Vulnerability of Landscape Carbon Fluxes to Future Climate and Fire in the Greater Yellowstone Ecosystem

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Abstract

More frequent fires under climate warming are likely to alter terrestrial carbon (C) stocks by reducing the amount of C stored in biomass and soil. However, the thresholds of fire frequency that could shift landscapes from C sinks to C sources under future climates are not known. We used the Greater Yellowstone Ecosystem (GYE) as a case study to explore the conditions under which future climate and fire regimes would result in tipping points of C source-sink dynamics. We asked: How great a change in climate and fire regime would be required to shift conifer forests in the GYE from a net C sink to a net C source? To answer this question, we developed downscaled climate projections for the GYE for three general circulation models and used these projections in a dynamic ecosystem process model (CENTURY version 4.5). We simulated C storage to year 2100 for individual forest stands under three fire-event pathways (fires at 90, 60, or every 30 years) and a reference simulation (no fire, representing the historical fire interval) under both future and current downscaled climate scenarios. Our results show that fire intervals less than approximately 90 years will cause lodgepole pine (Pinus contorta var. latifolia) forest stands to shift from a net C sink to a net C source, because the time between fires would be less than the time required to recover 85 percent of the C lost to fire. The capacity for fast post-fire regeneration of lodgepole pine from an aerial seedbank (serotinous cones) and the projected increase in lodgepole pine productivity under warmer climate conditions would not counter the consequences of fire-return intervals that were less than 90 years. In all future climate scenarios, decreases in fire-return interval are likely to reduce the potential of the GYE landscape to store C. The magnitude of this shift will depend on the future distribution of forest and non-forest ecosystems across the landscape, other constraints on fire patterns not considered here (fuels, ignition factors, and landscape management), and the accuracy of the fire-climate model as future climate diverges increasingly from the past.

Introduction

Forest managers in the western U.S. are facing more wildfires than ever before, and it is increasingly important for scientists and managers to anticipate the consequences of this trend. In subalpine forests of the northern Rocky Mountains, the number of large fires has increased in the past 25 years in association with warmer temperatures, earlier snowmelt, and longer fire seasons (Westerling et al. 2006, Running 2006). This trend is expected to continue with global warming (Tymstra et al. 2007, Littell et al. 2010). Yet, the consequences of increased fire frequency and climate warming for western forests remain uncertain. Increased fire occurrence is a prime concern of residents and land managers from state and federal agencies because of direct effects of fire on life, property, and resources (GAO 2007). More frequent fire may also trigger important ecological changes, and carbon (C) source-sink dynamics may be particularly vulnerable to altered fire regimes (e.g., Kurz et al. 2008, Balshi et al. 2009).

Our previous work, based on intensive field measurements in a chronosequence of 77 lodgepole pine (Pinus contorta var. latifolia) stands (Smithwick et al. 2009a, Kashian et al., in prep) and simulation models (Smithwick et al. 2009b) has shown that C and nitrogen (N) losses following stand-replacing fire are recovered within 70-100 years, well within the relatively long, average historical fire intervals (135 to 310 years) in lodgepole pine forests of the Greater Yellowstone Ecosystem (GYE; Schoennagel et al. 2003, 2004). When simulating C balance in lodgepole pine forests under projected future climates, our results also suggested the potential for an increase in net C storage (Smithwick et al. 2009b), because lodgepole pine productivity in the GYE may be limited, in part, by temperature and/or length of the growing season. Because C losses to fire are

relatively low and C stocks recover within the observed fire-return intervals (FRIs), we surmised that forests in the GYE would need to burn much more frequently than has occurred throughout most of the Holocene, where fire intervals were generally greater than 100 years (Whitlock et al. 2003), for C storage to be substantially altered (Kashian et al. 2006). However, the degree to which fire frequency would need to be increased that would lead to reductions in C storage has not been explored previously.

Our goal in this project was to advance scientific understanding of landscape-scale vulnerabilities of key western forest types to climate change. Our overall questions was: How great a change in climate and fire regime would be required to shift conifer forest communities in the GYE from a net C sink to a net C source? We aimed to identify the fire frequency at which conifer forests become net sources of C to the atmosphere (i.e., lower C storage in the future when compared to current conditions). The GYE is ideal for this study because its fire regime and vegetation dynamics are reasonably well understood (e.g., Romme and Despain 1989, Whitlock et al. 2003, Turner et al. 2003). In 1988, the extensive Yellowstone fires inaugurated a new era of major wildfires in the western U.S., and 20 years of intensive postfire research have provided many new insights into the consequences of large, severe wildfires in the Yellowstone ecosystem (Kashian et al. 2006, Schoennagel et al. 2008, Turner 2010). Lodgepole pine, the dominant tree species in Yellowstone National Park, can regenerate rapidly and abundantly after fire due to its serotinous cones (Turner et al. 1997), and the abundance of serotinous cones covaries spatially with elevation and historical fire frequency (Schoennagel et al. 2003). Although canopy fires consume fine litter, branches, and foliage, and kill live trees, relatively little of the C pools in tree boles, downed wood, and soil are combusted (Tinker and Knight 2000, Campbell et al. 2007).

Methods

Our approach combined a dynamic ecosystem model to project future C stocks under different climate scenarios and fire regimes. To identify how great a change in climate and fire regime would be required to shift vegetation from C source to C sink, we ran the ecosystem model CENTURY version 4.5 (Parton et al. 1987, Smithwick et al. 2009b) aspatially for the dominant vegetation communities in the GYE given a large fire event in 1988, and a range of estimated fire-return intervals and current and future climate conditions. Based on our previous work (Kashian et al. 2006, Kashian et al., in prep), we identified general patterns of fire regime and forest regeneration pathways across the region. Our goal was to focus on critical drivers that would be likely to result in observable and representative change across the landscape. We concluded that changes in C stocks would be most significant for transitions of forest to non-forest (rather than forest to forest only). Other studies have shown substantial differences in C stocks with stand age up to about 100 years, but less difference among conifer forest types (Bradford et al. 2008). Thus, our current modeling was focused on lodgepole pine, a representative forest type in the region. The model has to-date been additionally parameterized for warm-dry conifer (primarily Douglas fir (Pseudotsuga menziesii) forests in the GYE) and grasslands in the Lamar Valley; as validation data of C stocks in this ecosystem (Donato et al., in prep) become available, we will incorporate these vegetation types into our approach. However, to capture variation in recovery in lodgepole pine, we modeled two recovery pathways: fast (high pre-fire serotiny, more prevalent at elevations < 2400 m) and slow (low pre-fire serotiny, characteristic of elevations > 2400 m; Schoennagel et al. 2003). We expect that the slow recovery pathway will be representative of other vegetation types that lack serotinous cones and are likely to regenerate more slowly, for example, Douglas-fir or spruce-fir forests. All fires were prescribed to be highseverity, stand-replacing events.

To estimate current and future climate conditions, we used historical climate data and general circulation model (GCM) runs downscaled to the North American Land Data Assimilation system 1/8-degree latitude/longitude grid (12 x 12 km resolution). We used three AR4 GCMs (CCSM 3.0, CNRM CM 3.0, and GFDL CM 2.1) forced with the Intergovernmental Panel on Climate Change's (IPCC) Third Assessment Report: Special Report on Emissions Scenarios (SRES) A2 emissions pathway to generate a set of plausible climate futures for the western USA. The three GCMs used here are among a larger group that were assessed to adequately represent important aspects of western North American climate, including seasonality of temperature and precipitation and multiyear variability in sea surface temperatures (Daniel Cayan et al., unpublished). This particular subset of models was chosen because daily values for important variables such as temperature and precipitation were available for each GCM run, and these were required to force the hydrologic simulations used. The A2 emissions scenarios have been a frequent focus for impact assessment work because they were thought to represent a plausible high-end emissions scenario. However, for much of the past decade, emissions and atmospheric concentrations of greenhouse gases have exceeded the range of commonly used IPCC emissions scenarios, especially SRES A2. Consequently, given current and past emissions, the long lead times necessary to reduce future emissions, and the long atmospheric residence times of many greenhouse gases, climate projections using the SRES A2 CO_2 trajectory can no longer be considered a plausible representation of the future, nor representative of a "high" emissions scenario, but were used here given their availability.

Because current atmospheric concentrations exceed those represented in the SRES A2 scenarios, the climate scenarios used to derive our results can be considered conservative. GCM temperature and precipitation fields were downscaled using the constructed analogs method with bias correction (Maurer and Hidalgo 2008). Gridded historical climate data (temperature, precipitation, radiation, and wind speed) were obtained from Dr. Lettenmaier at the University of Washington and Dr. Maurer at the University of Santa Clara (Hamlet and Lettenmaier 2005). For the simulations of lodgepole pine forest, we used climate data from the grid centered on the Yellowstone Lake climate station, which is centrally located in the GYE and surrounded by lodgepole pine forest.

Productivity, mortality, and post-fire recovery were parameterized in CENTURY for lodgepole pine and warm-dry conifer trees based on empirical data (Tinker and Knight 2000, Pearson et al. 1987, Ryan and Waring 1992, Stump and Binkley 1993, Smithwick et al. 2009a, Kashian et al., in prep) and previous modeling efforts (Kashian et al. 2006, Smithwick et al. 2009b). The model was run in "savanna" mode, allowing for grass and tree competition for water and nutrients. For all simulations, we assumed a C3 grass parameterization available in CENTURY. Grass represented a small proportion of C stocks in mature stands but was a large and transient component of total C stocks for several years following fire. These large, transient pulses of post-fire grass were likely overestimated and future modeling efforts will be increasingly focused on grass dynamics in early post-fire years.

The fire-return intervals used in the CENTURY and landscape C modeling are based on understanding of the canopy seed bank and its influence on postfire regeneration. Specifically, Turner et al. (2007) demonstrated that lodgepole pine saplings are producing cones (including a few serotinous cones) by 15 years of age. Cone production begins at about the same age or even later in other conifer species of the GYE, and recent fires

that have burned young conifer forests (< 30 years) show minimal tree regeneration (Romme and Turner, personal observations). To encapsulate this rapid but variable trend in development of a canopy seed bank, we used a 30-year fire interval as a conservative estimate of the minimum FRI that would be followed by a very high likelihood of reforestation. If fire recurs at < 60 year intervals, seeds are present but in moderate quantities. By stand age of > 90 years, lodgepole pine trees are generally producing substantial numbers of cones. Although stands are likely to regenerate at different rates following a stand-replacing fire due to patterns in fire severity and pre-fire levels of serotiny (Turner et al. 2004), cone production is not limiting by age 90 years, and even initially sparse stands experience infilling (personal observations; Kashian et al. 2005, 2006). Empirical work along chronosequences of > 77 stands in the GYE (largely in Yellowstone National Park) indicated that most differences in N and C stocks occur at stand ages < 100 years (Smithwick et al. 2009a, Kashian et al., in prep).

Using these parameterizations for vegetation, climate, and fire, we performed a model experiment using a $4 \ge 4 \ge 2$ factorial design in which we considered four climate scenarios (historical plus the three GCMs), four fire-event pathways (no fires after 1988, a fire 90 years after the 1988 event, a fire 60 years after the 1988 event, and fires every 30 years after the 1988 event), and two recovery pathways (fast or slow).

Model output included live and dead pools (large wood, branches, leaves, coarse roots, fine roots), as well as active, slow, and passive pools in surface and soil, and relevant ecosystem processes such as respiration and decomposition. The time needed for forest C recovery following fire under both current and future climate scenarios was determined by comparing the time to recovery of pre-1988 C stocks (average of 1950-1987) of mature forest stands to that of both future periods (1970–2099) or averaged across the post-1988 simulation period (1989–2100). Total ecosystem C stocks varied little (< 10 percent) among future climate scenarios for a given fire-event pathway and were therefore averaged for the purposes of demonstrating the large differences in C stocks forecast among fire scenarios. Similarly, fast versus slow regeneration had a much smaller effect on total ecosystem C stocks than the timing of individual fire events. For simplicity, only fast recovery pathways from the CENTURY model are shown here.

Results

The modeled C storage between 1950 and 1987 in



Figure 1. Results from the CENTURY v.4.5 model simulations showing C stocks for total ecosystem carbon (g m-2; sum of live, dead, and soil pools) for four fire scenarios: No fires between 1989 and 2100, one fire 90 years following 1989; one fire at 60 years following 1989; fires every 30 years between 1989 and 2100. Data are averaged across 3 different climate scenarios (CCSM, CNRM, GFDL – see text for details).

lodgepole pine forests averaged 17,900 g C m⁻² (Figure 1). Simulation of the large fire in 1988 resulted in a 12 percent reduction in total C stocks from pre-fire levels-a relatively small reduction, largely due to the limited amount of biomass in the consumable pools (litter, foliage, fine branches) that was available to burn. Live pools were killed and converted to dead pools, but were not consumed. In the absence of subsequent fire (assuming historical fire-return intervals and therefore no fire in the post-1988 period), prefire C stocks were recovered by mid-century and, on average across the climate scenarios, continued to increase slowly through the end of the simulation. Under future climates and in the absence of subsequent fire, total C stocks were between 17 and 30 percent higher than historical C stocks. Increases in total ecosystem C under the future climates were stimulated by higher rates of net primary production of lodgepole pine with warmer temperature compared to the control simulation, although relative increases in productivity were less for the GFDL scenario (data not shown). For simulations assuming one fire event (90 year FRI), live and total C stocks were recovered following the 1988 fire before the 90-year fire event. However, for scenarios with FRIs at 60 or 30 years, live, dead, soil, and total C stocks did not recover prior to the next fire event, and total ecosystem C storage declined progressively through the future simulation period due to the lack of time for C recovery.

Averaged across the three future climate scenarios for the post-1988 fire period (1989–2099) and assuming fast recovery, total ecosystem C stocks at the end of the simulation period were 28 percent lower than historical stocks for the 60-year fire event and 66 percent lower than historical C stocks for the 30-year fire-interval scenario (Figure 2). In contrast, C stocks were within 5 percent of the pre-fire stocks for the 90-year fire-event scenario. These three fire scenarios suggest that fire events would need to be separated by 90 years or longer for recovery of C stocks, whereas more frequent fire events would lead to C losses relative to the historical average for mature forest stands. However, these simulations represent singular pathways of one or more fire events spaced exactly at 90, 60, or 30 years. In reality, fire sequences at any given location on the landscape will be best represented by a probabilistic distribution of fire events.

Discussion

Recent studies have emphasized the importance of understanding how changing climate and disturbance regimes—including wildfire—will alter the terrestrial C cycle (e.g., Kueppers and Harte 2005, CCSP 2007, 2008, Bond-Lamberty et al. 2007, Bowman et al. 2009, Frolking et al. 2009). Fire and recovery are fundamentally linked to regional C balance in forest landscapes, and other authors have suggested that terrestrial C sinks may be weakening (Fung et al. 2005, Canadell et al. 2007). We had suggested previously but had not demonstrated (e.g., Kashian et al. 2006, Smithwick et al. 2009b) what our current findings indicate: a threshold of fire-return interval beyond which current fire C stocks will not recover to their pre-fire levels. For lodgepole pine forests of the GYE, our simulations suggest this threshold may occur at a fire return interval of approximately 90 years.

Recent studies have documented an increase in the occurrence of large fires during the past few decades, with increases most pronounced in mid-elevation regions of the northern Rocky Mountains (Westerling et al. 2006, Morgan et al. 2008, Littell et al. 2009) due to increases in temperature and drier conditions. If fire frequency is reduced below the threshold identified here, forests will re-burn before they have re-accumulated the C lost in the previous fire. As a result, high-elevation Rocky Mountain



Figure 2. Carbon stocks (g m-2) for live, dead, soil, and total forest pools for historical (no fires between 1989 and 2100) and future fire (90-, 60-, or 30-year fire return interval (FRI)) under current or future climate. Future climate was averaged across three climate scenarios (see text).

forests could become C sources in the global C cycle, which could exacerbate global climate change. More frequent fires would also mean that mature and old-growth forests, which now cover large portions of high-elevation landscapes in the central and northern Rockies, will be increasingly replaced by young forests or even by nonforest vegetation during this century. The degree to which vegetation changes in response to warmer temperatures and longer growing seasons could potentially offset C losses is not known. For example, expansion of warm-dry conifer species or sagebrush steppe into non-vegetated areas could increase C stocks, whereas shifts from forest to non-forest vegetation would reduce C storage.

The capacity for fast post-fire regeneration of lodgepole pine from an aerial seedbank (serotinous cones) and the projected increase in lodgepole pine productivity under warmer climate conditions (Smithwick et al. 2009b) appear unlikely to counter reductions in fire-return interval that fall below 90 years. The magnitude of the shift in C balance due to shorter fire intervals in the future governs the ability of the forests to sequester C. Thus, the accuracy of future fire-climate models is critical for determining the degree to which C storage will be altered. Importantly, the specific timing of individual fires in a given location is likely to be more critical for determining the likelihood of forest recovery than projections of an average fire return interval in the future climate period. For example, net ecosystem production for Yellowstone National Park may be negative for about 30 years after the 1988 fires (Kashian et al. 2006), indicating even one or two additional fires as large as the 1988 fire would likely cause the GYE landscape to be a net C source over management timeframes. However, the specific time-path of the extreme fire years through the coming century must be estimated probabilistically.

Spatial variation in fuel, including potential shifts in dominant vegetation, is critical for understanding the spatial pattern in total ecosystem C stocks across the GYE landscape.

The magnitude of the shift in C balance will depend on the future distribution of forest and non-forest ecosystems across the landscape. A fundamental question is whether the current tree species and forest types will be able to persist in the GYE given projected climatic conditions and fire-return intervals. Some models suggest substantial changes in the geographic distribution of major tree species in the northern Rocky Mountain region, including the GYE (e.g., Bartlein et al. 1997, Coops and Waring 2011). For the work presented here, we assumed that the current dominant species were still present in

the GYE at the end of the twenty-first century for three reasons. First, our focus is on what will happen in the next 90 years; broad-scale biogeographic rearrangements like those depicted in Bartlein et al. (1997) probably will occur over a longer time period because of constraints on species migration, limitations to dispersal, etc. Second, we know that lodgepole pine persisted through variable climates and fire regimes during most of the Holocene (Whitlock et al. 2003), and the biogeographic models indicate that lodgepole pine and montane forests will still be present in the GYE a century from now even if their abundance is diminished (Bartlein et al. 1997, Rehfeldt et al. 2006). Finally, even if other conifer species replace the current dominants, the stand-level C dynamics probably will not be hugely different from what we are modeling for lodgepole pine; moreover, if future forests fail to regenerate altogether, then the tipping point from C sink to C source will be even more dramatic than our model predicts. However, the qualitative shift in fire regime predicted by our model underscores the importance of considering what vegetation types would be better suited to future climates in the GYE. Although projections of future vegetation condition were beyond the scope of the present project, it is an important priority for future work. To better forecast landscape C stocks for the *current* GYE, our next step is to parameterize CENTURY for additional ecosystem types that are present today. Few data exist for validation of C stocks for additional forest types in the northern Rocky region, although several related efforts are underway (e.g., Donato et al., in prep) that can inform this effort. Integration of these additional vegetation types and fire/climate responses will refine the sensitivity of our projected responses.

Whether we are likely to witness "tipping points" of C storage in the GYE during the twenty-first century, that is, sudden large and/or qualitative shifts in response to gradual or continuous changes in underlying driver variables, depends on the probabilistic projections of fire event pathways in conjunction with dynamic ecosystem modeling. The most striking potential tipping point identified here is that more frequent fire produces a qualitative shift in high-elevation Rocky Mountain forests from functioning as a C sink to a C source. Fire events that occur between 1988 and 2078 (90 years following the 1988 fire) have the potential to reduce C storage through the end of the simulation period (2099) if they re-burn forests that are < 90 years old. We had previously expected lodgepole pine ecosystems to be one of the most resilient Rocky Mountain forest types because of their historically long fire intervals and their capacity for rapid

recovery after fire (e.g., Kashian et al. 2006, Smithwick et al. 2009b). However, our analyses indicate that even lodgepole pine forests are vulnerable to projected climate change and the associated increase in burning during the twenty-first century. Ignoring the potential for future state changes, that is, shifts from forest to non-forest and from C sink to C source, and the spatial variation of these changes across heterogeneous landscapes, may lead to erroneous expectations for such values as biodiversity, productivity, and ecosystem C storage.

In conclusion, the modeling results shown here do not include projections of *future* vegetation distributions on the GYE resulting from future climate and fire, nor do the simulations describe well the site-specific time paths of actual fire events and recovery, which are likely to be heterogeneous over the landscape due to the interactions of ignition, fuels, topography, and microclimate. A major focus of our forthcoming papers will be to define path-specific trajectories of C fluxes that account for probabilistic fire events and variation in recovery rates for current vegetation types. Yet, our results do indicate that the C storage of GYE forests is extremely sensitive to projections in fire events over coming decades. Given recent projections of future fire-climate relationships (Littell et al. 2010, Westerling et al. 2006, Westerling et al., in prep), managers must be increasingly aware of the potential for novel vegetation-fire conditions, their heterogeneity across the landscape, and the potential for tipping points in critical ecosystem function such as C storage.

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References

- Balshi, M. S., A. D. McGuire, P. Duffy, M. Flannigan,
 D. W. Kicklighter, and J. Melillo. 2009.
 Vulnerability of Carbon Storage in North American
 Boreal Forests to Wildfires during the 21st Century.
 Global Change Biology 15:1491–1510.
- Bartlein, P. J., C. Whitlock, and S. L. Shafer. 1997. Future Climate in the Yellowstone National Park Region and its Potential Impact on Vegetation. *Conservation Biology* 11:782–792.
- Bond-Lamberty, B., S. D. Peckham, D. E. Ahl, and S. T. Gower. 2007. Fire as the Dominant Driver of Central Canadian Boreal Forest Carbon Balance. *Nature* 450:89.
- Bowman, D. M. J. S., J. K. Balch, P. Artaxo, W. J. Bond, J. M. Carlson, M. A. Chchrane, C. M. D'Antonio, R. S. DeFries, J. C. Doyle, S. P. Harrison, F. H. Johnston, J. E. Keeley, M. A. Krawchuk, C. A. Kull, J. B. Marston, M. A. Moritz, I. C. Prentice, C. I. Roos, A. C. Scott, T. W. Swetnam, G. R. Van Der Werf, and S. J. Pyne. 2009. Fire in the Earth System. *Science* 324:481–484.
- Bradford, J. B., R. A. Birdsey, L. A. Joyce, and M. G. Ryan. 2008. Tree Age, Disturbance History, and Carbon Stocks and Fluxes in Subalpine Rocky Mountain Forests. *Global Change Biology* 14:2882– 2897.
- Campbell, J., D. Donato, D. Azuma, and B. Law. 2007. Pyrogenic Carbon Emission from a Large Wildfire in Oregon, United States. *Journal of Geophysical Research-Biogeosciences* 112:G44014.
- Canadell, J. G., C. Le Quere, M. R. Raupach, C. B.
 Field, E. T. Buitenhuis, P. Ciais, T. J. Conway, N.
 P. Gillett, R. A. Houghton, and G. Marland. 2007.
 Contributions to Accelerating Atmospheric CO₂
 Growth from Economic Activity, Carbon Intensity, and Efficiency of Natural Sinks. *Proceedings of the* National Academy of Sciences 104(47):18866–18870.
- Climate Change Science Program (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 U.S. Climate Change Science Program and Subcommittee on Global Change Research. Asheville, North Carolina: National Oceanic and Atmospheric Administration, National Climatic Data Center.
- CCSP. 2008. The Effects of Climate Change on Agriculture, Land Resources, Water Resources, and Biodiversity. A report by the U.S. Climate

Change Science Program and Subcommittee on Global Change Research. Washington, D.C.: U.S. Environmental Protection Agency.

- Coops N. C., and R. H. Waring. 2011. A Process-Based Approach to Estimate Lodgepole Pine (*Pinus contorta Dougl*) Distribution in the Pacific Northwest under Climate Change. *Climatic Change* 105:313– 328.
- Frolking, S., M. G. Palace, D. B. Clark, J. Q. Chambers, H. H. Shugart, and G. C. Hurtt. 2009. Forest Disturbance and Recovery: A General Review in the Context of Spaceborne Remote Sensing of Impacts on Aboveground Biomass and Canopy Structure. *Journal of Geophysical Research* 114:G00E02.
- Fung, I. Y., S. C. Doney, K. Lindsay, and J. John. 2005. Evolution of Carbon Sinks in a Changing Climate. *Proceedings of the National Academy of Sciences* 102:11201–11206.
- Government Accountability Office (GAO). 2007. Climate change. Agencies Should Develop Guidance for Addressing the Effects on Federal Land and Water Resources. Report to Congressional Requesters GAO-07- 863. Washington, D.C.: GAO.
- Hamlet, A. F., and D. P. Lettenmaier. 2005. Producing Temporally Consistent Daily Precipitation and Temperature Fields for the Continental U.S. *Journal* of Hydrometeorology 6(3):330–336.
- Kashian, D. M., W. H. Romme, and M. G. Ryan. In preparation. Changes in Forest Carbon Stocks along Replicated Chronosequences in Yellowstone National Park, Wyoming, USA.
- Kashian, D. M., M. G. Turner, W. H. Romme, and C. G. Lorimer. 2005. Variability and Convergence in Stand Structure with Forest Development on a Fire-Dominated Landscape. *Ecology* 86:643–654.
- Kashian, D. M., W. H. Romme, D. B. Tinker, M. G. Turner, and M. G. Ryan. 2006. Carbon Storage on Landscapes with Stand-Replacing Fires. *Bioscience* 56:598–606.
- Kueppers, L. M., and J. Harte. 2005. Subalpine Forest Carbon Cycling: Short- and Long-Term Influence of Climate and Species. *Ecological Applications* 15:1984–1999.
- Kurz, W. A., G. Stinson, G. J. Rampley, C. C. Dymond, and E. T. Neilson. 2008. Risk of Natural Disturbances Makes Future Contribution of Canada's Forests to the Global Carbon Cycle Highly Uncertain. *Proceedings of the National Academy of Sciences* 105:1551–1555.
- Littell, J. S., D. McKenzie, D. L. Peterson, and A.

L. Westerling. 2009. Climate and Wildfire Area Burned in Western U. S. Ecoprovinces, 1916–2003. *Ecological Applications* 19:1003–1021.

- Littell, J. S., E. E. Oneil, D. McKenzie, J. A. Hicke, J. A. Lutz, R. A. Norheim, and M. M. Elsner. 2010. Forest Ecosystems, Disturbance, and Climatic Change in Washington State, USA. *Climatic Change* 102:129–158.
- Maurer, E. P., and H. G. Hidalgo. 2008. Utility of Daily Vs. Monthly Large-Scale Climate Data: An Intercomparison of Two Statistical Downscaling Methods. *Hydrology and Earth System Sciences* 12:551–563.
- Morgan, P., E. K. Heyerdahl, and C.E. Gibson. 2008. Multi-Season Climate Synchronized Forest Fires throughout the 20th Century, Northern Rockies, USA. *Ecology* 89:717–728.
- Parton, W. J., D. S. Schimel, C. V. Cole, and D. S. Ojima. 1987. Analysis of Factors Controlling Soil Organic Matter Levels in Great Plains Grasslands. *Soil Science Society of America Journal* 51:1173–1179.
- Pearson, J. A., D. H. Knight, and T. J. Fahey. 1987.
 Biomass and Nutrient Accumulation During Stand
 Development in Wyoming Lodgepole Pine Forests. *Ecology* 68:1966–1973.
- Rehfeldt, G. E., N. L. Crookston, M. V. Warwell, and J. S. Evans. 2006. Empirical Analyses of Plant-Climate Relationships for the Western United States. *International Journal of Plant Science* 167:1123– 1150.
- Romme, W. H., and D. G. Despain. 1989. Historical Perspective on the Yellowstone Fires of 1988. *Bioscience* 39:695–699.
- Running, S. W. 2006. Climate Change: Is Global Warming Causing More, Larger Wildfires? *Science* 313:927–928.
- Ryan, M. G., and R. H. Waring. 1992. Maintenance Respiration and Stand Development in a Subalpine Lodgepole Pine Forest. *Ecology* 73:2100–2108.
- Schoennagel, T., M. G. Turner, and W. H. Romme. 2003. The Influence of Fire Interval and Serotiny on Postfire Lodgepole Pine Density in Yellowstone National Park. *Ecology* 84:2967–2978.
- Schoennagel, T., T. T. Veblen, and W. H. Romme. 2004. The Interaction of Fire, Fuels, and Climate across Rocky Mountain Forests. *Bioscience* 54:661–676.
- Schoennagel, T., M. G. Turner, and E. A. H. Smithwick. 2008. Landscape Heterogeneity Following Large Fires: Insights from Yellowstone National Park, USA. *International Journal of Wildland Fire* 17:742–753.

Smithwick, E. A. H., D. M. Kashian, M. G. Ryan, and M. G. Turner. 2009a. Long-Term Nitrogen Storage and Soil Nitrogen Availability in Post-Fire Lodgepole Pine Ecosystems. *Ecosystems* 12:792–806.

Smithwick, E. A. H., M. G. Ryan, D. M Kashian, W.
H. Romme, D. B. Tinker, and M. G. Turner. 2009b.
Modeling the Effects of Fire and Climate Change on Carbon and Nitrogen Storage in Lodgepole Pine (*Pinus contorta*) Stands. *Global Change Biology* 15:535–548.

Stump, L. M., and D. Binkley. 1993. Relationships between Litter Quality and Nitrogen Availability in Rocky Mountain Forests. *Canadian Journal of Forestry Resources* 23:492–502.

Tinker, D. B., and D. H. Knight. 2000. Coarse Woody Debris Following Fire and Logging in Wyoming Lodgepole Pine Forests. *Ecosystems* 3:472–483.

Turner, M. G. 2010. Disturbance and Landscape Dynamics in a Changing World. *Ecology* 91:2833– 2849.

Turner, M. G., W. H. Romme, and D. B. Tinker. 2003. Surprises and Lessons from the 1988 Yellowstone Fires. *Frontiers in Ecology and the Environment* 1:351–358.

Turner, M. G., W. H. Romme, R. H. Gardner, and W. H. Hargrove. 1997. Effects of Fire Size and Pattern on Early Succession in Yellowstone National Park. *Ecological Monographs* 67:411–433.

Turner, M. G., D. M. Turner, W. H. Romme, and D. B.

Tinker. 2007. Cone Production in Young Post-Fire *Pinus contorta* Stands in Greater Yellowstone (USA). *Forest Ecology and Management* 242:119–126.

Turner, M. G., D. B. Tinker, W. H. Romme, D. M. Kashian, and C. M. Litton. 2004. Landscape Patterns of Sapling Density, Leaf Area, and Aboveground Net Primary Production in Post-Fire Lodgepole Pine Forests, Yellowstone National Park (USA). *Ecosystems* 7:751–775.

Tymstra, C., M. D. Flannigan, O. B. Armitage, and K. Logan. 2007. Impact of Climate Change on Area Burned in Alberta's Boreal Forest. *International Journal of Wildland Fire* 16:153–160.

Westerling, A. L., H. G. Hidalgo, D. R. Cayan, and T. W. Swetnam. 2006. Warming and Earlier Spring Increase Western U.S. Forest Wildfire Activity. *Science* 313:940–943.

Westerling, A.L., M.G. Turner, E. A. H. Smithwick,
W. H. Romme, M.G. Ryan, and K. Lubetki,
"Continued Warming Could Transform Greater Yellowstone Fire Regimes by Mid-21st Century. Proceedings of the National Academy of Sciences," in review, 2011.

Whitlock, C., S. L. Shafer, and J. Marlon. 2003. The Role of Climate and Vegetation Change in Shaping Past and Future Fire Regimes in the Northwestern US and the Implications for Ecosystem Management. *Forest Ecology and Management* 178:5– 21.