.5. Statistical analysis

TBA, LBA, soil water content and temperature, and soil respiration were analyzed using a two factor analysis of variance, within a completely randomized design, with repeated measures taken on one factor. Factors studied were stand and sampling date, plus their interaction; sampling date was the repeated measure. All terms in the repeated measures analysis were considered significant at $\alpha \leq 0.05$ and post hoc tests were conducted using Tukey's HSD. Statistical analyses used the GLM procedure in SAS (r.9.3 TS1M1, SAS Institute, Cary, NC). We used simple linear regressions to assess relationships between soil respiration and biotic (fine root biomass, TBA and LBA) and abiotic drivers (total monthly precipitation, maximum PPFD and soil moisture).

3. Results

Stand structure varied across the study area, as would be expected in a conifer forest undergoing disturbance and succession (Fig. S1). TBA, a proxy for determining aboveground and belowground vegetation productivity, was on average 40 $m^2\ ha^{-1}$ in the beetle infested stands and 70 $m^2\ ha^{-1}$ in UN (Table 1). LBA declined rapidly during the first three years of the study in BB07 and BB08, but declined gradually in BB09, while in UN it was unchanged during the five-year study (Table 1). BB07 and BB08 demonstrated tree mortality of 54% and 55%, respectively, after two years and 77% after three years following the infestation for both stands. The highest tree mortality of 82–83% was reported in BB07 during the fourth and fifth years following beetle infestation. In contrast, BB09 had a mortality of 9% in the first year and 29% in the second and third years of beetle infestation (Table 1).

Table 2
Peak growing season averages of soil water content (SWC) and temperature in uninfested (UN) and infested by beetles in 2009 (BB09), 2008 (BB08) and 2007 (BB07) stands, 2008–2012. Lower case letters demonstrate statistical significance of differences within a column and year at $\alpha \leq 0.05$ based on ANOVA Tukey's HSD test (DF = 5). N.A. – data not available and Inf. year – beetle infestation year.

Obs. year	Stand	Inf. year	SWC ($g\ g^{-1}$)	Soil temperature (°C)
2008	UN	0	N.A.	11.8 ± 0.35 a
	BB09	0	N.A.	12.2 ± 0.28 a
	BB08	0	N.A.	12.1 ± 0.12 a
	BB07	1	N.A.	12.5 ± 0.79 a
2009	UN	0	0.16 ± 0.03 b	17.5 ± 0.44 ab
	BB09	0	0.14 ± 0.03 b	16.6 ± 0.43 b
	BB08	1	0.36 ± 0.06 a	17.5 ± 0.62 ab
	BB07	2	0.23 ± 0.03 ab	19.2 ± 0.75 a
2010	UN	0	0.16 ± 0.06 a	9.2 ± 0.28 c
	BB09	1	0.12 ± 0.03 a	11.2 ± 0.19 b
	BB08	2	0.29 ± 0.04 a	9.3 ± 0.28 c
	BB07	3	0.23 ± 0.05 a	12.6 ± 0.43 a
2011	UN	0	0.19 ± 0.02 b	16.0 ± 1.17 a
	BB09	2	0.15 ± 0.02 b	13.6 ± 0.91 a
	BB08	3	0.33 ± 0.03 a	17.6 ± 0.91 a
	BB07	4	0.21 ± 0.02 b	15.2 ± 0.64 a
2012	UN	0	0.36 ± 0.07 a	22.6 ± 0.21 a
	BB09	3	0.27 ± 0.06 a	21.5 ± 0.76 a
	BB08	4	0.37 ± 0.06 a	21.9 ± 1.53 a
	BB07	5	0.32 ± 0.06 a	18.0 ± 0.77 b

Although seasonal variations were apparent in soil moisture and temperature, when analyzed by year the peak growing season soil water content was significantly higher in BB08 in 2009 and 2011 than other stands. Soil temperature was highest in BB07 in 2009 and 2010, and lowest in 2012 compared to the other stands (Table 2).

Soil respiration at all the stands in the lodgepole pine forest followed a seasonal pattern with differences among stands most pronounced during the middle of the growing season (Fig. 1). Across all four stands the mean soil respiration was 1.47 ± 0.09 $\mu mol\ m^{-2}\ s^{-1}$ during the early growing season, 2.14 ± 0.10 $\mu mol\ m^{-2}\ s^{-1}$ during the peak growing season, and 0.95 ± 0.08 $\mu mol\ m^{-2}\ s^{-1}$ during the late growing season. During the five peak growing seasons, June through early September, soil respiration was the lowest in BB07 (1.41 ± 0.11 $\mu mol\ m^{-2}\ s^{-1}$), followed by BB08 (1.95 ± 0.13 $\mu mol\ m^{-2}\ s^{-1}$), BB09 (2.46 ± 0.16 $\mu mol\ m^{-2}\ s^{-1}$), and the highest in UN (3.08 ± 0.21 $\mu mol\ m^{-2}\ s^{-1}$).

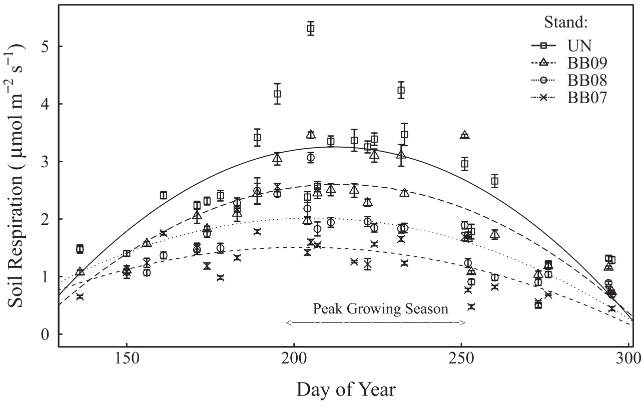

Fig. 1. Seasonal changes of soil respiration in stands with different beetle infestation histories in a lodgepole pine forest, southeastern Wyoming, 2008–2012. Stands were uninfested (UN) and infested by beetles in 2009 (BB09), 2008 (BB08) and 2007 (BB07). Error bar represents mean ± se of each sampling date (n = 5). The horizontal arrow indicates the peak growing season interval (DOY: 192–252). Fitted lines are parabolic fit of the data.

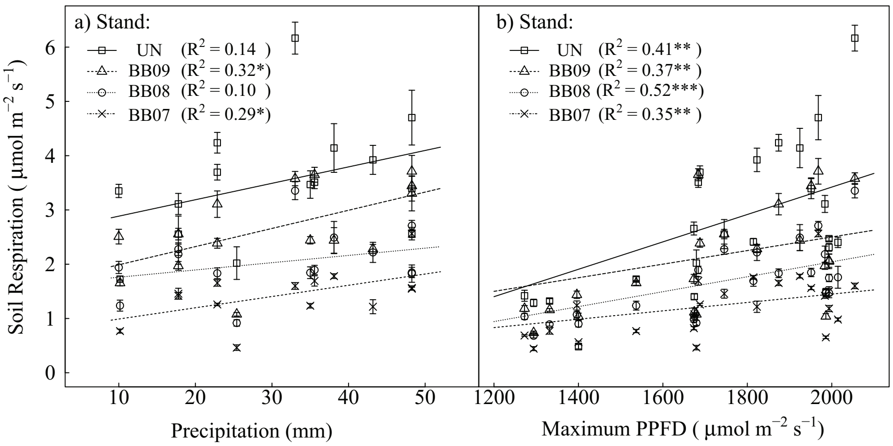

Fig. 2. Relationships of soil respiration with (a) total monthly precipitation and (b) mid-day photosynthetic photon flux density (maximum PPFD) during five growing seasons, 2008–2012. Stands were uninfested (UN) and infested by beetles in 2009 (BB09), 2008 (BB08), and 2007 (BB07). Precipitation data obtained from Wyoming SNOTEL Site Cinnabar Park (1046) – NRCS National Water and Climate Center. Statistical significance: $^{***}p < 0.0001$, $^{**}p = 0.001$, and $^{*}p = 0.01$.

Soil respiration was not correlated to soil temperature (Fig. S2) or air temperature (data not shown) across years or sites; neither was it correlated with soil water content (data not shown). However, soil respiration did increase with total monthly precipitation in some stands; 29% and 32% of variation in soil respiration was explained in BB07 ($p = 0.046$) and BB09 ($p = 0.029$), respectively, while no significant responses were observed at BB08 and UN (Fig. 2a). Observed daily maximum PPFD ranged from 1300–2000 μmol $\text{m}^{-2}\,\text{s}^{-1}$, and mid-day maximum PPFD was significantly and positively correlated to soil respiration at all stands, explaining 35%, 37%, 41% and 52% of the variability in BB07 ($p = 0.0025$), BB09 ($p = 0.0026$), UN ($p = 0.0010$) and BB08 ($p < 0.0001$), respectively, (Fig. 2b). The slope of this relationship appears to correlate with the degree to which each stand suffered beetle-induced mortality (Fig. 2b). In BB07, the stand first infested, the slope of the regression line was 0.0012, while in the uninfested stand it was more than double that, at 0.0029. In other words, with greater LBA, equal increases in maximum PPFD resulted in greater increases in soil respiration.

Supplementary material related to this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agrformet.2015.08.258.

Belowground and aboveground biotic changes significantly explained the variations in soil respiration following beetle infestation. Soil respiration was significantly correlated with both TBA ($R^2 = 0.51$, $p < 0.0001$; Fig. 3a), and more strongly with LBA ($R^2 = 0.66$, $p < 0.0001$; Fig. 3b). Forest die-off in response to beetle infestation progressed over the five years, with 20–32% mortality each year, in the first three years after beetle infestation, and declining to less than 10% mortality per year in the fourth and fifth years (Table 1). Across stands, peak growing season soil respiration declined significantly as forest mortality increased ($R^2 = 0.61$, $p < 0.0001$). Linear models suggest that if forest mortality reached 100%, soil respiration would be one-third the pre-beetle rate (Fig. 4a). Average rates of the peak growing season soil respiration were the highest in UN followed by BB09, BB08 and the lowest in BB07, but rates did not vary significantly within a stand over time since disturbance (Fig. 4b).

On average, fine root biomass was lower in BB07 ($115.6 \pm 20\,\text{g}\,\text{m}^{-2}$) and BB08 ($114.0 \pm 19\,\text{g}\,\text{m}^{-2}$) compared with BB09 ($288.7 \pm 33\,\text{g}\,\text{m}^{-2}$) and UN ($232.8 \pm 38\,\text{g}\,\text{m}^{-2}$), and root biomass was significantly correlated with LBA across all stands ($R^2 = 0.33$, $p = 0.04$; Fig. 5a). Furthermore, fine root biomass also significantly explained variation in soil respiration ($R^2 = 0.55$, $p = 0.0087$; Fig. 5b).

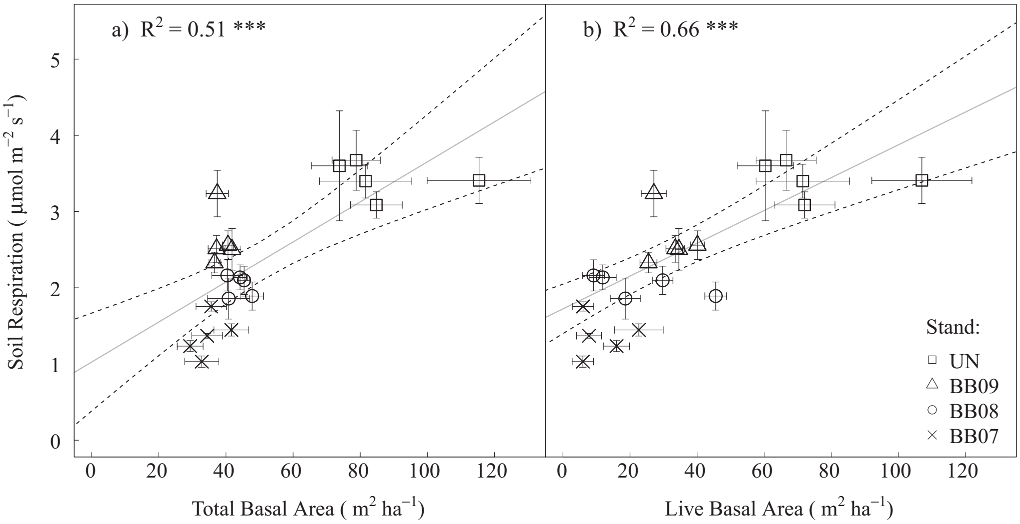

Fig. 3. Correlations of the peak growing season soil respiration with (a) total basal area and (b) live basal area at stands with different beetle infestation history, 2008–2012. Each data point represents the peak growing season average of five plots for that year ($n = 5$). Stands were uninfested (UN) and infested by beetles in 2009 (BB09), 2008 (BB08) and 2007 (BB07). Fitted line is a linear fit and dashed line represents 95% CI. Statistical significance: $^{***}p < 0.0001$, $^{**}p = 0.001$, and $^{*}p = 0.01$.

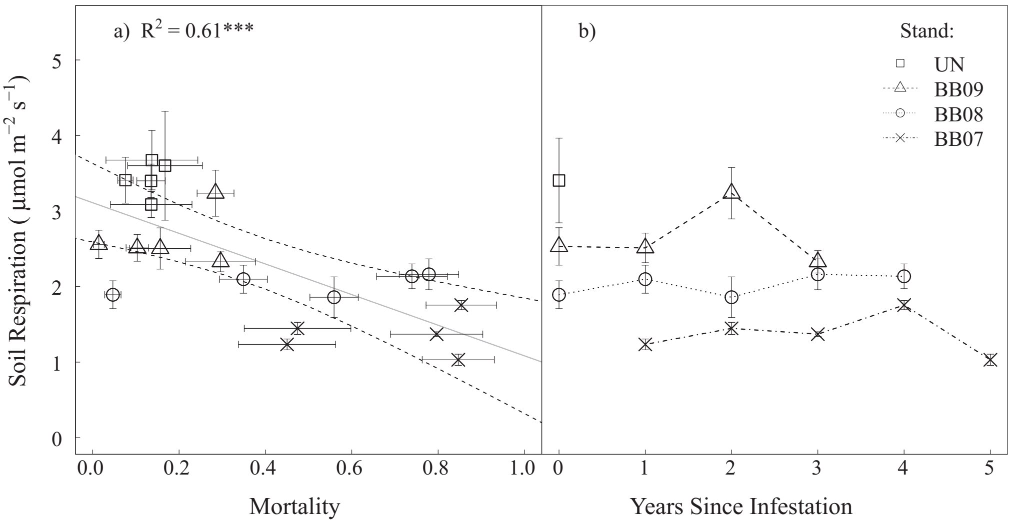

Fig. 4. Average peak growing season soil respiration rates in four stands; error bars represent standard error ($n = 5$). Stands were uninfested (UN) and infested by beetles in 2009 (BB09), 2008 (BB08) and 2007 (BB07). (a) Correlation between the peak growing season soil respiration and stand-level mortality including all four stands, 2008–2012. Mortality was calculated as 1 – (LBA/TBA). Fitted line is a linear fit and dashed line represents 95% CI. Statistical significance: ***$p < 0.0001$, **$p = 0.001$, and *$p = 0.01$. (b) Peak growing season soil respiration in each stand as a function of years since infestation.

4. Discussion

We expected that soil respiration would decline while forest mortality progressed, as observed by Högberg et al. (2001), and as demonstrated in our study across all stands (Fig. 4a). But we did not observe this at the stand level (Fig. 4b) despite that the roots and associated mycorrhizal fungi were dying in infested stands soon after water and nutrient flows in trees were terminated by beetles and associated blue stain fungi (Norton et al., 2015; Hubbard et al., 2013). Our results suggest that the contributions from autotrophic and heterotrophic respiration change over the course of beetle infestation and subsequent tree mortality. Beetle infestation results in a sudden decline in soil respiration under individual trees over approximately a three-month period (Hubbard et al., 2013). However, at the stand level, surviving trees and understory vegetation, combined with increased microbial respiration due to enhanced nutrient availability (Norton et al., 2015), appear to compensate for individual tree death. Thus, when viewed over a period of years in the post-infestation period, no decline in soil respiration within stands is evident. We attribute the differences among stands to be related to intrinsic ecological factors that led to larger, sparsely distributed trees in infested stands, and smaller trees within dense stands in other areas (Fahey and Knight, 1986). Soil respiration rates were correlated with TBA, demonstrating that initial differences among stands set the stage for ecosystem function, but SR was better correlated with LBA, indicating the importance of live roots and autotrophic processes at the ecosystem level (Fig. 3b). Compensating process, such as succession of understory vegetation (Norton et al., 2015), was more rapid in the sparse stands with lower TBA contributing to soil respiration and sustaining ecological functioning despite major mortality.

Other studies have suggested that soil respiration in forest ecosystems may be only slightly affected by disturbances (Bhupinderpal et al., 2003; Morehouse et al., 2008). Bhupinderpal et al. (2003) reported that a transient increase in isotope composition (δ^{13}C) of soil respiration was due to the use of stored carbohydrates in tree roots and decomposition of ectomycorhizal mycelium within two years following disturbance. We did not

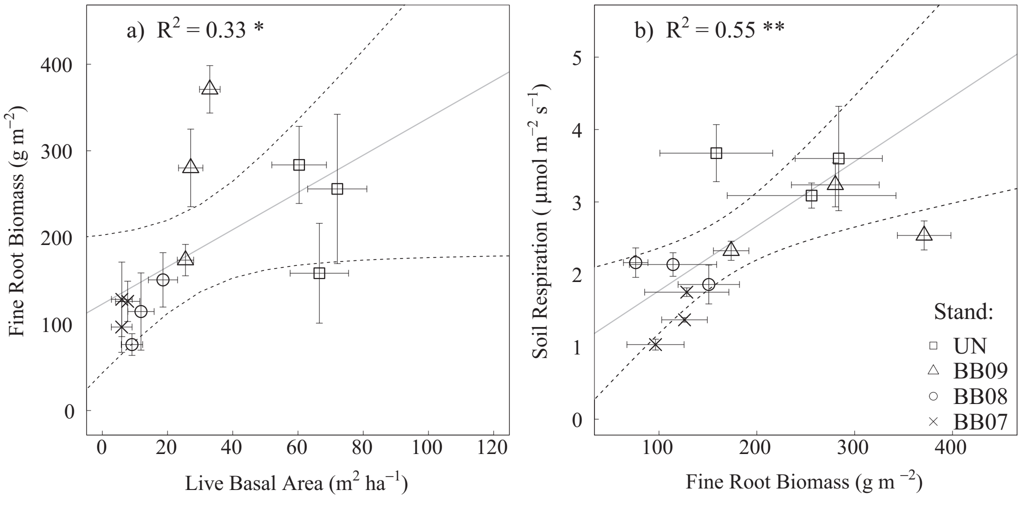

Fig. 5. Correlations (a) live basal area (LBA) versus fine root biomass and (b) fine root biomass versus soil respiration in stands with different mortality level following beetle infestation, 2010–2012. Each data point represents the average of five plots for that year ($n = 5$). Stands were uninfested (UN) and infested by beetles in 2009 (BB09), 2008 (BB08) and 2007 (BB07). Fitted lines are linear fits and dashed lines represent 95% CI. Statistical significance: ***$p < 0.0001$, **$p = 0.001$, and *$p = 0.01$.

find a transient increase in soil respiration that was reported by Bhupinderpal et al. (2003). It is possible that during our research the possible increase in soil respiration from the year-zero levels was not observed because of rapid forest die-off and subsequent reduction in root metabolism. However, soil respiration may rebound to pre-disturbance levels within five to six years (Moore et al., 2013) suggesting resilience in C cycling processes of high elevation forests across Western North America despite drastic disturbances. Furthermore, at the ecosystem level, disturbance may have a minor effect on fluxes, as surviving vegetation makes compensating contributions to carbon and water cycling (Reed et al., 2014).

Ecologists studying soil respiration highlight the role of interactions between aboveground and belowground ecosystem processes (Högberg and Read, 2006). There is a growing recognition that soil biological activities are predominantly influenced by recently produced aboveground C in the form of photosynthates (Högberg et al., 2001; Högberg and Read, 2006). The observed correlation in this study between soil respiration and maximum PPFD (Fig. 2b) supports this contention and is in agreement with a girdling experiment in a Scots pine forest (Högberg et al., 2001) where more than half of the substrate supplies for soil respiration originated from recent photosynthates. Similar to the girdling experiment results, beetle infestation causes both photosynthates and water flows to be terminated in trees within 2–3 months (Hubbard et al., 2013). However, spruce beetles, which also cause significant declines in ecosystem carbon uptake and water loss to the atmosphere, may take longer to kill trees (Frank et al., 2014). Canopy conductance of recently attacked trees dramatically declined indicating a drop in photosynthesis of individual trees during our study period (2008–2012) (Ewers; unpublished data) which is consistent with significantly reduced soil respiration (Hubbard et al., 2013). Thus, C supplied to the roots likely decreases rapidly following beetle infestation. The remaining soil respiration in dead stands can then be attributed to heterotrophic activity and/or surviving vegetation after two years following disturbance (Bhupinderpal et al., 2003).

On average, soil respiration earlier and later in the growing season contributed half of total soil respiration in the uninfested stand (Fig. 1). During these periods autotrophic respiration is expected to be minimal (Bhupinderpal et al., 2003), thus we attribute the sustained soil respiration flux to a shift toward more heterotrophic processes. We found characteristically low soil respiration for the entire growing season in infested stands (Fig. 1), although detailed the soil respiration response to beetle infestation is still uncertain. For instance, the lowest and least variable fine root biomass and peak growing season soil respiration occurred in the stands with more than 75% mortality (BB07; Table 1 and Fig. 5). Beetle infestation may accelerate dead root decomposition and, with additional resources in the form of N-rich needles, stimulate heterotrophs (Norton et al., 2015) for a short period following the infestation. Our findings differ from those of Högberg et al. (2001) in that we found N balance was strongly perturbed by beetle infestation. In contrast with beetle infestation, the girdling experiments mainly alter the carbohydrate flow to belowground and take much longer to kill lodgepole pine at this site than when combined with blue stain fungi (Knight et al., 1991). The ability of microbes to respond to the C inputs from beetle mortality could be related to the high levels of available N allowing a priming effect to occur (Morehouse et al., 2008; Norton et al., 2015).

In addition to direct experimental evidence showing that aboveground photosynthesis is well connected with soil respiration (Högberg et al., 2001; this paper), other indirect indices have been used in field measurements to describe this connection. For instance, aboveground vegetation production index (leaf area index, LAI) was a good predictor of changes in soil respiration on a global scale (Reichstein et al., 2003). Following this lead, we used the stand-level relative basal area of live trees as a proxy for aboveground plant productivity and fine root biomass as a proxy for belowground productivity and found strong and direct correlations between peak growing season soil respiration with both LBA (Fig. 3b) and fine root biomass (Fig. 5b). The lower soil respiration and fine root biomass in infested stands than in the uninfested stand suggest that an inverse correlation between soil respiration and stand mortality (Fig. 4a) is associated with changing root dynamics and tree root respiration (Högberg et al., 2001). Concurrently, the opening of canopies and available nutrients from the decomposition of newly added N-rich needle litter (Griffin et al., 2011; Norton et al., 2015) and root gap formation (Parsons et al., 1994) likely promoted the understory fine root growth (Stone and Wolfe, 1996; McMillin et al., 2003). Over time, this growth should increase the contribution of understory fine root respiration in soils, which will eventually compensate for the loss of live tree roots. Additionally, the photosynthetic efficiency of surviving vegetation may increase during post-disturbance canopy opening (Hubbard et al., 2013; Reed et al., 2014; Frank et al., 2014).

The increase in soil respiration we observed in response to total monthly precipitation, which accounted for 30% of variability in the observed soil respiration (Fig. 2a), was consistent with previous research that has shown that the seasonality of soil respiration may be controlled by moisture availability from precipitation events (Davidson et al., 1998; McCulley et al., 2005). During short term (days) rewetting events, soil respiration would most likely increase because of the reactivation of microbial activities (Barros et al., 1995) and microbial mineralization (Fierer and Schimel, 2003). On slightly longer timescales (weeks to months), precipitation will increase new root growth that increases root respiration (Luo and Zhou, 2006). For the stands studied here, changes in soil respiration were not dependent on infestation stages suggesting that the soil respiration increase due to rainfall events may be associated with prompt reactivation of microbial activity rather than new root growth (Fierer and Schimel, 2003; Högberg and Högberg, 2002). The reduction of canopy interception as mortality progresses (Biederman et al., 2014) may be coupled with reduced uptake of soil water by tree transpiration, as observed in a nearby forest (Hubbard et al., 2013), explaining our observations of enhanced soil water content in some stands in some years (Table 2). However, soil respiration was not strongly limited by moisture in this ecosystem. Thus, no correlations between soil respiration and soil moisture were observed, and the correlations with precipitation were not strong.

Sensitivity of soil respiration to seasonal variation of soil temperature is well known (Lloyd and Taylor, 1994), but this relationship did not explain temporal patterns in soil respiration for either infested or uninfested stands (Fig. S2). Although soil temperature was correlated with maximum PPFD ($R^2 = 0.21$, $p < 0.0001$), spatial variation in soil temperature was high, possibly because of canopy opening caused by beetle infestation. Boone et al. (1998) demonstrated that soil without roots and organic horizons responded sluggishly to temperature change; similarly, we observed that in infested stands with lower root biomass (Fig. 5b) the soil respiration rates were lower and not differentiated among years. We speculate that spatial variation in biotic factors related to mortality status overwhelmed the regulation of respiration rates by soil temperature, and reduced the predictability of soil respiration from soil temperature. The clarification of the temperature dependence of soil respiration in beetle infested and recovering forest ecosystems remains a question for future investigations.

The relationships among peak growing season soil respiration, stand-level LBA and soil fine root biomass (Figs. 3b and 5) observed here should aid in regional estimation and modeling of soil respiration changes due to widespread beetle infestations. While more data is needed linking soil respiration changes to reduction in canopy LAI, a variable most ecosystem process models use as the basis for gas and energy exchange, models that use LBA or live sapwood area may benefit by incorporating their relationships with soil respiration observed in this study. Combining these relationships with emerging remote sensing techniques to quantify mortality levels due to beetle infestation (Meddens and Hicke, 2014), and estimating live and dead tree basal area (Wolter et al., 2012), could provide additional inputs for improved estimations of changes in regional carbon budgets.

In conclusion, we observed that soil respiration varied among lodgepole pine stands owing to intrinsic differences in basal area, and did not change over the time frame of disturbance by beetle infestation in this study. We attribute this resilience of ecosystem functioning to compensating processes including vegetation survival, succession, and microbial respiration, and we recommend further studies on the underlying autotrophic and heterotrophic mechanisms contributing to soil respiration.

Acknowledgements

We thank D.H. Knight for introducing us to the study area and inspiring the biogeochemical studies; T.A. Surovell and D. Legg for assistance on data processing and statistical analysis; D.B. Tinker, T. Kelleners, and E. Traver for edits and suggestions in earlier drafts of the manuscript. Thanks to D. Reed, B. Mitra, C. Hudson, N. Brown, and numerous undergraduate students for assistance in the field and laboratory. This work was funded by the National Science Foundation (EAR-0910831), the Wyoming Water Development Commission, the USGS, the USDA National Institute of Food and Agriculture, McIntire – Stennis Project no. 0217074 and the WY Agricultural Experiment Station.

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