Carbon Storage on Landscapes with Stand-replacing Fires

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Many conifer forests experience stand-replacing wildfires, and these fires and subsequent recovery can change the amount of carbon released to the atmosphere because conifer forests contain large carbon stores. Stand-replacing fires switch ecosystems to being a net source of carbon as decomposition exceeds photosynthesis—a short-term effect (years to decades) that may be important over the next century if fire frequency increases. Over the long term (many centuries), net carbon storage through a fire cycle is zero if stands replace themselves. Therefore, equilibrium response of landscape carbon storage to changes in fire frequency will depend on how stand age distribution changes, on the carbon storage of different stand ages, and on postfire regeneration. In a case study of Yellowstone National Park, equilibrium values of landscape carbon storage were resistant to large changes in fire frequency because these forests regenerate quickly, the current fire interval is very long, the most rapid changes in carbon storage occur in the first century, and carbon storage is similar for stands of different ages. The conversion of forest to meadow or to sparser forest can have a large impact on landscape carbon storage, and this process is likely to be important for many conifer forests.

Keywords: carbon cycling, climate change, dead wood, decomposition, net ecosystem production

Coniferous forests contain more than one-third of all carbon stored in terrestrial ecosystems (Smith et al. 1993). Many of these forests are characterized by large, stand-replacing fires occurring at intervals of more than 100 years (Johnson 1992, Turner and Romme 1994) that control the storage and release of carbon from these systems. These fires and the recovery from them are important to regional carbon storage because carbon lost in stand-replacing fires is often a significant component of regional carbon budgets. Annual carbon losses resulting from fire in the Canadian boreal forest are estimated to be 10% to 30% of average net primary production (NPP) (Harden et al. 2000), and current climate models predict a 25% to 50% increase in the area burned in the United States over the next 100 years (Neilson and Drapek 1998, Dale et al. 2001). Understanding the effects of stand-replacing fires on landscape carbon storage over both short and long temporal scales is therefore critical to predicting future changes in the global carbon budget (Kasischke et al. 1995, Stocks et al. 1996).

The alteration of ecosystem carbon balance (net ecosystem production, or NEP) by fire varies with time. During a fire, a pulse of carbon is released to the atmosphere through combustion. A new forest usually regenerates after fire, but additional carbon is lost to the atmosphere as carbon dioxide (CO_2) from decomposing dead vegetation. If a stand replaces itself, all of the vegetation killed by the fire (often more than 50% of ecosystem carbon stores) will be decomposed but then eventually replaced by the regenerating forest, and the net carbon balance will be zero over the fire cycle. However, negative carbon storage—net carbon loss to the atmosphere—induced by fire can persist for over a century (Crutzen and Goldhammer 1993), and fire intervals in coniferous forest are often more than 100 years, so the appropriate timescale for understanding fire and carbon depends on the timescale of interest.

Short-term effects of fires (over years to decades) are important for predicting Earth's carbon balance over the next century, because greater fire frequency, extent, or severity will release much carbon through combustion and increase the forested area having negative NEP. If climate change significantly increases the area burned over the next century—and it may (Neilson and Drapek 1998, Dale et al. 2001)—these short-term effects are likely to influence atmospheric CO_2 concentration. Short-term effects of fire on carbon storage are

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regulated by the amount of carbon lost in combustion (Tinker and Knight 2000, Schuur et al. 2002, Litton et al. 2004), by the rate and amount of regeneration (Kashian et al. 2004, Litton et al. 2004), and by the amount of material from the prior stand that is decomposing (AuClair and Carter 1993, Turner et al. 1995, Kurz and Apps 1999). Fire severity affects combustion losses, especially for surface fuels (Kasischke and Johnstone 2005), and may also affect the rate and amount of vegetation recovery (Wirth et al. 2002).

Long-term effects of fire (over many centuries) on ecosystem carbon balance are regulated by processes that control postfire regeneration and by fire frequency. If the postfire stand has poor or no regeneration, forest growth will not replace the carbon lost through combustion and decomposition, and the net carbon storage over a fire cycle will decrease. Changing fire frequency will also affect the net carbon storage over a fire cycle because the amount of carbon stored in a stand and the rates of photosynthesis and decomposition vary with stand age (Kasischke 2000, Pregitzer and Euskirchen 2004). If changing climate alters the frequency and intensity of fires in forests, revegetation and patterns of carbon storage may also be affected.

Fire rarely entirely burns a large landscape, so landscape assessments (Harmon 2001, Dean et al. 2004) of fire effects on carbon cycling need to consider fire frequency and extent, and the distribution in stand ages that results from a given fire regime (Kurz and Apps 1999, Euskirchen et al. 2002, Pregitzer and Euskirchen 2004). More frequent fires will promote a higher proportion of young forests in the landscape, and young forests tend to store less carbon than older stands (because of lower biomass), although their rates of productivity are higher (Ryan et al. 1997). Assessments of carbon storage on landscapes also should consider variability in postfire regeneration (Kashian et al. 2004, Turner et al. 2004), because stands that fail to replace themselves will alter carbon storage. We suspect that incorporating effects of large disturbances at large spatial scales will improve predictions of the global carbon budget, because current models (e.g., Turner et al. 1995, Schulze et al. 2000) have used data based on mature forests over short time periods (French et al. 2000, Kasischke 2000) without incorporating these disturbance effects. Few carbon balance studies have estimated carbon pools and fluxes over large extents (e.g., Harmon 2001, Dean et al. 2004) or long temporal scales (e.g., Thornley and Cannell 2004).

In this article we outline the concepts used to examine changes in carbon storage on landscapes over short and long temporal scales, and examine the sensitivity or resilience of landscape carbon storage to changes in fire regimes. We describe the controls over carbon cycling at the stand level, and present an approach to examine carbon cycling for conifer forest landscapes subject to stand-replacing fires. We illustrate our approach using a case study for the lodgepole pine (*Pinus contorta* var. *latifolia* Engelm. ex S. Wats.)–dominated landscape of Yellowstone National Park. Although coniferous forest types vary in factors that affect carbon cycling, the general approach we present is applicable to most coniferous forests characterized by stand-replacing fires.

Short-term effects of fire on carbon cycling in coniferous forests

The immediate effect of stand-replacing fires on carbon storage in an ecosystem is a loss of carbon to the atmosphere via combustion. Stand-replacing fires typically kill live trees but consume only a fraction of the biomass, leaving behind killed trees as dead wood. The consumption of live and dead fuels during a fire in coniferous forests varies as a function of stand age and tree size (Kasischke et al. 1994), but fires oxidize stored carbon from pools such as foliage and small twigs, branches and cones, and dead wood (Tinker and Knight 2000, Schuur et al. 2002). The forest floor is nearly completely consumed in many coniferous forests (Litton et al. 2004), but its consumption may be highly variable where this layer is very thick (Kasischke and Johnstone 2005).

The carbon loss caused by combustion is obvious, but the strongest effect of fire on carbon cycling involves the balance between carbon lost through decomposing dead wood and carbon gained in growing vegetation. Stand-replacing fires kill living biomass in coniferous forests and reduce leaf area to near zero, causing NPP to approach zero immediately following the fire (Pearson et al. 1987). Decomposition of dead roots and boles for several decades following fires may release up to three times as much carbon into the atmosphere as the fire itself (AuClair and Carter 1993), and carbon loss may exceed assimilation by young postfire vegetation for several decades after the disturbance (Crutzen and Goldhammer 1993). Removal of the forest canopy and forest floor (Kasischke and Johnstone 2005) facilitates an increase in soil temperature and moisture as transpiration and interception are reduced, which may also result in higher decomposition if labile carbon is available (Landhaeusser and Wein 1993, Burke et al. 1997, Johnstone and Kasischke 2005). The difference between NPP and decomposition in upland systems closely approximates the net annual change in carbon storage (NEP), which is negative when carbon lost through decomposition exceeds that gained through photosynthesis.

As the forest reestablishes and decomposition slows, carbon accumulation in trees eventually compensates for carbon lost through decomposition (Crutzen and Goldhammer 1993), and NEP becomes positive (figure 1). NEP in coniferous forests may remain positive until the next stand-replacing fire, with annual biomass accumulation peaking in the fourth or fifth decade of stand development (Pearson et al. 1987) and slowly declining thereafter. As NPP declines with stand development (Ryan et al. 1997), NEP may again become slightly negative if decomposition of dead wood exceeds production (figure 1).

Soil in coniferous forests contains one of the largest stable pools of carbon in forest ecosystems (Bonan and Shugart 1989, Kasischke et al. 1995), and it is thought to be fairly stable even following wildfires (Harden et al. 2000, Wirth et al. 2002). Soil carbon in the upper soil horizons in Yellowstone National

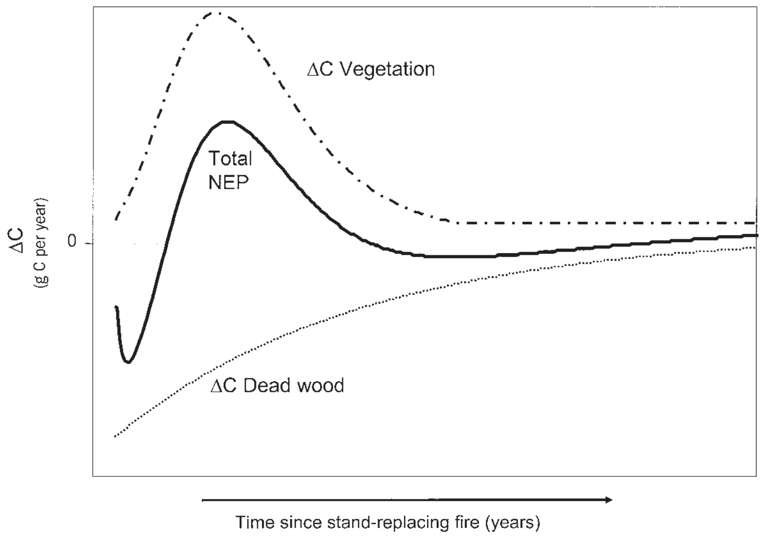

Figure 1. Hypothetical postfire net ecosystem production (NEP) trajectory for coniferous forests with vegetation and dead wood components. NEP is initially negative, and then increases with increasing net primary production (NPP) as trees reestablish, but eventually declines as NPP decreases while carbon is lost through decomposition of dead wood. Abbreviations: ΔC, change in carbon; g, gram.

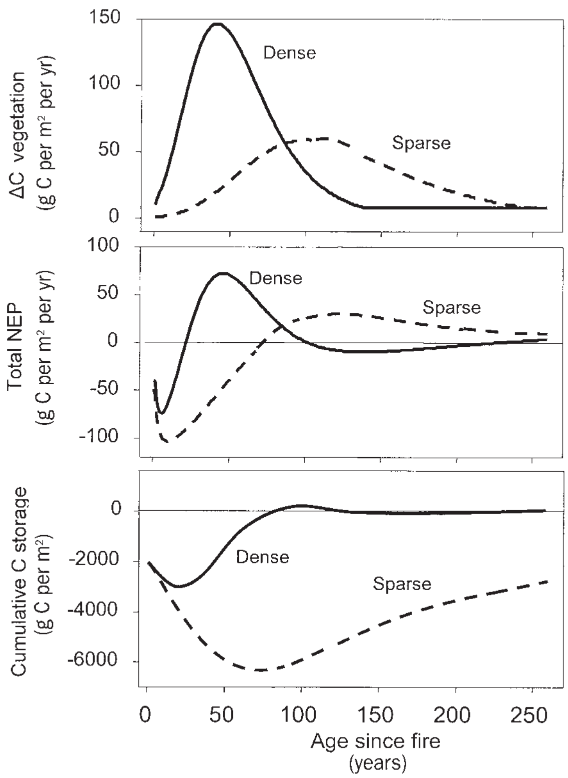

Figure 2. Change in carbon (ΔC) from live vegetation (top), total net ecosystem production (NEP; center), and cumulative C storage (bottom) for lodgepole pine stands with different structures. Stands of contrasting structure follow different trajectories of NEP, in large part because of different rates of C uptake and storage by vegetation. Abbreviations: g, gram; m^2, square meter; yr, year.

Park, for example, includes 2380 to 3580 grams (g) carbon per square meter (m^2) (37% to 47% of total ecosystem carbon) in regenerating (10-year-old) forests and 3380 g carbon per m^2 (20%) in mature (> 100-year-old) forests (Litton et al. 2004), suggesting that even long-term changes in the soil carbon pool are small. We therefore assume a stable soil carbon pool and focus on the interplay among living biomass, dead wood, and disturbance frequency in coniferous forests.

Long-term effects of fire on carbon cycling in coniferous forests

Stand-replacing fires may affect carbon cycling by altering the distributions of stand structure and stand ages across a landscape.

Variability in carbon storage with stand structure. The general trajectory of NEP is predictable (figure 1), but the specific trajectory of carbon storage in a stand is closely linked to postfire stand structure. The NEP trajectory for stands having low initial regeneration is very different from that for stands having dense regeneration. Studies following the Yellowstone fires have documented wide variability in postfire regeneration of pine seedlings (Kashian et al. 2004, Turner et al. 2004), which is strongly linked to postfire aboveground NPP (ANPP). Following the 1988 fires, stands with dense regeneration (> 10,000 seedlings per hectare [ha]) exhibited rapid canopy closure and high production (approximately 190 g carbon per m^2 per year), but sparse stands exhibited far lower values of ANPP (as low as 0.1 g carbon per m^2 per year) (Turner et al. 2004). Reconstructions of long-term trajectories of mature stands in Yellowstone demonstrate that initially variable postfire regeneration leaves a persistent legacy of heterogeneous stand structures for up to 200 years (Kashian et al. 2005), suggesting that initial variability in stand density may affect NEP trajectories over the long term.

We modeled long-term changes in NEP for sparse and dense stands using published data on ANPP in regenerating forests (Turner et al. 2004) and on carbon stocks (Smith and Resh 1999), and published (Litton et al. 2004) and unpublished data on standing and fallen dead wood in lodgepole pine stands in the Rocky Mountains (figure 2). Annual carbon stocks estimated empirically along a chronosequence for initially dense lodgepole pine stands (with the youngest stand averaging 12,500 stems per ha; Smith and Resh 1999) were used to model nonlinear trajectories of vegetation (including wood, foliage, and roots), forest floor, dead wood, and dead coarse roots over time. Stocks for sparse stands were estimated as a fraction of the stocks for dense stands, determined as the proportion of sparse to dense vegetation stocks on an annual basis. Stocks were converted to annual changes in each pool using the difference in carbon stocks in consecutive years. NEP was expressed as the sum of the changes in each of the four carbon pools each year. NEP for sparse stands was calculated assuming sparse regeneration following the burning of a dense prefire stand.

Stands of contrasting structure follow different trajectories of NEP, in large part because of different rates of carbon uptake and storage by vegetation. Dense stands accumulate more carbon at a higher rate than sparse stands because of physical differences in leaf area and available photosynthate, and NEP for a dense stand returns to a positive value following disturbance much earlier than for a sparse stand. However, NEP is positive for a shorter duration in dense stands, because of carbon loss resulting from the decomposition of dead wood produced by self-thinning several decades after the stand regenerates (figure 2). We estimated carbon lost to combustion as the sum of (a) carbon stored in the live foliage of trees, in the forest floor, and in herbaceous and shrub vegetation (Litton et al. 2004) and (b) 8% of carbon stored in dead wood (Tinker and Knight 2000). Using this value, recovery of carbon lost through combustion appears to be far slower in sparse stands. In fact, carbon lost in the fire may not be recovered even after 250 years if postfire tree density is very low (figure 2). These scenarios not only illustrate the potentially large differences in NEP for stands of different structure but suggest that the replacement of biomass for a given stand over multiple fire intervals is critical to the interaction between carbon storage and disturbances.

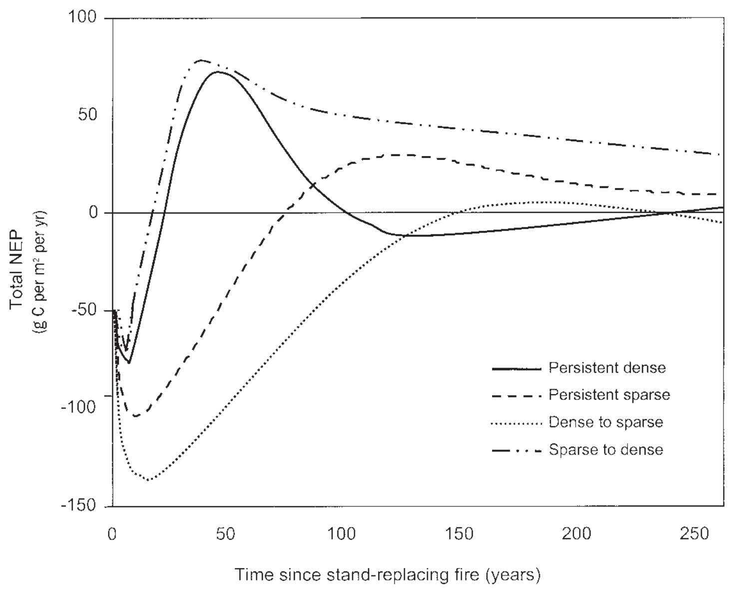

Figure 3. Hypothetical trajectories of net ecosystem production (NEP) for stands with persistent and changing relative density before and after stand-replacing fires. NEP will approach zero on a landscape with stands that replace themselves following stand-replacing fires. Abbreviations: C, carbon; g, gram; m², square meter; yr, year.

The importance of stand biomass replacement—that is, the regeneration of dense pine stands to dense rather than sparse stands—for NEP involves the link between the density of the newly regenerating stand and the decomposition of dead wood from the prefire stand. Assuming unchanging species composition, net carbon storage over the length of the fire interval should be near zero if biomass killed by the fire and decomposed is eventually replaced by the regenerating forest. Carbon storage in dense stands that regenerate densely and in sparse stands that regenerate sparsely should therefore approach zero over the length of a fire interval (figure 3). However, a sparse stand that regenerates densely will produce a low volume of dead wood but much regeneration to compensate for carbon loss through decomposition, resulting in a net carbon gain over the fire interval. A dense stand that regenerates to a sparse stand will result in a large amount of dead wood when it burns, but a decrease in vegetation when it regenerates, resulting in a net carbon loss (figure 3). A more extreme scenario is a type conversion from forest to grassland or meadow following fires; a lack of tree regeneration following fires would significantly reduce the amount of carbon stored in the ecosystem over the long term, especially in relation to the amount of carbon loss through decomposition.

The likelihood that stands will replace themselves depends strongly on the regeneration ecology of the dominant tree species. Species exhibiting cone serotiny (closed cones requiring high temperatures to open and release seeds), such as lodgepole pine in subalpine forests or jack pine (*Pinus banksiana* Lamb.) in boreal forests, store seeds within closed cones until fire occurs, promoting the dominance of these species over many fire intervals. Dense stands typically have many trees with serotinous cones and exhibit dense regeneration following fires (Schoenike 1976, Turner et al. 1997, Schoennagel et al. 2003), and sparse stands tend to have fewer trees with serotinous cones and regenerate sparsely following fires. Several authors examining serotinous species have shown that higher postfire stand density is associated with more frequent fire (Schoenike 1976, Givnish 1981, Schoennagel et al. 2003), such that increased fire frequency may create a directional change toward denser stands (Schoennagel et al. 2006). Conifer species that do not exhibit cone serotiny are less likely to regenerate densely regardless of prefire density—and thus are less likely to replace biomass following fires—and are more dependent on propagule input from nearby unburned forests and on environmental conditions in the first decade following the disturbance.

Stand age structure and changing fire frequency. Landscape carbon storage is the sum of the carbon budgets of each of the stands in the landscape, and therefore the carbon balance at the landscape level also depends on the distribution of stand ages across a heterogeneous landscape. Stands dominated by older, larger trees store large amounts of carbon and generally exhibit high carbon loss when disturbed compared with those dominated by younger, faster-growing trees (Schulze et al. 2000, Harmon 2001). A landscape should therefore shift between a carbon source (negative NEP) and sink (positive NEP) when the stand age distribution is altered (Kasischke et al. 1995, Kasischke 2000, Euskirchen et al. 2002, Pregitzer and Euskirchen 2004). Large fires quickly change the stand age distribution of a landscape, and changing fire frequency on the landscape will also change the age distribution over the long term (Kasischke et al. 1995, Gardner et al. 1996). If climate change increases fire frequency (Dale et al. 2001), the proportion of younger stands on the landscape will increase, more carbon will be released to the atmosphere via combustion, and less carbon will be stored on the landscape (Harmon et al. 1990, Schulze et al. 2000). This trend and the importance of landscape age structure have been demonstrated for shortened logging rotations using spatial simulation models on managed landscapes (Harmon et al. 1990, Euskirchen et al. 2002, Harmon and Marks 2002, Janisch and Harmon 2002).

Case study: Landscape-level carbon cycling on the Yellowstone landscape

We used the landscape of Yellowstone National Park as a case study to assess our conceptual approach to short- and long-term changes in landscape carbon storage on coniferous landscapes following large wildfires. About 250,000 ha of lodgepole pine forests (47% of all lodgepole pine forests in the park) burned in Yellowstone National Park in 1988 (Despain 1990), a disturbance that occurs on this landscape every 100 to 300 years (Romme 1982, Millspaugh et al. 2000). Specific parameters of this case study may not be applicable to all coniferous forests, but the example should provide a stimulus for further discussion and data collection in other types of coniferous forests with different disturbance regimes and ecological characteristics.

Short-term recovery of landscape carbon storage following the 1988 fires. We modeled recovery of carbon storage in Yellowstone using the data shown in figure 2, and additional data from pre- and post-1988 maps published by Despain (1990), to estimate changes in landscape NEP for 250 years following the 1988 fires (figure 4). The prefire NEP of the approximately 525,000 ha of lodgepole pine forests within Yellowstone National Park in 1987 was near zero—approximately 4.8 g carbon per m^2 per year. On the basis of published estimates of carbon pools (foliage, forest floor, herbaceous and shrub biomass, and partial dead wood; Litton et al. 2004) in the kinds of mature lodgepole pine stands in Yellowstone that burned in stand-replacing fires, we estimate direct carbon loss to the atmosphere during the 1988 fires to be about 1360 g per m^2. Other types of coniferous forests experience a more mixed fire regime that includes both nonlethal and stand-replacing fires (Wirth et al. 2002), resulting in variable consumption of the forest floor (Kasischke and Johnstone 2005), which may affect postfire regeneration (Johnstone and Chapin 2006). These sources of variation were not important in Yellowstone, where the surface organic layer is relatively thin and fires are mostly stand-replacing.

A total of about 1530 g carbon per m^2 is expected to be lost through decomposition and other postfire processes over 250 years following the 1988 Yellowstone fires (mostly during the first 30 years after the fire), supporting the results of those who documented higher carbon losses from postfire decomposition than from combustion in the fire itself (AuClair and Carter 1993, Kasischke et al. 1995, Wirth et al. 2002). We assumed no change in the soil carbon pool following the 1988 fires, but soil carbon in other types of coniferous forests—especially where the forests are associated with permafrost—may be more heavily influenced by changes in temperature regimes caused by variable consumption of the forest floor or by climate change (Kasischke et al. 1995, O'Neill et al. 2002, Bergner et al. 2004, Kasischke and Johnstone 2005).

The Yellowstone landscape should exhibit a large but short-duration carbon loss (i.e., act as a carbon source) followed by a long period as a moderate carbon sink (figure 4). Despite the presence of many stands on the landscape that have already recovered to prefire levels of ANPP (Turner et al. 2004), NEP is currently negative for the landscape as a whole and should remain so for approximately 35 years after the fire, as carbon losses from dead boles and coarse roots remain high within the burned area and in older unburned stands. This pattern is very similar to the postfire NEP estimated for boreal forests (negative for 25 to 37 years; Kasischke et al. 1995). We predict, from current conditions, that

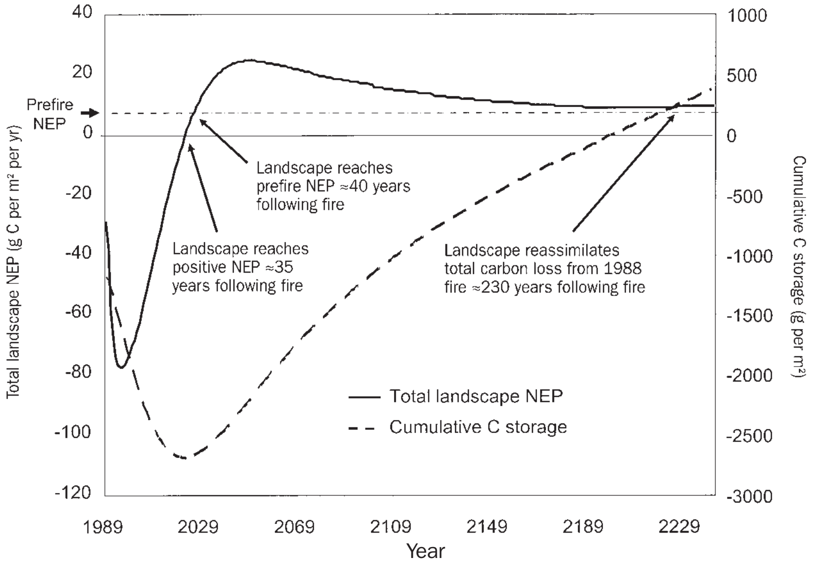

Figure 4. Predicted total net ecosystem production (NEP; solid line) and cumulative carbon (C) storage (dashed line) for lodgepole pine forests on the entire 525,000-hectare Yellowstone landscape following the 1988 fires. The landscape is expected to recover all C lost during and after the 1988 fires over the course of the fire interval. Abbreviations: g, gram; m^2, square meter; yr, year.

the Yellowstone landscape will reach prefire levels of NEP about 40 years after the 1988 fires, and that the total carbon lost (during and after the fires) will be recovered within about 230 years after the fires (figure 4). Thus this landscape appears resilient for carbon storage over the long term as a result of its long fire intervals, although it acts as a source of carbon over shorter time scales.

Long-term effects of fire in Yellowstone. Stand-replacing fires like the 1988 Yellowstone fires may affect carbon storage over the long term by altering stand age distributions and stand density distributions. However, very large changes in stand age or density distributions—perhaps including state conversions from forest to grasslands—are most likely necessary to shift carbon storage on large landscapes.

Stand age distributions. To evaluate the importance of altered fire frequency under plausible climate change scenarios, we applied the fire modeling results of Gardner and colleagues (1996) to our simulated landscape carbon budgets in Yellowstone National Park. We compared carbon stored on an approximately 80,000-ha portion of Yellowstone under (a) the current fire frequency (based on 20th-century data), (b) an increased fire frequency resulting from a dry climate simulation, and (c) a decreased fire frequency resulting from a wet climate simulation (table 1; Gardner et al. 1996). We estimated carbon stocks for each age class using the modeled estimates shown in figure 2; the sum of the products of the number of modeled hectares (table 1) and carbon stocks for each age class provides an estimate of landscape carbon stocks for each scenario (figure 5). The carbon stocks correspond to the equilibrium age distribution calculated from 1000 simulation years, and differences in carbon stocks represent differences in net landscape carbon balances among the scenarios.

Surprisingly, our simulations show that the changes in fire frequency expected under the climate change scenarios modeled by Gardner and colleagues (1996) had a negligible impact on landscape carbon storage over the long term. Following the 1988 fires and initially assuming an equal proportion of dense and sparse stands across the landscape, the landscape contains about 12.3 kilograms (kg) carbon per m^2; this value remained unchanged with increased fire frequency (–0.5%) or with less frequent fire (+0.5%) (figure 5). The simulations by Gardner and colleagues (1996) predict that 35% of the landscape will be occupied by stands under 150 years old in their increased fire frequency scenario, compared with 33% under current conditions (table 1). A shift in stand age distributions toward younger stands could cause a sizable loss of carbon from the landscape, but this shift apparently must be more substantial than predicted under the dry climate scenario of Gardner and colleagues (1996).

Stand density distributions. Long-term changes in the stand density distribution across a landscape imply changes in the ability of stands on a landscape to replace their biomass over multiple fire intervals. If dense stands were uncommon on the entire landscape (25%), landscape carbon stocks would lose 1.3 kg carbon per m^2 (–10%, for a total of 11.1 kg per m^2) with less frequent fire and 1.4 kg carbon per m^2 (–11%, for a total of 10.9 kg per m^2) with more frequent fire (figure 5). If changes in fire regimes resulted in the dominance (75%) of dense stands across the entire landscape, landscape carbon stocks would gain 1.3 kg carbon per m^2 (+10%, for a total of 13.7 kg per m^2) under a decreased fire frequency and about 1.4 kg carbon per m^2 (+11%, for a total of 13.6 kg per m^2) under an increased fire frequency, because denser stands accumulate carbon more rapidly after fire than sparse stands (figure 2). Under no scenario is change in landscape carbon storage extreme (maximum change = 1.4 kg carbon per m^2), which suggests that equilibrium landscape carbon storage is resistant to large changes in stand age or density distributions. A major type conversion, from forest to nonforest, would be required to produce a large change in carbon storage in our simulations. For example, if only 50% of stands regenerated on the landscape under current climate conditions, landscape carbon stocks would lose 3.2 kg carbon per m^2 (–26%). The loss would be 4.9 kg carbon per m^2 (–39%) if only 25% of stands regenerated.

Table 1. Proportions of an approximately 80,000-hectare portion of Yellowstone National Park occupied by four forest stand age classes, as determined by 10 sets of 1000-year simulations for three fire frequency scenarios by Gardner and colleagues (1996).

Age class (years)	Fire frequency scenario: Less frequent	Current	More frequent
0–50	0.11	0.12	0.13
51–150	0.18	0.21	0.22
151–250	0.32	0.34	0.35
> 250	0.39	0.33	0.30

Note: Increased fire frequency shifts the landscape slightly toward younger stands compared with current conditions, and decreased fire frequency shifts the landscape slightly toward older stands.

Causes of significant long-term carbon losses from coniferous landscapes

Our Yellowstone case study illustrates that increases in fire frequency are likely to have little effect on landscape carbon storage over the long term in this system, because most change in carbon balance occurs during the first few decades following the fire (figure 4), and changes in equilibrium carbon storage on a landscape would require that fire frequency be drastically shortened to within this window of change in carbon balance. Simple spreadsheet calculations of stand age distributions at increasing fire frequencies, assuming that half of each age class is burned during each fire event and that lodgepole pine forests regenerate after each event, suggest that a mean fire return interval of 80 years on the Yellowstone landscape—highly unlikely for this system—would still produce only about a 6% decrease from current landscape carbon stocks after 1000 simulation years of modeling. Such

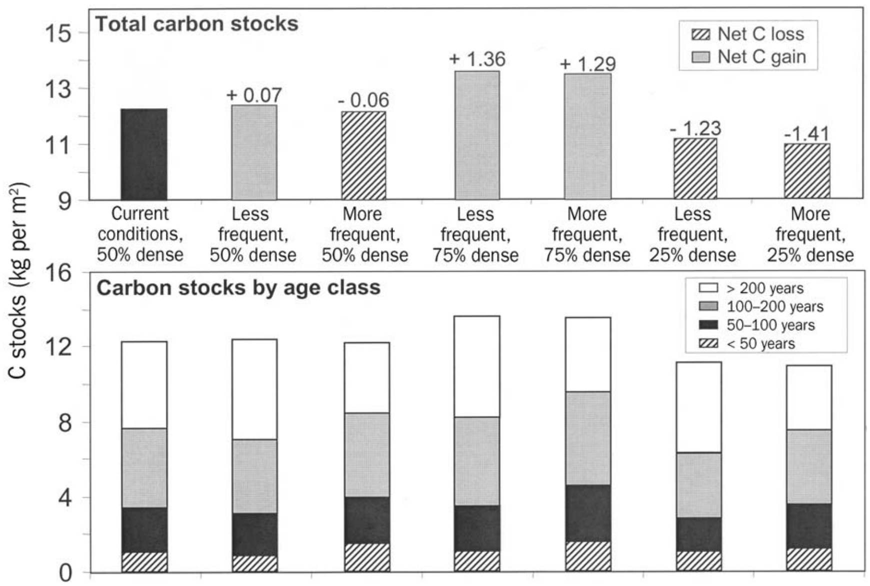

Figure 5. Total carbon (C) stocks (top) and C stocks by age class (bottom) of an 80,000-hectare portion of the Yellowstone landscape following 1000 simulation years under multiple fire frequency and density scenarios. Numbers above bars in top panel represent net changes in C stocks from current conditions, in kilograms C per square meter. Carbon stocks are more affected by shifts in the stand density distribution across the landscape than by shifts in stand age distributions.

an increase in fire frequency may be plausible in boreal forests, where fire intervals are currently shorter than in subalpine forests (Johnson 1992).

Our models for Yellowstone indicate that a significant state conversion appears to be necessary to create large changes in landscape-level carbon storage in subalpine coniferous forests, and perhaps in other coniferous forest types. Dramatic type conversions on landscapes, such as the conversion of forests to grasslands or shrublands, appear necessary to evoke large changes in equilibrium landscape carbon budgets. A lack of tree regeneration following disturbances would substantially reduce the amount of carbon accumulated and stored within the ecosystem during the fire cycle (Erb 2004) and would most likely result in a much larger loss of carbon from the system. A shift from dense to sparse stands, rather than shorter fire intervals alone, also may qualitatively change a landscape from a long-term sink to a source of carbon over the short term (figure 5), but several studies suggest that shortening fire intervals leads to directional changes toward denser stands on a landscape over the long term (Schoenike 1976, Givnish 1981, Schoennagel et al. 2006). Large-scale combustion of deep organic layers or melting of permafrost layers in boreal forests may also create large changes on landscapes where the majority of carbon is stored in organic material on the forest floor (Kasischke et al. 1995), and this would be likely to result in a larger loss of carbon to the atmosphere and a longer recovery time for landscape carbon storage.

Caveats and complications

We have considered changes in fire frequency and postfire tree density to be the most important factors affecting landscape carbon storage, but alterations in carbon storage may also result from changes in tree species composition that accompany changes in climate. Paleoecological studies in Yellowstone (Bartlein et al. 1997, Millspaugh et al. 2000) have shown almost no change in forest composition since the early Holocene for the lodgepole pine–dominated landscape of our case study. However, climate change on other coniferous landscapes may lead to species compositional changes accompanied by changes in stand density distributions, fire regimes, and carbon storage. Such changes may be especially important in boreal forests where decomposition is slower and permafrost is present (Kasischke et al. 1995).

Important differences exist in the processes driving landscape carbon storage in natural versus managed landscapes. Studies of carbon storage on managed landscapes have concluded that decreasing disturbance frequency will maximize carbon stocks on landscapes (Euskirchen et al. 2002), particularly in the Pacific Northwest (Harmon et al. 1990, Harmon and Marks 2002, Janisch and Harmon 2002), but these studies also note significant changes in carbon stocks at equilibrium when disturbances are more frequent. The major forest disturbance in the Pacific Northwest is clear-cut timber harvesting, which involves significant differences from wildfires in the removal and regeneration of live and dead biomass following a disturbance event. We estimated carbon lost through combustion during the 1988 Yellowstone fires to be about 8% of total ecosystem carbon (Tinker and Knight 2000). If the Yellowstone ecosystem were subjected to clear-cut harvesting in which all aboveground biomass was harvested and dead wood was burned with slash, about 62% of total ecosystem carbon would be removed from the system (although less would be returned to the atmosphere if stored in durable wood products). If we assume the removal of the dead wood carbon pool by postharvest burning, lengthening harvest rotations in Pacific Northwest systems results in more carbon stored in biomass (Harmon et al. 1990, Harmon and Marks 2002, Janisch and Harmon 2002). In unharvested coniferous landscapes, where fires remove a relatively small fraction of biomass, carbon stocks are less affected by the increasing frequency of disturbances, such that even large changes in age structure across the landscape do not result in large changes in carbon stocks.

Our primary conclusion from this conceptual study, that carbon storage in at least some coniferous forest landscapes is resistant to changes in fire frequencies over the long term, is based on equilibrium values that do not necessarily reflect carbon dynamics over shorter temporal scales. Our approach provides insights into the long-term, broadscale behavior of the system, but is less useful for understanding the interactions of climate change and landscape carbon storage at the shorter timescales reflected in human perspectives. For example, the Yellowstone landscape is resilient for carbon storage over a 300-year fire interval, but the landscape will release up to 2.7 kg carbon per m^2 over the next 40 years (figure 4). This pulse of carbon to the atmosphere will be sequestered by the landscape over the long term, but the occurrence across the globe of fires similar in size and severity to those in 1988 would have a large effect on the global carbon budget over the next half-century regardless of the ability of individual landscapes to recover carbon over the next few centuries. Policy regulating atmospheric carbon focuses by its nature on the short term, and most human concerns regarding the global carbon budget lie within the next 50 to 100 years. Moreover, the time required for full recovery of carbon lost in Yellowstone (approximately 230 years) is nearly as long as the maximum time between large fires (approximately 300 years), and thus even relatively small changes in climate that shorten or lengthen the fire interval in Yellowstone may be important to the landscape's ability to store carbon following a single fire event. At a global scale, large, stand-replacing fires in coniferous forests during the next several decades will result in large releases of carbon that may affect atmospheric CO_2 levels.

Conclusions

Stand-replacing fires on coniferous landscapes affect carbon cycling and storage over large spatial extents and long time periods, and understanding these relationships is important for predicting future changes in atmospheric carbon. Stand-replacing fires alter the balance between carbon gained through tree growth and carbon lost through decomposition of dead wood, and may shift the landscape from a carbon sink to a carbon source for several decades following the disturbance. Increasing fire frequency due to climate change, therefore, will increase the amount of carbon released to the atmosphere in the short term, which may have important effects on the global carbon budget. As long as forests continue to regenerate over the long term, however, equilibrium values of landscape carbon storage are resistant to changes in disturbance frequency, because stand-replacing fires remove relatively little biomass from the landscape, large amounts of carbon are stored in dead wood, and fire intervals would have to be shortened drastically (and probably unrealistically for many systems) to effect a change in long-term carbon storage. Thus a significant state change—such as a large-scale shift toward sparser stands or the conversion of coniferous forests to grasslands—is probably necessary to evoke changes in equilibrium values of landscape carbon storage. Increasing fire frequency with climate change has short-term as well as long-term effects for carbon storage, however, and short-term implications may be significant in terms of their feedbacks with global climate change.

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