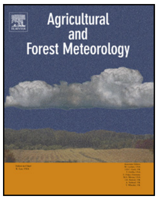
Agricultural and Forest Meteorology 214–215 (2015) 201–207

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

B. Borkhuu [a,*], S.D. Peckham [a,e], B.E. Ewers [a,c], U. Norton [b,c], E. Pendall [a,c,d]

[a] Department of Botany, University of Wyoming 3165, 1000 E. University Ave., Laramie, WY 82071, USA
[b] Department of Plant Sciences, 3354, 1000 E. University Ave., Laramie, WY 82071, USA
[c] Program in Ecology, University of Wyoming, USA
[d] Hawkesbury Institute for the Environment, University of Western Sydney, Pernith, NSW 2751, Australia
[e] Confederated Tribes of the Umatilla Indian Reservation, 46411 Timíne Way, Pendleton, OR 97801, USA

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 $1.4 \pm 0.1\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$ in stands with lowest LBA to $3.1 \pm 0.2\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$ 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).

---

[*] Corresponding author. Present address: 2800 E. Garfield Street Apt #B101, Laramie, WY 82070, USA.
E-mail address: bujidmaa2009@gmail.com (B. Borkhuu).

http://dx.doi.org/10.1016/j.agrformet.2015.08.258
0168-1923/© 2015 Elsevier B.V. All rights reserved.

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 ≤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.