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Observations and modeling of aboveground tree carbon stocks and fluxes following a bark beetle outbreak in the western United States

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Abstract

Bark beetle epidemics result in tree mortality across millions of hectares in North America. However, few studies have quantified impacts on carbon (C) cycling. In this study, we quantified the immediate response and subsequent trajectories of stand-level aboveground tree C stocks and fluxes using field measurements and modeling for a location in central Idaho, USA that experienced an outbreak of mountain pine beetle (*Dendroctonus ponderosae* Hopkins). We measured tree characteristics in lodgepole pine (*Pinus contorta*) plots spanning a range of structure and mortality conditions. We then initialized the forest vegetation simulator, an individual tree-based model, with these measurements and simulated the response of aboveground production of C fluxes as well as trajectories of C stocks and fluxes in the coming decades. Mountain pine beetles killed up to 52% of the trees within plots, with more larger trees killed. C stocks in lodgepole pine were reduced by 31–83% following the outbreak, and plot-level C fluxes decreased 28–73%. Modeled C stocks increased nearly continuously following the infestation, recovering to preoutbreak levels in 25 years or less. Simulated aboveground tree C fluxes increased following the immediate postoutbreak decrease, then subsequently declined. Substantial variability of C stocks and fluxes among plots resulted from the number and size of killed and surviving trees. Our study illustrates that bark beetle epidemics alter forest C cycling unlike stand-replacement wildfires or clear-cut harvests, due in part to incomplete mortality coupled with the preference by beetles for larger trees. The dependency of postoutbreak C stocks and fluxes on stand structure suggests that C budget models and studies in areas experiencing mountain pine beetle disturbances need to include size distribution of trees for the most accurate results.

Keywords: bark beetle, carbon storage, *Dendroctonus ponderosae*, forest disturbance, forest growth simulation, forest vegetation simulator, insect outbreak, *Pinus contorta*

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Introduction

Changes in atmospheric carbon dioxide in recent decades have resulted in global climate change, and future projections of CO_2 emissions are expected to continue to modify climate (IPCC, 2007). Exchanges of carbon (C) between the land surface and the atmosphere are important components of the global C cycle. Natural disturbances such as insect outbreaks have large impacts on C budgets through extensive tree mortality (CCSP, 2007, 2008). However, few studies exist to quantify C exchange as a result of these processes, and additional research is needed to increase understanding of the processes involved and improve predictions of future trajectories of atmospheric CO_2.

Insect epidemics result in tree mortality across millions of hectares in North America annually, with substantial effects on forest ecosystem processes (Mattson & Addy, 1975; Romme *et al*., 1986; Veblen *et al*., 1991; Raffa *et al*., 2008). Tree mortality from outbreaks can lead to significant decreases and subsequent recovery of vegetation productivity in temperate and boreal forests (Romme *et al*., 1986; Kurz & Apps, 1999; Hicke *et al*., 2002; Kurz *et al*., 2008a). In addition, insect disturbances cause increased heterotrophic respiration associated with the decomposition of killed trees (Kurz *et al*., 2008a). As a result of these modifications to productivity and respiration, these disturbances may result in and/or prolong periods during which forest ecosystems act as sources of atmospheric C rather than sinks (Kurz & Apps, 1999; Volney & Fleming, 2000).

In western North America, bark beetle species (Coleoptera: Curculionidae, Scolytinae) attack and kill many species of conifers. Mountain pine beetle (*Dendroctonus ponderosae* Hopkins) is a particularly damaging species, affecting millions of hectares of forest in recent decades in British Columbia and the western

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United States (Kurz *et al.*, 2008a; USDA Forest Service, 2009). Bark beetles preferentially attack larger trees with thicker bark and phloem, which may be more suitable in terms of nutritional value, overall quantity, protection from natural enemies, extreme temperatures, and sapwood drying (Reid *et al.*, 1967; Safranyik & Carroll, 2006). In larger [>16 cm diameter at breast height (DBH)] size classes, 50–100% of lodgepole pine (*Pinus contorta*, a favored host of the insect) forests have been killed by mountain pine beetle, with reductions of 0–30% in smaller (<16 cm DBH) size classes (Amman & Baker, 1972; Jorgensen & Mocettini, 2005). This bias toward larger trees killed by mountain pine beetle suggests a proportionally larger impact on C stocks than number of trees.

Bark beetle outbreaks often differ from other large-scale forest disturbances such as stand-replacement wildfire or clear-cut harvest because nonhost tree species as well as smaller host trees survive these epidemics. Surviving trees often respond to decreases in overstory competition by increasing growth (Roe & Amman, 1970; Cole & Amman, 1980), depending on tree size, crown condition, and/or species (Lewis Murphy *et al.*, 1999). The number of surviving trees, their growth release, and factors that determine growth release need to be considered when evaluating impacts of outbreaks on C budgets.

Past studies have discussed bark beetle impacts in terms of tree stem volume and/or biomass. Severity of outbreaks is often reported as stem volume in killed trees (e.g., USDA Forest Service, 1985; Hall & Moody, 1994). Several studies have discussed the response of biomass, basal area, or growth of individual trees. Using a forest growth model, Coates & Hall (2005) predicted basal area following an outbreak in three stands, finding recovery within 20–80 years. Amman (1975) and Cole & Amman (1980) studied postoutbreak tree growth rates and observed growth increase among individual trees.

Few studies, however, have specifically addressed insect outbreak impacts on C budgets, particularly among individual trees at the scale of plots, stands, or forest landscapes before and following disturbance. Romme *et al.* (1986) used aboveground stem volume increment as an index for primary productivity over a 20-year period among four stands affected by a mountain pine beetle infestation in Yellowstone and Grand Teton National Parks. They reported recovery or near-recovery of preoutbreak stand stem volume increment within 15 years among four stands. Hicke *et al.* (2002) suggested that a series of spruce budworm outbreaks in eastern North America were responsible for large increases in forest net primary production (NPP) in that region several decades later. Seidl *et al.* (2008) report that projected climatic change will increase damage in Norway spruce (*Picea abies*) forests using modeled bark beetle (*Ips typographus*) outbreaks, which in turn will reduce total forest C stocks over a 100-year period in most stands. In other stands modeled over a similar time period, tree mortality caused by bark beetles ultimately increased total C stocks, particularly in unharvested stands with higher components of suppressed and/or relatively young trees. Kurz & Apps (1999) showed that an increase in disturbances, primarily insect outbreaks and fire, were responsible for switching managed Canadian forests from C sinks to sources in the latter part of the 20th century. Finally, Kurz *et al.* (2008a) quantified the impact of the ongoing mountain pine beetle infestation in British Columbia on C fluxes, showing that this disturbance will cause forests there to be net sources of C to the atmosphere for several decades.

Although these studies have quantified insect outbreak effects on C budgets, additional understanding is needed to assess effects related to the wide variety of structural and compositional vegetation changes induced by outbreaks. Silvicultural decisions made at local scales in pursuit of C management objectives (Dillard *et al.*, 2008) often involve the manipulation of forest structure and species composition. Furthermore, the complexity of possible changes in forest structure and species composition resulting from bark beetle outbreaks results in considerable variation of beetle effects on long-term forest C sequestration (Seidl *et al.*, 2008). Thus, studies are needed to quantify disturbance effects on structure, species composition, and corresponding C budgets at local and regional scales.

Our objectives in this study were to assess the impact of a mountain pine beetle infestation on plot-level C stocks and fluxes with measurements and modeling. We measured tree characteristics in the field to establish tree mortality and resulting amount of C in killed trees. We then initialized the forest vegetation simulator (FVS) growth model with these measurements to estimate preoutbreak and immediate postoutbreak aboveground tree C fluxes and to predict future trajectories of C stocks and fluxes.

Using simulation modeling, the difficulties of obtaining repeated measurements over decades and of identifying older beetle-killed stands for use in a chronosequence study can be overcome. FVS has several advantages when assessing C stocks and fluxes. First, the model incorporates the effects of tree competition on individual tree and stand productivity via three methods: tree mortality predictions based on stand density, stand-level growth limitations based on competition among all trees, and limitations of the growth rate of trees in less competitive canopy positions.

Second, FVS uses empirical size/growth relationships to capture changing physiological constraints faced by large trees and associated declines in productivity (Magnani *et al*., 2000; Ryan *et al*., 2006; Greenwood *et al*., 2008). Third, because FVS is an individual tree-based model, it allowed us identify trees killed by beetles and assess their effects as well as follow the fate of individual surviving trees to assess their growth response after the disturbance.

Methods

Study area

Our study site was in the Sawtooth National Recreation Area (SNRA), Idaho, USA (Fig. 1). Conifer species that occur at the study site include primarily lodgepole pine and to lesser degree Douglas-fir (*Pseudotsuga menziesii* var. menziesii), subalpine fir (*Abies lasiocarpa*), whitebark pine (*Pinus albicaulis*), and/or limber pine (*Pinus flexilis*) (Steele *et al*., 1981). The climate is characterized by long, cold winters (January average temperature is −7 °C) and mild, arid summers (July average temperature is 14 °C) (NOAA, 2002).

A disturbance history of mixed severity fires (Crane & Fischer, 1986; Schmidt *et al*., 2002) and bark beetle outbreaks (Jorgensen & Mocettini, 2005) has led to a diverse mosaic of stand structures, many of which are multiaged. The study area is largely managed as a National Recreation Area, with an emphasis on allowing processes of disturbance and recovery to occur with as little interference as possible from human activities. Wildfires are still frequently suppressed, but insect outbreaks are not, and processes of ecological recovery occur with minimal human intervention. Currently the area is experiencing a widespread and severe mountain pine beetle outbreak, which increased from endemic levels to an epidemic beginning in the late 1990s (Jorgensen & Mocettini, 2005). Based on visual assessment and aerial survey information (USDA Forest Service, 2006), most trees measured in this study were attacked between 2001 and 2004.

Fig. 1 Study location in the Sawtooth National Recreation Area, Idaho, USA.

Field measurements to quantify initial disturbance impacts

Field measurements were used to establish present stand structure and species composition, estimate C stocks, mortality severity, and to initialize model simulation projects. We used plot locations collected in a separate study that was designed to assess landscape-scale impacts of the outbreak. From those plots, 12 plots were selected for this study to illustrate ranges of forest structure, species composition, and mortality conditions at the time of the outbreak.

During the summer 2007, all trees >7 cm in DBH were measured within each 400 m^2 (11.28 m radius) circular plot. Species, DBH, total height, height to base of live crown, and condition (live, killed before outbreak, or killed during outbreak) were recorded. To focus on live lodgepole pine trees and those killed by beetles, we removed from our model simulations trees identified as dead before the outbreak or dead trees of other species.

Simulation of future C stocks and fluxes

We used the FVS, a (Stage, 1973; Dixon, 2003), to estimate present and future C fluxes and future C stocks using field measurements for model initialization. FVS is a model that predicts individual tree growth based on state variables derived from individual tree and plot characteristics, and is classified as a distance-independent, individual-tree model (Munro, 1974), in contrast to other model types that include whole stand, diameter class, or gap process models (Crookston & Dixon, 2005). In this study, the model was used to compare biomass (C stocks) and growth rates (C fluxes) among outbreak-affected plots, as well as the same plots modeled as if outbreak-caused mortality had not occurred.

Growth was estimated for individual trees based on tree characteristics and interactions, then summed to provide plot-level estimates. Individual tree variables included species, stem DBH (1.37 m above root collar), and crown ratio (the ratio of the distance from the base of the live crown to the tree top, to total tree height). For each tree record, FVS computes the tree's percentile rank in the total plot distribution of tree basal area, which is also used for growth prediction (Dixon, 2003). Plot-level variables include slope, aspect, elevation, tree density, and a measure of site potential. To simplify modeling efforts and focus on differences relating to forest structure, tree mortality, and species composition, model input variables related to the overall growth environment (i.e., aspect, elevation, and latitude) were held constant for all model runs. We used the Teton variant of FVS in which we suppressed 'background' tree mortality. Simulation time step, or growth cycle duration, was specified as 5 years. For each growth cycle, the model predicts tree mortality and changes in stem diameter, height, crown ratio, and crown width for all trees. Plot-level characteristics are summarized at the end of each growth cycle based on live individual tree records. Changes in tree diameter were predicted for individual trees using the large tree (>7.6 cm DBH) submodel within FVS (Crookston & Dixon, 2005). We also used the small tree (<7.6 cm DBH) growth

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model in a sensitivity study to identify the effect of including seedling establishment following outbreak collapse.

FVS computes growth by predicting the inside-bark diameter increment squared (DDS) (Cole & Stage, 1972; Stage, 1973; Wykoff, 1990; Dixon, 2003):

$$\begin{aligned}\ln(\mathrm{DDS}) = {} & \beta 1 + (2\mathrm{SI} + \beta 3 \sin(\mathrm{ASP} - 0.7854)) \\ & + (\beta 4 \cos(\mathrm{ASP} - 0.7854)) + (\beta 5\mathrm{SL}) \\ & + (\beta 6\mathrm{SL2}) + \beta 7 \ln(\mathrm{DBH})) + (\beta 8\mathrm{BAL}) \\ & + (\beta 9\mathrm{CR}) + (\beta 10\mathrm{CR2}) + (\beta 11(\mathrm{DBH})2) \\ & + (\beta 12 + \beta 13(\mathrm{CCF}/100)) \qquad (1)\end{aligned}$$

where SI is species site index, ASP is a coefficient relating to plot aspect, SL is plot slope (percent), DBH is tree DBH (inches), BAL is total basal area in trees larger than the subject tree ($\mathrm{ft}^2\,\mathrm{acre}^{-1}$), CR is a tree's live crown ratio (compacted) expressed as the percent of total tree height occupied by a live crown, CCF is stand crown competition factor, and the β's are species-specific coefficients. For this study, SI, ASP, and SL were all prescribed to be 50, 0, and 5%, respectively.

Diameter increment (DI) was derived using:

$$\mathrm{DI} = \sqrt{\mathrm{DBH}_{\mathrm{ib}}^2 + \mathrm{DDS}} - \mathrm{DBH}_{\mathrm{ib}} \qquad (2)$$

where $\mathrm{DBH}_{\mathrm{ib}}$ is the DBH inside the bark. The small tree growth prediction model differs slightly from the large tree model in that it predicts height growth first, then diameter growth as a function of height growth (Dixon, 2003).

DBH, CR, BAL, and CCF all describe characteristics of forest structure that influence tree growth. Larger trees (greater DBH) with larger crowns (greater CR) have higher growth. Initial CR was specified using field measurements of height and height to base of crown. BAL and CCF are indicators of tree competition that reduce individual tree growth. BAL is a measure of tree dominance. CCF is a relative measure of stand density based on tree diameters (Krajicek *et al*., 1961) that simulates the effect of increased competition for limited light resources, as well as soil water and nutrient resources. A CCF value of 100 indicates that tree crowns will just touch in an unthinned, evenly spaced stand.

Density-related mortality was predicted based on the relationship between the stand density index (SDI, Reineke, 1933) of a given growth cycle and the maximum SDI for the stand. In the model, density-related mortality begins at approximately 55% of maximum SDI and peaks at 85%. Maximum SDI values for individual species reflect the maximum observed trees per acre for a given quadratic mean diameter among hundreds of Forest Inventory and Analysis and other survey plots throughout the area used to develop the Teton Variant. Mortality in the model occurs at a rate sufficient to ensure the number and size of trees within a given site does not exceed that which has been observed in nature.

FVS was initialized by populating tree lists with our field measurements for each plot. Simulations predicted growth for the growth cycle before 2007 ('preoutbreak') as well as for growth cycles following the outbreak ('postoutbreak'). Two runs were conducted for each plots: one 200-year simulation with observed outbreak-related mortality applied to tree records ('attacked' plots) and, for comparison, one run with no outbreak-caused mortality ('unattacked' plots). The unattacked simulations allowed us to evaluate postoutbreak trajectories of C stocks and fluxes that respond to changing stand conditions, tree growth, and mortality occurring in the absence of outbreak mortality, thus providing a clearer picture of the role of the beetle epidemic.

Among the 12 plots included in this study, we provide more detailed analysis for four plots. These four plots demonstrate ranges of stand structure and observed growth decreases resulting from outbreak-related mortality, as well as subsequent values relative to pre- and/or immediate postoutbreak conditions. More detailed analyses of these plots are provided to identify causal factors.

Calculation of C stocks and fluxes

For each growth cycle, total aboveground tree C stocks were calculated from stem diameter using allometric equations from Jenkins *et al*. (2003). The average fraction of C in tree biomass was assumed to be 0.5 (Penman *et al*. 2003). Aboveground production of tree C (APTC) was calculated for individual trees as the difference between the aboveground tree C stocks of two consecutive growth cycles divided by the number of years in that cycle, providing an annual mean flux. For plot-level APTC, the growth of trees killed by the FVS mortality submodel within a time step was included. APTC differs from NPP in that fine and coarse root production, shrub and herbaceous production, and litterfall are not included. However, changes of annual forest biomass or stemwood increment have been considered roughly comparable to changes of aboveground NPP (Smith & Resh, 1999). C stocks and fluxes were summed for all trees to calculate plot-level totals.

Results

Preoutbreak conditions

We measured 625 trees on the 12 plots, and 528 (84%) were lodgepole pine. Before the epidemic, plots typically had 1200–1500 trees ha^{-1} (Fig. 2a). Seven plots had minimal or no nonhost tree species ($\leq 5\%$), and two plots (1 and 3) had significant contributions of nonhost species (mostly subalpine fir and Douglas-fir). Trees were concentrated in the smaller size classes (Fig. 2b); the largest trees (>35 cm DBH) were nonhost species.

Aboveground tree C averaged $49\,\mathrm{Mg\,C\,ha}^{-1}$ (range: 30–90 $\mathrm{Mg\,C\,ha}^{-1}$) across plots with 71% in lodgepole pine (Fig. 2c). Nonhost species typically contributed only a minor amount of C to a plot, with the exception of Plots 1 and 3. Intermediate size classes contained large amounts of C as a result of many trees (Fig. 2d). Modeled APTC simulated with FVS was on the order of $2\,\mathrm{Mg\,C\,ha}^{-1}\,\mathrm{yr}^{-1}$ (Fig. 2e), also concentrated in the intermediate size classes (Fig. 2f).

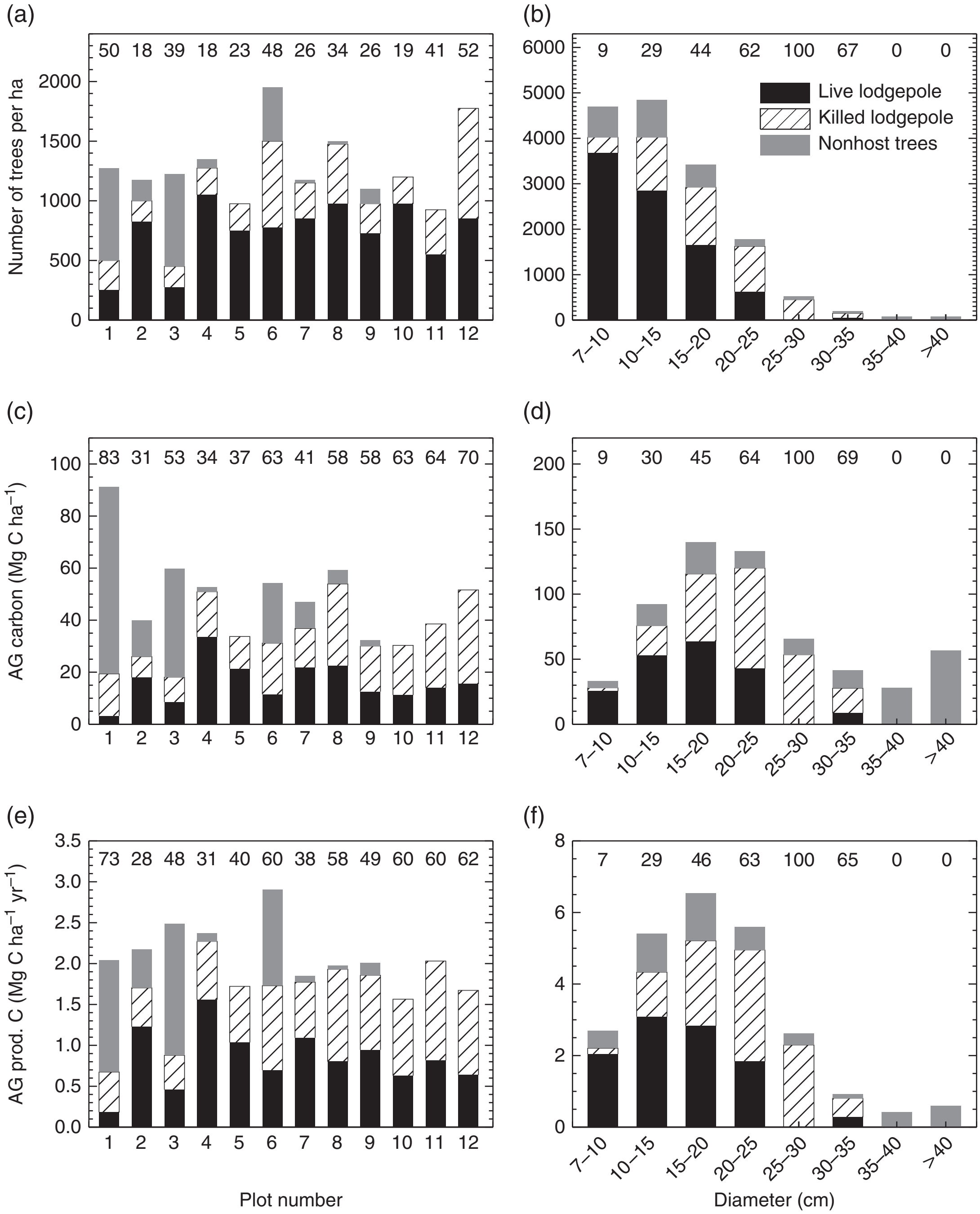

Fig. 2 Number of trees per ha [top row, (a), (b)], aboveground tree C stocks (Mg C ha^{-1}) [middle row, (c), (d)], and aboveground production of C (Mg C ha^{-1} yr^{-1}) [bottom row, (e), (f)] for each plot within study site [left column, (a), (c), (e)] and for all trees across plots [right column, (b), (d), (f)]. Black bars: number of live lodgepole pine remaining after outbreak. Hatched bars: number of lodgepole pine killed by outbreak. Gray bars: number of nonhost tree species. Numbers across top indicate percentage of variable in lodgepole pine killed by outbreak compared with all lodgepole pine.

Immediate response following mountain pine beetle outbreak

Field measurements indicated mountain pine beetles had killed 174 lodgepole pines (33% of lodgepole pine or 28% of all tree species). Plots had 18–52% of lodgepole pine killed in the outbreak (numbers, top of Fig. 2a). Larger lodgepole pines were killed preferentially by beetles (Fig. 2b). C in killed lodgepole pine averaged

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18.9 Mg C across plots, or 54% of all lodgepole pines; these killed lodgepole pines contained 38% of all C within the plots (i.e., considering all species). C in killed lodgepole pine represented 31–83% of the C in lodgepole pine as a result of the epidemic (Fig. 2c); C in killed lodgepole pine was highest in the 15–30 cm size classes (Fig. 2d). Modeled APTC of lodgepole pine decreased 28–73% following the outbreak (Fig. 2e), with the largest reductions in the intermediate size classes.

Trajectories of aboveground tree C stocks and fluxes: example plots

Trajectories of C stocks and fluxes simulated by FVS in four plots (4, 6, 10, 11) illustrate different temporal patterns (Fig. 3; trajectories for all plots shown in Fig. S1 and S2). Plot 4 had relatively higher aboveground tree C stocks and fluxes among all study plots and had relatively lower losses to beetle attack (Fig. 2). Beetles killed several of the largest trees and a few smaller trees, but postoutbreak stand structure included numerous large trees (>20 cm DBH; Fig. 3a). C stocks recovered quickly following this minimal impact, increasing to the preoutbreak value in 5 years (Fig. 3e) and to C stocks of a simulated unattacked plot in 96 years. APTC decreased somewhat following the epidemic and increased only slightly afterward (Fig. 3i). Modeled fluxes in both attacked and unattacked simulations declined dramatically following the outbreak as the trees aged. Postoutbreak APTC in the attacked

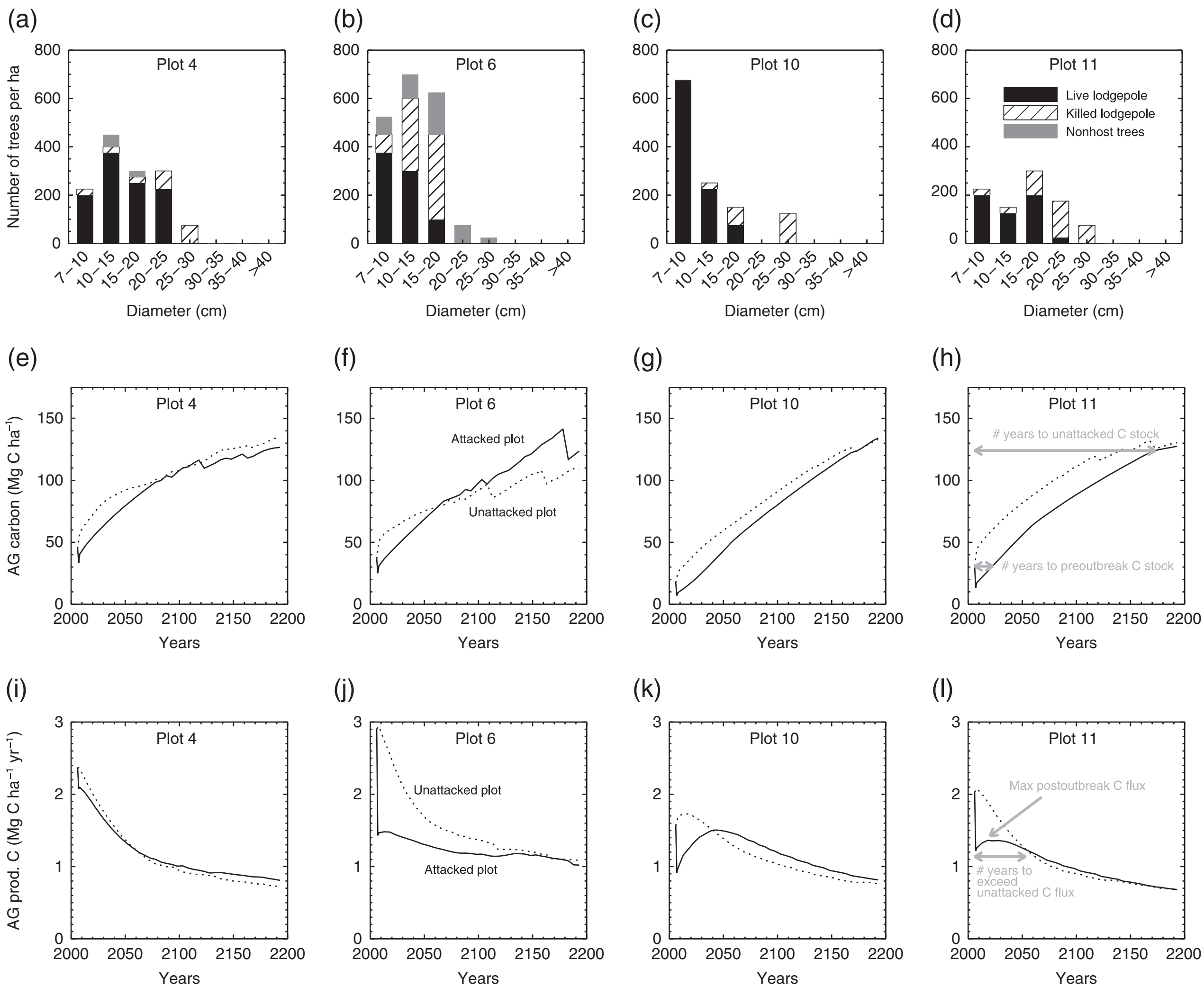

Fig. 3 Example plots (columns) showing range of mortality and recovery patterns. (top row) Size distribution of number of trees. Black bars: surviving lodgepole pine; hatched bars: lodgepole pine killed by mountain pine beetle; gray bars: nonhost trees. Trajectories of modeled aboveground tree C stocks (Mg C ha^{-1}) (middle row) and production (bottom row) of C (Mg C ha^{-1} yr^{-1}). (h) and (l) describe metrics of response and recovery used in Fig. 4 (gray) for simulations with outbreak-caused mortality ('attacked' plot, solid curve) and without ('unattacked plot,' dotted curve).

simulation equaled that of the unattacked simulation in 56 years.

Plot 6 had slightly higher preoutbreak stocks and fluxes as Plot 4 but substantially higher mortality. Beetles killed 48% of the lodgepole pine in Plot 6, representing 63% of the C and 62% of APTC in lodgepole pine. Plot 6 had less basal area of large ($\geq$ 20 cm DBH) trees before the outbreak, and substantial mortality occurred among lodgepole pine 10–20 cm DBH (Fig. 3b); surviving trees included large nonhost species and smaller (7–15 cm DBH) diameter lodgepole pine. Despite a substantial postoutbreak reduction, C stocks reached the preoutbreak value in 7 years, and despite having consistently lower APTC, simulated attacked C stocks exceeded unattacked C values in 56 years. The C stocks of attacked stands eventually exceeded the unattacked versions due to the density-dependent mortality of trees simulated by FVS (revealed by a flattening of the C stock trajectory in Fig. 3f) that removed C in the unattacked simulation as the plot aged. APTC increased slightly following the postoutbreak decrease, but declined again within a few years (Fig. 3j), taking 161 years to reach fluxes of the unattacked simulation.

Plot 10 exhibited a substantially different trajectory of APTC than Plots 4 and 6 (Fig. 3k). Plot 10 had lower stocks and fluxes than Plots 4 and 6 and no nonhost trees. Surviving trees were limited to size classes $<$20 cm DBH, with the majority of these trees $<$10 cm DBH (Fig. 3c). Postoutbreak APTC decreased by 41% but quickly increased to 96% of preoutbreak growth, overtaking APTC of the unattacked simulation in 35 years and substantially exceeding the unattacked growth for the next 150 years (Fig. 3k). Aboveground tree C stocks quickly increased to the preoutbreak amount in 14 years (Fig. 3g), although recovery to the C of the unaffected run took 167 years, partly as a result of minimal density-dependent tree mortality in the unaffected simulation.

Plot 11 had slightly higher preoutbreak values and similar percentage reductions in postoutbreak C stocks and fluxes as Plot 10, yet did not have the same large postoutbreak increase in APTC (Fig. 3l). Postoutbreak C was larger in Plot 11 than in Plot 10, and importantly, there were more surviving large trees and far fewer surviving small trees (Fig. 3d). Postoutbreak aboveground tree C increased to the preoutbreak C in 16 years, similar to Plot 10, and never equaled the amount of the unattacked simulation following the outbreak. Postoutbreak APTC increased slightly after the disturbance but only achieved 67% of the preoutbreak growth before declining. APTC exceeded that of the unattacked simulation in 48 years as a result of the rapid reduction of APTC in the unattacked simulation.

Drivers of response of aboveground tree C stocks and fluxes

Various metrics were explored to capture the immediate postoutbreak response and subsequent trajectories of C stocks and fluxes (see Table 1 for list and Fig. 3 for examples). These metrics were calculated using C stocks and fluxes of trees from all species within a plot, and so values differ from the values presented for lodgepole pine only in Fig. 2. We investigated relationships among these metrics to identify drivers of postoutbreak aboveground tree C stocks and fluxes.

Table 1 Drivers of aboveground tree carbon (C) stocks and fluxes following mountain pine beetle outbreak

Process			Value	Related to
Aboveground tree C	Immediate postoutbreak response		6–65% decrease	# trees killed; beetles preferentially kill larger trees
	Recovery	# years to preoutbreak value	1–25 years	% of postoutbreak decrease in aboveground tree C
		# years to unattacked simulation	56–185 years (4 plots never recovered)	# trees killed and trajectory of unattacked simulation
Aboveground production of tree C	Immediate postoutbreak response		12–51% decrease	Immediate postoutbreak response of C stocks
	Recovery	Maximum % of preoutbreak value	51–96%	Negatively related to immediate postoutbreak response of flux and positively related to % C in small trees
		# years to postoutbreak unattacked simulation	29–161 years	Relatively constant among plots (30–60 years)

Metrics calculated using all tree species.

Higher percent C in killed trees following beetle outbreaks were associated with higher percent number of lodgepole pine killed by the beetle (Fig. 4a). Because beetles prefer larger diameter trees, the percent C in killed trees exceeded the percent number of trees killed. There was some variability in this relationship, however. Plots 9 and 10 had most of their lodgepole pine $\geq$15 cm DBH killed, and as a result experienced 60% reduction of C in live lodgepole pine. Plots 5 and 7, on the other hand, had similar percentages of trees killed, but had more surviving trees $\geq$15 cm DBH and experienced a lower amount of C in killed trees.

Following the outbreak, C stocks recovered to preoutbreak values in 1–25 years. Not surprisingly, the percent C in killed trees as a result of the disturbance was a strong driver of time to recovery (Fig. 4b). Percent C in killed trees also influenced the time for C stocks to recover to values of unattacked simulations (30–160 years, not shown). However, this recovery metric was also affected by the prediction of C stocks of unattacked simulations, which were reduced to varying degrees by density-dependent tree mortality included in FVS.

Unlike C stocks, which increased steadily following the end of the outbreak, C fluxes exhibited first an initial increase after the outbreak followed by a subsequent decrease, with substantial variation among plots (as illustrated in Fig. 3). Immediate decreases in APTC (as a percentage of preoutbreak values) were inversely related to immediate decreases in aboveground tree C stocks (Fig. 4c). However, Plot 6 was a notable exception to this relationship. It had intermediate percent C in killed trees; however, it had the greatest postoutbreak decrease in APTC because a) it had the highest preoutbreak APTC due to an abundance of trees 7–15 cm DBH and no trees $\geq$20 cm DBH, and b) mortality was concentrated in the more productive intermediate size classes (10–20 cm DBH). Conversely, Plot 4 appeared as a possible outlier for opposite reasons: C in killed trees was concentrated in larger ($\geq$20 cm DBH) size classes, which had less APTC per amount of aboveground tree C stocks due to APTC limitations associated with tree size. As a result, in this plot the proportional decrease of aboveground tree C stocks was, relative to other plots, associated with a smaller proportional decrease of APTC.

After the initial decrease in APTC, fluxes increased somewhat within a few years, then declined again. Maximum postoutbreak APTC was governed by two factors. First, the amount of APTC decrease following the disturbance was a major influence, though the linear least squares relationship produced a relatively low R^2 of 0.39 (Fig. 4d). Inspection of the residuals led to the second factor: the capability of a plot to increase growth following the disturbance. This capacity, as indicated by the percent maximum APTC relative to immediate postoutbreak APTC, is determined by the number of small vs. large trees. Large numbers of small trees permitted relatively greater postoutbreak increases of APTC; the presence of large, dominant trees implied reduced capacity for increased growth. Differences of postoutbreak growth response associated with tree size were apparent within individual tree growth data (not shown) and broader representations of stand structure such as stem diameter size distribution, captured by the percent aboveground tree C in trees $<$15 cm DBH (Fig. 4e). A multiple linear regression analysis was performed using this percent C in small trees and immediate postoutbreak percent decrease in APTC as explanatory variables and maximum postoutbreak APTC as a percentage of preoutbreak APTC as the response variable. This statistical model produced an $R^2 = 0.88$ and an RSME = 3.9%, indicating a greatly improved fit over the relationship that used the immediate postoutbreak percent decrease in APTC alone ($R^2 = 0.39$, Fig. 4d).

The time for APTC to reach that of unattacked simulations was relatively constant among most plots (30–60 years, data not shown). The exception to this was Plot 6, which took 161 years as a result of the substantial postoutbreak decrease in APTC (50%) and minimal capacity to increase growth after the disturbance as represented by the low percent C in small trees (30%, Fig. 4e).

We did not measure seedlings in our field plots, and so did not include them in our FVS modeling. The Teton variant of FVS does not simulate seedling establishment timing or amount, but this can be manually included by the modeler. Establishment has the potential to affect the trajectories of C stocks and fluxes, however. The sensitivity of outbreak-related changes in C stocks and fluxes to postoutbreak seedling establishment was assessed by adding lodgepole pine seedlings at a density of 300 ha^{-1} to plot 12, which had relatively high beetle-caused mortality. This addition increased APTC in the first 75 years following the disturbance, within minimal differences after that (Fig. 5). The maximum increase was 11% over the simulation with the outbreak in year 2033. Differences in C stocks were minimal over much of the run, though after 120 years density-dependent tree mortality in the run with seedling establishment reduced C compared with the run without establishment.

Discussion

The infestation of mountain pine beetle killed about 1/3 of lodgepole pine across all our plots, with up to 52% killed within a plot. Because beetles kill larger trees preferentially, these killed trees represented

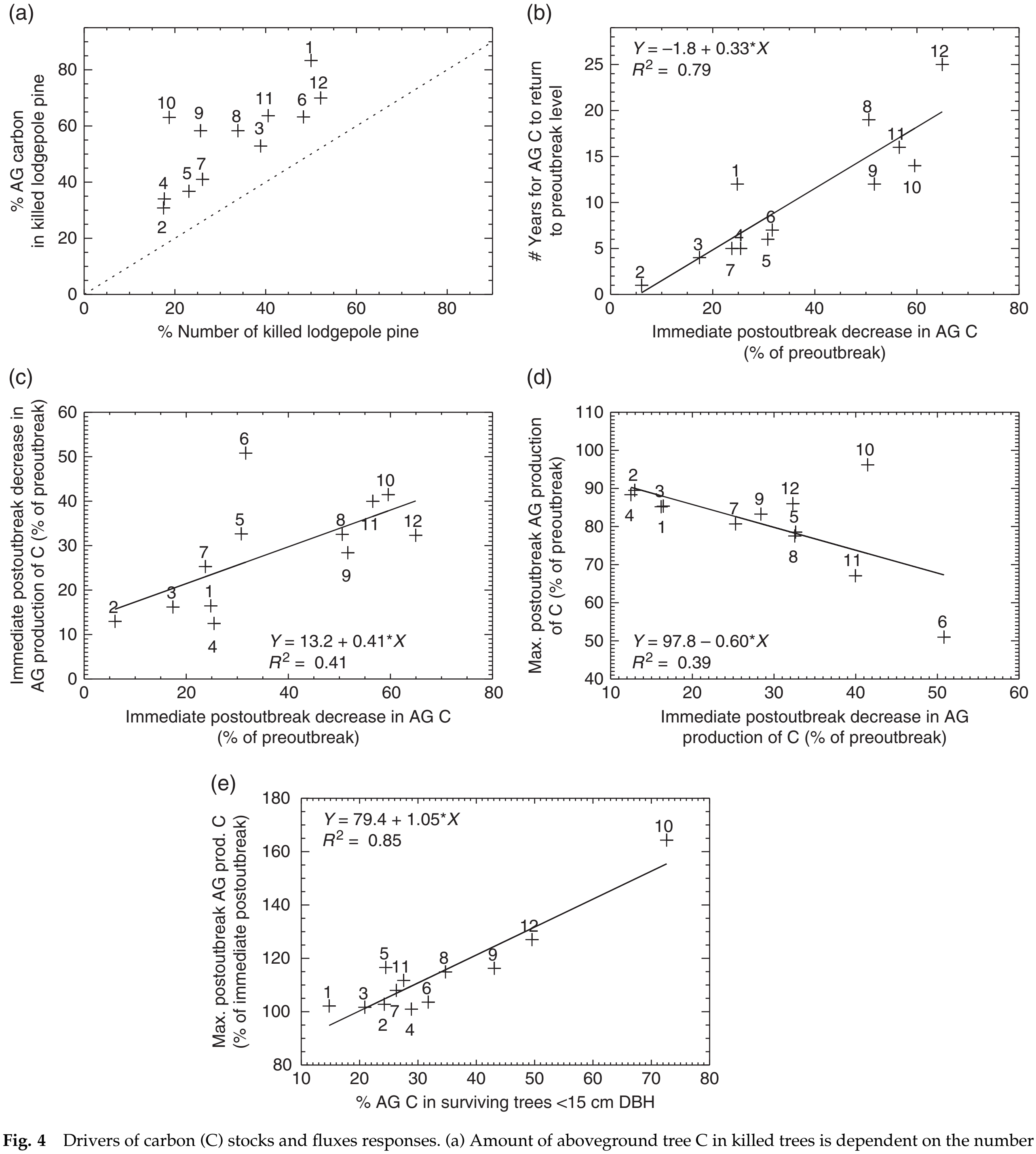

Fig. 4 Drivers of carbon (C) stocks and fluxes responses. (a) Amount of aboveground tree C in killed trees is dependent on the number of lodgepole pine killed (dotted line id 1 : 1 line). (b) Time to preoutbreak values of aboveground tree C stocks is dependent on the postoutbreak decrease in C stocks. (c) Postoutbreak decrease of aboveground production of C is dependent on the postoutbreak decrease in C stocks. (d) Maximum postoutbreak aboveground production of C is dependent on immediate postoutbreak reduction in this variable (note: model fit improved when percent C in small trees also considered; see text). (e) Ability of a plot to increase aboveground production of C following the disturbance is dependent on the percentage of C in small trees. Values include host and nonhost tree species. Numbers indicate plot numbers; solid lines are results of linear regression.

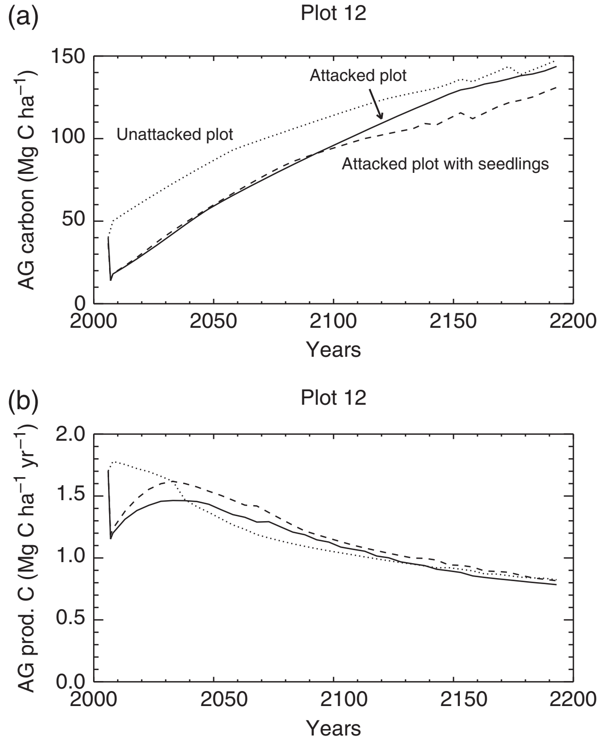

Fig. 5 Sensitivity of trajectories of aboveground tree C stocks and production of carbon to seedling establishment.

proportionally larger values of C stocks and aboveground tree C production in killed trees within stands. Maximum plot-level (all species) decreases were 65% for C stocks and 52% for APTC.

Plot-level C recovered to preoutbreak values in 25 years or less. C stocks recovered to values from unattacked simulations in 50–160 years; time to recovery depended on both the postoutbreak response of APTC in attacked simulations as well as the density-dependent-caused tree mortality in unattacked simulations that reduced plot-level C.

Following the outbreak, APTC never recovered to preoutbreak values due to declining productivity based on stand structure (evident in unattacked simulations). APTC in some plots exhibited relatively large increases after the immediate postoutbreak decrease as surviving trees grew faster; APTC in other plots increased only slightly.

Variability in the patterns of C stocks and fluxes among plots following the epidemic was caused by several factors. First, the number of trees killed within plots was a contributor as well as the size of those killed trees. More and larger trees killed resulted in greater decreases in C stocks and APTC and longer recovery times. A second factor was the size distribution of surviving trees. Plots with many remaining small ($\leq$20 cm DBH) trees and no larger trees increased APTC following the outbreak as the survivors capitalized on increased resource availability by increasing their growth rate. In contrast, large ($\geq$20 cm DBH) survivors increased their growth rates to a lesser extent as these trees were already dominant within a plot and were closer to (or had already reached) maximum APTC associated with size-related productivity limitations.

Simulated C stocks and fluxes were comparable to others reported in the northern Rocky Mountains for forests of similar structure and species composition (Fahey, 1983; Pearson *et al.*, 1987; Smithwick *et al.*, 2009). The initial rise and peak of APTC predicted by FVS following the simulated disturbance is consistent with flux patterns widely observed as leaf area moves toward and attains a maximum (Oliver & Larson, 1996). Using a forest growth model, Coates & Hall (2005) predicted postoutbreak basal area among three plots and reported recovery of preoutbreak basal area within 20–80 years, depending on the percent of basal area killed by bark beetles, which varied 18–81%. In one plot with outbreak-related mortality of 96% of basal area, basal area did not recover during the course of a 100-year simulation.

Romme *et al.* (1986) examined differences in annual stem volume increment before the onset and following the collapse of a mountain pine beetle outbreak in several stands in northwest Wyoming. Among three stands, they observed recovery of aboveground wood production (postoutbreak stem volume increment as a percentage of preoutbreak levels) similar to that observed in this study. In contrast to our study, in one stand, Romme *et al.* observed significant increases of overstory stem volume increment relative to preoutbreak rates. This increase may have reflected an outbreak that occurred in a stand of relatively small, sparse trees, leaving small, widely spaced survivors that had a high capacity to increase growth.

Our simulations extended almost 200 years. During that time, plots are likely to experience another disturbance such as wildfire or bark beetle outbreaks. In addition, the region will almost certainly will experience significant warming that may lead to increases in growth following disturbances (Smithwick *et al.*, 2009). These effects were not captured by the modeling.

Our study did not quantify impacts on belowground C stocks, heterotrophic respiration, or on the net C flux between the ecosystem and the atmosphere. Observations within 2 years of an infestation of bark beetles recorded no change in soil respiration (Morehouse *et al.*, 2008), although modeled long-term accumulations of soil C were reported by Seidl *et al.* (2008) in Norway spruce forests affected by *I. typographus*. Additional soil

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C measurements, eddy covariance measurements, and/or modeling that include heterotrophic respiration are required to evaluate the complete response of ecosystem C to these disturbances.

Our study assessed plot responses for a range of beetle-caused mortality in central Idaho. Landscape-scale impacts to C budgets are of interest to scientists and land managers. The extent to which the plots used in our study are representative of the entire outbreak in Idaho, i.e., up-scaling to a landscape C budget, requires additional research.

Mortality caused by the SNRA mountain pine beetle outbreak affected short and long-term vegetation C storage through alterations of stand structure and species composition. Other disturbances that cause similar changes in structure would produce similar stand responses. For instance, tree mortality caused by other insects such as balsam wooly adelgid (*Adelges piceae*) or Douglas-fir beetle (*D. pseudotsugae* Hopkins) have the potential to affect forest structure in ways similar to the mountain pine beetle outbreak discussed in this study, with similar consequences for forest C budgets.

Conclusions

Increased emphasis and attention is paid to assessing and managing forest C emissions and sequestration (Dillard *et al*., 2008). Our findings inform both general management strategies and site-specific decisions, which often include silvicultural manipulation of tree species composition, size distribution, and tree density before and following disturbance events with similar effects. Among stands similar to those included in this study, the increased growth of surviving trees may not fully replace the productivity associated with beetle-killed trees. On the other hand, C stocks reached pre-outbreak levels after 25 years or less, which is less than significant outbreak return intervals observed in British Columbia (Taylor *et al*., 2006). Time required for 'recovery' of C stocks can vary widely depending on whether recovery is defined relative to preoutbreak or unattacked conditions (Table 1; <25 or 56–185 years, respectively), with different implications for C flux management. Variation of immediate (<25 years) post-outbreak C flux is most important when recovery of C stocks is defined relative to preoutbreak conditions. Conversely, long-term (>50 years) variation of C flux has greatest importance for recovery of postoutbreak C stocks relative to unaffected stands.

Postdisturbance seedling establishment may play some role in mitigating short-term negative impacts on annual C sequestration associated with bark beetle outbreaks and similar disturbances (Kurz *et al*., 2008b). At the same time, in the absence of postdisturbance seedling germination, the stands included in this study exhibited significant resiliency of C storage to beetle-caused mortality.

Our results illustrated substantial differences in the response of C stocks and fluxes following a bark beetle outbreak. To a large degree, differences were related to pre- and postoutbreak stand structure and variable growth release of surviving trees, implying that accurate simulation of C cycling following such events needs to include these variables. Furthermore, studies that assess landscape- to continental-scale impacts of bark beetle outbreaks need to account for spatial variability in resulting tree mortality and postoutbreak stand structure in addition to quantifying the extent of the outbreak. Distribution of tree sizes/ages within a stand has important implications for postdisturbance forest C cycling that may not be fully represented by single estimates of overall stand age.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Figure S1. Plot trajectories of aboveground carbon stocks for each plot. Attacked simulations are shown with solid lines, unattacked simulations with dotted lines.
Figure S2. Same as Figure S1 but for aboveground production of carbon.