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

David E Reed¹,²,³, Brent E Ewers¹,⁴ and Elise Pendall¹,⁴,⁵

¹ University of Wyoming, Program in Ecology, 1000 E. University, Laramie WY 82071, USA
² University of Wyoming, Department of Atmospheric Science, 1001 E. University, Laramie WY 82071, USA
³ Dickinson College, Department of Physics and Astronomy, PO Box 1773, Carlisle PA 17013, USA
⁴ University of Wyoming, Department of Botany, 1001 E. University, Laramie WY 82071, USA
⁵ Hawkesbury Institute for the Environment, University of Western Sydney, Locked Bag 1797, Penrith, NSW 2751, Australia

E-mail: david.edwin.reed@gmail.com

Received 25 June 2013, revised 19 August 2014
Accepted for publication 9 September 2014
Published 10 October 2014

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 CO₂ 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 CO₂ uptake to water vapor loss) did not change. Between 2009 and 2011, canopy water conductance increased from 98.6 to 151.7 mmol H₂O 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 CO₂ 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 CO₂ exchange. These results agree with an emerging consensus in the literature demonstrating CO₂ and H₂O 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
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 CO2 uptake, increase in decomposition rates, decreasing leaf area and stem density (Edenburg et al 2012), and changes to the water cycle (Mikkelsen 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, CO2 fluxes are primarily controlled by water availability (Pastor and Post 1986). Lack of available water can limit CO2 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 (Edenburg 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 (Mikkelsen 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 CO2 (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, Edenburg 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 (Mikkelsen et al 2013), potentially increasing CO2 uptake in surviving trees (Law et al 2002). Increasing CO2 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 (Mikkelsen 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 Edenburg et al 2012 and Mikkelsen 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 (Edenburg et al 2012). To quantify ecosystem CO2 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 CO2 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 (Grosemannia 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 CO2 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 (HF01SC; Hukselux, 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 CO2 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) (Brümer et al. 2012).

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

where \( \Delta \) is the rate of change of the saturation specific humidity with air temperature, \( \rho \) is dry air density, \( c_p \) is the specific heat capacity of dry air, \( \gamma \) is the psychrometric constant, \( \lambda_c \) 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, 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 CO2 flux and radiation data were used to fit a Michaelis–Menten light response curve (Harley et al. 1992, Falge et al. 2001) to the data.

\[
NEP = \frac{A_{\max}}{A_{\max} + \Phi_0 \, R_s} - R_{eco} \tag{2}
\]

Solar radiation was used for the incoming radiation term, \( R_s \), to estimate quantum yield (\( \Phi_0 \)) 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 (\( R_{eco} \)) was also calculated with VPD limiting GEP, using light response curves and day-time data, following Lasslop et al. (2010). \( R_{eco} \) 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 \( R_{eco} \) 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 (Steudito 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 CO₂ and water flux parameters of \( g_t, R_{ecO}, R_{ecO,D}, \Phi_t, A_{max}, GEP, \) 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 CO₂ 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 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
significantly (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 CO2 fluxes

Average NEP did not change among years even as tree mortality increased dramatically, with net CO2 uptake by the ecosystem remaining high throughout all three growing seasons (figures 1(a), 2(a)). Average values of Φa of diffuse light increased in 2010 and 2011, as compared to 2009 (p < 0.05) (figures 2(b)–(d) and table 2). Ecosystem Amax, and GEP did not change (p > 0.05) among years in this study (figures 2(e), (f)). While Reco was generally smaller than RDeco, 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 gc 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 gc in 2010 and 2011 both increased (p < 0.05) from 2009 (table 2).

The relationship between ecosystem gc 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 gc in 2010 (p < 0.05) with a positive relationship between the variables. gc 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 CO2 mg−1 H2O, which was statistically comparable (p < 0.05) to our results in 2009 and 2011. Average water and CO2 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.

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

| Predictor | ET 2009 (mg H2O m−2 s−1) | ET 2010 (mg H2O m−2 s−1) | ET 2011 (mg H2O 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) |
|-----------|--------------------------|--------------------------|--------------------------|----------------------------------------|----------------------------------------|----------------------------------------|
| Rn (W m−2) | 0.00                     | 0.01b                    | 0.00                     | 0.07                                   | 0.45                                   | 0.12                                   |
| VPD (kPa)  | 0.60                     | 1.25b                    | 1.79b                    | −17.66                                 | 65.54b                                 | 57.12                                  |
| Soil moisture (%) | −1.18                 | −0.78                    | 4.42                     | 398.64                                 | −9.78                                  | 3.80                                   |

* p < 0.05.

b p < 0.01.

Figure 2. Weekly averages of (a) net ecosystem productivity, (b) ecosystem respiration (Rec, calculated from light response curves), (c) ecosystem respiration (RDeco, 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.
Table 2. Mean CO₂ 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 (μmol 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 (μ mole m⁻² s⁻¹) | eWUE With intercept not fixed at zero (μmol CO₂ mg⁻¹ H₂O) | Intercept of eWUE (μmol CO₂ 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 CO₂ m⁻² s⁻¹) | Intercept of WUE (μmol CO₂ mg⁻¹ H₂O) | 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)      | — | — | — | — |
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 CO2 and water exchange were evaluated by normalizing growing season average \( g_* \), \( R_{eco} \), \( R_{eco, d} \), \( \Phi_0 \), \( A_{max} \), GEP, eWUE and WUE by LAI (table 4). The LAI-normalized values of \( g_* \), \( A_{max} \), \( \Phi_0 \) and GEP were higher in 2011 than in 2009 (\( p < 0.05 \)) and scaled \( \Phi_0 \) of diffuse radiation increased every year (\( p < 0.05 \)). Both \( \Phi_0 \) and \( \Phi_d \) 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 \( g_* \) and thus ET increased. Carbon cycling results were also not as expected, with \( A_{max} \), \( R_{eco} \), \( R_{eco, d} \), and GEP all not changing, while only diffuse light \( \Phi_d \) 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 \( \Phi_d \) increased. While there is no pre-outbreak data from this study, the \( A_{max} \) values found (19.6–21.1 \( \mu \text{mol} \text{m}^{-2} \text{s}^{-1} \)) were similar to those in other temperate forest zones (Whitehead and Gower 2001). In a mixed northern hardwood forest experimental treatment, CO2 uptake was sustained through similarly high canopy defoliation (Gough et al 2013).

Ecosystem parameter of diffuse light \( \Phi_d \) 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 \( \Phi_d \) increased from 2009 and 2010 as well. Seasonal patterns in \( \Phi_d \) 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 \( \Phi_d \) 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 CO2 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 CO2 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 CO2 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 \(A_{\text{max}}\) (μmol m\(^{-2}\) s\(^{-1}\)) | LAI Normalized eWUE with intercept not fixed at zero (μmol CO2 mg\(^{-1}\) H2O) | LAI Normalized intercept of eWUE (μmole CO2 m\(^{-2}\) s\(^{-1}\)) | LAI Normalized NEP (μmol m\(^{-2}\) s\(^{-1}\)) | LAI Normalized GEP (μmol 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)                                     | 0.052 (0.02)                                    | 1.43 (0.71)                                     | 1.29 (0.50)                                     | 3.09 (0.31)                                     | 1.03 (0.84)                                     | 1.89 (0.52)                                     | 4.33 (0.27)                                     | 1.03 (0.84)                                     | 1.89 (0.52)                                     | 4.33 (0.27)                                     |
| 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)                                     | 0.055 (0.02)                                    | 1.29 (0.76)                                     | 1.99 (0.57)                                     | 3.51 (0.26)                                     | 1.03 (0.84)                                     | 1.89 (0.52)                                     | 4.33 (0.27)                                     | 1.03 (0.84)                                     | 1.89 (0.52)                                     | 4.33 (0.27)                                     |
| 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)                                     | 0.069 (0.02)                                    | 1.03 (0.84)                                     | 1.89 (0.52)                                     | 4.33 (0.27)                                     | 1.03 (0.84)                                     | 1.89 (0.52)                                     | 4.33 (0.27)                                     | 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 $\Phi_a$ 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 $\Delta_{\text{max}}$ 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 (Edenburg 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 $g_s$, both $\Phi_a$ and diffuse light $\Phi_d$, $\Delta_{\text{max}}$, 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 $g_s$, 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 (Fletcher 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 ($\Phi_d$)
increased over the outbreak, and changes were primarily attributed to declining canopy leaf area. The interaction between ecosystem WUE and CO₂ 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 CO₂ and water fluxes while emphasizing the need for such mechanisms to be included in process models of forest recovery after insect-induced mortality.

Acknowledgments

The authors thank two anonymous reviewers for the improvements to this work based on their comments, J Angstmann, C Rumsey, D King, and F Whitehouse for field site management as well as Yost R and Zippy P for small mammal deterrence at the field site. This work was funded by National Science Foundation, UW Agriculture Experiment Station, Wyoming Water Development Commission, the United States Geological Survey, and the Wyoming NASA Space Grant Consortium.

References

Adelman J D, Ewers B E and Mackay D S 2008 Use of temporal patterns in vapor pressure deficit to explain spatial autocorrelation dynamics in tree transpiration *Tree Physiol.*, **28** 647–58

Amiro B D et al 2006 Carbon, energy and water fluxes at mature and disturbed forest sites, Saskatchewan, Canada Agric. Forest Meteorol., **136** 237–51

Amiro B D et al 2010 Ecosystem carbon dioxide fluxes after disturbance in forests of North America J. Geophys. Res.-Biogeosci., **115** G00K02

Ayres M P and Lombardero M A J 2000 Assessing the consequences of global change for forest disturbance from herbivores and pathogens Sci. Total Environ., **262** 263–86

Baldocchi D D, Hicks B B and Camara P 1987 A canopy stomatal resistance model for gaseous deposition to vegetated surfaces Atmos. Environ. (1967), **21** 91–101

Baldocchi D D, Luxmoore R J and Hatfield J L 1991 Discerning the forest from the trees: an essay on scaling canopy stomatal conductance Agric. Forest Meteorol., **54** 197–226

Bearell L A, Maxwell R M, Clow D W and McCray J E 2014 Hydrological effects of forest transpiration loss in bark beetle-impacted watersheds *Nat. Clim. Change* **46** 481–6.

Biederman J A, Brooks P D, Harpold A A, Goichis D J, Gutmann E, Reed D E, Pendall E and Ewers B E 2014 Multiscale observations of snow accumulation and peak snowpack following widespread, insect-induced lodgepole pine mortality *Ecology Hydrology*, **7** 150–62

Bowler R, Fredeen A L, Brown M and Andrew Black T 2012 Residual vegetation importance to net CO₂ uptake in pine-dominated stands following mountain pine beetle attack in British Columbia, Canada Forest Ecol. Manage., **269** 82–91

Brown M, Black T A, Nesci Z, Foord V N, Spittlehouse D L, Fredeen A L, Grant N J, Burton P J and Troslynow J A 2010 Impact of mountain pine beetle on the net ecosystem production of lodgepole pine stands in British Columbia Agric. Forest Meteorol., **150** 254–64

Brown M G et al 2012 The carbon balance of two lodgepole pine stands recovering from mountain pine beetle attack in British Columbia Agric. Forest Meteorol., **153** 82–93

Brümmer C et al 2012 How climate and vegetation type influence evapotranspiration and water use efficiency in Canadian forest, peatland and grassland ecosystems Agric. Forest Meteorol., **153** 14–30

Burton P J 2010 Striving for sustainability and resilience in the face of unprecedented change: the case of the mountain pine beetle outbreak in British Columbia *Sustainability*, **2** 2403–23

Cao M and Woodward F I 1998 Dynamic responses of terrestrial ecosystem carbon cycling to global climate change *Nature*, **393** 249–52

Carignan R, D’arcy P and Lamontagne S 2000 Comparative impacts of fire and forest harvesting on water quality in boreal shield lakes *Can. J. Fish. Aquatic Sci.*, **57** 105–17

Clark K L, Skowronski N and Hom J 2010 Invasive insects impact forest carbon dynamics Glob. Change Biol., **16** 88–101

Cowan I R and Farquhar G D 1977 Stomatal function in relation to leaf metabolism and environment *Symp. Soc. Exp. Biol.*, **31** 471–505

Dale V H et al 2001 Climate change and forest disturbances *Biogeochemistry*, **51** 723–34

Deluca T H and Zouhar K L 2000 Effects of selection harvest and prescribed fire on the soil nitrogen status of ponderosa pine forests *Forst Ecol. Management*, **138** 263–71

Dixon R K, Solomon A M, Brown S, Houghton R A, Trexier M C and Winsiekwski J 1994 Carbon pools and flux of global forest ecosystems *Science*, **263** 85–90

Edsberg S L, Hicke J A, Brooks P D, Pendall E G, Ewers B E, Norton U, Goichis D, Gutmann E D and Meddens A J H 2012 Cascading impacts of bark beetle-caused tree mortality on coupled biogeochemical and biogeochemical processes *Front. Ecol. Environ.*, **10** 416–24

Emmerich W E 2007 Ecosystem water use efficiency in a semiarid shrubland and grassland community *Rangeland Ecol. Manage.*, **60** 464–70

Ewers B E, Oren R, Kim H S, Bohrer G and Lai C T 2007 Effects of hydraulic architecture and spatial variation in light on mean stomatal conductance of tree branches and crowns *Plant Cell Environ.*, **30** 483–96

Falge E et al 2001 Gap filling strategies for defensible annual sums of net ecosystem exchange Agric. Forest Meteorol., **107** 43–69

Fletcher N 1976 Patterns of leaf resistance to lodgepole pine transpiration in wyoming *Agric. Forest Meteorol.*, **17** 1–9

Goetz S J et al 2012 Observations and assessment of forest carbon dynamics following disturbance in North America *J. Geophys. Res.*, **117** G02022

Gough C M, Hardiman B S, Nave L E, Bohrer G, Maurer K D, Vogel C S, Nadelhoffer K J and Curtis P S 2013 Sustained carbon uptake and storage following moderate disturbance in a Great Lakes forest *Ecol. Appl.*, **23** 1202–15
Gough C M, Vogel C S, Harrold K H, George K and Curtis P S 2007 The legacy of harvest and fire on ecosystem carbon storage in a north temperate forest Glob. Change Biol. 13 1935–49

Goulden M L, Winston G C, Mcmillan A M S, Litvak M E, Read E L, Rocha A V and Elliot J R 2006 An eddy covariance mesonet to measure the effect of forest age on land-atmosphere exchange Glob. Change Biol. 12 2146–62

Gower S T, Kucharik C J and Norman J M 1999 Direct and indirect estimation of leaf area index, fAPAR, and net primary production of terrestrial ecosystems Remote Sens. Environ. 70 29–51

Granier A, Biron P and Lemoine D 2000 Water balance, transpiration and canopy conductance in two beech stands Agric. Forest Meteorol. 100 291–308

Gu L, Baldocchi D, Verma S B, Black T A, Vesala T, Falge E M and Dowdy P R 2002 Advantages of diffuse radiation for terrestrial ecosystem productivity J. Geophys. Res. 107(D6)

Gu L H et al 2005 Objective threshold determination for nighttime eddy flux filtering Agric. Forest Meteorol. 128 179–97

Harley P C, Thomas R B, Reynolds J F and Strain B R 1992 Modeling photosynthesis of cotton grown in elevated CO2 Plant Cell Environ. 15 271–82

Harmon M E, Bond-Lamberty B, Tang J and Vargas R 2011 Heterotrophic respiration in disturbed forests: a review with examples from North America J. Geophys. Res.: Biogeosci. 116 G00K04

Hicke J A et al 2012 Effects of biotic disturbances on forest carbon cycling in the United States and Canada Glob. Change Biol. 18 7–34

Horst T and Lenschow D 2009 Attenuation of scalar fluxes measured with spatially-displaced sensors Bound.-Layer Meteorol. 130 275–300

Horst T W 2000 On frequency response corrections for eddy covariance flux measurements Bound.-Layer Meteorol. 94 517–20

Hubbard R M, Rhodes C C, Elder K and Negron J 2013 Changes in transpiration and foliage growth in lodgepole pine trees following mountain pine beetle attack and mechanical girdling Forest Ecol. Manage. 289 312–7

Katul G G, Palmroth S and Oren R 2009 Leaf stomatal responses to Hubbell R M, Rhoades C C, Elder K and Negron J 2006 An eddy covariance mesonet to measure the effect of forest age on land-atmosphere exchange Glob. Change Biol. 12 2146–62

Gower S T, Kucharik C J and Norman J M 1999 Direct and indirect estimation of leaf area index, fAPAR, and net primary production of terrestrial ecosystems Remote Sens. Environ. 70 29–51

Granier A, Biron P and Lemoine D 2000 Water balance, transpiration and canopy conductance in two beech stands Agric. Forest Meteorol. 100 291–308

Gu L, Baldocchi D, Verma S B, Black T A, Vesala T, Falge E M and Dowdy P R 2002 Advantages of diffuse radiation for terrestrial ecosystem productivity J. Geophys. Res. 107(D6)

Gu L H et al 2005 Objective threshold determination for nighttime eddy flux filtering Agric. Forest Meteorol. 128 179–97

Harley P C, Thomas R B, Reynolds J F and Strain B R 1992 Modeling photosynthesis of cotton grown in elevated CO2 Plant Cell Environ. 15 271–82

Harmon M E, Bond-Lamberty B, Tang J and Vargas R 2011 Heterotrophic respiration in disturbed forests: a review with examples from North America J. Geophys. Res.: Biogeosci. 116 G00K04

Hicke J A et al 2012 Effects of biotic disturbances on forest carbon cycling in the United States and Canada Glob. Change Biol. 18 7–34

Horst T and Lenschow D 2009 Attenuation of scalar fluxes measured with spatially-displaced sensors Bound.-Layer Meteorol. 130 275–300

Horst T W 2000 On frequency response corrections for eddy covariance flux measurements Bound.-Layer Meteorol. 94 517–20

Hubbard R M, Rhodes C C, Elder K and Negron J 2013 Changes in transpiration and foliage growth in lodgepole pine trees following mountain pine beetle attack and mechanical girdling Forest Ecol. Manage. 289 312–7

Katul G G, Palmroth S and Oren R 2009 Leaf stomatal responses to vapour pressure deficit under current and CO2-enriched atmosphere explained by the economics of gas exchange Plant Cell Environ. 32 968–79

Krishnan P, Black T A, Jassal R S, Chen B and Nesic Z 2009 Interannual variability of the carbon balance of three different-aged Douglas-fir stands in the Pacific Northwest J. Geophys. Res.: Atmos. 114 G04011

Kuglitsch F, Reichstein M, Beer C, Carrara A, Ceulemans R, Granier A, Janssens I, Koestner B, Lindroth A and Loustau D 2008 Characterisation of ecosystem water-use efficiency of European forests from eddy covariance measurements Biogeosci. Discuss. 5 4481–519

Kurz W A, Dymond C C, Stinson G, Rampley G J, Neilson E T, Carroll A L, Ebata T and Safranyik L 2008a Mountain pine beetle and forest carbon feedback to climate change Nature 452 987–90

Kurz W A, Stinson G, Rampley G J, Dymond C C and Neilson E T 2008b Risk of natural disturbances makes future contribution of Canada’s forests to the global carbon cycle highly uncertain Proc. Natl. Acad. Sci. USA 105 1551–5

Lasslop G, Reichstein M, Papale D, Richardson A D, Arndt A, Arrêt A, Stoy P and Wohlfahrt G 2010 Separation of net ecosystem exchange into assimilation and respiration using a light response curve approach: critical issues and global evaluation Glob. Change Biol. 16 187–208

Law B E et al 2002 Environmental control over carbon dioxide and water vapor exchange of terrestrial vegetation Agric. Forest Meteorol. 113 97–120

Law B E, Goldstein A H, Anthoni P M, Unsworth M H, Pance J A, Bauer M R, Fracheboud J M and Hultman N 2001 Carbon dioxide and water vapor exchange by young and old ponderosa pine ecosystems during a dry summer Tree Physiol. 21 299–308

Lee X, Massman W and Law B 2004 Handbook of Micrometeorology: A Guide for Surface Flux Measurement and Analysis (Dordrecht: Kluwer)

Liu S et al 2011 Simulating the impacts of disturbances on forest carbon cycling in North America: processes, data, models, and challenges J. Geophys. Res.: Biogeosci. 116 G00K08

Loescher H W, Hanson C V and Oechel T W 2009 The psychrometric constant is not constant: a novel approach to enhance the accuracy and precision of latent energy fluxes through automated water vapor calibrations Hydrometeorol. 10 1271–84

Mackay D S, Ahl D E, Ewers B E, Gower S T, Burrows S N, Samanta S and Davis K J 2002 Effects of aggregated classifications of forest composition on estimates of evapotranspiration in a northern Wisconsin forest Glob. Change Biol. 8 1253–65

Mackay D S, Ewers B E, Loranty M M and Kruger E L 2010 On the representativeness of plot size and location for scaling transpiration from trees to a stand J. Geophys. Res. 115 G02016

Masker J G, Huang C, Wolfe R, Cohen W, Hall F, Kutler J and Nelson P 2008 North American forest disturbance mapped from a decadal Landsat record Remote Sens. Environ. 112 2914–26

Massman W J 2000 A simple method for estimating frequency response corrections for eddy covariance systems Agric. Forest Meteorol. 104 185–98

Mcdowell N et al 2008 Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? New Phytologist 178 719–39

Mikkelsen K, breakup L, Maxwell R, Stednick J, Mcrayer J and Sharp J 2013 Bark beetle infestation impacts on nutrient cycling, water quality and interdependent hydrological effects Biogeochemistry 115 1–21

Monson R K, Prater M R, Hu J, Burns S P, Sparks J P, Sparks K L and Scott-Denton L E 2010 Tree species effects on ecosystem water-use efficiency in a high-elevation, subalpine forest Oecologia 162 491–504

Nijssen B and Lettenmaier D P 1999 A simplified approach for predicting shortwave radiation transfer through boreal forest canopies J. Geophys. Res. 104 27859–68

Parsons W J, Miller S L and Knight D H 1994 Root-gap dynamics in a lodgepole pine forest: ectomycorrhizal and nonmycorrhizal fine root activity after experimental gap formation Can. J. Forest Res. 24 1531–8

Pastor J and Post W 1986 Influence of climate, soil moisture, and succession on forest carbon and nitrogen cycles Biogeochemistry 2 3–27

Pataki D E, Oren R and Smith W K 2000 Sap flux of co-occurring species in a western subalpine forest during seasonal soil drought Ecology 81 2557–66

Phillips N, Bond B J, Mcdowell N G and Ryan M G 2002 Canopy and hydraulic conductance in young, mature and old Douglas-fir trees Tree Physiol. 22 205–11

Ponton S, Flanagan L B, Astl K P, Johnson B G, Morgenstern K, Kljun N, Black T A and Barr A G 2006 Comparison of ecosystem water-use efficiency among Douglas-fir forest, aspen forest and grassland using eddy covariance and carbon isotope techniques Glob. Change Biol. 12 294–310

Pugh E and Small E 2012 The impact of pine beetle infestation on snow accumulation and melt in the headwaters of the Colorado River Ecohydrology 5 467–77

Raffa K F, Aukema B H, Bentz B J, Carroll A L, Hicke J A, Turner M G and Romme W H 2008 Cross-scale drivers of...
natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions BioScience 58 501–17
Reichstein M et al 2005 On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm Glob. Change Biol. 11 1424–39
Rhoades C C et al 2013 Biogeochemistry of beetle-killed forests: explaining a weak nitrate response Proc. Nat Acad. Sci. 110 1756–60
Roy J, Mooney H A and Saugier B 2001 Terrestrial global productivity (New York: Academic)
Running S W 1980 Environmental and physiological control of water flux through pinus contorta Can. J. Forest Res. 10 82–91
Schuepp P H, Leclerc M Y, Macpherson J I and Desjardins R L 1990 Footprint prediction of scalar fluxes from analytical solutions of the diffusion equation Bound.-Layer Meteorol. 50 355–73
Smith W K 1980 Importance of aerodynamic resistance to water use efficiency in three conifers under field conditions Plant Physiol. 65 132–5
Spitters C J T 1986 Separating the diffuse and direct component of global radiation and its implications for modeling canopy photosynthesis: II. Calculation of canopy photosynthesis Agric. Forest Meteorol. 38 231–42
Steduto P and Albrizio R 2005 Resource use efficiency of field-grown sunflower, sorghum, wheat and chickpea: II. Water use efficiency and comparison with radiation use efficiency Agric. Forest Meteorol. 130 269–81
Thompson M T D, Larry T and Blackard J A 2005 Wyoming’s Forests, 2002. Resour. Bull. RMRS-RB-6. Fort Collins, CO: US Department of Agriculture, Forest Service, Rocky Mountain Research Station 148 p
Valentini R et al 2000 Respiration as the main determinant of carbon balance in European forests Nature 404 861–5
Vanloocke A, Twine T E, Zeri M and Bernacchi C J 2012 A regional comparison of water use efficiency for miscanthus, switchgrass and maize Agric. Forest Meteorol. 164 82–95
Webb E K, Pearman G I and Leurig R 1980 Correction of flux measurements for density effects due to heat and water vapor transfer Q. J. R. Meteorol. Soc. 106 85–100
Whitehead D and Gower S T 2001 Photosynthesis and light-use efficiency by plants in a Canadian boreal forest ecosystem Tree Physiol. 21 925–9
Yamaoka Y, Swanson R H and Hiratsuka Y 1990 Inoculation of lodgepole pine with four blue-stain fungi associated with mountain pine beetle, monitored by a heat pulse velocity (HPV) instrument Can. J. Forest Res. 20 31–6
Zhang J and Marshall J D 1994 Population differences in water-use efficiency of well-watered and water-stressed western larch seedlings Can. J. Forest Res. 24 92–9
Zhang L-M et al 2006 Seasonal variations of ecosystem apparent quantum yield (α) and maximum photosynthesis rate (Pmax) of different forest ecosystems in China Agric. Forest Meteorol. 137 176–87
Zimmermann R, Schulze E D, Wirth C, Schulze E E, Mcdonald K C, Vygodskaya N N and Ziegler W 2000 Canopy transpiration in a chronosequence of Central Siberian pine forests Glob. Change Biol. 6 25–37