Carbon stocks of trees killed by bark beetles and wildfire in the western United States

2013 Environ. Res. Lett. 8 035032

(http://iopscience.iop.org/1748-9326/8/3/035032)

OPEN ACCESS
IOP Publishing
Environmental Research Letters
Environ. Res. Lett. **8** (2013) 035032 (8pp)
doi:10.1088/1748-9326/8/3/035032

Carbon stocks of trees killed by bark beetles and wildfire in the western United States

Jeffrey A Hicke[1], Arjan J H Meddens[1], Craig D Allen[2] and Crystal A Kolden[1]

[1] Department of Geography, University of Idaho, Moscow, ID 83844-3021, USA
[2] US Geological Survey, Fort Collins Science Center, Jemez Mountains Field Station, Los Alamos, NM 87544, USA

E-mail: jhicke@uidaho.edu

Received 7 June 2013
Accepted for publication 9 August 2013
Published 29 August 2013
Online at stacks.iop.org/ERL/8/035032

Abstract
Forests are major components of the carbon cycle, and disturbances are important influences of forest carbon. Our objective was to contribute to the understanding of forest carbon cycling by quantifying the amount of carbon in trees killed by two disturbance types, fires and bark beetles, in the western United States in recent decades. We combined existing spatial data sets of forest biomass, burn severity, and beetle-caused tree mortality to estimate the amount of aboveground and belowground carbon in killed trees across the region. We found that during 1984–2010, fires killed trees that contained 5–11 Tg C year^{-1} and during 1997–2010, beetles killed trees that contained 2–24 Tg C year^{-1}, with more trees killed since 2000 than in earlier periods. Over their periods of record, amounts of carbon in trees killed by fires and by beetle outbreaks were similar, and together these disturbances killed trees representing 9% of the total tree carbon in western forests, a similar amount to harvesting. Fires killed more trees in lower-elevation forest types such as Douglas-fir than higher-elevation forest types, whereas bark beetle outbreaks also killed trees in higher-elevation forest types such as lodgepole pine and Engelmann spruce. Over 15% of the carbon in lodgepole pine and spruce/fir forest types was in trees killed by beetle outbreaks; other forest types had 5–10% of the carbon in killed trees. Our results document the importance of these natural disturbances in the carbon budget of the western United States.

Keywords: bark beetle outbreaks, forest disturbances, forest carbon cycling, western United States

S Online supplementary data available from stacks.iop.org/ERL/8/035032/mmedia

1. Introduction

Forests play important roles in the carbon cycle (Denman *et al* 2007). Globally, tree regrowth following harvest and deforestation contributes substantially to the net carbon fluxes between the land and atmosphere (Goodale *et al* 2002, Canadell *et al* 2007, Pan *et al* 2011). Forest disturbances are significant regulators of carbon cycling (Odum 1969), and tree killing disturbances, including severe wildfire and bark beetle outbreaks, affect forest carbon cycling through multiple processes. Carbon uptake by the forest ecosystem through photosynthesis is immediately reduced following tree mortality. Fires release carbon directly to the atmosphere via combustion of vegetation and soil. Tree mortality moves carbon from live to dead pools, which begin to release carbon back to the atmosphere via heterotrophic respiration. After disturbance, remaining vegetation (surviving overstory trees and understory seedlings, saplings, shrubs, and herbs) increases growth, altering the net carbon flux. Effects can last decades as killed trees decompose and new vegetation slowly establishes and grows (Hicke *et al* 2003, Amiro *et al* 2010, Edburg *et al* 2011).

Wildfires and insect outbreaks have affected millions of hectares in the western United States in recent decades. Fires are important natural disturbances across North America (Kasischke *et al* 2011), and in the western US alone fires burned an estimated mean of 760 000 ha year^{-1} during 1980–2000 (Littell *et al* 2009). Bark beetle outbreaks kill trees from Mexico to Alaska (Salinas-Moreno *et al* 2004, Raffa *et al* 2008). Cumulative mortality area since 1997 from bark beetle-killed trees has exceeded 5 Mha (Meddens *et al* 2012). Mountain pine beetles (*Dendroctonus ponderosae*) in lodgepole pine (*Pinus contorta* var. *latifolia*) forests have been particularly damaging, causing 63% of the mortality (Meddens *et al* 2012). However, additional bark beetles, including piñon ips (*Ips confusus*), Douglas-fir beetle (*Dendroctonus pseudotsugae*), and western balsam bark beetle (*Dryocoetes confusus*), have caused substantial tree mortality.

Forest disturbances, including wildfire and insect outbreaks, play important roles in the North American carbon budget (CCSP 2007, Kasischke *et al* 2013). Substantial carbon is released by direct combustion of forests (Wiedinmyer and Neff 2007, French *et al* 2011, Ghimire *et al* 2012). Fires also generate dead organic matter that affects postdisturbance carbon fluxes (Harmon *et al* 2011, Ghimire *et al* 2012, Kashian *et al* 2013). Insect outbreaks can also significantly impact carbon cycling (Hicke *et al* 2012). The mountain pine beetle outbreak in British Columbia caused forests there to switch from being a slight carbon sink to a significant carbon source for decades (Kurz *et al* 2008). However, not all biotic disturbances result in such significant effects. The severity of tree mortality within a given area, type of biotic disturbance agent (particularly growth reducers versus tree killers), and number and size of surviving trees are important influences on net carbon fluxes (Hicke *et al* 2012).

Although large forest fires and bark beetle outbreaks in the western United States have been documented (Littell *et al* 2009, Meddens *et al* 2012), no studies to date have assessed the impact of these disturbances on the regional carbon cycle. Quantifying effects on carbon stocks for each disturbance type leads to a greater understanding of the role of each in governing carbon cycling in the forests of the western United States.

Here we use the area of trees killed by wildfire and bark beetle outbreaks to estimate the amount of carbon in killed trees. Although changes in carbon stocks do not directly translate into net ecosystem fluxes (e.g., net biome productivity), broad scale, spatially explicit quantification of carbon in killed trees can be estimated with simple approaches, whereas analogous estimates of carbon fluxes require extensive inputs and more complex modeling. Our objective was to combine estimates based on observations of areas disturbed by wildfire and bark beetles and carbon stocks to quantify the spatial and temporal characteristics of carbon in killed trees during the last few decades in the western United States.

2. Methods

Our study area encompassed forested areas of the western United States. Detailed information exists for this area on bark beetle outbreaks, wildfire burn severity, forest cover, and carbon stocks for recent decades on a spatially explicit basis at fairly high spatial resolution.

To compute carbon in trees killed by bark beetles, we used the annual area of mortality produced by Meddens *et al* (2012). Mortality area is the summed crown area of killed trees, and is different from 'area affected' often reported because mortality area does not include the contribution from live trees. USDA Forest Service Aerial Detection Surveys (ADS) report damage attributes, including beetle and tree species and number of trees killed in the survey year, recorded by observers in planes. Annual records from 1997–2010 were converted from attribute information within polygons to a 1 km grid containing the number of killed trees for different bark beetle species. Meddens *et al* (2012) used trees killed per hectare to calculate mortality area using species-specific crown diameters from a USDA Forest Service Forest Health Monitoring data set (Meddens *et al* 2012). These crown diameters were from both stand-grown and open-grown trees, thereby increasing the mean crown diameter and accommodating the preference of larger diameter trees by bark beetles (Shore and Safranyik 1992). This process resulted in a 'lower estimate' of mortality area. An upper estimate of mortality area was also produced by applying adjustment factors to the lower estimate that were derived by comparing the lower estimate to beetle-caused tree mortality from fine resolution remotely sensed imagery (Meddens *et al* 2012). Three adjustment factors were calculated in three different forest types across the western US (in order of increasing value: pinyon pine, whitebark pine, lodgepole pine). The adjustment factor using the pinyon pine imagery was used for tree mortality in pinyon pine only, assuming that aerial surveys were more accurate in more open woodlands. To be conservative, Meddens *et al* (2012) used the largest adjustment factor, in lodgepole pine killed by mountain pine beetle, for that tree/beetle combination only, and used the intermediate adjustment factor (in whitebark pine killed by mountain pine beetle) for all other host tree species. More recent analyses of lodgepole pine stands attacked by mountain pine beetle suggest an average adjustment factor in that tree/beetle combination close to that of the whitebark pine adjustment factor. Therefore, in this study, we added a third ('middle') estimate using only the pinyon pine adjustment factor for that tree species and the whitebark pine adjustment factor for all other tree species. Because this middle estimate is based on comparisons with highly accurate classifications of tree mortality using fine-scale remotely sensed imagery, we view the middle estimate as the most realistic of the three. The year of mortality area corresponds to the year of detection by ADS, not the year of attack.

Tree mortality from forest fires was computed using the Monitoring Trends in Burn Severity (MTBS) maps of burn severity from 1984–2010 (Eidenshink *et al* 2007). MTBS maps fires >405 ha (1000 acres) at 30-m spatial resolution in the western United States; this threshold represents 95% of area burned across the US (Zhu and Eidenshink 2007) and a higher percentage of total area burned in some forests dominated by stand-replacing fire (Kolden *et al* 2012). Burn severity classes were estimated by MTBS using thresholds of the Landsat-based spectral index of differenced normalized burn ratio (dNBR). These thresholds were arbitrarily assigned on a per-fire basis and have not been directly evaluated by MTBS, so there is some uncertainty as to how much mortality was associated with each class. To address this uncertainty, we considered two estimates of tree mortality by fire: one using high-severity burned areas only, and a second based on moderate + high-severity burned areas. This choice was supported by a review of published studies (Ghimire *et al* 2012), that reported tree mortality of 40–60% for moderate-severity fires and 70–99% for high-severity fires, although the severity classifications in the reviewed studies are not necessarily equivalent to those of MTBS. At the scale of western United States forests, the carbon in trees killed in low-severity fires is minimal (Ghimire *et al* 2012).

To mask out nonforest burned areas, we developed a 30 m forest mask based on three data sets. Land cover data based on satellite imagery only reflect land cover at the time of image acquisition, and we noted misclassification in land cover databases in some forested areas burned just before imagery was acquired. Therefore, we combined two Landsat-based land cover data sets (USGS National Land Cover Dataset (NLCD) and LANDFIRE Existing Vegetation Types (EVT)) with modeled potential vegetation representing pre-EuroAmerican settlement land cover (LANDFIRE Biophysical Settings (BPS)). We identified forest classes in the NLCD and EVT data sets, and combined the two with a geospatial union. We added potentially forested areas from BPS except in locations currently identified as agriculture by EVT. We then combined the forest mask with the two burn severity estimates and aggregated the 30-m data to 1-km spatial resolution by calculating the percentage of a 1-km grid cell containing high or moderate + high severity 30-m grid cells. The resulting maps of burn severity (high- and moderate + high-severity) in forested areas estimated the percentage area of tree mortality caused by forest fires.

We then overlaid tree mortality with spatial data of carbon stocks in trees. For the latter, we used the aboveground live forest biomass map produced by Blackard *et al* (2008), who modeled biomass from USDA Forest Service Forest Inventory and Analysis plots and MODerate Imaging Spectroradiometer (MODIS) imagery acquired in 2001, land cover, climate, topography, and other ancillary variables. We aggregated 250-m biomass data to 1-km resolution and converted aboveground live biomass to total live carbon stocks by (1) adding an estimate of belowground biomass modeled as a function of aboveground biomass (Cairns *et al* 1997) (their Equation (1) in table 3) and (2) multiplying by 0.5 to compute carbon (Schlesinger 1997).

Because we noted relatively low biomass in recently disturbed forested areas compared with surrounding undisturbed forests (for example, in the Yellowstone area burned in 1988), we produced a corrected carbon stocks map representing undisturbed conditions. To do so, we identified disturbed areas before 2001 from the bark beetle mortality area and moderate + high-severity burned areas. We calculated the mean carbon stock in undisturbed locations for each major forest type (Ruefenacht *et al* 2008) within each ecoregion (Olson *et al* 2001) in the western United States. In disturbed locations, we used the maximum of the carbon stock from this mean and the Blackard *et al*-based estimate described in the previous paragraph. The corrected biomass map resulted in a 14–16% increase in cumulative carbon in trees killed by beetles and fires for the region and study period. Most significantly, carbon in trees killed by fires increased from 11 to 25 Tg in 1988 associated with the Yellowstone fires. In other years, the increase was minor, usually less than 1–2 Tg C.

To compute carbon in killed trees, we multiplied the percentage mortality area maps (annual for each of bark beetles and forest fires) by the carbon stock map. We summed carbon in killed trees in each forest type using a classification developed from MODIS imagery (250-m spatial resolution) (Ruefenacht *et al* 2008) that we aggregated to 1 km. We also summed carbon in killed trees by ecoregion defined by the World Wildlife Fund (Olson *et al* 2001) for better visual presentation in figures. We calculated the percentage of carbon in killed trees within ecoregions and forest types by using the total carbon in all trees for each ecoregion and forest type. When reporting cumulative values across time, we did not account for any decomposition during the time period.

Estimates of the amount of carbon in harvested trees in the western United States were derived from a national USDA Forest Service report on forest resources (Smith *et al* 2009). Average annual removals in ft^3 were reported based on national inventory databases developed for 1976, 1986, 1996, and 2006 (i.e., averages from prior years). We multiplied removals by the ratio of total volume to merchantable volume to account for foliage, bark, branches, and roots. We then used specific gravities for the Pacific Southwest, Pacific Northwest (averaged east and west values), and Rocky Mountains (averaged north and south values) as well as a conversion factor from biomass to carbon (0.5) from Smith *et al* (2005) to convert volume to carbon.

3. Results

Between 1997 and 2010, fires and beetles together killed trees that contained >100 Tg C (table 1). The most realistic middle estimate for bark beetles and the higher estimate for fires resulted in 486 Tg C in killed trees during this time period. The middle estimate for bark beetles was 47% greater than the higher estimate for fires. The amount of carbon in killed trees by fires (higher estimate) and beetles (middle estimate) consisted of 3% and 6%, respectively, of the

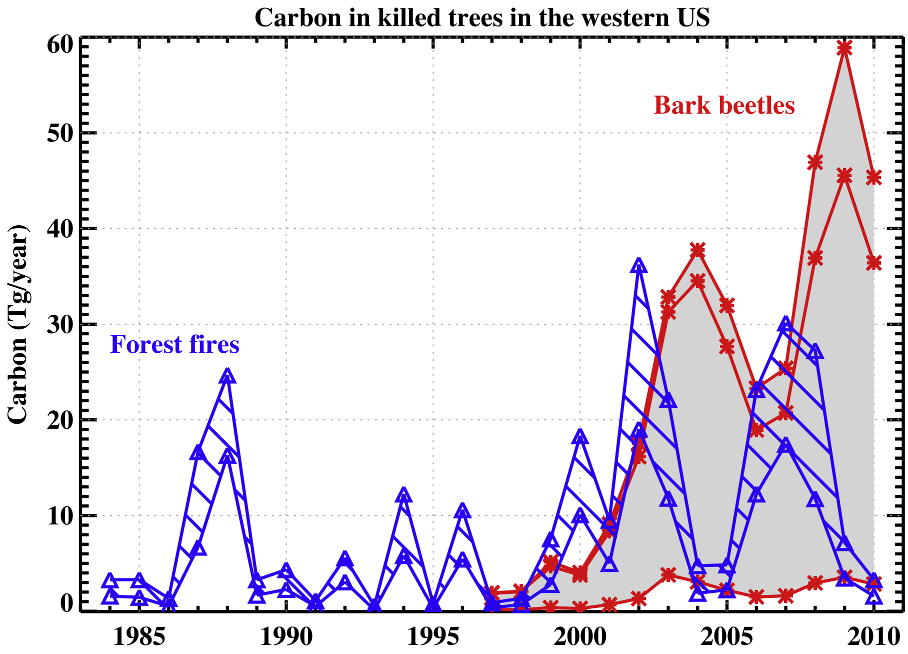

Figure 1. Carbon in trees killed by major bark beetle species (1997–2010; red lines representing upper, middle, and lower estimates; gray shading indicates range between lower and upper estimates) and forest fires (1984–2010; blue lines; hatching indicates range between moderate- and moderate + high-severity burned areas).

Table 1. Carbon in trees killed by forest fires, bark beetles, and harvest.

	Time period	Cumulative carbon in killed trees		Annual mean C in killed trees (Tg C year^{-1})
Disturbance type		Tg C	% of total tree C	
Forest fires	1984–2010	146–285	2.4–4.6%	5.4–10.5
	1997–2010	100–197	1.6–3.2%	7.2–14.1
Bark beetles	1997–2010	25–342 (289[a])	0.4–5.5% (4.7[a])	1.8–24.4 (20.6[a])
Harvest	1976			49.4[b]
	1986			49.4
	1996			29.1
	2006			29.9

[a] Most realistic middle estimate for bark beetles.

[b] Annual average from inventory database developed for listed year.

total tree carbon in the western United States. An additional 46–88 Tg C was associated with trees killed by forest fires during 1984–1996, a time of reduced burned area compared with the later period. The sum of carbon in trees killed by these two natural disturbances slightly exceeded the estimate from harvest in recent decades, and was less than that from harvest in the 1970s and 1980s (table 1).

Time series of the amount of carbon in killed trees reveals several years of substantial tree mortality caused by fires (figure 1). Notable high forest fire years included 1987–1988, 2000, 2002–2003, and 2006–2008. In other years, the amount of carbon associated with fire-killed trees was typically fairly low, less than 5–6 Tg C year^{-1}. Bark beetles killed increasing numbers of trees during 1997–2010. Although there were a few years of declines, the amount of carbon in trees killed by beetles rose from <5 Tg C in 1997 to a peak of 45 Tg C (middle estimate) in 2009. Two major sets of outbreaks caused these patterns. First, ips beetles, fir engravers, Douglas-fir beetles, spruce beetles, and other unspecified bark beetles attacked trees throughout much of the western United States in 2002–2005, after which outbreaks of these beetles subsided (Meddens *et al* 2012). At the same time, populations of mountain pine beetle were increasing and continued to remain high through 2010, resulting in the peak of carbon in killed trees during the latter part of the study period. In addition to causing a greater cumulative amount of carbon in killed trees, beetles also were associated with more carbon in killed trees during any individual year than forest fires (i.e., the maximum annual carbon in killed trees from beetles, 45 Tg C in 2009, exceeded that from wildfire, 35 Tg C in 2002).

Spatial patterns illustrate large variability in the amount of carbon killed by beetles and fire (figure 2 and supplementary information, available at stacks.iop.org/ERL/8/035032/mmedia). Patterns do not change significantly among lower, middle, and higher estimates, so here we present results associated with the most realistic middle estimate for bark beetles and the moderate + high-severity estimate for forest fires. For fires, higher amounts of C in killed trees occurred in the middle Rocky Mountains and the Siskiyou Mountains of California and Oregon, where ecoregion totals exceeded 35 Tg C for the 1984–2010 period. In terms of percentage carbon in killed trees (compared with total tree

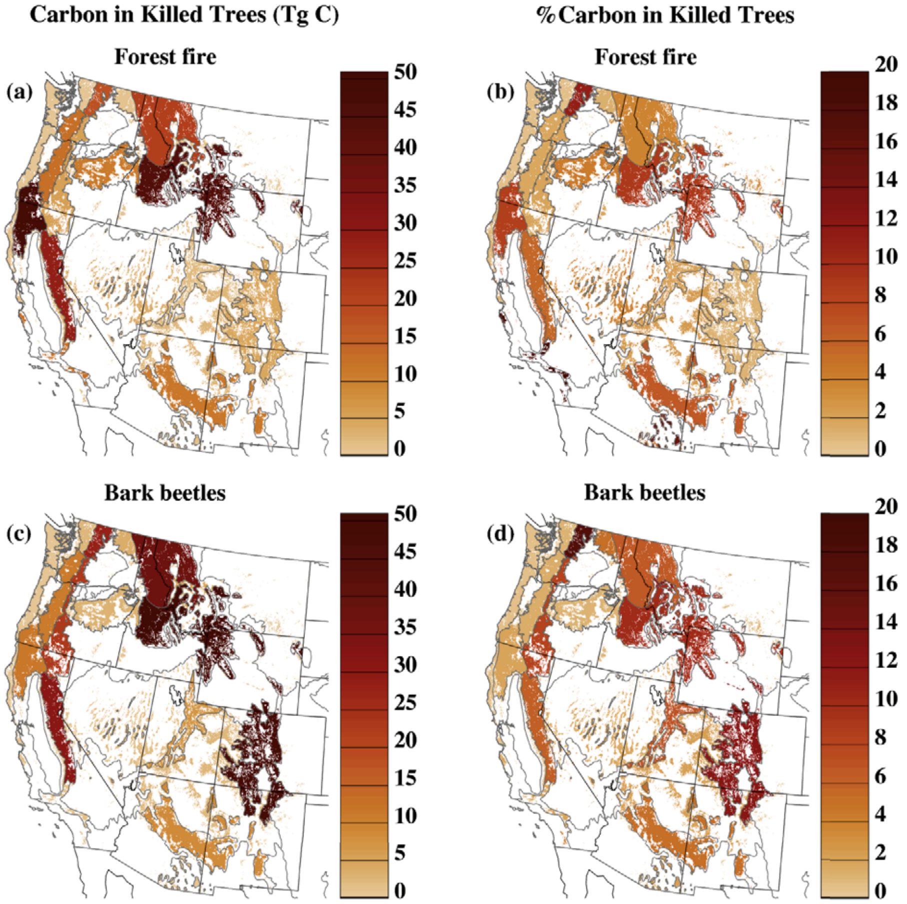

Figure 2. Cumulative carbon by ecoregion and over time in trees killed by bark beetles and forest fires in ((a), (c)) Tg C and ((b), (d)) percentage of total forest carbon within ecoregion. (a), (b) Forest fires (1984–2010; moderate + high-severity burned areas). (c), (d) Bark beetles (1997–2010; middle estimate). Total for each ecoregion is plotted for all forested pixels within that ecoregion.

C) within ecoregions, the highest percentage occurred in the forests of coastal southern California (>18%), and values of 4–11% occurred in the Rocky Mountains, northern Cascades, and northern California.

Ecoregional totals of C (summed over time) in trees killed by bark beetles were typically greater than those from fires. The Rocky Mountains and Sierra Nevada experienced especially large effects on carbon, on the order of 30–50 Tg C. Carbon in killed trees exceeded 10% of the total tree C in the southern and middle Rocky Mountains and northern Cascades. In terms of total C, fires were more significant than beetle outbreaks in coastal northern California and Oregon, northeastern Oregon, and parts of the Southwest.

Fire and beetle impacts to C stocks varied substantially by forest type (figure 3). The large areas of lower-elevation pinyon pine killed by pinyon ips beetle translated into relatively low amounts of carbon (figure 3). Forests at somewhat higher elevations (ponderosa pine and especially Douglas-fir) were more affected, with 60–80 Tg C in trees killed by beetles and fires. We note that impacts within a given forest type may be associated with other tree species; substantial lodgepole pine mortality was included in the Douglas-fir forest type, for instance. Lodgepole pine forests were subjected to widespread mortality from beetles and to a lesser degree from fires: 20% and 7% of the total tree carbon in this forest type were in trees killed by beetles and fires, respectively. Higher-elevation spruce/fir forests were also heavily impacted. Beetles were more significant disturbances than fires in lodgepole and spruce/fir forest types, and fires and beetles were similar in magnitude in the other coniferous forest types.

4. Discussion

Our analysis estimated the effects of beetle outbreaks and forest fires in terms of carbon in killed trees. We accounted for several processes to more realistically represent carbon impacts than simply using affected area reported by the Aerial Detection Surveys (beetles) and burned area (fires). For beetles, we used a data set of mortality area that represents the area of killed trees, not the affected area (which includes live trees) (Meddens *et al* 2012). For fires, we limited burned areas to forests only and considered only more severely burned areas that represent tree mortality. For both disturbance types, we accounted for variability in forest cover and tree size by utilizing spatial biomass data. Our data sets were derived from observations, increasing the confidence of our results.

We found that the most realistic middle estimate for bark beetles was associated with more C in killed trees

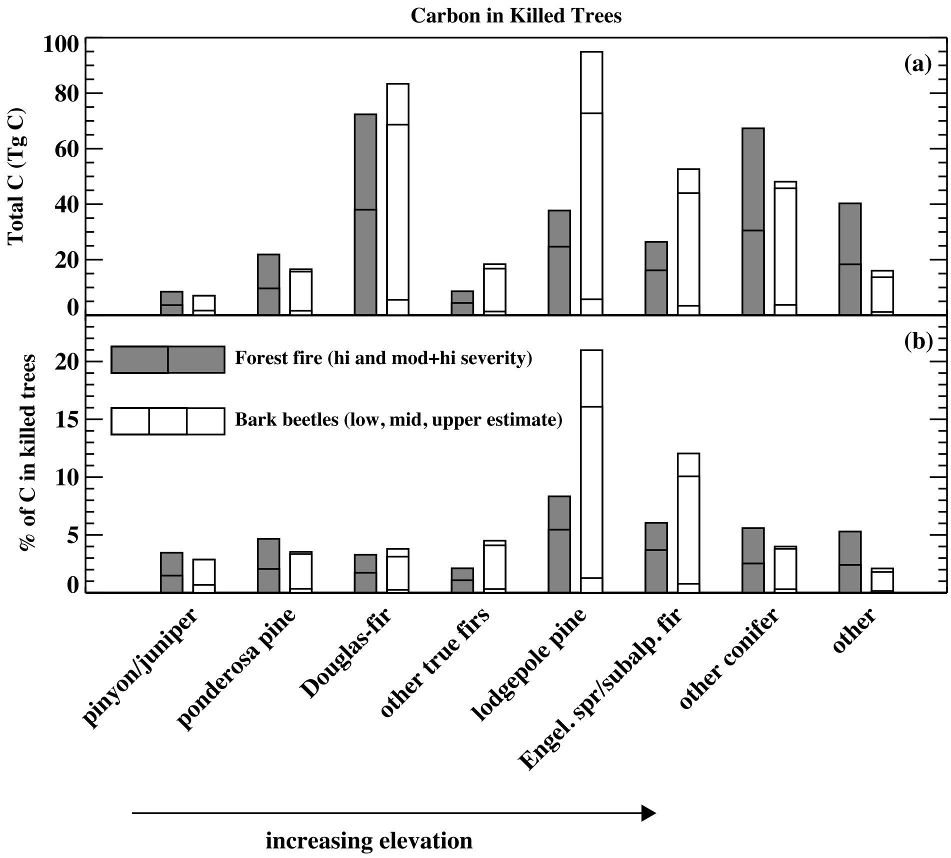

Figure 3. Cumulative carbon by forest type and over time in trees killed by bark beetles (1997–2010) and forest fires (1984–2010) in (a) Tg C and (b) per cent carbon in killed trees within forest type. Forest types (except 'other conifer' and 'other') sorted by elevation (Daubenmire 1966, Allen *et al* 1991).

than either estimate for fires, even when including a longer study period for fires. The lower estimate for bark beetles, however, was substantially lower than either estimate for fires. Most of the bark beetle-caused impacts on carbon were caused by mountain pine beetle killing lodgepole pine throughout much of the western United States. Together, C impacts of the higher estimates of these natural disturbances were of similar magnitude to that from harvesting in the two most recent decades, illustrating the importance of these natural disturbance types in the forests of the western United States. We note that postdisturbance carbon dynamics differ among these three disturbances even for similar amounts of mortality. For example, (a) fires affect all vegetation, including understory trees, shrubs, and herbs as well as soil, suggesting slower recovery; (b) stands that experience beetle outbreaks have surviving overstory (nonhost) and understory trees, suggesting faster recovery; and (c) harvesting removes carbon from the stand, altering subsequent decomposition.

Significant mountain pine beetle outbreaks happened in the early to mid-1980s, affecting 0.4–2 Mha year^{-1} (comparable to the affected area in the late 2000s) (USDA Forest Service 2012). Including these outbreaks would substantially increase our estimated cumulative impacts on carbon stocks. However, because spatial information about these outbreaks is lacking, these older outbreaks were not included in this analysis.

Our upper estimate of carbon in trees killed by bark beetles (285 Tg C) is less than that from a recent outbreak of mountain pine beetle in British Columbia (471 Tg C; Kurz *et al* 2008) despite similar areas of mortality (Meddens *et al* 2012). Several factors may contribute to this. First, some of the outbreak in British Columbia occurred after the end of the Meddens *et al* study (2012), corresponding to an additional 30 Tg C. Second, 63% of the beetle-caused mortality in the western United States was in lodgepole pine, whereas 94% of the British Columbia mortality was in lodgepole pine. The remainder of the mortality in the United States occurred in lower-biomass forest types (23% lower biomass than US lodgepole pine stands). Third, lodgepole pine stands in British Columbia have higher biomass than those from the US: the mean aboveground biomass in lodgepole pine stands in the western United States (100 Mg ha^{-1}) (Blackard *et al* 2008) is about 66% of that of forests in the montane cordillera (interior) region of British Columbia (all forest types; 152 Mg ha^{-1}) (Penner *et al* 1997). Finally, some of the difference may be attributable to differences in methodology.

Previous studies have reported the amount of carbon associated with fires in the United States. Our results agree with those of Ghimire *et al* (2012), who used a combination of carbon cycle modeling and forest inventories for carbon and burned severities from MTBS. Their estimate of 10.5 Tg C year^{-1} for carbon in killed trees is the same as our upper estimate, and good agreement occurs in the two time series. The amount of tree carbon released by combustion during fires should be less than the total amount of carbon in trees killed by fires (reported in this study). Two studies report combustion emissions in the United States, although the reported estimates include carbon from combustion of components of forest ecosystems (e.g., litter) in addition to trees, making comparisons difficult. van der Werf *et al* (2010) reported a mean combustion emission of 9 Tg C year^{-1} during 1997–2009 for the conterminous United States, slightly less than our upper estimate of carbon in trees killed by fires, but for a larger region. Wiedinmyer and Neff (2007) reported that 29 Tg C year^{-1} resulted from combustion emissions in the western United States in 2002–2006. This amount is higher than the total carbon in killed trees in our study, although the time period of the Wiedinmyer and Neff study (2007) was a period when large fires occurred and, as noted above, includes contributions from dead organic matter.

We produced a large range of estimated carbon impacts, and although we provide guidance about the most realistic beetle effect, each of the disturbance data sets has notable uncertainties. Bark beetle-caused tree mortality was recorded by trained observers in planes, suggesting uncertainty associated with this subjectivity. Although we reduced uncertainty by using collocated fine spatial resolution imagery to compute adjustment factors and produce a more realistic middle estimate, the large number of observers, their range in skills and experience, and variability in flying conditions imply that uncertainty in the number of killed trees remains. Field evaluations and consistent classification thresholds are also needed to translate spectral burn severity indices more accurately into fire-caused tree mortality.

Our study is a key first step toward quantifying impacts of these disturbances on the carbon cycle, and a more complete assessment should include additional components. We estimated the carbon in killed trees; this carbon is then shifted to dead carbon pools, which slowly decompose over decades, except for the combustion losses during fires (Kashian *et al* 2006, Edburg *et al* 2011). Additional studies are needed to estimate these carbon fluxes as well as regrowth. Killed trees no longer take up carbon from the atmosphere through photosynthesis, and decompose over several decades (Hicke *et al* 2012). Based on observations and modeling, we expect that areas with substantial tree mortality will be carbon sources in the first decade or so following beetle attack or fire and become weaker carbon sinks for a long period (Amiro *et al* 2010, Edburg *et al* 2011). Effects on carbon fluxes are more challenging to estimate than effects on C stocks, in part because of the difficulty of observing or modeling fluxes over large regions. However, flux studies such as those by Ghimire *et al* (2012), who investigated wildfires, are needed to better understand the full effect of disturbances on the carbon cycle. Furthermore, low-severity fires also modify forest carbon cycling and need to be included when considering a full accounting of the effects of fire.

5. Conclusions

We used spatially explicit maps of biomass, wildfires, and bark beetle-caused tree mortality to quantify how fire and beetle disturbances affect carbon in killed trees in the western United States in the past several decades. We found that during this time period, bark beetles resulted in more carbon in killed trees than wildfires, and that together, fires and beetles were associated with a similar amount of carbon in killed trees as harvesting. The period since 2000 has been subject to a particularly large area of tree mortality from fires and beetle outbreaks. Fires affected lower-elevation forest types more than higher-elevation forest types, whereas beetle outbreaks also affected upper montane and subalpine forest types.

Forest disturbances are also important in areas outside the western United States. The ready availability of spatially explicit databases facilitated our study of the western United States, yet such information is lacking or limited in other locations. Furthermore, a full assessment of the impacts of these disturbances on regional carbon cycling requires investigation of fluxes in addition to stocks. One means of doing so uses ecosystem models. Our results provide a comparison for these modeling studies.

Given expected continued warming, we anticipate that fires and beetle outbreaks will become more extensive and/or severe (Karl *et al* 2009, Bentz *et al* 2010). Because forest carbon cycling will continue to be substantively affected by these disturbance agents, fires and bark beetle outbreaks will continue to play major roles in the North American carbon budget (CCSP 2007).

Acknowledgments

Support was provided by the USGS Western Mountain Initiative (Award Number G09AC00337), Los Alamos National Laboratory (Subcontract Number 193703-1), NOAA (Award Number NA090AR4310194), the National Science Foundation (Award Number EAR-0910928), the USDA Forest Service Western Wildland Environmental Threat Assessment Center (Agreement Number PNW-08-JV-1126900-082), and NASA (Agreement Number NNX11AO24G S03). We thank Ben Bright for assistance with data processing, and anonymous reviewers whose comments improved the letter.

References

Allen R B, Peet R K and Baker W L 1991 Gradient analysis of latitudinal variation in Southern Rocky Mountain forests *J. Biogeogr.* **18** 123–39

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

Bentz B J, Régnière J, Fettig C J, Hansen E M, Hayes J L, Hicke J A, Kelsey R G, Negrón J F and Seybold S J 2010 Climate change and bark beetles of the western United States and Canada: direct and indirect effects *Bioscience* **60** 602–13

Blackard J A *et al* 2008 Mapping US forest biomass using nationwide forest inventory data and moderate resolution information *Remote Sens. Environ.* **112** 1658–77

Cairns M A, Brown S, Helmer E H and Baumgardner G A 1997 Root biomass allocation in the world's upland forests *Oecologia* **111** 1–11

Canadell J G, Le Quere C, Raupach M R, Field C B, Buitenhuis E T, Ciais P, Conway T J, Gillett N P, Houghton R A and Marland G 2007 Contributions to

accelerating atmospheric CO_2 growth from economic activity, carbon intensity, and efficiency of natural sinks *Proc. Natl Acad. Sci. USA* **104** 18866–70
CCSP 2007 *The First State of the Carbon Cycle Report (SOCCR): The North American Carbon Budget and Implications for the Global Carbon Cycle. A Report by the US Climate Change Science Program and the Subcommittee on Global Change Research. National Oceanic and Atmospheric Administration* (Asheville, NC: National Climatic Data Center)
Daubenmire R 1966 Vegetation: identification of typal communities *Science* **151** 291–8
Denman K L *et al* 2007 Couplings between changes in the climate system and biogeochemistry *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* ed S Solomon, D Qin, M Manning, Z Chen, M Marquis, K B Averyt, M Tignor and H L Miller (Cambridge: Cambridge University Press)
Edburg S L, Hicke J A, Lawrence D M and Thornton P E 2011 Simulating coupled carbon and nitrogen dynamics following mountain pine beetle outbreaks in the western United States *J. Geophys. Res.* **116** G04033
Eidenshink J, Schwind B, Brewer K, Zhu Z, Quayle B and Howard S 2007 A project for monitoring trends in burn severity *Fire Ecol.* **3** 3–12
French N H F *et al* 2011 Model comparisons for estimating carbon emissions from North American wildland fire *J. Geophys. Res.—Biogeosci.* **116** G00K05
Ghimire B, Williams C A, Collatz G J and Vanderhoof M 2012 Fire-induced carbon emissions and regrowth uptake in western US forests: documenting variation across forest types, fire severity, and climate regions *J. Geophys. Res.* **117** G03036
Goodale C L *et al* 2002 Forest carbon sinks in the Northern Hemisphere *Ecol. Appl.* **12** 891–9
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.* **116** G00K04
Hicke J A, Asner G P, Kasiske E S, French N H F, Randerson J T, Collatz G J, Stocks B J, Tucker C J, Los S O and Field C B 2003 Postfire response of North American boreal forest net primary productivity analyzed with satellite observations *Glob. Change Biol.* **9** 1145–57
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
Karl T R, Melillo J M and Peterson T C (ed) 2009 *Global Climate Change Impacts in the United States* (Cambridge: Cambridge University Press)
Kashian D M, Romme W H, Tinker D B, Turner M G and Ryan M G 2006 Carbon storage on landscapes with stand-replacing fires *Bioscience* **56** 598–606
Kashian D M, Romme W H, Tinker D B, Turner M G and Ryan M G 2013 Postfire changes in forest carbon storage over a 300-year chronosequence of *Pinus contorta*-dominated forests *Ecol. Monogr.* **83** 49–66
Kasischke E S, Amiro B D, Barger N N, French N H F, Goetz S J, Grosse G, Harmon M E, Hicke J A, Liu S and Masek J G 2013 Impacts of disturbance on the terrestrial carbon budget of North America *J. Geophys. Res.—Biogeosci.* **118** 303–16
Kasischke E S, Loboda T, Giglio L, French N H F, Hoy E E, de Jong B and Riano D 2011 Quantifying burned area for North American forests: implications for direct reduction of carbon stocks *J. Geophys. Res.* **116** G04003
Kolden C A, Lutz J A, Key C H, Kane J T and Wagtendonk J W V 2012 Mapped versus actual burned area within wildfire perimeters: characterizing the unburned *Forest Ecol. Manag.* **286** 38–47
Kurz W A, Dymond C C, Stinson G, Rampley G J, Neilson E T, Carroll A L, Ebata T and Safranyik L 2008 Mountain pine beetle and forest carbon feedback to climate change *Nature* **452** 987–90
Littell J S, McKenzie D, Peterson D L and Westerling A L 2009 Climate and wildfire area burned in western US ecoprovinces, 1916–2003 *Ecol. Appl.* **19** 1003–21
Meddens A J H, Hicke J A and Ferguson C A 2012 Spatiotemporal patterns of observed bark beetle-caused tree mortality in British Columbia and the western United States *Ecol. Appl.* **22** 1876–91
Odum E P 1969 Strategy of ecosystem development *Science* **164** 262–70
Olson D M *et al* 2001 Terrestrial ecoregions of the world: a new map of life on Earth *Bioscience* **51** 933–8
Pan Y *et al* 2011 A large and persistent carbon sink in the world's forests *Science* **333** 988–93
Penner M, Power K, Muhairwe C, Tellier R and Wang Y 1997 Canada's forest biomass resources: deriving estimates from Canada's forest inventory *Information Report* BC-X-370 (Victoria: Pacific Forestry Centre, Canadian Forest Service)
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
Ruefenacht B *et al* 2008 Conterminous US and Alaska forest type mapping using forest inventory and analysis data *Photogramm. Eng. Remote Sens.* **74** 1379–89
Salinas-Moreno Y, Mendoza M G, Barrios M A, Cisneros R, Macıas-Samano J and Zuniga G 2004 Areography of the genus Dendroctonus (Coleoptera: Curculionidae: Scolytinae) in Mexico *J. Biogeogr.* **31** 1163–77
Schlesinger W H 1997 *Biogeochemistry: An Analysis of Global Change* (San Diego, CA: Academic)
Shore T L and Safranyik L 1992 *Susceptibility and Risk Rating Systems for the Mountain Pine Beetle in Lodgepole Pine Stands* (*BC-X-336*) (Victoria: Forestry Canada, Pacific Forestry Centre)
Smith J E, Heath L S, Skog K E and Birdsey R A 2005 *Methods for Calculating Forest Ecosystem and Harvested Carbon with Standard Estimates for Forest Types of the United States* (*GTR* NE-343) (Newtown Square, PA: USDA Forest Service Northeastern Research Station)
Smith W B, Miles P D, Perry C H and Pugh S A 2009 *Forest Resources of the United States, 2007* (*General Technical Report* WO-78) (Washington, DC: USDA Forest Service, Washington Office)
USDA Forest Service 2012 *Major Forest Insect and Disease Conditions in the United States: 2010 Update* (*FS-988*) (Washington, DC: USDA Forest Service)
van der Werf G R, Randerson J T, Giglio L, Collatz G J, Mu M, Kasibhatla P S, Morton D C, DeFries R S, Jin Y and van Leeuwen T T 2010 Global fire emissions and the contribution of deforestation, savanna, forest, agricultural, and peat fires (1997–2009) *Atmos. Chem. Phys.* **10** 11707–35
Wiedinmyer C and Neff J C 2007 Estimates of CO_2 from fires in the United States: implications for carbon management *Carbon Balance Manag.* **2** 10
Zhu Z and Eidenshink J 2007 Assessment of spatial and temporal fire severity trends in the United States *Proc. 4th Int. Wildland Fire Conf. (Sevilla, Spain)*