Impacts of beetle-induced forest mortality on carbon, water and nutrient cycling in the Rocky Mountains

Elise Pendall, Brent Ewers, Urszula Norton, Paul Brooks, W.J. Massman, Holly Barnard, David Reed, Tim Aston, John Frank

Conifer forests across western North America are undergoing a widespread mortality event mediated by an epidemic outbreak of bark beetles of the genus Dendroctonus and their associated bluestain fungi (Ophiostoma spp.). As of late 2009, beetles have impacted over 600,000 hectares in northern Colorado and southern Wyoming (US Forest Service aerial survey estimates), with the majority of mature lodgepole pine (Pinus contorta) and Engelmann spruce (Picea engelmannii) expected to be dead by 2012 (Figure 1; Figure 2). While bark beetles are native to North American forests, the importance of insect outbreaks on water, C and N cycling has increased in recent years as a result of past timber management, fire exclusion, recent warming trends and drought (Allen et al. 2010). A recent modeling study suggests that CO₂ emissions from beetle-induced lodgepole pine mortality in British Columbia, Canada may be similar in magnitude as stand-replacing fires (Kurz et al 2008).

Current Bark Beetle Activity in Wyoming From the 2009 Aerial Detection Survey

Figure 1: Current bark beetle activity in Wyoming
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Experimental girdling of lodgepole pines led to a 92% increase in water outflow, compared to a 277% increase resulting from clearcutting (Knight et al. 1991). Despite the enormity of the currently spreading bark beetle epidemic, little is known of its impact on carbon, water and nitrogen cycles.

Bark beetles spend much of their life as larvae under the bark of host trees, feeding on phloem. Although healthy host trees can repel beetles through enhanced resin production, their defenses are overwhelmed by mass attacks synchronized by pheromones. Tree death occurs through occlusion of xylem by blue-stain fungus carried by the beetles, resulting in death of trees within months of attack (Figure 3; Knight et al. 1991). While the beetle has several hosts, lodgepole pine is especially important due to its large spatial extent, its timber, recreational and wildlife habitat values, and its controls over carbon, water and nutrient cycles in mid-elevation forests of the central Rockies (Knight et al. 1991) including southern Wyoming. Beetle mortality of Engelmann spruce is a concern in subalpine forests, where snowpack accumulates in the headwaters of rivers that supply Western cities with most of their water.

While predictive understanding of the bark beetle epidemic is improving, much less is known about its subsequent impact on plant succession and carbon, water and nutrient cycling. Much of the current understanding has been hypothesized from comparisons to fire research or simulated with models (Kurz et al. 2008). Forest managers believe that lodgepole pine is likely to become re-established following bark beetle mortality (Jenkins et al. 2008), but the rate of recovery and resulting stand density and productivity are impossible to predict with current knowledge. Furthermore, successional trajectories at upper and lower forest boundaries may not be predictable from stand dynamics of the recent past. On annual to decadal timescales, the responses of C, water and nutrient cycling to the beetle epidemic are linked to forest stand dynamics, particularly leaf area index (LAI), as suggested by our hypotheses, presented in Figure 4.

Near our study area in the Medicine Bow Mountains (Figure 1), beetle attacks were simulated by girdling trees on small experimental patches with the main objective of studying effects on water and N cycling. The girdling treatment increased discharge below the rooting zone (Knight et al. 1991). Extensive spruce beetle mortality was associated with increased streamflow in Colorado (Bethlahmy 1974) and Montana (Potts, 1984). However, other key components of the water cycle, such as...
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Figure 4. Postulated time course of ecosystem characteristics and biogeochemical responses to MPB attack over 3 year study period in our catchment ecosystems. MPB preferentially kills larger diameter host trees in open stands, leading to spatial variability in mortality patterns and impacts (indicated by dashes). TOP: Tree mortality is associated with rapid loss of LAI, decreased transpiration, NPP and canopy interception (yellow). A pulse of needle litterfall begins during the second year after attack, and is associated with peaks of decomposition (Rh) and DOM export to streams (blue). BOTTOM: Decreased LAI and transpiration lead to increases in soil moisture and temperature (red). Reduced N uptake by trees enhances N availability (green), which may be inhibited by terpenes the first year after attack.

Evapotranspiration, have not previously been studied. Our initial sap flux data suggests that within a month of beetle attack and introduction of bluestain fungus, transpiration per tree is reduced to less than half (Figure 5). Water availability following beetle attack is likely to determine in large part the immediate responses of subsequent C and N cycling. Parsons et al. (1994) found that girdling patches with at least 15 trees resulted in significantly greater concentrations of inorganic N while dissolved organic N decreased. Indeed, surviving trees are crucial to retaining N in stands (Knight et al. 1991). How much of this extra available N will be taken up by the next generation of trees, potentially enhancing growth and C sequestration, or lost to streams or denitrifying processes is still unknown.

We are studying ecosystem responses to beetle-induced lodgepole and spruce mortality at middle and upper elevation forests using eddy covariance at Chimney Park (CP) and the Glacier Lakes Ecosystem Experiments Site (GLEES), Wyoming (Figure 6a, b). The GLEES Ameriflux site (41.3642° N; 106.23995° W; 3126 m) has been in operation since 1999, and is dominated by Englemann spruce and subalpine fir (Abies lasiocarpa). Recent data from GLEES suggest a decline in forest C uptake and water loss (Figure 7). The CP site (41.068° N, 106.1195° W 2740 m elevation) has been operating since spring,
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2009, and is dominated by lodgepole pine that has been subjected to varying management regimes in the past several decades. Preliminary data suggest that during the 2009 growing season, mortality had not yet impacted water or CO2 fluxes. A unique aspect of our study is the carbon and water budgets at the tower scale as well as in zero - and first-order drainages via intensive studies of snow hydrology (Figure 8), soil water, respiration and trace gas fluxes within stands varying in time since beetle attack.

Clearly, many unknowns exist regarding forest regeneration and C, N and water cycling following beetle attack. Regeneration, or succession, will define the trajectory of forest stand dynamics for the coming century, and the plant communities that are established in the wake of the epidemic will regulate biogeochemical and water cycles over the decadal time frame of succession. Past timber management appears to have affected the rate of infestation and extent of mortality, and will thus also impact regeneration. Our present focus is on short-term (3-year) responses to the current bark beetle outbreak and will set the stage for continued longer-term monitoring (5-10 years and beyond). Our study areas are valuable because of their proximity accessibility in all seasons, and extensive ecological research that has been previously conducted there (e.g., Knight et al. 1991; Parsons et al. 1994; Musselman 1994). Thus, we expect that this initial study should generate mechanistic understanding of immediate

Figure 6. A. GLEES AmeriFlux scaffold; B. CP tower.

Figure 7. Annual CO2 and H2O fluxes from the GLEES AmeriFlux site (negative means uptake by the forest ecosystem).
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ecosystem responses and also provide a platform for future studies.

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contact:

Elise Pendall
pendall@uwyo.edu

Department of Botany & Program in Ecology, University of Wyoming, Laramie

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