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Impact of mountain pine beetle induced mortality on forest carbon and water fluxes

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Abstract

Quantifying impacts of ecological disturbance on ecosystem carbon and water fluxes will improve predictive understanding of biosphere—atmosphere feedbacks. Tree mortality caused by mountain pine bark beetles (*Dendroctonus ponderosae*) is hypothesized to decrease photosynthesis and water flux to the atmosphere while increasing respiration at a rate proportional to mortality. This work uses data from an eddy-covariance flux tower in a bark beetle infested lodgepole pine (*Pinus contorta*) forest to test ecosystem responses during the outbreak. Analyses were conducted on components of carbon (C) and water fluxes in response to disturbance and environmental factors (solar radiation, soil water content and vapor pressure deficit). Maximum CO_2 uptake did not change as tree basal area mortality increased from 30 to 78% over three years of beetle disturbance. Growing season evapotranspiration varied among years while ecosystem water use efficiency (the ratio of net CO_2 uptake to water vapor loss) did not change. Between 2009 and 2011, canopy water conductance increased from 98.6 to 151.7 mmol H_2O m^{-2} s^{-1}. Ecosystem light use efficiency of photosynthesis increased, with quantum yield increasing by 16% during the outbreak as light increased below the mature tree canopy and illuminated remaining vegetation more. Overall net ecosystem productivity was correlated with water flux and hence water availability. Average weekly ecosystem respiration, derived from light response curves and standard Ameriflux protocols for CO_2 flux partitioning into respiration and gross ecosystem productivity, did not change as mortality increased. Separate effects of increased respiration and photosynthesis efficiency largely canceled one another out, presumably due to increased diffuse light in the canopy and soil organic matter decomposition resulting in no change in net CO_2 exchange. These results agree with an emerging consensus in the literature demonstrating CO_2 and H_2O dynamics following large scale disturbance events are dependent not only on tree mortality but also on the remaining and new vegetation responses because mortality and recovery occur at the same time.

Keywords: ecosystem disturbance, forest mortality, ecosystem fluxes, carbon cycle

1. Introduction

Biosphere carbon (C) cycling is highly dynamic and tightly coupled with global climate change (Cao and Woodward 1998). Understanding controls of the C cycle within the biosphere is vital to constraining uncertainty and improving

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predictive understanding of ecosystem responses to disturbance (Kurz *et al* 2008b, Liu *et al* 2011). Globally, forests account for up to 80% of terrestrial aboveground C and ~40% of belowground C (Dixon *et al* 1994, Roy *et al* 2001). Changes in factors regulating the C cycle have large global C implications, especially when potential positive feedbacks to climate change are considered (Dale *et al* 2001).

Forests in the US and Canada have 2–3% areal disturbance rates per year, primarily due to harvest and forest fire (Masek *et al* 2008). Harvest and fire disturbance impacts on ecosystems have been widely studied, including mechanisms controlling water quality (Carignan *et al* 2000), nitrogen cycling (DeLuca and Zouhar 2000) and net C cycling (Gough *et al* 2007). The mountain pine bark beetle (*Dendroctonus ponderosae*) infestation in the United States and Canadian Rockies is larger than any previously recorded outbreak (Kurz *et al* 2008a, Raffa *et al* 2008). Bark beetle impacts on ecosystem mechanisms may be similar to other disturbances (Ayres and Lombardero 2000, Hicke *et al* 2012). These include predicted reduction in plant CO_2 uptake, increase in decomposition rates, decreasing leaf area and stem density (Edburg *et al* 2012), and changes to the water cycle (Mikkelson *et al* 2013). Ecosystem responses are also expected to be complex and variable both in space and time, owing to patchy vegetation dynamics during the mortality event with succession happen simultaneously (Rhoades *et al* 2013).

In temperate ecosystems, CO_2 fluxes are primarily controlled by water availability (Pastor and Post 1986). Lack of available water can limit CO_2 uptake below maximum potential of a given leaf area during dry years (Law *et al* 2002). When mountain pine beetles first appear, their attack affects water use of individual trees as they and their symbiotic blue-stain fungi reduce transpiration in infected trees (Edburg *et al* 2012, Yamaoka *et al* 1990, Hubbard *et al* 2013). Reduced transpiration from infected trees has been shown to alter water cycling processes, increasing soil moisture and drainage at the stand scale (Mikkelson *et al* 2013), and impacting snowpack dynamics (Biederman *et al* 2014, Pugh and Small 2012) and runoff (Bearup *et al* 2014). Water cycling changes are also expected to alter C cycling (Brown *et al* 2010, Brown *et al* 2012).

Carbon and water cycling are inherently linked through stomatal conductance within leaves by the transpirational loss of water while photosynthesis assimilates atmospheric CO_2 (Katul *et al* 2009, Cowan and Farquhar 1977). Variation in ecosystem water use efficiency (WUE), defined as the ratio of ecosystem C gain to evapotranspiration (ET), is primarily linked to water availability of forested ecosystems (Ponton *et al* 2006). WUE is dependent on species present as well as canopy structure in the ecosystem (Monson *et al* 2010). Ecosystem canopy conductance, derived from ET measurements, can indicate decoupling of the C and water cycles (Granier *et al* 2000). For example, decoupling could occur in response to disturbance if canopy transpiration is reduced more than photosynthesis, or if water loss from soil evaporation increases under a more open canopy. Thus, changes in WUE may be a useful indicator of disturbance effects on ecosystem processes.

Mountain pine beetle disturbances are expected to release soil C to the atmosphere over long time scales due to increases in the decay of soil C pools coupled in the short term with reduced photosynthetic uptake (Goetz *et al* 2012, Edburg *et al* 2012, Harmon *et al* 2011, Hicke *et al* 2012). The net effect of both processes reduces net ecosystem productivity (NEP). However, it has been shown that tree mortality associated with disturbance can increase soil water availability (Mikkelson *et al* 2013), potentially increasing CO_2 uptake in surviving trees (Law *et al* 2002). Increasing CO_2 uptake from surviving trees can balance photosynthesis reduction from disturbance (Gough *et al* 2013). If evaporation does not increase enough to compensate for reduced transpiration due to bark beetle infestation (Hubbard *et al* 2013), ET from the ecosystem should decline (Mikkelson *et al* 2013). By monitoring NEP, ET, WUE and canopy conductance during the course of an outbreak, the changing controls of C and water cycling can be characterized separately from the effects of wet or dry years.

Review papers by Edburg *et al* (2012) and Mikkelson *et al* (2013) highlight expected changes to bark beetle impacted ecosystems. These include canopy mortality and soil water increases, both of which have cascading impacts on carbon and water cycles. The mechanism causing mortality by bark beetle infestation is similar to that of extreme drought stress (Yamaoka *et al* 1990, McDowell *et al* 2008). Therefore, we expect soil water content and ET responses to be similar to those of drought. Carbon cycling, as a balance of photosynthesis and respiration, will be controlled largely by different time scales of mortality, needle fall, and litter decomposition (Edburg *et al* 2012). To quantify ecosystem CO_2 and water fluxes following a mountain pine beetle outbreak, we examined eddy-covariance data over three growing seasons as mortality increased within the tower footprint. We hypothesized that (1) bark beetle caused mortality will increase radiation and soil moisture while decreasing water flux to the atmosphere, (2) ecosystem WUE and canopy conductance will decrease as mortality increases during the course of the outbreak, (3) a decrease in photosynthesis and increase in respiration will cause net CO_2 uptake to decline throughout the duration of the outbreak.

2. Methods

2.1. Site description

The study site is located in the Medicine Bow Range in Southeast Wyoming, near Chimney Park (41.37N 106.53W) at 2770 m elevation. The forest is primarily even aged with the last stand replacing fire 135 years ago and is composed of lodgepole pine (*Pinus contorta*, 81.2% basal area of study site), aspen (*Populus tremuloides*, 11.2%), and Engelmann spruce (*Picea engelmannii*, 0.8%). The area of the lodgepole pine forest vegetation extended 3 km in all directions from the eddy covariance tower. Mountain pine beetles (*D. ponderosae*) and the associated symbiotic blue-stain fungi (*Grosmannia clavigera*) were first observed at the site in summer

2007 and mortality within the study site was up to 79% in 2011.

Mean annual temperature of all three years at the site was 6.1 °C and monthly mean temperatures ranged from −7.3 °C (January) to 14.6 °C (August). The majority of precipitation falls during the winter months as snow. Maximum snow pack accumulations reached a snow water equivalent of 27.8 cm in 2010 and 28.4 cm in 2011, based on winter surveys done approximately one week before the snow pack turned isothermal (Biederman *et al* 2014). Snow melt generally occurs near the first week of May (Biederman *et al* 2014), and is associated with fully saturated soil and overland flow.

Average canopy height varied between 8.7 m and 16.2 m and the overall slope of the study area was under 2%. The longitudinal extent of the tower footprint was calculated based on average wind speed, average friction velocity, sensor height, zero plane displacement height and roughness length (Schuepp *et al* 1990). The tower footprint had a maximum straight line distance of 875 m to the west and 200 m to both the north and south, well within the extent of the forest study area. More than 95% of the average 30 min wind direction values were from the west.

2.2. Eddy covariance and environmental instrumentation

Above-canopy half-hour eddy-covariance measurements of water vapor flux (ET), sensible heat flux and CO_2 flux began at the field site in January 2009. The eddy-covariance tower (18 m) was equipped with an open-path infrared gas analyzer (17.7 m) (LI-7500; LI-COR, USA), a sonic anemometer (17.7 m) (CSAT3; Campbell Scientific, USA), a four-component net radiometer (CNR1; Kipp & Zonen, the Netherlands) (17.1 m), and temperature and relative humidity sensors (HMP45C; Vaisala, Finland) (17.7 m and 3.7 m). Diffuse and direct photosynthetically active radiation at the top of the canopy was estimated based on Spitters (1986), using location of the field site and time of year. Transfer of radiation through the canopy was modeled based on Nijssen and Lettenmaier (1999), with an attenuation coefficient of 0.8 for both radiation types that is typical for pine canopies (Gower *et al* 1999). Soil moisture probes (CS616; Campbell Scientific, USA) were installed at 0–15 and 15–45 cm soil depths while two soil heat flux plates (HFP01SC; Hukseflux, Netherlands) were installed at a depth of 5 cm. Previous work at this study site (Parsons *et al* 1994) showed that >90% of roots are found within 40 cm of the surface, so both depths of soil moisture probes were averaged into one value based on weighted lengths of the probes. Growing season was defined as May 1st through October 1st and coincides with the average snow-free time period. Instruments for eddy covariance measurements were recorded at 10 Hz while all other sensors were recorded as half-hourly averages with a digital data logger (CR5000 or CR1000; Campbell Scientific, USA).

Ecosystem flux data were processed using MATLAB (2010a, The MathWorks) in the manner described in Lee *et al* (2004) including de-spiking the raw time series (Dale *et al* 2001) (Matlab code is contained as an appendix), addressing calibration drifts (Loescher *et al* 2009), coordinate rotation and planar fitting (Finnigan *et al* 2003), correcting for the time lag due to spatially separate sensors (Horst and Lenschow 2009), spectral corrections (Horst 2000, Massman 2000) and finally the WPL correction (Webb *et al* 1980). A friction velocity threshold of 0.089 m s^{-1} was established to screen out data based on Gu *et al* (2005), which included normalizing at diurnal and seasonal scales night-time CO_2 fluxes using temperature response functions described in Gu *et al* (2002). All data with a friction velocity below this threshold were removed from our analysis, which accounted for only 1.4% of the total.

2.3. Canopy conductance

The Penman–Monteith equation was rearranged to give an expression for the ecosystem canopy conductance (g_c) (Brümmer *et al* 2012).

$$\frac{1}{g_c} = \frac{\rho\, c_p\, \mathrm{VPD}}{\gamma \lambda_v \mathrm{ET}} + \frac{1}{g_a}\left[\frac{\Delta}{\gamma}\left(\frac{R_n - G}{\lambda_v \mathrm{ET}} - 1\right) - 1\right], \quad (1)$$

where Δ is the rate of change of the saturation specific humidity with air temperature, ρ is dry air density, c_p is the specific heat capacity of dry air, γ is the psychrometric constant, λ_v is the latent heat of vaporization and g_a is the aerodynamic (boundary layer) conductance. R_n, G, and VPD are measured net radiation, soil heat flux and vapor pressure deficit (VPD), respectively, from the site. A top-down ecosystem canopy conductance approach (Baldocchi *et al* 1991) was applied (Baldocchi *et al* 1987) that solved a nonlinear least squares curve fitting algorithm that fit both g_c and g_a at weekly time steps.

2.4. Light response curves

Ecosystem CO_2 fluxo and radiation data were used to fit a Michaelis–Menten light response curve (Harley *et al* 1992, Falge *et al* 2001) to the data.

$$\mathrm{NEP} = \frac{A_{\max}\ \Phi_a\ R_i}{A_{\max}\ + \Phi_a R_i} - R_{\mathrm{eco}}. \quad (2)$$

Solar radiation was used for the incoming radiation term, R_i, to estimate quantum yield (Φ_a) as the slope of the curve at low light levels and maximum assimilation $(A_{\max})$ as the asymptotic value at high light levels. Ecosystem respiration (R_{eco}) was estimated from curve fits using incoming solar radiation data. Curve fit parameters were calculated weekly over the course of the growing season in a manner similar to Zhang *et al* (2006). Weeks with less than 65% data coverage (Falge *et al* 2001) were discarded from this analysis.

Ecosystem respiration $(R_{\mathrm{eco}D})$ was also calculated with VPD limiting GEP, using light response curves and day-time data, following Lasslop *et al* (2010). $R_{\mathrm{eco}D}$ was used to calculate gross ecosystem productivity (GEP) from NEE. Time series were gap-filled at the 30 min scale (Reichstein *et al* 2005) only for short gaps (less than one day) during the flux partitioning algorithm. Both GEP and $R_{\mathrm{eco}D}$ values were averaged to daily time scales.

2.5. Water use efficiency

WUE on an ecosystem scale (eWUE) was defined as the slope of NEP to ET (VanLoocke *et al* 2012, Emmerich 2007), where positive NEP indicates uptake by the ecosystem. WUE was defined as the slope of GEP to ET (Law *et al* 2002); the values of eWUE will be somewhat smaller than WUE (Steduto and Albrizio 2005). Thirty minute fluxes were averaged on a weekly basis, again disregarding weeks with less than 65% of data. eWUE was calculated for each growing season as the mean of the weekly eWUE values following Law *et al* (2002) for WUE.

2.6. Scaling by leaf area index (LAI) and statistical analysis

The CO_2 and water flux parameters of g_c, R_{eco}, R_{ecoD}, Φ_a, A_{max} , GEP, eWUE and WUE were normalized by yearly LAI values to convert parameters from a ground area basis to a leaf area basis. This was done to separate the yearly changes in the ecosystem parameters from the effect of a decline in the canopy leaf area. LAI measurements were taken once a year at 20 representative plots within the eddy-covariance footprint with a plant canopy analyzer (LAI-2000; LI-COR, USA). LAI was scaled to ecosystem level using a paint-by-numbers approach (Mackay *et al* 2002) that aggregated stand estimate of tree level basal area distributions data from 20 representative plots up to the ecosystem level of 144 plots. Four classes of tree basal area distributions were created that were similar to the four stands of trees measured for soil and tree temperature and moisture. Each of these four stands of trees were then considered representative of any of the 144 plots of the footprint that were most similar to them. Tree basal area and condition were measured annually in the 144 plots arrange along the tower footprint to track mortality due to beetle infestation. Basal area was used to estimate mortality at the footprint scale because basal area has been shown to be an appropriate scale for transpiration in ate lodgepole pine (Adelman *et al* 2008) and in other forest studies (Mackay *et al* 2010, Ford *et al* 2007). Autocorrelation of time series variables was addressed by computing differences between time steps of CO_2 and ET fluxes while t-tests were used to statistically test for differences in parameters. MATLAB was used for all statistical and analytical work (MATLAB version 7.10.0. Natick, Massachusetts: The MathWorks, 2010).

3. Results

3.1. Controls of ecosystem fluxes

NEP (figure 1(a)) and ET (figure 1(b)) dynamics along with environmental controls of net radiation (figure 1(c)), VPD (figure 1(d)), and soil moisture (figure 1(e)) are shown against increasing site mortality, expressed as affected basal area percent (figure 1(f)). Site mortality expressed by density of trees was 38%, 55% and 68% in 2009, 2010 and 2011 respectively; lower than mortality by basal area due to bark beetle host selection favoring larger diameter trees. Net radiation and VPD were similar among years, but soil water

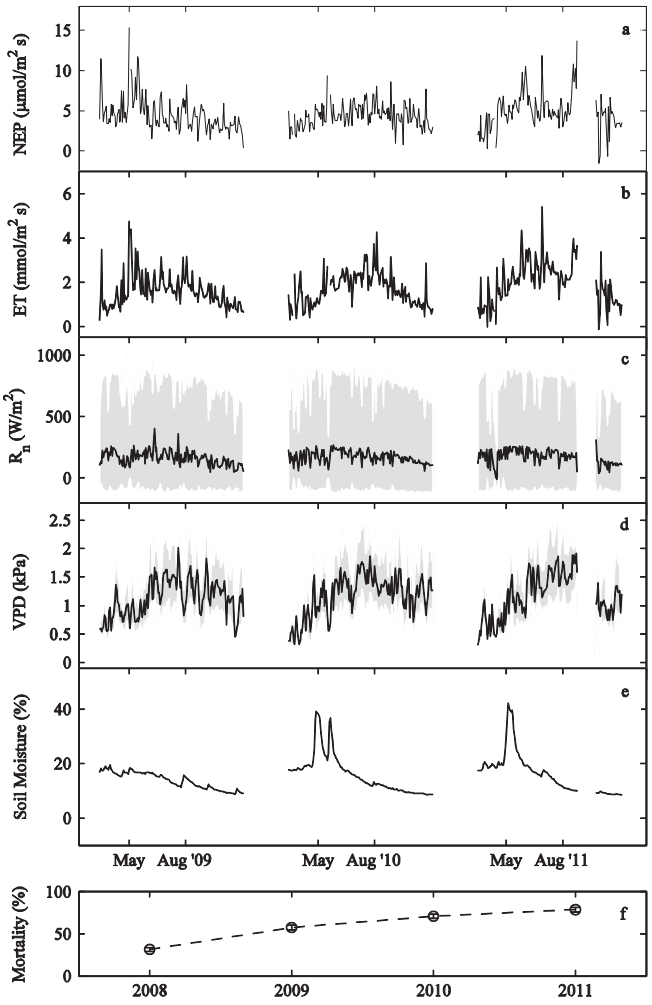


Figure 1. Seasonal variation in daily (24 h) average of (a) net ecosystem productivity at 17.7 m height, (b) ecosystem evapotranspiration flux at 17.7 m height, (c) net radiation at 17.1 m height with daily minimum and maximum values as shading, (d) mean vapor pressure deficit at 17.1 m height with minimum and maximum values as shading, (e) volumetric soil water content in the 0–0.45 m layer during the growing seasons of 2009–11 with tick labels relating to the 1st day of the month. Tree mortality percentage (of basal area) within the tower footprint by year for 2008–11 is shown in panel (f).

content increased in 2010 and 2011. Snow melt began earlier in 2009 and full soil saturation was not observed during the growing season that year (Biederman *et al* 2014). In terms of snowpack, 2011 was a very wet year, and snow-water equivalent was estimated to be between 140% and 200% above the 30-year average from SNOTEL (Snowpack Telemetry) sites around the region. Despite the above-average snowpack in 2011, soil water content reached typical values by the end of the growing season. However, average ET was higher in the late growing season in 2011 than the other two years.

Regression analyses of ET values showed weak and non-significant ($p > 0.05$) responses to soil moisture, net radiation, and vapor pressure deficit across the years of the study and regression slope coefficients between ET and soil moisture of all years are shown in table 1. Net radiation was a weak driver of ET in 2010. Regression coefficients for VPD were

Table 1. Regression slope coefficients for ET and canopy conductance as functions of environmental drivers (net radiation (R_n), vapor pressure deficit (VPD), soil moisture, and ET) for all three site years, excluding regression intercepts. Significant coefficients are in gray.

	Response					
Predictor	ET 2009 (mg H_2O m^2 s^{-1})	ET 2010 (mg H_2O m^{-2} s^{-1})	ET 2011 (mg H_2O m^{-2} s^{-1})	Canopy Conductance 2009 (mmol m^{-2} s^{-1})	Canopy Conductance 2010 (mmol m^{-2} s^{-1})	Canopy Conductance 2011 (mmol m^{-2} s^{-1})
R_n (W m^{-2})	0.00	0.01[a]	0.00	0.07	0.45	0.12
VPD (kPa)	0.60	1.25[b]	1.79[b]	−17.66	65.54[a]	57.12
Soil moisture (%)	−1.18	−0.78	4.42	398.64	−9.78	3.80
	—	—	—	—	—	—

[a] $p < 0.05$.
[b] $p < 0.01$.

significant ($p < 0.05$) in 2010 and 2011, and as expected, an increase in VPD was linked to an increase in ET. The coefficients did not vary among years ($p > 0.05$).

3.2. Interannual variations in ecosystem WUE, canopy conductance and CO_2 fluxes

Average NEP did not change among years even as tree mortality increased dramatically, with net CO_2 uptake by the ecosystem remaining high throughout all three growing seasons (figures 1(a), 2(a)). Average values of Φ_a of diffuse light increased in 2010 and 2011, as compared to 2009 ($p < 0.05$) (figures 2(b)–(d) and table 2). Ecosystem A_{max} , and GEP did not change ($p > 0.05$) among years in this study (figures 2(e), (f)). While R_{eco} was generally smaller than R_{ecoD}, as expected due to high degree of VPD control over transpiration within lodgepole pine (Pataki *et al* 2000), both respiration estimates showed no differences between years ($p > 0.05$) as well.

Ecosystem g_c increased in the middle of the growing season, compared to early season values (weeks 8–15) in both 2010 and 2011 (figure 3(a)). The growing season average g_c in 2010 and 2011 both increased ($p < 0.05$) from 2009 (table 2).

The relationship between ecosystem g_c and the driving variables soil moisture, net radiation, and VPD, showed no change among years (table 1). VPD was the only statistically significant predictor of g_c in 2010 ($p < 0.05$) with a positive relationship between the variables. g_c was not significantly related to net radiation or soil moisture.

eWUE and WUE showed no significant change among successive years (figure 4, table 2). All three study years had non-zero intercept terms for eWUE and WUE relationships between water and carbon dioxide. Ecosystem WUE measured at the same study area using gas exchange of shoots (Smith 1980) was 0.13 μmol CO_2 mg^{-1} H_2O, which was statistically comparable ($p < 0.05$) to our results in 2009 and 2011. Average water and CO_2 fluxes from all three years of this study were lower than fluxes measured using the gas exchange method by Smith (1980) as expected when comparing whole forest canopies to fully illuminated shoots.

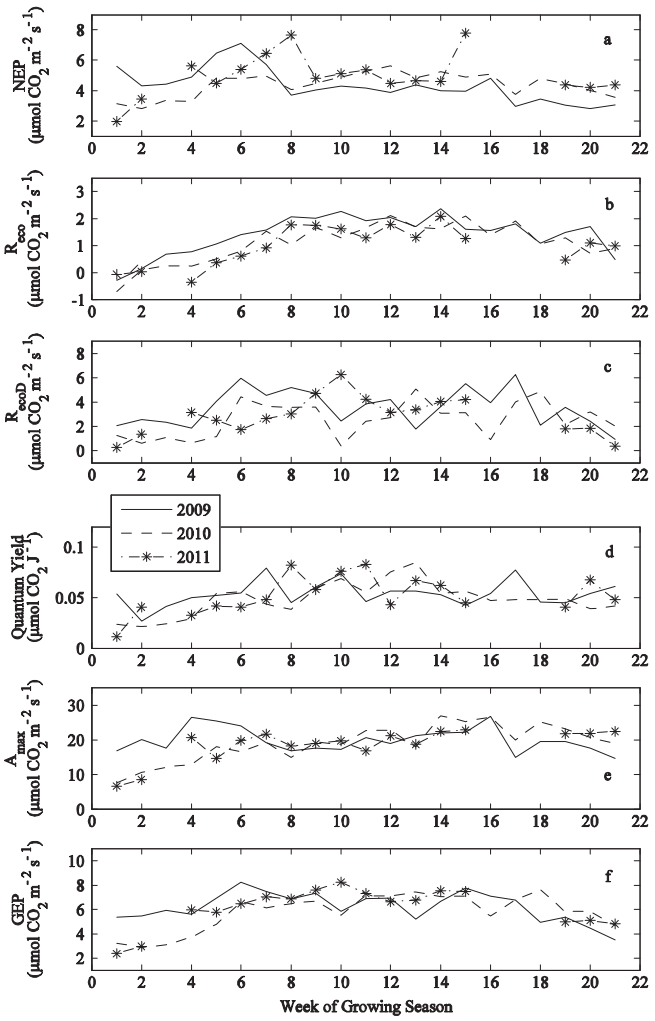


Figure 2. Weekly averages of (a) net ecosystem productivity, (b) ecosystem respiration (R_{eco}, calculated from light response curves), (c) ecosystem respiration (R_{ecoD}, including VPD limitation), (d) ecosystem quantum yield, (e), maximum ecosystem assimilation rates and (f) gross ecosystem production during the growing season for site years 2009–11.

3.3. LAI decline and ecosystem parameters

As mortality increased (figure 1(f)), LAI non-significantly ($p > 0.05$) declined from 2.16 in 2009 to 1.69 in 2011 while diffuse and direct solar radiation transfer through the canopy increased (table 3). Diffuse light at the top of the canopy made up 45% of the incoming solar radiation. Below canopy, both diffuse and direct light increased as a percentage of total

Table 2. Mean CO_2 and water parameters for all three site years from the middle of the growing season (weeks eight through 15) with 95% confidence interval in parentheses.

Year	Canopy conductance (mmol m^{-2} s^{-1})	Ecosystem respiration (μmol m^{-2} s^{-1})	VPD limited ecosystem respiration (μmol m^{-2} s^{-1})	Quantum yield (μmol m^{-2} s^{-1})/(W m^{-2})	Quantum yield of diffuse light (μmol m^{-2} s^{-1})/(diffuse W m^{-2})	A_{max} (μmole m^{-2} s^{-1})	eWUE With intercept not fixed at zero (μmol CO_2 mg^{-1} H_2O)	Intercept of eWUE (μmol CO_2 m^{-2} s^{-1})
2009	98.59 (14.10)	2.00 (0.22)	3.91 (1.08)	0.054 (0.008)	0.065 (0.002)	19.6 (1.9)	0.072 (0.06)	2.32 (1.82)
2010	145.38 (28.27)	1.67 (0.30)	2.96 (1.11)	0.062 (0.012)	0.066 (0.003)	21.1 (3.4)	0.061 (0.02)	2.54 (0.72)
2011	151.67 (25.72)	1.60 (0.25)	4.13 (0.87)	0.064 (0.013)	0.071 (0.002)	19.8 (1.8)	0.095 (0.04)	1.46 (1.44)
Year	WUE With Intercept Not Fixed at Zero (μmol CO_2 mg^{-1} H_2O)	Intercept of WUE (μmol CO_2 m^{-2} s^{-1})	NEP (μmol m^{-2} s^{-1})	GEP (μmol m^{-2} s^{-1})	—	—	—	—
2009	0.113 (0.05)	3.08 (1.53)	2.78 (1.08)	6.69 (0.68)	—	—	—	—
2010	0.107 (0.05)	2.51 (1.48)	3.86 (1.11)	6.82 (0.50)	—	—	—	—
2011	0.117 (0.04)	1.75 (1.42)	3.18 (0.87)	7.31 (0.45)	—	—	—	—

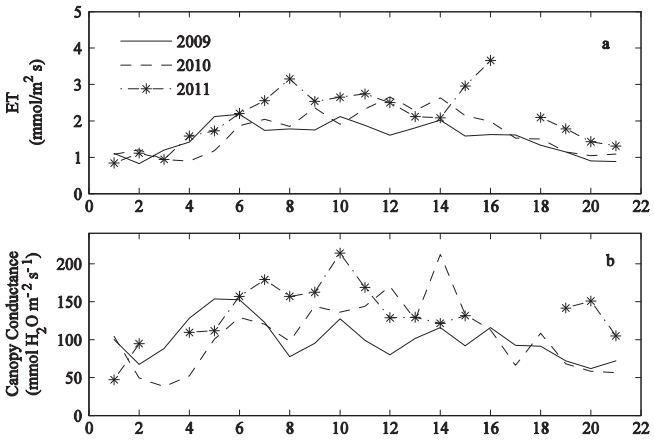


Figure 3. Weekly averages of (a) ecosystem evapotranspiration flux and (b) ecosystem canopy conductance during the growing season for site years 2009–11.

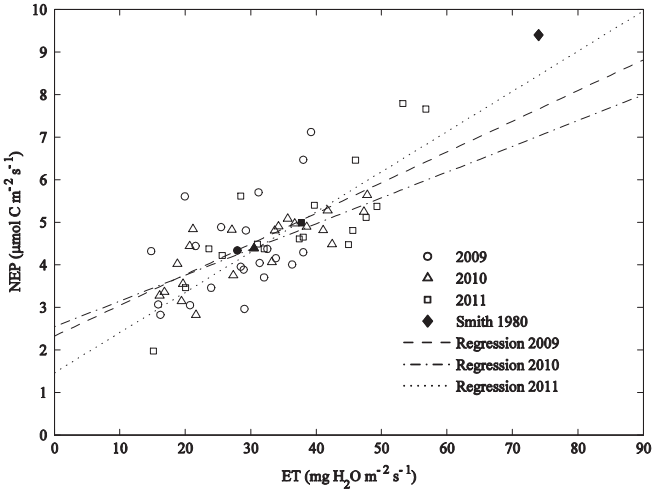


Figure 4. Weekly average water (ET) and CO_2 (NEP) flux with fitted linear regression lines by year. Filled symbols are average ecosystem water use efficiency by year. Literature value from Smith (1980) is included.

Table 3. Values of measured LAI expressed in m^2 of leaf area per m^2 ground area, modeled below canopy diffuse light and below canopy direct light, expressed as a percentage of above canopy solar radiation.

Year	Leaf area index ($m^2\ m^{-2}$)	Below canopy diffuse light (%)	Below canopy direct light (%)
2009	2.16	7.9%	9.7%
2010	1.94	9.6%	11.6%
2011	1.69	11.7%	14.2%

incoming above canopy solar radiation. This increase in below canopy radiation was caused by the declining LAI.

Effects of mortality-induced changes in canopy structure on ecosystem CO_2 and water exchange were evaluated by normalizing growing season average g_c, R_{eco}, R_{ecoD}, Φ_d, A_{max}, GEP, eWUE and WUE by LAI (table 4). The LAI-normalized values of g_c, A_{max}, Φ_d and GEP were higher in 2011 than in 2009 ($p < 0.05$) and scaled Φ_d of diffuse radiation increased every year ($p < 0.05$). Both Φ_d and Φ_d of diffuse radiation were not significantly different in 2009 and 2010 (table 2).

4. Discussion

Results from this study show little change in the relationship between environmental drivers and fluxes during a major beetle outbreak, contrary to expectations. Water cycling within the ecosystem was complex, with eWUE not changing during the study while ecosystem g_c and thus ET increased. Carbon cycling results were also not as expected, with A_{max}, R_{eco}, R_{ecoD}, and GEP all not changing, while only diffuse light Φ_d increased.

During the course of the mountain pine beetle outbreak, the prediction that ecosystem photosynthesis would decrease (Edburg *et al* 2012) was not supported as the maximum assimilation parameter from the ecosystem light response curve and GEP from flux partitioning did not change and Φ_d increased. While there is no pre-outbreak data from this study, the A_{max} values found (19.6–21.1 μmole $m^{-2}\ s^{-1}$) were similar to those in other temperate zone forests (Whitehead and Gower 2001). In a mixed northern hardwood forest girdling experimental treatment, CO_2 uptake was sustained through similarly high canopy defoliation (Gough *et al* 2013).

Ecosystem parameter of diffuse light Φ_d increased between 2010 and 2011. This is likely due to declines in LAI and canopy shading causing increased diffuse light penetration in the canopy similar to that found in a spruce beetle epidemic (Dale *et al* 2001). Increases in diffuse light have been linked to higher ecosystem productivity in other work (Gu *et al* 2002). Once the change in LAI was incorporated, diffuse light Φ_d increased from 2009 and 2010 as well. Seasonal patterns in Φ_d can be explained by variations in temperature among different forest types (Zhang *et al* 2006). As temperature was not significantly different among years, the observed increase in Φ_d and diffuse canopy light throughout the study period is likely to contribute to the consistent NEP despite increasing mortality between all three years, as suggested by Gough *et al* (2013). Diffuse light within the canopy has a large effect on stomatal conductance at the leaf and canopy level (Ewers *et al* 2007) and net CO_2 uptake from an ecosystem (Law *et al* 2002, Gough *et al* 2013). This work suggests that diffuse light impacts can be extended to forest disturbances and future process modeling should incorporate canopy light attenuation models that explicitly handle diffuse light.

With LAI declining throughout the beetle outbreak, increased amounts of modeled diffuse and direct light below the canopy allow more efficient CO_2 uptake throughout the canopy as well as in the understory (Gu *et al* 2002). However, the needle drop process by dead trees is delayed at least two years after bark beetle infestation (Edburg *et al* 2012) thus the decline in LAI is lagged relative to mortality. Further, there are differences in LAI that attenuates radiation and LAI that no longer contributes to gas exchange before it falls off the dead trees illustrating the difference between LAI measured

Table 4. Mean CO_2 and water parameters normalized by LAI values for each year with 95% confidence interval in the mean in parenthesis.

Year	LAI Normalized canopy conductance (mmol m^{-2} s^{-1})	LAI Normalized ecosystem respiration (μmol m^{-2} s^{-1})	LAI Normalized VPD limited ecosystem respiration (μmol m^{-2} s^{-1})	LAI Normalized quantum yield (μmol m^{-2} s^{-1})/(W m^{-2})	LAI Normalized quantum yield of diffuse light (μmol m^{-2} s^{-1})/(diffuse W m^{-2})	LAI Normalized A_{max} (μmole m^{-2} s^{-1})	LAI Normalized eWUE with intercept not fixed at zero (μmol CO_2 mg^{-1} H_2O)	LAI Normalized intercept of eWUE (μmole CO_2 m^{-2} s^{-1})
2009	45.64 (6.53)	0.92 (0.10)	1.81 (0.50)	0.025 (0.004)	0.030 (0.001)	9.05 (0.86)	0.033 (0.03)	1.07 (0.84)
2010	74.94 (14.57)	0.85 (0.16)	1.54 (0.57)	0.032 (0.006)	0.034 (0.002)	10.86 (1.74)	0.031 (0.01)	1.31 (0.37)
2011	89.75 (15.22)	0.95 (0.15)	2.44 (0.52)	0.038 (0.008)	0.042 (0.001)	11.76 (1.04)	0.056 (0.02)	0.86 (0.85)
Year	LAI Normalized WUE with intercept not fixed at zero (μmol CO_2 mg^{-1} H_2O)	LAI Normalized intercept of WUE (μmole CO_2 m^{-2} s^{-1})	LAI Normalized NEP (μmol m^{-2} s^{-1})	LAI Normalized GEP (μmol m^{-2} s^{-1})	—	—	—	—
2009	0.052 (0.02)	1.43 (0.71)	1.29 (0.50)	3.09 (0.31)	—	—	—	—
2010	0.055 (0.02)	1.29 (0.76)	1.99 (0.57)	3.51 (0.26)	—	—	—	—
2011	0.069 (0.02)	1.03 (0.84)	1.89 (0.52)	4.33 (0.27)	—	—	—	—

by light attenuation and effective LAI. Lag in LAI decline would explain the change noted in Φ_a in 2010 and 2011 rather than at the start of the 2008 infestation. Canopy light-C interaction is hypothesized to increase in magnitude as the canopy continues to open and is one mechanism contributing to sustained A_{max} and CO_2 uptake values despite the mortality, in opposition to hypothesis 3. This process is also shown in the results of Brown *et al* (2012), Bowler *et al* (2012), and Amiro *et al* (2010) wherein CO_2 uptake recovery from insect disturbances happens much more quickly than previously anticipated, considering the high mortality rates. This could be partly because trees that survive the mortality event take advantage of the extra water and nutrients that occur as root gaps form (Parsons *et al* 1994) and remaining trees grow faster (Hubbard *et al* 2013). Our results show that the 20% surviving trees and rapidly growing understory of lodgepole pine forests is a key feature leading to forest NEP and ET resiliency after bark beetle disturbance as suggested by overall indicators of forest management resiliency, similar to sustainable timber harvest management (Burton 2010).

The responses of ecosystem respiration, from light response curves and flux partitioning, showed no change, similar to the results of Brown *et al* (2012). This is likely a result of increased heterotrophic respiration and soil C decay (Edburg *et al* 2012, Harmon *et al* 2011) compensating for decreased autotrophic respiration as infested trees die. However, increased autotrophic respiration from residual vegetation responding to the increased light, water and nutrient environment cannot be ruled out. Ecosystem respiration is a main determinant of C balance in forests (Valentini *et al* 2000) so the predicted potential switch from a net CO_2 sink to a CO_2 source from modeling studies (Kurz *et al* 2008a, Kurz *et al* 2008b) is not supported from this site.

When normalized by LAI, several increases in ecosystem parameters appeared between years, including g_c, both Φ_a and diffuse light Φ_d, A_{max}, and GEP. This suggests changes in ecosystem CO_2 and water functions are linked to changing canopy area, similar to the gypsy moth defoliation results of Clark *et al* (2010). This LAI normalized ecosystem response could provide an additional perspective on the contribution of autotrophic processes to ecosystem respiration; changes in LAI should be considered as scalars of fluxes in future ecological disturbance studies.

In contrast to our expectation in hypothesis 2 and the work of Brown *et al* (2012), we found that both eWUE and WUE did not change with increasing mortality but were similar to values reported for shoots in an undisturbed, nearby forest (Smith 1980). Along with increased ecosystem g_c, this suggests the water flux signal is still dominated by transpiration. However the ecosystem transpiration is likely to include an increased understory proportion and may not have transitioned to an increased evaporation to transpiration state. If eWUE or WUE had dropped, as we expected, that would suggest more evaporation from the ecosystem per unit of CO_2 uptake. However, eWUE or WUE can also remain constant even under high water stress (Zhang and Marshall 1994); indeed spruce trees dying from blue-stain induced mortality from spruce beetles continue to photosynthesize while they inevitably die (Dale *et al* 2001).

When considering ecosystem water and CO_2 fluxes, total ET is related to the current age of the forest (Amiro *et al* 2006, Goulden *et al* 2006, Zimmermann *et al* 2000) while eWUE and WUE are both a function of water availability and stand age (Krishnan *et al* 2009). Values of water and CO_2 fluxes from saplings are likely higher than from either a mixed or single aged mature forest (Law *et al* 2001, Phillips *et al* 2002). While the overall (three-year average) CO_2 flux at this site was 49% lower as compared to Smith (1980), it is likely due in large part to intrinsic difference between saplings and mature ecosystems. In general, the eWUE and ecosystem flux values for all three site years were not out of range compared to other evergreen conifer study sites from the FLUXNET (Law *et al* 2002) and European (Kuglitsch *et al* 2008) synthesis studies; furthermore the observed lack of response of C cycling to mortality was similar to other forest disturbance results (Gough *et al* 2013, Gough *et al* 2007).

ET was not controlled by the expected environmental drivers of net radiation, VPD and soil water content and hypothesis 1 is rejected. In healthy pine forests in the Rocky Mountains, ET has been shown to be strongly related to leaf water potential (Running 1980) which is likely controlled by soil water content and VPD (Fetcher 1976, Pataki *et al* 2000). Even though year to year environmental control of water flux did not change during this study, mortality levels were already high (>50%) when flux measurements started. It is possible that ET declines had occurred prior to the start of this study in 2009. However, the smaller than expected response in ET is supported by the work of Biederman *et al* 2014, where stream flow amounts and water isotopic data from the same watershed as this study confirms that ET fluxes do not decrease and even increase as mortality increases. The possibility that surviving trees and re-growth are compensating for high mortality has been proposed by Mikkelson *et al* (2013) and seen in Biederman *et al* (2014), Rhoades *et al* (2013), and Hubbard *et al* (2013). Our work is the first to examine eWUE after mountain pine beetle mortality and contributes to an emerging literature that mountain pine beetles do not have consistent, large ecosystem consequences to water and carbon cycling. Our work combined with other recent papers illustrates that ecosystem resilience to insect-fungi induced mortality must be incorporated into predictions of future forests.

5. Conclusion

This study quantified the impacts of tree mortality induced by an insect epidemic on water and CO_2 cycling and can be used to better understand environmental controls of these fluxes during the course of a large disturbance. Ecosystem WUE did not significantly change during the outbreak and was comparable values from undisturbed forests. An increase in GEP was found between 2009 and 2011. Ecosystem respiration and the efficiency of ecosystem to uptake CO_2 with light (Φ_a)

increased over the outbreak, and changes were primarily attributed to declining canopy leaf area. The interaction between ecosystem WUE and CO_2 uptake in the near future will determine if the ecosystem will be net C source or sink.

As mortality levels off due to lack of suitable sized host trees for the beetles, understory dynamics are expected to play a much larger role in C balance as the ecosystem recovers from the disturbance. Healthy, undisturbed lodgepole pine forests are characterized by a lack of understory vegetation and dry soils. However, beetle-induced mortality increases understory light and soil water and nutrient availability through root gaps. This shift in forest characteristics increases the importance of sub-canopy processes in regulating ecosystem CO_2 and water fluxes while emphasizing the need for such mechanisms to be included in process models of forest recovery after insect-induced mortality.

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