

Modeling the effects of fire and climate change on carbon and nitrogen storage in lodgepole pine (*Pinus contorta*) stands

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Abstract

The interaction between disturbance and climate change and resultant effects on ecosystem carbon (C) and nitrogen (N) fluxes are poorly understood. Here, we model (using CENTURY version 4.5) how climate change may affect C and N fluxes among mature and regenerating lodgepole pine (*Pinus contorta* var. *latifolia* Engelm. ex S. Wats.) stands that vary in postfire tree density following stand-replacing fire. Both young (postfire) and mature stands had elevated forest production and net N mineralization under future climate scenarios relative to current climate. Forest production increased 25% [Hadley (HAD)] to 36% [Canadian Climate Center (CCC)], compared with 2% under current climate, among stands that varied in stand age and postfire density. Net N mineralization increased under both climate scenarios, e.g., +19% to 37% (HAD) and +11% to 23% (CCC), with greatest increases for young stands with sparse tree regeneration. By 2100, total ecosystem carbon (live + dead + soils) in mature stands was higher than prefire levels, e.g., +16% to 19% (HAD) and +24% to 28% (CCC). For stands regenerating following fire in 1988, total C storage was 0–9% higher under the CCC climate model, but 5–6% lower under the HAD model and 20–37% lower under the Control. These patterns, which reflect variation in stand age, postfire tree density, and climate model, suggest that although there were strong positive responses of lodgepole pine productivity to future changes in climate, C flux over the next century will reflect complex relationships between climate, age structure, and disturbance-recovery patterns of the landscape.

Keywords: CENTURY, serotiny, tree density, Yellowstone

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Introduction

Changes in climate and disturbance frequency are likely to affect future terrestrial ecosystem productivity in temperate coniferous forests but the relative effects of disturbance and climate are uncertain (Schimel *et al.*, 1997; Kurz & Apps, 1999; Dale *et al.*, 2001). The landscape mosaic of forest age and productivity is rarely considered, potentially affecting the net landscape

response to disturbance events and climate change. Kurz & Apps (1999) were among the first to assess the importance of the landscape age mosaic on regional carbon (C) storage. Recently, model projections by Albani *et al.* (2006) showed that future C storage in the eastern United States (US) to year 2100 will be determined largely by forest regrowth following harvesting, and Vetter *et al.* (2005) suggested legacy age-class distributions accounted for 17% of the C sink in coniferous forests in Europe. In addition, variation in stand density may contribute up to 20% of the error in age and net primary productivity (NPP) relationships

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(Chen *et al.*, 2002), suggesting that postdisturbance regeneration and stand structure may affect future C flux. Together, these studies suggest that assessments of future C balance depend on understanding the range in forest responses to disturbances and future climate. Here, we present modeling scenarios to estimate changes in C and nitrogen (N) storage in response to predicted changes in climate among mature and regenerating forest stands that vary in tree density following stand-replacing fire. We additionally characterize the extent to which fire frequencies would have to change to alter net C balance under current climate.

Infrequent, stand-replacing fires characterize the disturbance regime in most forested areas of Yellowstone National Park, located in the northwestern corner of Wyoming, in the western US (Romme & Despain, 1989). Mean fire return intervals (FRIs) range from 192 ± 90 (mean ± 1 SD) at low elevations (<2300 m) and 276 ± 87 at high elevations (>2300 m) (Schoennagel *et al.*, 2003). Like other large, infrequent disturbances, these stand-replacing fires initiate heterogeneity in ecosystem function (Turner *et al.*, 1997, 2003, 2004; Foster *et al.*, 1998), providing a natural setting for exploring responses to disturbance across broad scales. For example, in 1988, stand-replacing fire burned $>35\%$ of Yellowstone National Park (YNP) (approximately 174 000 ha). The 1988 fire season was a result primarily of severe climate conditions rather than variation in fuel abundance, fuel structure, or stand age (Habeck & Mutch, 1973; Romme & Despain, 1989; Schoennagel *et al.*, 2005). Most of the fires were severe surface, in which dead needles remained on the trees for 1–2 years following fire, or crown fires, in which canopy needles were consumed; in both cases, the tree canopy was killed and the shallow organic matter on the forest floor was consumed. Establishment of lodgepole pine (*Pinus contorta* var. *latifolia* Engelm. ex S. Wats.) seedlings under these stand-replacing fires was a function of fire severity (severe-surface or crown), but was dominated by patterns of serotiny across the park. Postfire sapling density ranged six orders of magnitude following the fire and total aboveground (tree, shrub, and herbaceous) NPP in 1999 ranged from 0.04 to $15.12 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ (Turner *et al.*, 2004). Variability in basal area increment and leaf area index (LAI) may persist for at least 125 years following fire (Kashian *et al.*, 2005a) and variation in stand density may persist for up to 200 years (Kashian *et al.*, 2005b). Thus, following the 1988 fires, landscape patterns in stand age and tree density were altered that have the potential to affect ecosystem function for over a century. However, patterns in forest structure and stand age are rarely considered in estimates of future C flux across landscapes (Euskirchen *et al.*, 2002).

Understanding the impact of stand-replacing disturbances on C flux is critical given that fires are likely to increase in frequency and severity. Climate change is expected to reduce mean FRIs in temperate and boreal coniferous forests of North America. Flannigan *et al.* (2005) suggest that the area burned in Canada may increase 74–118% by the end of the century in a $3 \times \text{CO}_2$ scenario, potentially resulting in an increase of annual burned area in Canada from 1.8 Mha presently to >3 Mha in future climates. The increase in area burned across the conterminous US is predicted to increase from 4% to 31% between 1995 and 2100 (Bachelet *et al.*, 2003). In particular, midelevation forests in the western US exhibited increased large-wildfire frequency in the mid-1980s in response to increased spring and summer temperatures and an earlier spring snow melt (Westerling *et al.*, 2006). Specifically, YNP is centered on the subalpine elevation range highlighted by Westerling *et al.* (2006) as having experienced the greatest vulnerability to fire due to altered climate patterns. Thus, understanding the interaction between large fire events, climate and postfire patterns in stand structure and age in YNP may have broad implications for understanding fire and climate interactions in other parts of the western US.

To understand forest responses to fire and climate we asked two questions. First, how will climate change over the next century affect future C storage and N availability in both mature (i.e., unburned) and young (i.e., burned) stands, and, specifically, how does variability in tree density among young stands affect the response to altered climate? We used two projected climate scenarios to forecast C and N storage and fluxes for both low and high density forest stands recovering from fire in 1988 and compared results against simulations using a Control (i.e., current) climate. In this question, and throughout the paper, we account for effects of altered temperature and precipitation to year 2100 but the effects of altered CO_2 concentrations on plant production were not simulated. Second, we asked, how does shortening the FRI affect C storage and N availability? We compared C and N fluxes for two FRIs and for sparse and dense stand recovery. Because the average FRI for YNP exceeds the length of the available climate projection dataset, modeling transient effects of climate with repeated fire events in the future period was beyond the scope of the paper and current climate conditions were used to answer this question. The model was parameterized for mature lodgepole pine forests in the region and results were compared with the literature. In addition, we compared our results to published data for YNP on projected trajectories of C storage in sparse and dense stands (Kashian *et al.*, 2006).

Materials and methods

Study area

Yellowstone National Park is located on high-elevation forest plateaus ranging in elevation from 1900 to 2900 m (Romme & Turner, 1991). Approximately 80% of the park is dominated by lodgepole pine but subalpine fir [*Abies lasiocarpa* (Hook.) Nutt.], Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), whitebark pine (*Pinus albicaulis* Engelm.) and Douglas-fir (*Pseudotsuga menziesii* Franco.) may be locally abundant. Annual average precipitation is 61.9 cm (9/1978–9/2005 Normals, Western Regional Climate Center, Old Faithful). Average total snow fall is 541.8 cm, with an average depth of 33.0 cm. Average monthly maximum temperature is 9.6 °C (–2.0 °C in January and 23.6 °C in July) and average monthly minimum temperature is –7.4 °C (–17.8 °C in January and 3.9 °C in July). Most soils in YNP are derived from relatively infertile rhyolitic substrates, intermixed with small areas of less infertile soils derived primarily from andesitic substrates and lake-bottom sediments.

The CENTURY model

CENTURY (Parton *et al.*, 1987) is a deterministic ecosystem model that simulates the flow of nutrients and water among vegetation and soil compartments, and which includes the effects of management and/or natural disturbances such as fire. We used version 4.5 for all simulations. Here, we present new parameterization of the model for lodgepole pine forests. Allocation parameters for leaf, fine branch, large wood, coarse root, and fine root pools were calculated from values in the literature by dividing pool-specific NPP estimates by total NPP (Table 1). Production allocation patterns were switched from young to mature allocation at 30 years. Optimum temperature for tree production was set to 18 °C (Scott, 1970; Dykstra, 1974). Maximum projected LAI was assumed to be 4 m² m^{–2} (Litton, 2002; Kashian *et al.*, 2005a). Version 4.5 of CENTURY allows for C:N ratios of leaves, fine roots, fine branches, large wood, and coarse wood to vary from minimum to maximum rates; however, there is limited information on the range of C:N ratios for lodgepole pine forests in YNP and we relied on results from Pearson *et al.* (1987) to calculate a constant value for each pool. In version 4.5, N inputs are calculated as a function of precipitation and were not used to parameterize productivity rates. Wood decay constants were estimated from the literature (Fahey, 1983; Tinker & Knight, 2000, 2001; Kueppers *et al.*, 2004). Variability in density following the 1988 fires was attributed largely to variation in

Table 1 Lodgepole pine tree and site parameters used in CENTURY

Latitude/longitude	44.36°/110.3°
Soil characteristics	
Sand (%)	55
Silt (%)	30
Clay (%)	15
Rock (%)	25
Bulk density	0.96
pH	5.10
C/N ratios*	
Foliage C/N	51
Fine root C/N	175
Large wood C/N	1778
Coarse root C/N	382
Fractional allocation parameters (stand age > 30 years)†	
Foliage	0.48
Fine roots	0.17
Fine branch	0.05
Large wood	0.27
Coarse root	0.03
Mortality rates (per year)‡	
Foliage	0.04 (per month)
Fine roots	0.071
Fine branches	0.0036
Large wood	0.00070
Coarse root	0.00043

*Pearson *et al.* (1987).

†Arthur & Fahey (1992), Smith & Resh (1999), Litton (2002); assumed fine roots were 27% of production allocation.

‡Litton (2002).

prefire stand serotiny (Turner *et al.*, 1997), a parameter not available in the model. Therefore, variability in postfire tree density was parameterized by modifying the rate of postfire biomass accumulation by altering competition for light and resources between grasses and trees using the variable, SITPOT. Carbon accumulation curves were sensitive to this variable, allowing the comparison of carbon trajectories of sparse and dense stands to published estimates (see 'Model corroboration').

Fire removes user-specified fractions of live tree (leaves, fine branches, and large wood), root, and dead wood pools, and modifies postfire surface nutrient concentrations (Table 2). Fire-killed trees were immediately transferred to downed wood pools, so postfire snags were not simulated. Ninety percent of snags fall within 15 years (Tinker & Knight, 2000), suggesting the effect of standing vs. fallen wood decay rates is minimal (mean fire interval of 172 or 293 years). However, because snags may represent 67% of total dead wood in burned stands (Tinker & Knight, 2000), we modified

Table 2 User-specified parameters used to simulate fire disturbance in CENTURY based on published estimates in the literature (Tinker & Knight, 2000; Kashian *et al.*, 2006)

Parameters	Values
Fraction of live tree pools removed by fire	
Live leaves	0.90
Live fine branches	0.90
Live large wood	0.05
Live fine root	0.00
Live coarse root	0.00
Fraction of dead tree and litter pools removed by fire	
Standing dead	0.25
Litter	0.90
Dead fine branches	0.90
Dead large wood	0.10
Fraction of N returned to system following fire	
Live leaves	0.30
Fine branches	0.30
Large wood	0.30

decay rates of dead wood to allow for slower decomposition.

The simulations

Historical (1895–1993) climate in YNP was generated by climate data that were spatially extrapolated from observed station data (Daly *et al.*, 1994). The climate data were developed for the conterminous US on a grid consisting of cells that were $0.5^\circ \times 0.5^\circ$ (latitude/longitude), and we used the grid cell corresponding to the location of the National Climatic Data Center climate station at Old Faithful ($44^\circ 27'$ latitude, $110^\circ 50'$ longitude). To bring the model into equilibrium, we used mean climate data from the detrended climate series (Kittel *et al.*, 2004).

Fire years were determined a priori from a Poisson distribution of FRIs for low and high elevation lodgepole pine forests (Schoennagel *et al.*, 2003). Mean FRI were 172 and 293 years, which fall within the confidence intervals reported by Schoennagel *et al.* (2003). Given the relatively long fire intervals, a 5000-year baseline simulation was required to ensure equilibrium conditions. Following the 5000-year baseline simulation, the model was run with historical climate (1895–1993) (Kittel *et al.*, 2004). During this historical period, we simulated young stands that burned in 1988 as well as mature stands that did not experience fire in 1988. Future climate conditions (1994–2100) were specified using the (1) Hadley2 (HAD) or (2) Canadian Climate Center 1 (CCC) climate models, or (3) a Control climate that represented 'current' climate conditions (average climate of years 1978–1987). Average annual precipita-

tion in YNP is predicted to increase 21 cm (HAD) to 32 cm (CCC) (Fig. 1a and b). Most increases (>4 cm month $^{-1}$) are expected in February, March, October, November, and December, with smaller changes from May to September (-2.0 to 3 cm month $^{-1}$). Average annual maximum temperatures are expected to increase 2.8 °C (HAD) to 4.3 °C (CCC) (Fig. 1c and d). January maximum temperatures are expected to increase 3.5 °C (HAD) to 9.1 °C (CCC). July maximum temperatures are expected to decrease 0.4 °C (CCC) or increase 3.8 °C (HAD). Average annual minimum temperature is expected to increase 4.7 °C (HAD) to 9.1 °C (CCC) (Fig. 1e and f). The most dramatic increase is predicted for minimum January temperatures which are predicted to increase 5.8 °C (HAD) to 11.1 °C (CCC).

Calculations

To quantify the relative effect of climate change on young (with sparse or dense recovery following fire in 1988) and mature stands (Question 1), we compared C and N storage under the three future climate scenarios (HAD, CCC, Control; average of years 2091–2100) minus that in the current period (average of years 1978–1987). To explore the effect of reducing fire intervals using current climate (Question 2), we compared C and N storage from the last 1000 years of the baseline simulation for stands with sparse and dense recovery for the two FRIs. Average stand ages were 120 and 176 years, for 172 and 293 intervals, respectively.

Results

Model corroboration

Model estimates of C storage under equilibrium climate and historical fire frequencies were similar to published values for mature forests (Table 3). Live C ranged between 8650 and 11 799 g C m $^{-2}$ and dead C ranged between 2819 and 3551 g C m $^{-2}$, depending on the fire frequency and postfire density. Tree aboveground C (leaves, fine roots, and large wood) was 47–51% of total ecosystem C (TEC), within the range reported by Kueppers & Harte (2005) of 28–64% among subalpine forests in Colorado. Large dead wood C was 13–14% of TEC, at the middle of range (2–28%) reported by Kueppers & Harte (2005). Productivity ranged from 336 to 373 g C m $^{-2}$ yr $^{-1}$, within the range of published values for mature lodgepole pine stands in Wyoming (Table 3).

Model estimates of live pool N ranged from 18.5 to 21.9 g N m $^{-2}$, comparable to published estimates (Table 3). Dead pool N ranged from 5.8 to 7.2 g N m $^{-2}$, just below the range reported by Fahey *et al.* (1985). Soil N was also lower than reported by Fahey *et al.* (1985) but

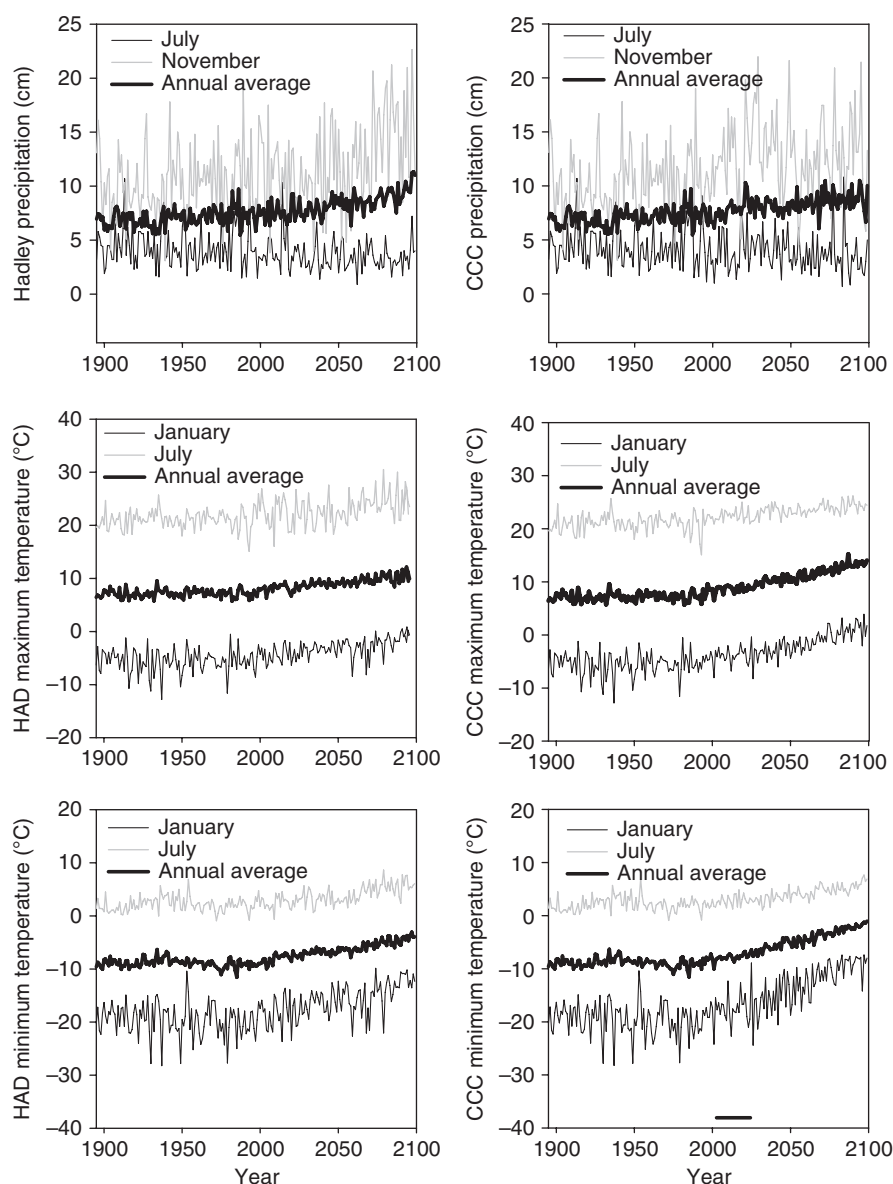


Fig. 1 Climate data (Kittel *et al.*, 2004) used in the simulations between years 1985 and 2100 (a) Hadley (HAD) precipitation (cm), (b) CCC precipitation (cm) (c) HAD maximum temperature ($^{\circ}\text{C}$), (d) Canadian Climate Center (CCC) maximum temperature ($^{\circ}\text{C}$), (e) HAD minimum temperature ($^{\circ}\text{C}$), (f) CCC minimum temperature ($^{\circ}\text{C}$).

soil N averaged 91% of total ecosystem N, similar to other studies (Knops *et al.*, 2002; Page-Dumbroese & Jurgensen, 2006). Soil net N mineralization averaged $3.5 \text{ g N m}^{-2} \text{ yr}^{-1}$, comparable to that reported by Romme & Turner (2004) for a 120-year old lodgepole forest.

Trajectories of live C accumulation for young stands were similar to those predicted by Kashian *et al.* (2006) (Fig. 2). Specifically, all CENTURY simulations were within the envelope of predictions made by Kashian *et al.* (2006) for live C accumulation in sparse and dense stands. Compared with simulations by Kashian *et al.*

(2006), CENTURY may underestimate live C storage for stands with dense regeneration between 50 and 200 years and may slightly overestimate C storage for stands with sparse regeneration, thus providing a conservative estimate for the influence of postfire tree density on C and N storage.

Question 1: climate, stand age, and tree density

Trajectories of postfire forest C production depended on whether stands regenerated sparsely or densely, with sparse stands having both lower and more variable

Table 3 Comparison of observed data from mature lodgepole pine forests relative to model-simulated baseline conditions (average of last 1000 years of a 5000 simulation) for Poisson mean fire intervals (293 or 172) for sparse or dense stands

Variable	Simulated				Observed
	172		293		
	Dense	Sparse	Dense	Sparse	
Net primary productivity (NPP) (g C m ⁻² yr ⁻¹)	373	336	373	349	288–420*
Live C (g C m ⁻²)					
Leaves	254	248	254	250	300†
Fine branches	394	320	402	352	431†
Large wood	7991	6294	8909	7815	7909†
Coarse roots	2029	1666	2099	1874	2148 (1913–2697)†
Fine roots	135	123	135	127	68 (57–82)†
Total live C	10 803	8650	11 799	10 419	10 869 (10 634–11 418)
Dead wood C (g C m ⁻²)					
Fine branches	491	399	503	444	868‡
Large wood	2396	1968	2494	2226	1878‡
Coarse roots	547	452	555	498	548‡
Total dead wood C	3434	2819	3551	3168	3294‡
Soil organic matter C (g C m ⁻²)					
	2915	2726	2943	2833	3376 (2366–4123)‡
Total system C	17 153	14 196	18 293	16 420	17 539 (16 294–18 835)
Live N (g N m ⁻²)					
Leaves	5.0	4.9	5.0	4.9	5.8–6.8§, 4.5–7.4¶
Fine branches	3.4	2.8	3.5	3.0	5.7–6.0§, 2.9–6.2¶
Large wood	7.0	5.8	7.2	6.4	5.4–5.7§
Coarse roots	5.3	4.4	5.5	4.9	0.5–0.8§, 8.6–12.0¶
Fine roots	0.8	0.7	0.8	0.7	3.8–4.0§, 0.69–0.98¶
Total live N	21.5	18.5	21.9	20.0	21.2–23.3§, 16.7–26.6¶
Dead wood N (g N m ⁻²)					
Fine branches	4.2	3.4	4.3	3.8	
Large wood	1.4	1.1	1.4	1.3	
Coarse roots	1.4	1.2	1.5	1.3	
Total dead wood N	7.0	5.8	7.2	6.4	8.6–16.7§
Soil organic matter N (g N m ⁻²)					
	287.0	270.1	289.7	279.8	315–860§
Total system N	315.5	294.3	318.8	306.2	345–900

*Smith & Resh (1999); low value for 260-year old stand, high value for 100-year old stand.

†Live pool C equal to the average of mature stands ($n = 4$) (Litton, 2002).

‡Dead wood C and soil organic matter C pools equal to the average of mature stands ($n = 4$) (Litton, 2002).

§Fahey *et al.* (1985); live coarse root N is for lateral roots > 2 mm.

¶Live N pools were calculated from % N values (Litton, 2002; Metzger *et al.*, 2006) multiplied by pool biomass (Litton, 2002).

production following fire (Fig. 3). By 2100, forest C production was independent of stand age or postfire density. Instead, relative changes in forest C production depended on the climate model that was used. For example, C production increased +2% under current climate, +25% under the HAD scenario (376–500 g C m⁻² yr⁻¹) and +36% under the CCC scenario (376–589 g C m⁻² yr⁻¹).

For mature stands, TEC storage (live + dead + soil) increased under future climate scenarios (Fig. 4).

Increases were greatest under both the HAD and CCC climate scenarios. TEC increased +16% to 19% for the HAD scenario and +24% to 28% for the CCC scenario. TEC increased +6% to 10% under the current climate, presumably because these stands were only 120 years old in 1988 and thus continued to accumulate C throughout the simulation. The range in response among mature stands within a given climate scenario reflects legacy C storage from the baseline simulations when stands regenerated sparsely or densely in

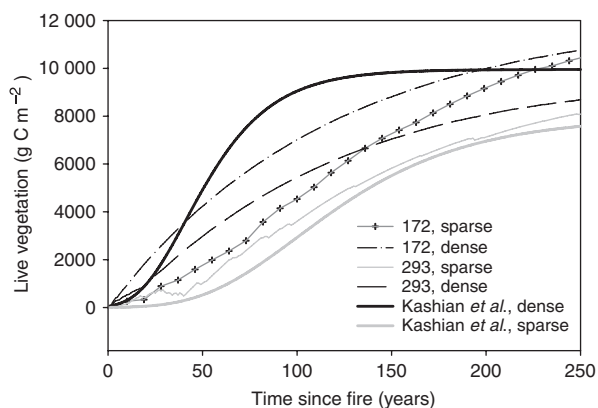


Fig. 2 Comparison of CENTURY trajectories of regeneration for sparse and dense stands compared with published estimates (Kashian *et al.*, 2006).

response to fire. For young, regenerating stands (i.e., those that burned in 1988), TEC in the future period was generally lower than the prefire years. Under the Control climate, TEC was 20–37% lower by 2100, depending on postfire stand density. Under the HAD climate, TEC was –5% to 16% lower. However, under the CCC scenario, TEC was +0% to 9% higher in the future period. Thus, the increased productivity under the CCC scenario resulted in a net C sink by 2100 in young stands, whereas both the HAD scenario and the Control climate scenario resulted in stands that were net sources of C by 2100.

Increases in live and dead wood C were largely responsible for the increases in total C in mature stands. Live wood C increased +8% to 12% under the current climate, +22% to 26% under the HAD climate, and +32% to 36% under the CCC climate (Fig. 5). For young, regenerating stands, live wood C remained –30% to 61% lower under the current climate and –5% to 23% lower under the HAD scenario, but was +0% to 13% higher under the CCC scenario. For dead wood C, mature stands had higher dead wood C by 2100 (+4% to 14%) and young stands had lower amounts (–13% to 50%), despite a large pulse of dead wood immediately following the fire event (Fig. 5).

Soil net N mineralization averaged 3.2 g N m⁻² yr⁻¹ in the prefire period and either remain unchanged or increased in the future period (Fig. 6). In mature stands, soil net N mineralization did not increase under the Control climate, but increased slightly with the future climate scenarios [to 3.6 g N m⁻² yr⁻¹ (HAD) and to 3.9 g N m⁻² yr⁻¹ (CCC)]. In young (burned) stands, there was a short-term increase in net N mineralization. By 2100, net N mineralization was only slightly higher, up to 3.4 g N m⁻² yr⁻¹ under the Control climate, but was between 14% and 39% higher for the HAD and

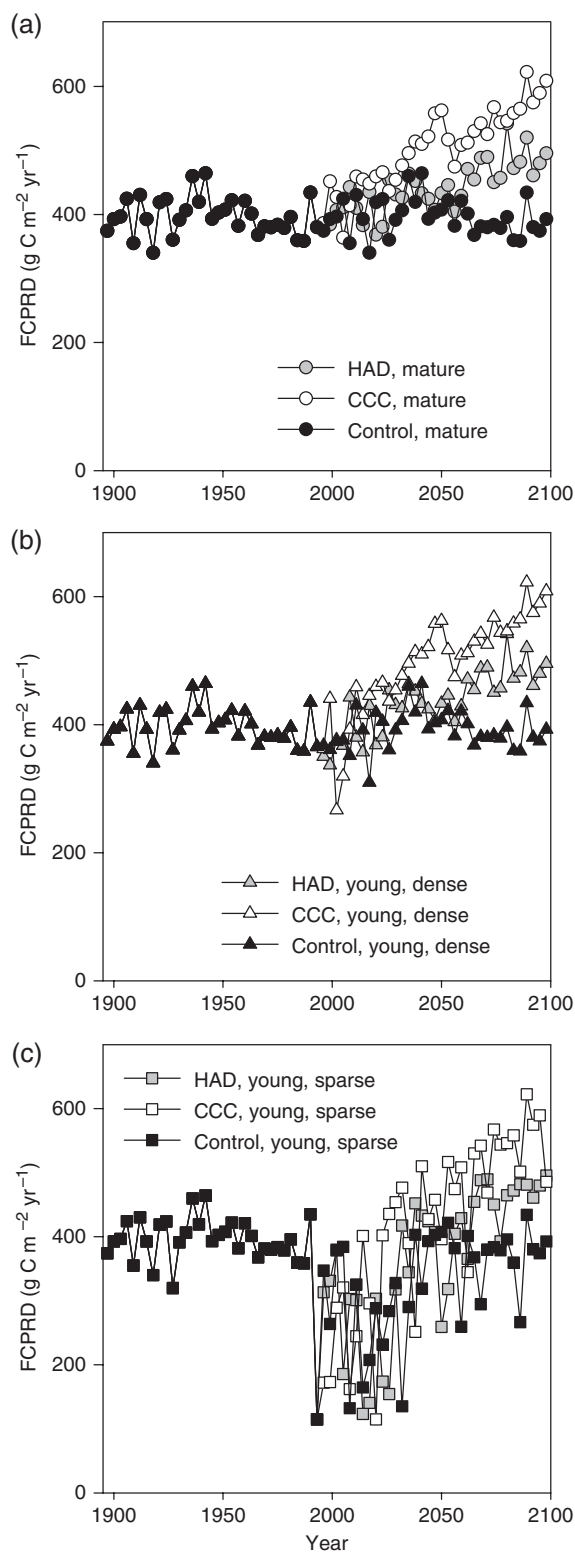


Fig. 3 Lodgepole pine simulated forest C production (FCPRD) (g C m⁻²) for (a) mature, (b) dense, or (c) sparse young stands regenerating following stand-replacing fire in 1988 for the three climate scenarios [Canadian Climate Center (CCC), Hadley (HAD), or Control (current climate)].

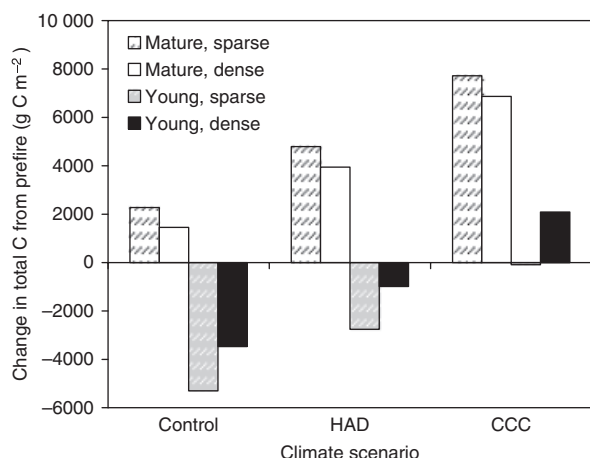


Fig. 4 Percent difference in total C storage (live + dead + soil) between future and current period for the Hadley (HAD), Canadian Climate Center (CCC), and Control (i.e., current) climate scenarios. Positive differences reflect net C gain by the ecosystem relative to the atmosphere whereas negative differences reflect net C loss.

CCC climate, with the highest net N mineralization ($5.0 \text{ g N m}^{-2} \text{ yr}^{-1}$) in the CCC climate with sparse regeneration.

Total ecosystem N was unchanged ($\pm 1\%$) under all future simulations due to the large storage of N in the soil, which was relatively resistant to variation in climate, stand age, or tree density. Relative changes in live and dead wood N pools equaled those of C because C:N ratios did not change. In absolute terms, the greatest increase in N storage was in mature stands with the CCC climate, which resulted in an increase of 3.4 g N m^{-2} . The greatest reduction in N was in young stands with sparse regeneration under the Control climate, which resulted in a net loss of 2.3 g N m^{-2} relative to the prefire period.

In 1989, 1 year following fire, TEC was 7.6% lower than in 1988, supporting the idea of low net C losses following stand-replacing fire (Tinker & Knight, 2000; Kashian *et al.*, 2006). Fire also resulted in minimal net N losses ($<0.04\%$, or $<5.8 \text{ g N m}^{-2}$; difference in total ecosystem N between 1988 and 1989). Thereafter, decomposition losses exceeded productive gains such that, under the CCC climate, net ecosystem carbon balance (NECB) was negative for >30 years following the 1988 fire event (Fig. 7). Then, NECB remained positive through the end of the simulation.

Despite consistently positive NECB by 2050, recovery of prefire C stocks with the CCC climate required between 95 and 109 years for dense and sparse stands, respectively. With the HAD and Control climate, prefire C stocks were not recovered by year 2100 (112 years following fire in 1988) and were between 74% and 96%

of prefire C storage. Using the average NECB between 2050 and 2100, we calculated potential increases in C stocks beyond 2100. This calculation indicated that prefire C stocks would be reached between 194 and 219 years following fire for the Control simulations, which is very similar to the 230 years estimated by Kashian *et al.* (2006). With the HAD climate, we calculated that 1988 prefire C stocks would be recovered 133–136 years following fire.

Question 2: fire frequency and tree density

Total ecosystem C storage varied 22% among simulated FRIs and postfire stand densities under current climates. The long FRI (average = 293 years) and dense tree regeneration resulted in the greatest total C and N stores among the simulations (Table 3), while the short FRI (average = 172 years) and the sparse tree regeneration resulted in the least C and N storage.

Soil organic matter C and N were resilient to changes in FRI and densities specified by the model, changing 7.4% and 7.7%, respectively, among FRIs and densities. Because soil N was $>90\%$ of total ecosystem N, the maximum difference in total N was 6.8% among FRIs and densities. Total N in live and dead biomass varied 16% and 20% among scenarios, with greater N storage in stands of longer FRI and higher postfire tree density.

Discussion

Our modeling simulations showed a strong positive effect of climate on future C production in both young (e.g., regenerating) and mature stands. Importantly, our results suggest that productivity responses to fire may be faster with climate warming scenarios than with the current climate. However, because of substantial C losses by the fire event, net changes in stand C balance by the year 2100 depended on the interaction between postfire tree density and the climate scenario that is chosen. The results support earlier hypotheses that the Yellowstone landscape is relatively resilient to reductions in fire frequency and that changes in stand density following disturbance are likely to have a large effect on net C balance (Kashian *et al.*, 2006).

Globally, there is a general trend toward increased forest productivity under altered climates, although both site-specific influences and effects of disturbances are unclear (Loustau *et al.*, 2005; Boisvenue & Running, 2006; Morales *et al.*, 2007). Recent analysis of lodgepole pine in central British Columbia suggests that lodgepole pine productivity may increase 7% with a 2°C increase in mean annual temperature, and compared with other commercially important species in British Columbia, lodgepole pine may show the greatest positive response

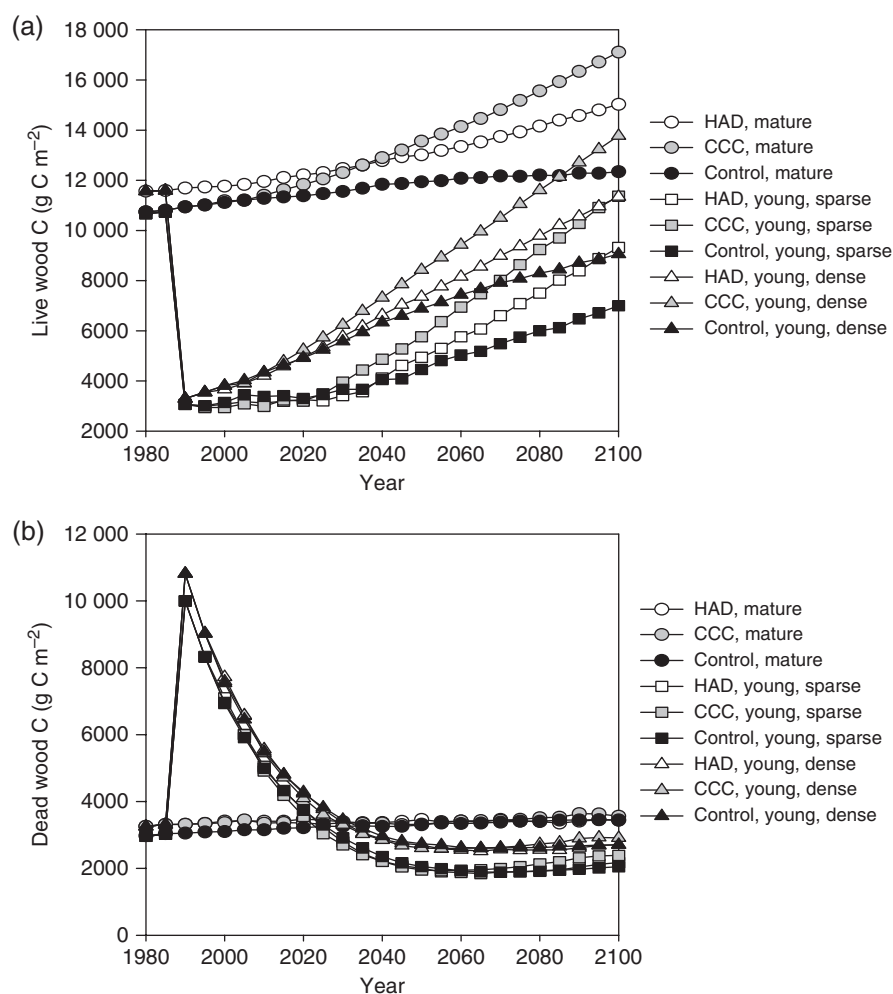


Fig. 5 Simulated (a) live C stocks or (b) dead C stocks (gC m^{-2}) for mature or young (dense or sparse) lodgepole pine stands regenerating following stand-replacing fire in 1988 under the three climate scenarios [Hadley (HAD), Canadian Climate Center (CCC), Control (current climate)].

to climate change (Nigh *et al.*, 2004). Tree-ring analysis has shown that lodgepole pine growth has been limited historically by summer moisture stress but stimulated by warm autumn temperatures (Villalba *et al.*, 1994). In subalpine forests in the western US, lodgepole pine forests may see increased growth with warmer, longer growing seasons if precipitation is not limiting (Kueppers & Harte, 2005). Notably, the optimum temperature for lodgepole pine production was set to 18°C , which is reached much earlier in the growing season (May) under the CCC climate scenario compared with the Control climate model (mid-June), suggesting an earlier warming. Thus, results shown here support observed increases in lodgepole pine due to favorable temperature and precipitation that are predicted by the Kittel *et al.* (2004) climate database.

Where productivity is limited by N availability, increases in N inputs via atmospheric deposition or

increased decomposition could enhance increases in productivity, along with favorable changes in climate. We expected this response to be particularly strong in lodgepole pine ecosystems, where N is tightly cycled (Fahey & Knight, 1986). Model results showed that N availability increased under both the HAD and CCC climate scenario in both mature and young stands, which would support the modeled increases in productivity. The fact that net N mineralization did not increase under the Control climate suggests that elevated nutrient availability was stimulated by projected changes in climate. Several mechanisms may explain elevated N availability under our climate scenarios. In CENTURY, N inputs increase with increased precipitation, which could directly increase N availability, allowing for increased plant production. In addition, the grass N pool in the understory, which was present in sparse stands, would have resulted in higher N

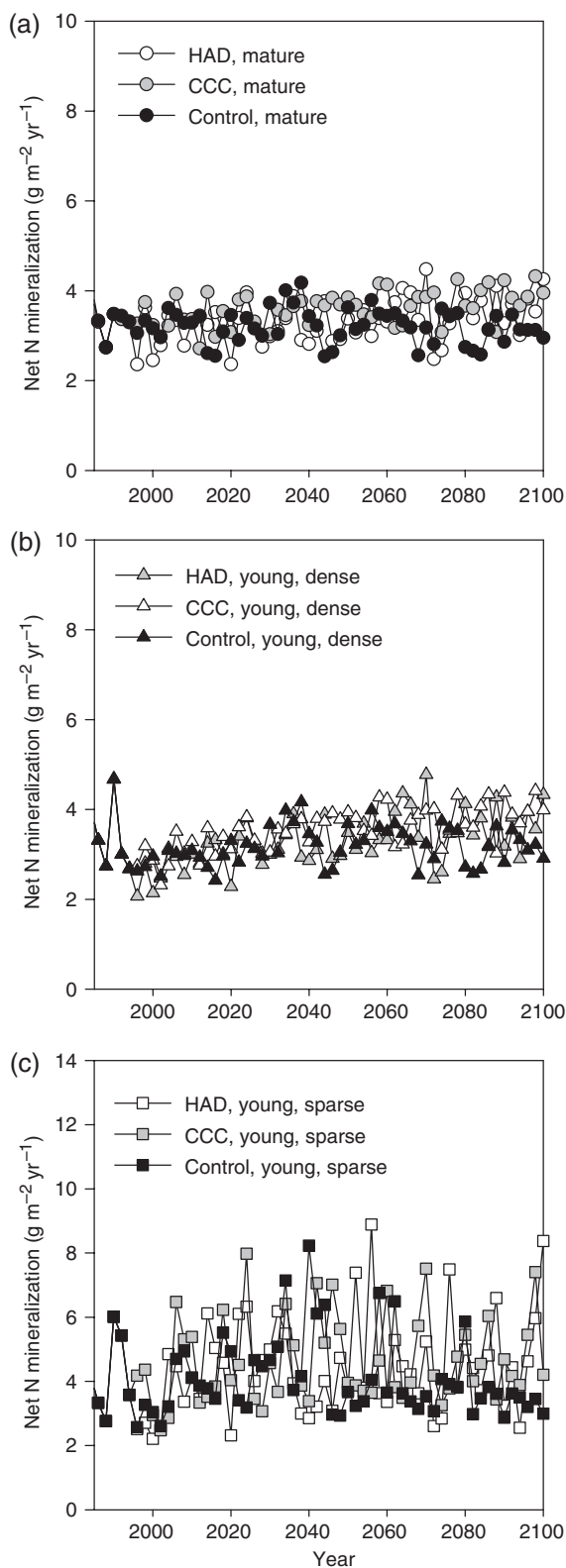


Fig. 6 Lodgepole pine simulated net N mineralization ($\text{g N m}^{-2} \text{yr}^{-1}$) for (a) mature, (b) dense, or (c) sparse young stands regenerating following stand-replacing fire in 1988 for the three climate scenarios [Canadian Climate Center (CCC), Hadley (HAD), or Control (current climate)].

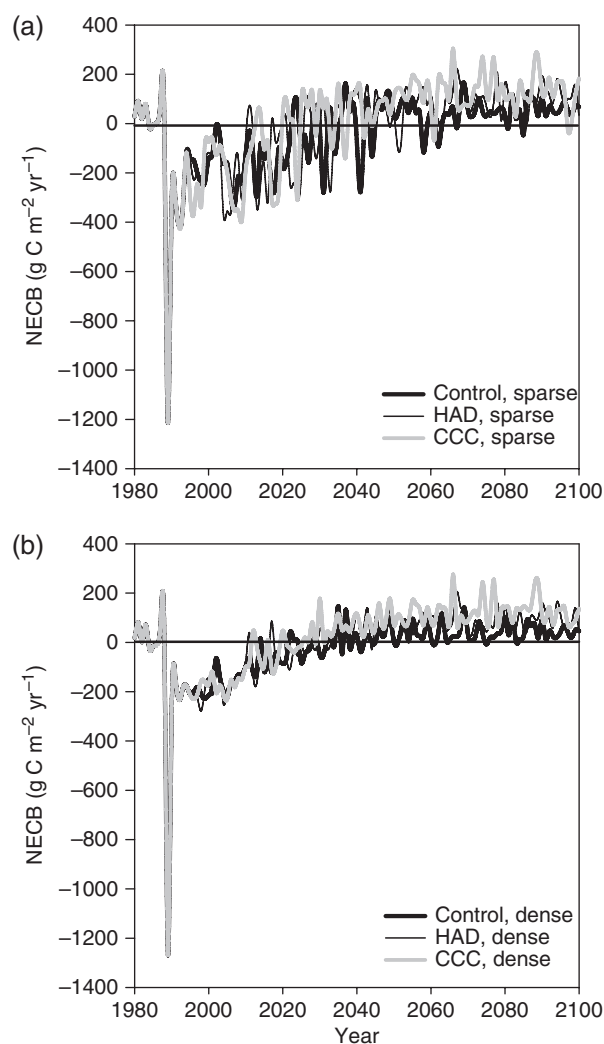


Fig. 7 Net ecosystem carbon balance (NECB), $\text{g C m}^{-2} \text{yr}^{-2}$ for (a) sparse and (b) dense lodgepole pine forest stands regenerating following stand-replacing fire in 1988 for the three climate scenarios [Canadian Climate Center (CCC), Hadley (HAD), or Control (current climate)].

availability when this labile N source decomposed. Higher net N mineralization rates were observed in sparse stands. Finally, the warmer temperatures and higher precipitation may also produce conditions that are more favorable for decomposition, increasing N turnover directly. Importantly, our results do not reflect potential changes in productivity due to CO_2 fertilization or changes in water or nutrient-use efficiency, both of which may modify potential C productivity and alter responses to elevated CO_2 (Liu *et al.*, 2005; Reich *et al.*, 2006). The combined changes in CO_2 concentration, climate, and tree physiology are likely to result in more complex patterns in C production than presented here (Neilson & Drapek, 1998; Cramer *et al.*, 2001; Hanson *et al.*, 2005).

Climate variability remains the primary influence on fire in YNP and fire suppression and land-use changes, which are known to affect C storage across broad regions (Caspersen *et al.*, 2000; Pacala *et al.*, 2001), have had little impact on YNP (Schoennagel *et al.*, 2004). However, the simulations did not include low severity fires, pathogens, insects, windthrow, or other disturbances that operate in the YNP and are likely to affect C storage and N cycling. Another simplification in the model is the prescription of historical fire events rather than their dynamic simulation. Probability distributions based on historical fire records are commonly used to estimate FRIs, and the distributions used in the model reflect published estimates of historical fire frequency in YNP (Schoennagel *et al.*, 2006). With increasing fire frequency (Flannigan *et al.*, 2005; Westerling *et al.*, 2006), it is likely that historical fire records may not be a good proxy for prescribing future FRIs, and a more dynamic fire model is needed (e.g., Bachelet *et al.*, 2003). In Yellowstone, current postfire establishment patterns are largely a function of prefire serotiny but it is unclear how postfire establishment patterns may be altered under future climates. The dynamic interaction between future climate and fire frequency remains a critical research need.

Our results suggest that it would take a minimum of 95 years to recover total C stocks lost by fire in 1988 with dense tree regeneration and the CCC climate, which predicts the most rapid increases in plant production. With more mild (HAD) or neutral (Control) climate, total C stocks may not return to prefire levels for 194 and 219 years. These results confirm earlier theoretical predictions that C storage in Yellowstone is resistant to changes in FRI (Kashian *et al.*, 2006), and suggest that increases in climate productivity may reduce recovery times, further enhancing ecosystem resistance to changes in FRIs.

Our results suggest that recovery of total N stocks would be rapid because of the low N storage in above-ground pools and modest N losses. In a recent field-based study in northwestern US, N losses by fire were estimated to be <1% to 6% of total N in *P. contorta* stands (Page-Dumroese & Jurgensen, 2006). In sparse stands, a substantial grass understory may also facilitate N recovery via increased N stocks immediately following fire and via its relatively rapid incorporation into soil organic matter. However, in order to parameterize differences in stand density with CENTURY, we may have overestimated average grass biomass in young stands. Recent work in YNP suggests that grass C is $30 \pm 35 \text{ g C m}^{-2}$ (average $\pm 1 \text{ SD}$), with a range of <1 to 118 g C m^{-2} among stands of varying age and density (Forester *et al.*, 2007). CENTURY predicts $56 \pm 35 \text{ g C m}^{-2}$, on average between 1989 and 2100, but a similar range of $6\text{--}104 \text{ g C m}^{-2}$.

Overall, our results suggest that FRIs would need to be dramatically reduced to affect long-term N and C storage in the Yellowstone ecosystem due to low above-ground N losses via combustion, the large soil N pool, and relatively fast recovery of aboveground C pools. Specifically, a 22% reduction in C storage would be reached by replacing the average FRI typical of high elevations (293 years) with that typical of low elevations (172 years) and switching the postfire successional pathway from dense to sparse. Such changes represent an upper bound of C change, because changes in average FRI and successional pathways are likely to be more gradual over the coming century. Therefore, we suggest this result reflects a substantial resiliency of YNP to changes in FRI in terms of C storage. Alteration in postfire tree density had a greater effect on C storage than changing the FRI. For example, lengthening the FRI from 172 to 293 would increase C storage 2225 g C m^{-2} for sparse stands, but increasing postfire density alone would result in an increase of 2957 g C m^{-2} .

However, over timescales relevant to current ecosystem management, a single large fire event may be important for forecasting transient changes in C and N storage. In our simulations, future changes in climate resulted in increases in lodgepole pine C and N stocks that greatly exceeded pre-1988 levels in mature stands. Although stand-replacing fire postponed this C sequestration potential, productivity over the next century was enhanced by a warmer climate. It follows that the mix of young and mature stands on the landscape, as a function of their disturbance history, may affect net landscape C flux. More specifically, the net C balance by the end of the projected period was dependent on postfire tree density and the specific climate model that was used. Given that postfire lodgepole pine tree density varies widely across YNP, this variation is likely to be substantial among individual forest stands for a given climate scenario. This suggests the importance of understanding the spatial variability of postfire stand structures across other fire-dominated conifer landscapes.

Although our analysis was not spatially explicit, primarily due to the lack of a robust stand density map across YNP, we are able to calculate the potential effect of our results at the landscape scale by using published estimates of the range in stand densities following the 1988 fire. Turner *et al.* (2004) calculated that 64% of the burned landscape was high density ($>1001 \text{ trees ha}^{-1}$) and 36% was low density ($<1000 \text{ trees ha}^{-1}$). Weighting our model estimates by these areas provides a coarse measure of landscape C storage potential in recovering forests. In the CCC scenario, young forests were a large C sink or small source

by 2100, depending on postfire density (+2091 to -86 gC m^{-2} for dense and sparse, respectively). Weighted by the area in each density class, the burned landscape would be a net sink of 1307 gC m^{-2} by 2100 due to the very strong sink strength of dense stands even though they occupied less of the burned area. In the HAD scenario, all young stands were C sources (-988 to -2759 gC m^{-2}), resulting in the burned landscape being a C source of -1625 gC m^{-2} . Under the Control climate, young stands were also net sources (-3470 to -5280 gC m^{-2} for dense and sparse, respectively), resulting in a net source of -4128 gC m^{-2} . Mature stands were net sinks under all model scenarios, storing between 1453 gC m^{-2} (Control climate) and 7718 gC m^{-2} (CCC climate) more C in the future period, translating to a weighted sink strength between 3813 and 7174 gC m^{-2} .

In summary, potential C sequestration in YNP ranged from a C sink to source due to variation in stand age, climate scenarios projected for the region, and postfire stand density. Stand age is increasingly appreciated as a controlling factor for understanding landscape C flux (Kurz & Apps, 1999; Euskirchen *et al.*, 2002; Smithwick *et al.*, 2006). Morales *et al.* (2007) showed that the choice of the general circulation model strongly influenced C balance in Europe. However, this study is the first to show that variation in postfire tree density may influence C flux under climate change scenarios. Moreover, more frequent large fires in Yellowstone may result in greater variation in stand density across the landscape (Schoennagel *et al.*, 2006), which would accentuate the patterns in C flux modeled here. Spatially explicit models of C potential are needed in YNP and other forests experiencing stand-replacement fire to refine these estimates.

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