CHAPTER 11.

The Influence of Mountain Pine Beetle Outbreaks on Carbon Productivity and Storage in Central U.S. Rockies Lodgepole Pine Forests

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INTRODUCTION

Recent widespread and severe bark beetle outbreaks in western North America have resulted in larger carbon (C) pools in beetle-killed trees than in fire-killed trees (Hicke and others 2013). Mortality from these outbreaks modifies forest structure, changes the course of forest development, and affects nutrient and carbon cycling at multiple scales of time and space (Edburg and others 2012, Hansen 2014, Hicke and others 2012). Knowledge of post-outbreak C productivity (the rate of stand-level C accumulation from live plants) and storage (the amount of C biomass held in stands at a point in time) will aid prediction of regional forest C balance (i.e., the net rate of C accumulation or loss from the ecosystem) (Kashian and others 2013). More information is needed to understand the possible contributions of post-outbreak stands to atmospheric carbon dioxide (CO_2) content. For example, Kurz and others (2008) suggest that the recent outbreaks in western Canada were large enough to increase global atmospheric CO_2, whereas eddy covariance data suggest that post-outbreak stands are near C neutral (Brown and others 2012, Moore and others 2013).

Cycles of birth, growth, death, and renewal occur at all ecological scales, including entire ecosystems (Holling 1992). In lodgepole pine (*Pinus contorta*) systems, stand-replacing wildfires may occur at intervals up to 300 years or more (Arno 1980). A disturbance-adapted species, lodgepole pine rapidly recolonizes burned landscapes, typically forming pure, even-aged stands (Lotan and others 1985) that become increasingly susceptible to mountain pine beetle (*Dendroctonus ponderosae*) outbreaks as trees grow into diameters favored by beetles, usually after stand ages of 80 years (Amman and others 1977). Recurring outbreaks are possible thereafter every 20–50 years (Alfaro and others 2004, Cole and Amman 1980). These outbreaks are partial disturbances that kill varying amounts of overstory pines and generally leave nonpines (e.g., fir and spruce) and understory pines undamaged (Hansen 2014).

These beetle-caused changes in stand structure and subsequent stand development modify C productivity (i.e., the rate of C accumulation in live plants) for decades after infestation. Although the death of each beetle-killed tree immediately results in reduced stand-level productivity, surviving trees accelerate growth because of reduced competition for resources. Moreover, seedlings are commonly recruited into beetle-caused canopy gaps (Hansen 2014). Thus, productivity can recover to pre-outbreak levels, with recovery times ranging from 5 to 56 years (Edburg and others 2011, Kashian and others 2013, Pfeifer and others 2010, Romme and others 1986). Meanwhile, C productivity in uninfested even-aged stands typically reaches maximum rates within a few decades after stand establishment then slowly diminishes over the life of the stand (Ryan and others 1997). In lodgepole pine stands, this peak occurs at age 24–60 years and declines to 16–48 percent of peak values by age 200–350 years (Kashian and others 2013, Pearson and others

1987, Ryan and Waring 1992). It is therefore possible that frequent partial disturbances, such as from beetle outbreaks, might stimulate C productivity by returning stand development to conditions similar to earlier, more productive stages (Kimmins 1987).

The impact of outbreaks on C storage is confounded by rate changes in pool inputs (i.e., C productivity) and outputs (i.e., C release via decomposition). As outlined above, input rates initially decline but productivity will recover to levels at or, possibly, above pre-outbreak rates. Output rates will vary by substrate type (e.g., fallen needles will decompose within a few years whereas infested boles will persist for decades) and beetle-caused changes in stand structure will modify microclimates, affecting process rates. All of these rate changes vary with time, and long-term patterns (e.g., > 100 years) must be considered to fully understand the influence of outbreaks.

Our objectives were to measure and model the effects of mountain pine beetle outbreaks on C productivity and storage in lodgepole pine type of the central U.S. Rockies. Various aspects of this subject have been examined by previous investigators (Edburg and others 2011, Kashian and other 2013, Pfeifer and others 2010, Romme and others 1986). We present the most comprehensive analysis to date, combining empirical and simulated data to examine short- and long-term C responses among undisturbed and infested lodgepole pine stands. We installed plots in undisturbed and infested stands, with a range of time since infestation (3–80 years), to quantify C storage, C productivity, and decomposition of litter and fine woody debris. We augmented these observations with growth and yield model simulations of C storage and productivity under developmental trajectories with and without mountain pine beetle infestation.

METHODS

After consultation with U.S. Forest Service entomologists, we identified potential field sites in lodgepole pine type with and without evidence of previous mountain pine beetle infestation in three landscapes of the central U.S. Rockies (fig. 11.1). These stands were dominated by lodgepole pine, including the understory for most stands, although some stands also had varying amounts of subalpine fir, Engelmann spruce, Douglas-fir, and/or whitebark pine. Each landscape included an uninfested, mature class of plots with stand ages 118–145 years old. Additional disturbance history classes were: (1) uninfested old-growth (> 200 years old); (2) stands with an outbreak c. 1984; (3) stands with an outbreak c. 1974; (4) stands with an outbreak c. 1930; and (5) stands with an initial outbreak c. 1930 and subsequent outbreak c. 1999–2006 (note that not all classes were available at each of the three landscapes; see Hansen and others 2015). To minimize environmental differences, plot locations were randomly selected within each landscape and disturbance history class using restrictions on elevation, aspect, and slope (e.g., 300-m elevation "window"). Thirty-six plots were installed during 2008–2009 and monitored

Figure 11.1—Plot locations (circles) at three landscapes with undisturbed and mountain pine beetle-infested lodgepole pine stands. Infested stands represented a range of time since disturbance. The green polygons represent lodgepole pine distribution.

for at least 3 years. Sampling methods were based on U.S. Department of Agriculture, Forest Service, Forest Inventory and Analysis phase 3 protocols (USDA Forest Service 2008). These include measurements of over- and understory trees, downed woody material, vegetation, and soils (fig. 11.2). Some protocols were modified to meet the needs of our study, and additional measurements were included to estimate litterfall and decomposition rates. Carbon pool sizes were calculated by multiplying biomass, estimated from allometric equations (Lambert and others 2005), by component-specific

Figure 11.2—A survey crew sampling downed woody materials in a lodgepole pine stand infested by mountain pine beetles about 10 years earlier, Sawtooth National Forest, Idaho. (photo by Matt Hansen, U.S. Department of Agriculture Forest Service)

C concentrations (e.g., foliage, bark, stemwood) derived by analyzing off-plot tree tissue samples. All plots were remeasured 3 years after the original surveys and plot-level C productivity was estimated as the difference in total C storage (adjusted to an annual basis) plus litterfall C. Forest floor decomposition rates were estimated by dividing the C mass by the annual litterfall C flux. We also measured 1-year mass loss of litterbags and tongue depressors, the latter a proxy for fine woody debris. Net ecosystem C balance (i.e., the net rate of C accumulation or loss from live and dead biomass) was calculated by subtracting estimated decomposition rates of snags, downed woody materials, and forest floor from estimates of C productivity (see Hansen and others 2015 for full details).

We used the Forest Vegetation Simulator (FVS) (Dixon 2002) to augment our field data and simulated development with and without mountain pine beetle disturbance. These simulations allowed us to examine complete chronosequences of C productivity and storage, rather than discrete post-outbreak intervals dictated by availability of suitable plots. Moreover, pre-outbreak stand conditions were held constant with the simulations, thus overcoming confounding influences due to environment and initial stand structure. Note that the empirical and simulated data were not intended as validation for each other; rather, each method has inherent advantages and disadvantages and using both methods enhances the data from which to infer beetle-caused impact to C cycling. Input data sources were our field data as well as “bare-ground” conditions, the latter initiated with median values of postfire seedling density as well as snag, downed woody material, and forest floor biomasses measured from recently burned stands. FVS has > 20 regionally specific variants; we used the Tetons and Utah variants. One-hundred-year simulations were created based on the field data (i.e., mature stands) and 200-year simulations with the bare-ground data (i.e., newly established stands). For simulations with mountain pine beetle disturbance, we used the FVS-Mountain Pine Beetle extension and manually scheduled infestations every 40 years beginning at stand age 100 years. To demonstrate the influence of infestation severity, we ran bare-ground simulations using the default mortality algorithms as well as simulations with reduced mortality rates. The simulations included regeneration at each 10-year time step with a pulse of lodgepole regeneration one time step after any infestation; this mimics post-outbreak recruitment observed in the field (Hansen 2014). Using the same allometric equations used to estimate biomass for our field data, we calculated aboveground C in the trees with additional compartments (e.g., nontree vegetation, snags, forest floor, and roots) estimated using the Fire and Fuels Extension of FVS. Carbon productivity was calculated by dividing the time step C accumulation in trees by the number of years in the time step (see Hansen and others 2015 for details of FVS keywords and settings used). We derived net ecosystem C balance by comparing total C storage at each 10-year time step; increasing total C storage was considered to indicate positive net C balance (i.e., C sink), whereas decreasing total C storage was considered to indicate negative C balance (i.e., C source).

We used generalized linear mixed models to detect differences among the disturbance history classes for the field and simulated data. Additional analyses were conducted using combined disturbance history classes (e.g., uninfested mature and old-growth compared to all infested disturbance history classes). In a preliminary analysis, we tested for differences among the three landscapes by comparing C productivity and storage among the uninfested mature class plots. Because no significant differences were found, we analyzed all data from the three landscapes in single models using "landscape" as a random variable (see Hansen and others 2015 for full details).

RESULTS AND DISCUSSION

Total system C storage was not significantly different among most disturbance history classes using the field data; the only significant difference was between old-growth plots and plots infested a second time c. 2002 (fig. 11.3). Combined infested classes, however, had about 19 percent less total C than combined undisturbed classes. The outbreaks redistributed C from the live overstory compartment to the snags/downed woody material compartment. Time since outbreak diminished these differences; the oldest post-outbreak class plots (infested c. 1930) were not significantly different from the undisturbed class plots for any

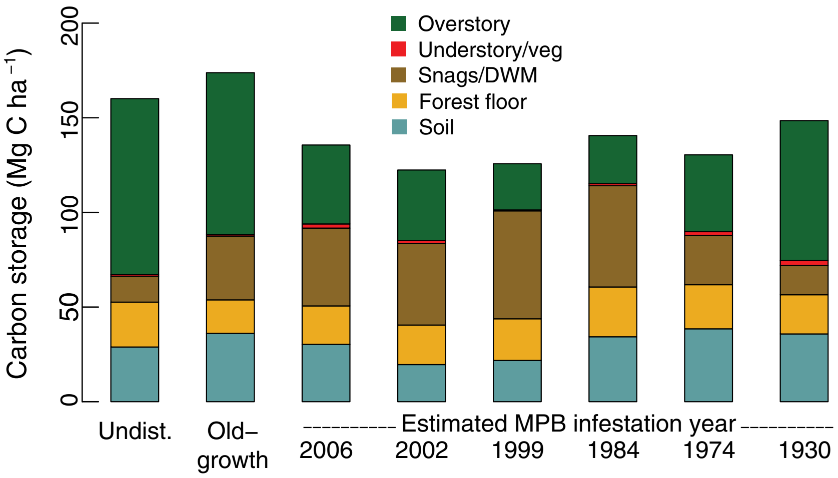


Figure 11.3—Mean carbon storage by compartment among disturbance history classes. Total system carbon (C) storage was significantly different only between old-growth plots and plots infested a second time c. 2002. Combined infested-class plots, however, had significantly less (about 19 percent) total C than combined undisturbed and old-growth plots. Carbon storage by compartment was significantly different among the disturbance history classes. Most notably, infestations transferred C from live overstory to dead compartments although the plots infested c. 1930 were not significantly different than the undisturbed plots for any compartment (see Hansen and others 2015 for full details). Note: DWM = downed woody material; MPB = mountain pine beetle.

compartment. Results from the FVS-simulated data were generally similar. For simulations based on the field data, trajectories with repeated beetle disturbance averaged 1–30 percent less total C storage than did undisturbed trajectories. For simulations based on the bare-ground data, trajectories with repeated beetle disturbance had 7–34 percent less average total C storage than did undisturbed trajectories, depending on outbreak severity and FVS variant (fig.11.4). In summary, C storage is reduced by mountain pine beetle outbreaks, but levels remain robust because C is transferred from live to dead compartments, and decomposition is drawn out over many decades (fig. 11.3). These results support Pfeifer and others' (2010) conclusion that lodgepole pine C storage is resilient to mountain pine beetle disturbance.

Carbon productivity results using the field data were similar to the C storage results in that undisturbed and infested class plots were not significantly different (with one pairwise exception; fig. 11.5, top panel), whereas *combined* infested class plots had about 19 percent less C productivity than combined undisturbed class plots. From the field data-based FVS simulations, Utah variant, 100-year averaged C productivity results indicated no significant differences between trajectories with and without repeated mountain pine beetle (MPB) outbreaks. Results using the Tetons variant were variable depending on whether the stand had been previously infested. Among undisturbed stands, trajectories without MPB infestation had greater 100-year averaged C productivity than did trajectories with repeated mountain pine beetle outbreaks, whereas the opposite was the case for stands with previous infestation (Hansen and others 2015). Temporal patterns of post-outbreak C productivity can be seen in results from simulations using bare-ground simulations, Tetons variant (fig. 11.6). Using the default beetle-caused mortality algorithm, C productivity was decreased after an outbreak but generally rebounded to values at or above that of the undisturbed trajectory within 20–30 years. Moreover, the reduced severity

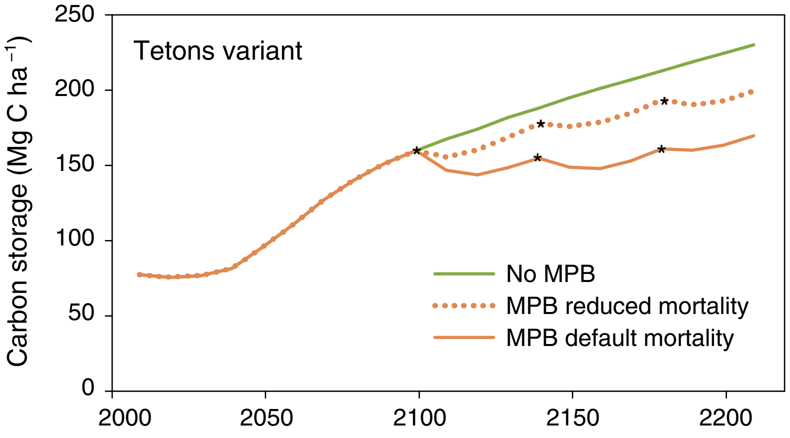
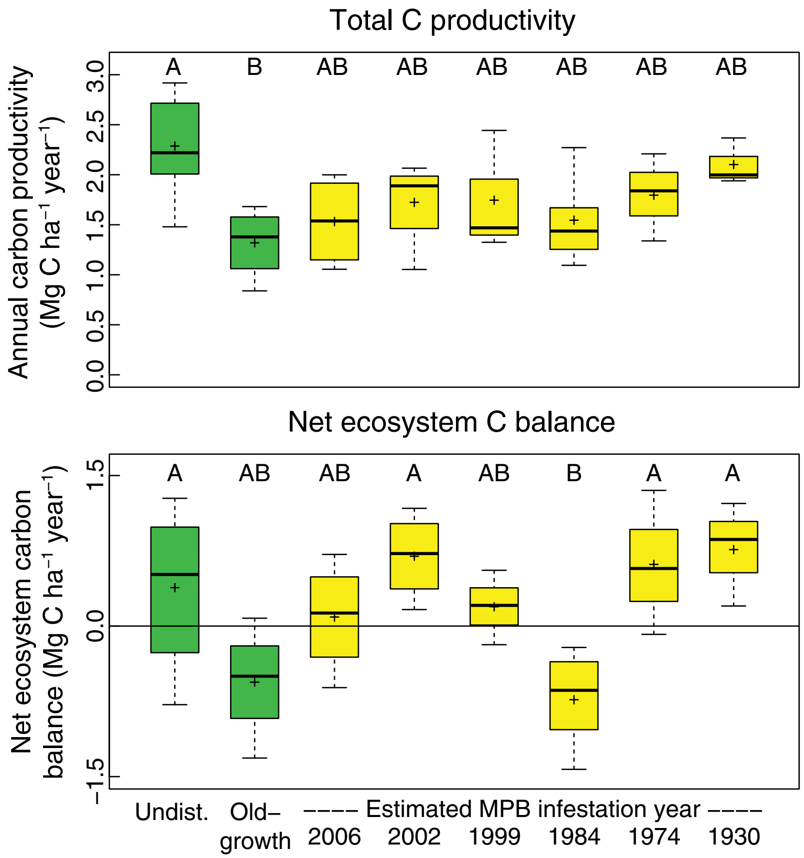


Figure 11.4—FVS-simulated total system carbon storage through time, with and without repeated mountain pine beetle outbreaks using bare-ground data and the Tetons variant. The asterisks indicate outbreak events. Results using the Utah variant were comparable (Hansen and others 2015). Note: MPB = mountain pine beetle.



Total C productivity

Net ecosystem C balance

Figure 11.5—Boxplots of total carbon (C) productivity (top panel) and net ecosystem C balance (bottom panel) among disturbance history classes (empirical data). Green boxes indicate disturbance history classes without evidence of beetle infestation and yellow boxes indicate infested classes. Solid lines are the medians, plusses are the means, boxes represent the 25th and 75th percentiles, and whiskers are 1.5 times the interquartile range. Disturbance history classes with the same letter within each panel were not significantly different using multiple range tests (α = 0.10). Note: MPB = mountain pine beetle.

simulation showed heightened C productivity, relative to the undisturbed trajectory, for each 10-year time step after the first outbreak. In this case, C productivity of the surviving trees is predicted to accelerate such that 10-year production more than compensates for the partial loss of canopy trees. Bare-ground results using the Utah variant (not shown; see Hansen and others 2015) were comparatively moderate in that 200-year averaged C productivity of the default and reduced severity trajectories was only about 3 percent higher than that of the undisturbed trajectory.

We expected to observe changes in forest floor dynamics because of increased litterfall from infested trees followed by reduced litterfall thereafter from the reduced surviving canopy. Instead, we found almost no differences in forest floor pool sizes (fig. 11.3), litterfall, or forest floor decomposition rates among the disturbance history classes in the field (Hansen and others 2015). Multiple factors suggest that beetle-caused changes in forest floor inputs and outputs will be ephemeral and difficult to detect: (a) annual litterfall may include up to 20 percent of total needle volume even without beetle-caused mortality; (b) many trees survive outbreaks, and the timing of infestation of trees within a stand occurs over several years rather than a single year; (c) timing of needle fall from infested trees is likewise a distribution rather than a discrete event; (d) pine needles are a relatively high quality substrate for decomposition and 50 percent of

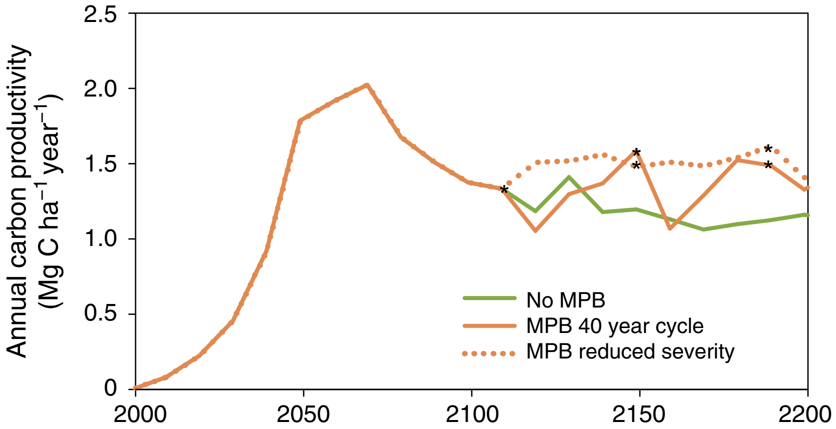


Figure 11.6—FVS-simulated C productivity through time, with and without repeated mountain pine beetle outbreaks using bare-ground data and the Tetons variant. The asterisks indicate outbreak events. Results using the Utah variant differed in that post-outbreak productivity was relatively reduced (Hansen and others 2015). Note: MPB = mountain pine beetle.

fresh litter mass can be lost in as little as 2 years. Nevertheless, it is reasonable to expect that outbreaks likely cause at least some increase in litterfall during the early post-outbreak years with a concomitant (albeit short-lived) increase in forest floor pool size. Thereafter, the decrease in litterfall may be offset by the warmer, drier post-outbreak environment, which slows decomposition and results in stable forest floor pool size as the overstory recovers along with litterfall rates.

Field data–derived estimates of net ecosystem C balance found that, with one exception, the infested disturbance history classes were near C neutral to net C sinks with mean values not significantly different from those of undisturbed plots (fig. 11.5, bottom panel). FVS simulations based on the field data similarly showed that stands generally remained net C sinks despite repeated beetle outbreaks (Hansen and others 2015). An exception for this was found with previously uninfested stands that became net C sources for 10–30 years depending on stand age and infestation severity. Simulations based on the bare-ground data likewise showed that recently infested stands became net C sources for 10–20 years before switching to net C sinks (downward and upward trends of infested trajectories in fig. 11.4). A key reason infested stands remain relatively C neutral is because most C in lodgepole pine systems is held in tree boles. Beetle-killed snags can remain standing for 10 years or more with very little decomposition. Even after falling, snags may remain elevated off the ground (fig. 11.2), and even fallen boles in direct contact with the soil can take multiple decades to decompose (Hansen 2014). The temporary loss of live lodgepole from beetle infestation (i.e., reduced C input rates) is more important to net C balance than the increase in dead substrates (i.e., decomposition potential or output rates) (Kashian and others 2013, Moore and others 2013). Thus, the potential for beetle outbreaks to temporarily switch stands from net C sinks to net C sources is dependent on factors such as stand age, infestation severity, and disturbance history. Also, because of increasing diversity of stand ages, species composition, and size classes with increasing spatial scales, stand-level effects will be muted at the landscape scale.

CONCLUSIONS

Mountain pine beetle outbreaks significantly modify C productivity and storage in central U.S. Rockies lodgepole pine ecosystems by redistributing C from live (sinks) to dead pools (sources). Impacted stands recover to, if not above, pre-outbreak rates within a few decades (fig. 11.6). Moreover, decreases in total C storage range from 1–34 percent, according to our simulation results, and total C storage among post-outbreak stands is considerable (figs. 11.3 and 11.4). This is because decomposition of killed trees (i.e., C output rate) proceeds relatively slowly whereas C productivity recovery to pre-outbreak rates (i.e., input rate) occurs more quickly. Ecosystem creation and destruction is inevitable (Holling 1992) and mountain pine beetle is one agent of reorganization in that cycle. Lodgepole pine systems rely on disturbance (Lotan and others 1985) and are resilient to impacts from mountain pine beetle with respect to C storage and productivity.

CONTACT INFORMATION

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