Postfire changes in forest carbon storage over a 300-year chronosequence of *Pinus contorta*-dominated forests

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Abstract. A warming climate may increase the frequency and severity of stand-replacing wildfires, reducing carbon (C) storage in forest ecosystems. Understanding the variability of postfire C cycling on heterogeneous landscapes is critical for predicting changes in C storage with more frequent disturbance. We measured C pools and fluxes for 77 lodgepole pine (*Pinus contorta* Dougl. ex Loud var. *latifolia* Engelm.) stands in and around Yellowstone National Park (YNP) along a 300-year chronosequence to examine how quickly forest C pools recover after a stand-replacing fire, their variability through time across a complex landscape, and the role of stand structure in this variability.

Carbon accumulation after fire was rapid relative to the historical mean fire interval of 150–300 years, recovering nearly 80% of prefire C in 50 years and 90% within 100 years. Net ecosystem carbon balance (NECB) declined monotonically, from 160 g C·m^{-2}·yr^{-1} at age 12 to 5 g C·m^{-2}·yr^{-1} at age 250, but was never negative after disturbance. Decomposition and accumulation of dead wood contributed little to NECB relative to live biomass in this system. Aboveground net primary productivity was correlated with leaf area for all stands, and the decline in aboveground net primary productivity with forest age was related to a decline in both leaf area and growth efficiency. Forest structure was an important driver of ecosystem C, with ecosystem C, live biomass C, and organic soil C varying with basal area or tree density in addition to forest age. Rather than identifying a single chronosequence, we found high variability in many components of ecosystem C stocks through time; a >50% random subsample of the sampled stands was necessary to reliably estimate the nonlinear equation coefficients for ecosystem C. At the spatial scale of YNP, this variability suggests that landscape C develops via many pathways over decades and centuries, with prior stand structure, regeneration, and within-stand disturbance all important. With fire rotation projected to be <30 years by mid century in response to a changing climate, forests in YNP will store substantially less C (at least 4.8 kg C/m^2 or 30% less).

Key words: carbon; chronosequence; lodgepole pine; net ecosystem carbon balance; net ecosystem production; Pinus contorta *var.* latifolia; *postfire succession; Yellowstone National Park, Wyoming, USA.*

INTRODUCTION

Forests are a substantial store of carbon (C) in terrestrial environments (Dixon et al. 1994, Schimel 1995, Houghton 1996), and C cycling in forests is strongly shaped by disturbance and subsequent regrowth (Vitousek and Reiners 1975, Pearson et al. 1987, Kasischke 2000, Gower et al. 2001, Chen et al. 2002). Forests are important to the global C budget (Pacala et al. 2001, Bradford et al. 2008, Pan et al. 2011), especially because forest C uptake in North America and Europe is an important offset of anthropogenic C emissions that contribute to climate change (Murray et al. 2000, Papadopal 2000, Parker et al. 2000, Schulze et

al. 2000, CCSP 2007, Pan et al. 2011). Quantifying changes in forest C after disturbances is therefore essential for managing future C emissions, especially given uncertainties about forest C storage under future climate scenarios (Janisch and Harmon 2002, Metsaranta et al. 2010, 2011, McKinley et al. 2011). Specifically, quantifying the rate of recovery of C pools is necessary for understanding how disturbances influence local, regional, and global C budgets (AuClair and Carter 1993, Houghton 1996, Burke et al. 1997, Amiro 2001).

Fires are unique among disturbances in that they cause an immediate C loss to the atmosphere via combustion of foliage, small twigs and cones, portions of larger branches, and dead wood (Tinker and Knight 2000, Schuur et al. 2002). Organic matter in the soil is partially consumed, with losses from organic horizons

typically much greater than losses from mineral horizons (Kasischke et al. 1995, Rothstein et al. 2004, Kashian et al. 2006; but see Bormann et al. [2008] for a study where high-intensity fire promoted substantial losses of organic C from mineral horizons). Carbon losses to combustion generally represent only a small fraction of total ecosystem C (Stocks 1989, Dixon and Krankina 1993, Kasischke 2000), because fires consume only a small fraction of tree biomass, and much C remains in the postfire stand as dead wood when the trees are killed.

Fire changes forest C storage by affecting the presence and abundance of live and dead biomass following the event. Forest C storage for ecosystems shaped by stand-replacing disturbances is driven mainly by the balance between C accumulation in growing vegetation (Ryan et al. 1997) and C loss through decomposition following a disturbance. This balance largely determines the net accumulation of C in an ecosystem, or net ecosystem carbon balance (NECB, Chapin et al. 2006), and NECB changes markedly over the life of the stand (Kashian et al. 2006). Until recently, net ecosystem production (NEP) has been used in the literature to describe net C accumulation and is analogous to NECB in this regard (Chapin et al. 2006). Severe disturbances such as stand-replacing fires can shift stands to a source of atmospheric C immediately following the event when vegetation is sparse, net primary productivity (NPP) is very low, and the stand is dominated by decomposing, fire-killed trees (Crutzen and Goldhammer 1993, Janisch and Harmon 2002, Amiro et al. 2010). If young stands dominate a landscape, the entire landscape is likely to be a C source (Harmon et al. 1990, Schulze et al. 2000, Janisch and Harmon 2002), at least until C pools in affected stands recover. When C accumulation in regenerating vegetation compensates for C lost through decomposition, NECB becomes positive, the stand shifts to a C sink (Crutzen and Goldhammer 1993), and NECB then gradually decreases toward zero over the life of the stand. Landscapes dominated by older stands are therefore likely to be small C sinks (NECB near zero) with large C storage (Kasischke et al. 1995, Kasischke 2000, Euskirchen et al. 2002, Pregitzer and Euskirchen 2004, Luyssaert et al. 2008) even when current production declines (Schulze et al. 2000, Harmon 2001). An emphasis on empirical data quantifying postfire C storage has increased over the last decade, especially for coniferous forests (Wirth et al. 2002, Law et al. 2003, Bond-Lamberty et al. 2004, Rothstein et al. 2004), but this information is still very limited.

In addition to stand age, Kashian et al. (2006) illustrated the importance of landscape variability in stand density for NEP following stand-replacing fires. Large stand-replacing fires create tremendous structural heterogeneity in regenerating postfire forests (Turner et al. 1997, 2004, Kashian et al. 2004) that may persist for decades or centuries before stand structural convergence occurs across the landscape (Kashian et al. 2005b). In Yellowstone National Park the heterogeneity of sapling density across the landscape 10–20 years following large stand-replacing fires has been associated with variability in stand productivity (Reed et al. 1999, Turner et al. 2004), C allocation (Litton et al. 2003), and C storage (Litton et al. 2004). Carbon pools have been described for stands of contrasting density within the same age class (Litton et al. 2004), but few empirical data exist that compare changes in C storage over the life of stands with contrasting density (Kashian et al. 2006).

Increases in frequency of disturbances—particularly stand-replacing fires—in a future warmer, drier climate will likely lower C storage in forests (Kasischke et al. 1995, Fearnside 2000, Harden et al. 2000, Metsaranta et al. 2010, 2011), even if fire replaces older, slower-growing trees with younger trees having higher NPP (Rothstein et al. 2004). Forest C losses may be most pronounced if fires become too frequent and tree regeneration fails, converting forests to meadow or shrub ecosystems (Kashian et al. 2006). Recent increases in fire activity (Flannigan and Van Wagner 1991, Amiro 2001, Westerling et al. 2006) suggest climate warming and associated alterations to hydrology are already changing disturbance regimes. Climate-driven changes in fire regimes in the current century (Westerling et al. 2011) will likely create more extensive changes in terrestrial ecosystem structure and function than physiological responses of organisms to changes in temperature, precipitation, or CO_2 (Dale et al. 2001).

We developed a 300-year chronosequence of 77 lodgepole pine (*Pinus contorta* Dougl. ex Loud var. *latifolia* Engelm.) stands in Yellowstone National Park (Wyoming, USA) to determine patterns of changes and variability in C pools and fluxes after stand-replacing wildfires. Our goal was to describe the magnitude of C loss and the timing of its recovery during postfire succession for a diversity of stand ages and structures as a means of accounting for realistic heterogeneity on complex landscapes. We asked:

1) How quickly do forest C pools recover after a stand-replacing fire and what controls the recovery rate?
2) How variable are C pools within and among stand ages, and is this variability related to the structural variables of basal area and tree density?
3) How well do chronosequences function in answering questions about long-term changes in C storage?

METHODS

Study area

Our study area was the forested area within and immediately surrounding Yellowstone National Park (YNP), located in the northwest corner of Wyoming and adjacent portions of Montana and Idaho, USA (4427′ N, 11 038′ W). The climate in Yellowstone is cool throughout the year, averaging a maximum of 9.6°C and a minimum of −7.4°C (23.6°C and 3.9°C during the growing season) in the approximate center of the study

area (Western Regional Climate Center, Old Faithful RAWS [remote automatic weather station]).[8] The growing season is typically dry; annual precipitation averages 62 cm, with only 15–35% of the average amount falling as rain between early June and mid-October (Despain 1990). Total snowfall averages 540 cm, with an average depth of 33 cm between mid-October and early July. Most soils in YNP are rhyolitic in origin and are infertile, interspersed with more fertile soils of andesitic or lacustrine origin. All study sites were located on rhyolitic soils with sandy loam textures characterized by low clay content (Litton et al. 2004).

YNP is located on several subalpine plateaus of volcanic origin ranging from about 1900 to 2900 m in elevation. The combination of extensive, dry, infertile soils, large stand-replacing fires over many centuries, and recurring insect outbreaks allow lodgepole pine to dominate almost 80% of the forested area of YNP. Lodgepole pine forest composition in YNP may shift toward longer-lived, more shade-tolerant species (Lotan and Critchfield 1990), but lodgepole pine often remains the predominant species even at ages of >350 years (Despain 1990, Kashian et al. 2005b). Subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) and Engelmann spruce (*Picea engelmannii* Parry ex Engelm) in YNP are typically dominant only in local areas of high moisture and more fertile soils of andesitic origin.

YNP contains a complex mosaic of lodgepole pine stand ages that have resulted from centuries of stand-replacing wildfires (Romme and Despain 1989). Approximately 45% of the park was burned by large stand-replacing wildfires in 1988, resulting in an abundance of young regenerating lodgepole pine stands with stem density ranging over five orders of magnitude (Kashian et al. 2004, Turner et al. 2004) within a patchwork of older stands up to more than 400 years old (Romme and Despain 1989, Tinker et al. 2003). As a result, stand ages are present in YNP from nearly every decade since the late 1600s (Romme and Despain 1989), though stands 40–70 years old are less frequent.

Chronosequence development and sampling

We developed a replicated chronosequence of 77 lodgepole pine stands (Fig. 1) to examine C storage and fluxes in stands from 12 to >300 years old during the summers of 2004 through 2006. Lodgepole pine forests in YNP are ideal for a chronosequence study because of the relatively gentle topography, uniform soils, dominance of a single overstory species (Despain 1990), and a relatively natural disturbance regime that has created a mosaic of stand age, tree size, tree density, and amount and size of dead wood (Romme and Knight 1982, Turner et al. 1997, 2004, Kashian et al. 2004). Stands were sampled for five age classes (<25, 40–70, 80–130, 170–230, and >250 years old) to ensure equal representation of stand ages present across the YNP landscape.

Stands within an age class were spatially separated by 1 km or more. Within each age class we established three classes of tree density for stands younger than 130 years (low, moderate, and high density) and two classes of mountain pine beetle activity (present or absent) for stands older than 170 years. Stands were placed into density classes based on self-thinning trajectories presented in Kashian et al. (2005b). Stand ages were determined using stand age maps when available (Romme and Despain 1989, Tinker et al. 2003), or from tree increment cores sampled from 8–10 dominant trees per stand. Four to six replicate stands in each age, tree density, or beetle category (total 77 stands) were selected and measured using a stratified random sampling design that ensured representation of the full range of values in each category.

All soil and vegetation sampling at each stand was completed using three 10×50 m plots separated by 50 m (less if conditions precluded wider spacing), with the location of the center plot chosen at random within the stand. All stands were ≥5 ha in area, a minimum of 100 m from roads or trails, and originated from a stand-replacing fire with no detectable anthropogenic disturbance. Ecosystem C storage was measured by summing C stored in aboveground and belowground live biomass, standing and fallen dead wood, dead coarse roots and root collars, organic soil, and mineral soil (Table 1). Two C fluxes were measured: annual wood production in trees and litterfall; aboveground net primary production (ANPP) was estimated as the sum of these two components.

Allometric equation development

Allometric equations for aboveground and belowground biomass of lodgepole pine were developed specifically for the study area using three lodgepole pine stands in the adjacent Caribou-Targhee National Forest. To assess the influence of stand age and density on model equations, we selected a young, dense stand (~65 years old, 2452 trees/ha); a young, sparse stand (~65 years old, 725 trees/ha); and an older sparse stand (~165 years old, 674 trees/ha) for allometric development. All three sites were located on soils similar to those found in YNP and at similar elevation. Aboveground tree biomass was harvested from a total of 46 trees across the range of tree sizes within the three stands, and 24 root systems were excavated to develop allometric equations between easily measurable tree characteristics (dbh, tree height) and above- and belowground tree biomass components. Harvesting and equation development were conventional and the details are given in Appendix B.

Vegetation C pools

We estimated C in live overstory trees (dbh >4 cm diameter at 1.4 m), saplings (trees <4 cm dbh and all trees shorter than 1.4 m), coarse roots (>2 mm), fine roots, standing dead trees, dead coarse roots and root
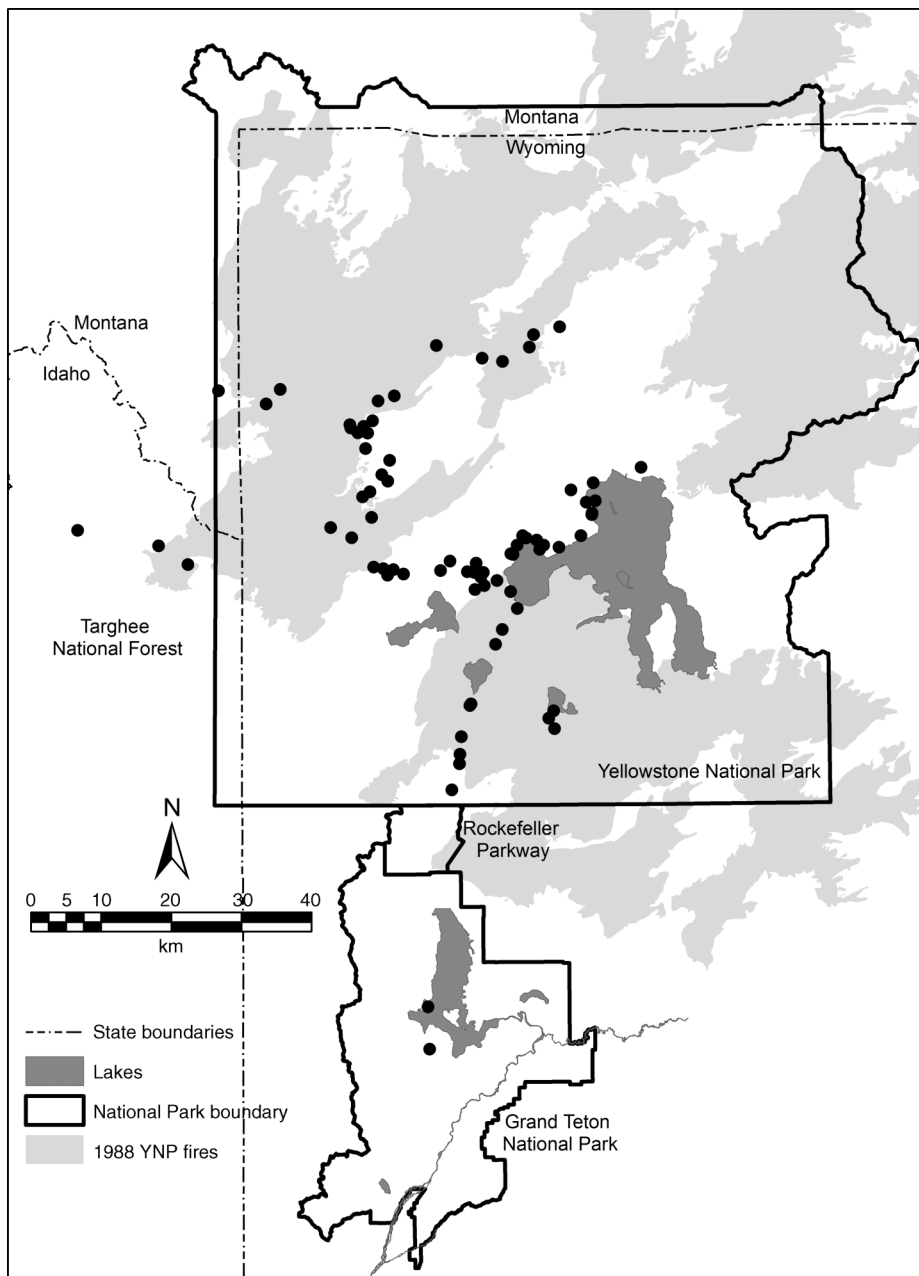
Fɪɢ. 1.   Locations of 77 chronosequence stands (solid black circles) distributed across the Greater Yellowstone Ecosystem. Sixteen of the stands were located within the area burned in 1988.

collars, and downed dead wood by estimating biomass multiplied by carbon fraction determined from subsamples (Table 2). A subsample of 29 stands in this study aged 131–335 years old revealed that herbs and shrubs represented <0.1% of total ecosystem carbon, and Litton et al. (2004) reported that this pool represented <0.7% of total ecosystem carbon for stands <25 years old. As such, we did not include biomass or carbon estimates of herbs and shrubs in this study. All subsamples for C were dried at 65°C, ground in a Wiley

Mill to pass through a size 40 mesh (0.5 mm^2) and analyzed on a LECO-100 CHN analyzer (LECO Corporation, St. Joseph, Michigan, USA).

Allometric equations (Table 3; Litton et al. 2003, Turner et al. 2004) were used to determine aboveground biomass in live overstory trees at each study site. Diameter at breast height (dbh), sapwood basal area, total tree height, and height to the base of the live crown were measured on 30 trees selected randomly within the three sample plots of each stand (10 trees per plot) to

TABLE 1.   Summary of field methods for sampling biomass pools; all sampling occurred in three 10×50 m plots per stand.

Biomass pool	Measured variables	Methodology in each plot
Stand basal area	diameter at breast height (dbh)	measured on all trees >4 cm dbh in two 50-m belt transects per plot; used for double sampling
Live overstory trees	dbh, sapwood basal area, total tree height, height to the base of the live crown	sampled on 10 random trees per plot and used with allometric equations; adjusted values to plot with double sampling
Saplings	basal diameter	24 randomly selected saplings per plot; used with allometric equations by Turner et al. (2004).
Tree coarse roots (>2 mm)	dbh	sampled on 10 random trees per plot and used with allometric equations; adjusted values to plot with double sampling
Sapling coarse roots (>2 mm)	basal diameter	24 randomly selected saplings per plot; used with allometric equations by Litton et al. (2003).
Fine roots	fine-root biomass	five 30-cm-deep soil cores per plot; corrected for ash-free mass.
Downed dead wood	diameter and/or count using planar intercept method	eight 15.2-m transects per plot classified into decay classes defined by Maser et al. (1979)
Standing dead trees	dbh	measured in two 50-m belt transects per plot; used with allometric equations by Pearson et al. (1984)
Dead coarse roots (<25 years)	dbh	measured in two 50-m belt transects per plot; used with allometric equations by Pearson et al. (1984)
Root collars (>25 years)	basal diameter	measured in two 50-m belt transects per plot
Organic soil	organic soil biomass	measured with 900-cm^2 sampling frames in five random locations per plot
Mineral soil	soil bulk density	five 30-cm-deep soil cores per plot sampled directly below organic soil sample
Litterfall	annual litterfall biomass	sampled for 2–3 years in four 0.14-m^2 litter traps per plot

calculate mean tree biomass of the 30-tree sample. Mean basal area of the stand was measured by sampling the dbh of all trees >4 cm dbh within 50-m belt transects run along the long axis of each plot boundary; belt widths were varied so as to sample a minimum of 150 trees per stand (mean, 50 trees per plot). Double sampling (Cochran 1977) adjusts plot biomass for the difference between stand basal area and the basal area of the 30-tree sample. Data from Litton et al. (2003), collected with the same methods, was used for 12 of the stands <25 years old. Biomass for saplings in stands

>40 years old was estimated using basal diameter measurements of 72 randomly selected saplings per stand (24 saplings per plot) and allometric equations developed for lodgepole pine saplings in YNP by Turner et al. (2004).

Biomass of coarse roots of trees was estimated using the same 30-tree sample and double sampling design as for aboveground biomass using the equation in Table 3. Coarse-root biomass for saplings was estimated using the equations developed for 13-year old saplings in YNP by Litton et al. (2003). Carbon content for tree and

TABLE 2.   Carbon content of biomass pools for lodgepole pine forests in Yellowstone National Park (USA).

	% C			
Pool	Mean	SE	N	Source
Aboveground tree woody biomass	43.5	0.06	84	subsample of stands >40 years old
Tree foliage	53.1	0.12	631	subsample of stands >40 years old
Aboveground sapling woody biomass	46	0.13	48	sample of all stands <25 years old
Sapling foliage	50.1	0.14	222	sample of all stands <25 years old
Tree coarse roots	43.5	0.06	84	subsample of stands >40 years old
Sapling coarse roots	46	0.13	48	sample of all stands <25 years old
Fine roots	34.9	0.32	359	average content across all 77 stands
Dead-wood Class I	48.8	0.21	18	subsample of all stand ages
Dead-wood Class II	49.2	0.12	18	subsample of all stand ages
Dead-wood Class III	50.2	0.23	18	subsample of all stand ages
Dead-wood Class IV	51.2	0.30	18	subsample of all stand ages
Dead-wood Class V	49.9	1.07	18	subsample of all stand ages
Standing dead trees	49	0.11	36	average of dead-wood classes I and II
Root collars	49.9	0.24	90	average of five dead-wood classes
Organic soil	28.1	0.60	182	average content across all 77 stands
Mineral soil	1.1	0.04	365	average content across all 77 stands
Litterfall	50.4	0.16	195	average content across all 77 stands

Note: C content was determined using an average value of multiple samples from each biomass pool. Biomass estimates were converted to C by multiplying dry mass by C content.

TABLE 3. Allometric equations for predicting dry biomass (kg) of nine different above- and belowground components of lodgepole pine in the Greater Yellowstone Ecosystem.

Biomass component	Equation†	n	R^2‡
Total aboveground	$0.201 \times \mathrm{dbh}^{2.199}$	46	0.96
Bole	$0.020 \times \mathrm{dbh}^{1.535} \times \mathrm{HT}^{1.447}$	46	0.97
Branches	$0.117 \times \mathrm{dbh}^{3.133} \times \mathrm{HT}^{-1.705}$	46	0.84
Fine fuels I (twigs and foliage)	$0.536 \times \mathrm{dbh}^{2.445} \times \mathrm{HT}^{-1.237}$	46	0.81
Fine fuels I (twigs and foliage)	$0.150 \times \mathrm{dbh}^{1.961} \times (\mathrm{HT} - \mathrm{CB})^{-0.347}$	46	0.87
Foliage	$0.104 \times \mathrm{dbh}^{2.419} \times \mathrm{HT}^{-1.055}$	46	0.82
Total coarse root	$0.021 \times \mathrm{dbh}^{2.281}$	24	0.94
Root crown	$0.015 \times \mathrm{dbh}^{2.222}$	24	0.84
Lateral roots	$0.006 \times \mathrm{dbh}^{2.386}$	24	0.94
Total tree	$0.268 \times \mathrm{dbh}^{2.124}$	24	0.98

† All equations are of the form Biomass (dry kg) = $a \times \mathrm{dbh}^b$ or $a \times \mathrm{dbh}^b \times X^c$, where a, b, and c are coefficients to the nonlinear regression equation, dbh is diameter at 1.37 m (in cm), and X is either tree height (HT) or height from the ground to the base of the live crown (HT − CB) in m.

‡ R^2 is calculated as 1 − (residual sum of squares)/(corrected sum of squares).

sapling coarse roots was assumed to be the same as for aboveground wood. Fine-root biomass (<2 mm, 0–30 cm mineral soil depth) was estimated using 15 soil cores per stand (6.35 cm diameter, five per plot). The upper 30 cm of the mineral soil profile captures 80–90% of the fine roots in lodgepole pine stands (Pearson et al. 1984). Subsamples of fine roots were combusted in a muffle furnace to correct final biomass estimates for ash-free mass.

Down dead-wood biomass (dead wood on the ground) was estimated using the planar intercept method along 24 15.2-m transects run perpendicular to the 50-m belt transects (eight transects per plot; total, 366 m per stand) as described by Brown (1974). All dead wood >7.5 cm in diameter was classified into five decay classes as defined by Maser et al. (1979), with wood density and C content determined for each class. Samples of down wood from each of the five decay classes was collected from three stands in each of the five age classes sampled in this study (15 stands total) and analyzed for C content using the method previously described.

Biomass in standing dead trees was estimated by measuring all standing dead trees within the same 50-m belt transects used for live biomass sampling. Site-specific equations used to estimate live-tree biomass were not applicable to standing dead trees because they include fine branches and foliage not present on standing dead trees. We used equations developed for lodgepole pine in southeastern Wyoming (Pearson et al. 1984) to estimate the biomass of standing dead boles and branches because those equations do not require a height measurement. Carbon content of standing dead trees was estimated as the mean C content of dead wood in decay classes I and II (49%). Biomass in root crowns was estimated by measuring the basal diameter of root collars located within the 50-m belt transects and the equation in Table 3. Dead coarse roots are a large pool of C in recently burned stands, and these values were taken from Litton et al. (2004) for 12 of the stands <25

years old. Dead coarse-root biomass for the remaining four stands <25 years old was determined using allometric equations developed by Pearson et al. (1987) and exponential decay coefficients developed for lodgepole pine roots in southeastern Wyoming (Yavitt and Fahey 1982). Dead coarse roots were assumed to be well incorporated into the mineral soil (sampled as a separate C pool) in stands >25 years old. Biomass for root crowns was converted to C using the average C content of the five decay classes (49.9%).

Soil C pools

We estimated mass of the organic horizon (fine litter, or needles, bark, cones, and branches < 0.6 cm in diameter) using 900-cm² sampling frames, by collecting all organic material from five random locations in each plot. Mineral soil was collected immediately below the organic soil sample to a depth of 30 cm using a soil tube 6.35 cm in diameter (five samples/plot). The five mineral and organic soil samples were separately combined by plot, and the organic samples weighed in the field and subsampled. Samples were then dried to a constant mass at 65°C and ground on a Wiley mill to pass through a size 40 (0.5-mm²) mesh screen. Subsamples of the organic and mineral soil samples were processed overnight on a roller mill, and analyzed for C content on the LECO-100 CHN analyzer. Subsamples of organic soil biomass were combusted in a muffle furnace to correct final biomass estimates for ash-free mass. Mineral soil C (0–30 cm) was estimated from measured C content and bulk density estimated from dry mass and core volume. Mineral soil was not sampled below 30 cm because we could not consistently core below 30 cm.

ANPP and LAI

We estimated aboveground net primary productivity (ANPP) as the sum of annual biomass increment of trees and saplings and annual litterfall because ANPP is an important flux, and leaf area (expressed as leaf-area

index, LAI) because LAI is often correlated with productivity. Variability of ANPP divided by LAI indicates differences in photosynthesis or partitioning of photosynthesis (Waring 1983). Annual tree biomass increment for 12 of the 16 stands <25 years old was sampled in 2000 and 2001 and reported in Litton et al. (2004). For stands >25 years old we sampled two increment cores perpendicular to each other in 2004 and 2005 from each of the 30 trees measured for height and measured the past 5-yr diameter growth. Sapling diameter increment was measured on basal disks (Litton et al. 2004). We determined annual biomass increment using the equations in Table 3 and measured diameter and height increments or the equations in Litton et al. (2004) and Turner et al. (2004). ANPP of shrubs and herbs was not included because this carbon pool represented a very small fraction of total ecosystem C, although we acknowledge that herbs and shrubs could be a much more significant contributor to ANPP, particularly in stands <25 years (Litton et al. 2004). Litterfall was collected annually for 2–3 years in four 0.14-m^2 litter traps per plot, which may underestimate litterfall by excluding loss to consumers, decomposition, and leaching. Litterfall samples were prepared as above for biomass. Annual litterfall was estimated as annual collected litterfall biomass plus annual foliage biomass increment, estimated with the allometric equations described above.

Projected, one-sided leaf-area index (m^2/m^2) was determined for stands >40 years old using the 30-tree measurements in each stand and the foliar biomass equation in Table 3. Biomass was converted to leaf area using 9.52 m^2/kg (Kaufman and Troendle 1981). After adjusting with double sampling (Cochran 1977), stand total LAI was converted to projected LAI by dividing by 3.21 (Kaufman et al. 1982). For stands <25 years old, values of LAI were taken from Litton et al. (2004).

Analysis of the chronosequence

We evaluated how well the chronosequence stands represented the Yellowstone landscape by comparing them to randomly sampled burned and unburned lodgepole pine stands across YNP (n = 40 stands in each class). We estimated (1) live and dead prefire basal area of stands that burned in 1988 for comparison with the same variables in chronosequence stands <25 years old; (2) live and standing dead basal area of stands >100 years old that did not burn in 1988 for comparison with the same variables in the chronosequence stands >100 years old, and (3) for comparison with the "new" dead wood pool of the <25-yr-old stands. In stands burned in 1988 we measured dbh of trees alive in 1988 (distinguishable by a lack of stem char because of water in phloem and xylem when burned) in two 5 × 50 m belt transects separated by 30 m. In stands not burned in 1988, we measured dbh of trees selected with a 20 BAF (basal-area factor) prism (Forestry Suppliers, Jackson, Mississippi, USA) in 10 variable-radius plots.

Data analysis

Stand was the sample unit in this study; values presented here are means of three plots per stand. Tree density declines substantially and exponentially across the chronosequence (Kashian et al. 2005b), so that differences in stand density within an age class are relative across age classes rather than absolute (i.e., very high or low tree densities have very different ecological implications at age 12 compared to age 200). Therefore, we analyzed the effect of tree density by computing an index of relative tree density for each age class as (tree density)/(maximum tree density) (range, 0 to 1). We also assessed the importance of basal area as a structural variable, measured at the tree base for stands <25 years old and at 1.4 m for stands >25 years old.

Patterns in C pools with age were examined using least-squares nonlinear regression. The importance of relative tree density and basal area in explaining variation in C pools was assessed by examining patterns in the residuals of the nonlinear equation regressed against linear or quadratic equations with these variables. Differences in C pools for stands affected and unaffected by mountain pine beetle were assessed with analysis of variance. Relationships between variables were assessed using linear regression, multiple linear regression, or quadratic regression. Statistics were assessed using SPSS version 17 (SPSS Science 2008) and SAS version 9.3 (SAS Institute 2011), and a significance level of alpha = 0.05 was used for all analyses.

RESULTS

Allometric equations

Nine allometric models were developed for all measured tree components with R^2 values ranging from 0.81 to 0.97 (Table 3). Plots of residuals vs. dbh did not show evidence of bias or any evidence of the influence of tree density or stand age for any of the nine models. Equations for total aboveground biomass, total tree biomass, and root biomass included dbh as the only independent variable, but all other components also contained tree height or height to crown base in the model (Table 3).

Vegetation C pools

Carbon in live trees averaged 7070 ± 465 g C/m^2 (mean ± SE), varied from 33 to 14 400 g C/m^2 across the chronosequence, and increased with stand age following a Michaelis-Menton function (Fig. 2A). Aboveground biomass was 81% of live biomass C (6030 ± 404 g C/m^2), coarse-root biomass was 9% of live biomass C (988 ± 40 g C/m^2) and fine-root biomass was 10% of live biomass C (245 ± 16 g C/m^2). Live C averaged 46% of total ecosystem C across all stands, ranging from <1% in the youngest stands to nearly 80% in a 131-yr-old stand. Residuals from the nonlinear equation were correlated with both relative tree density
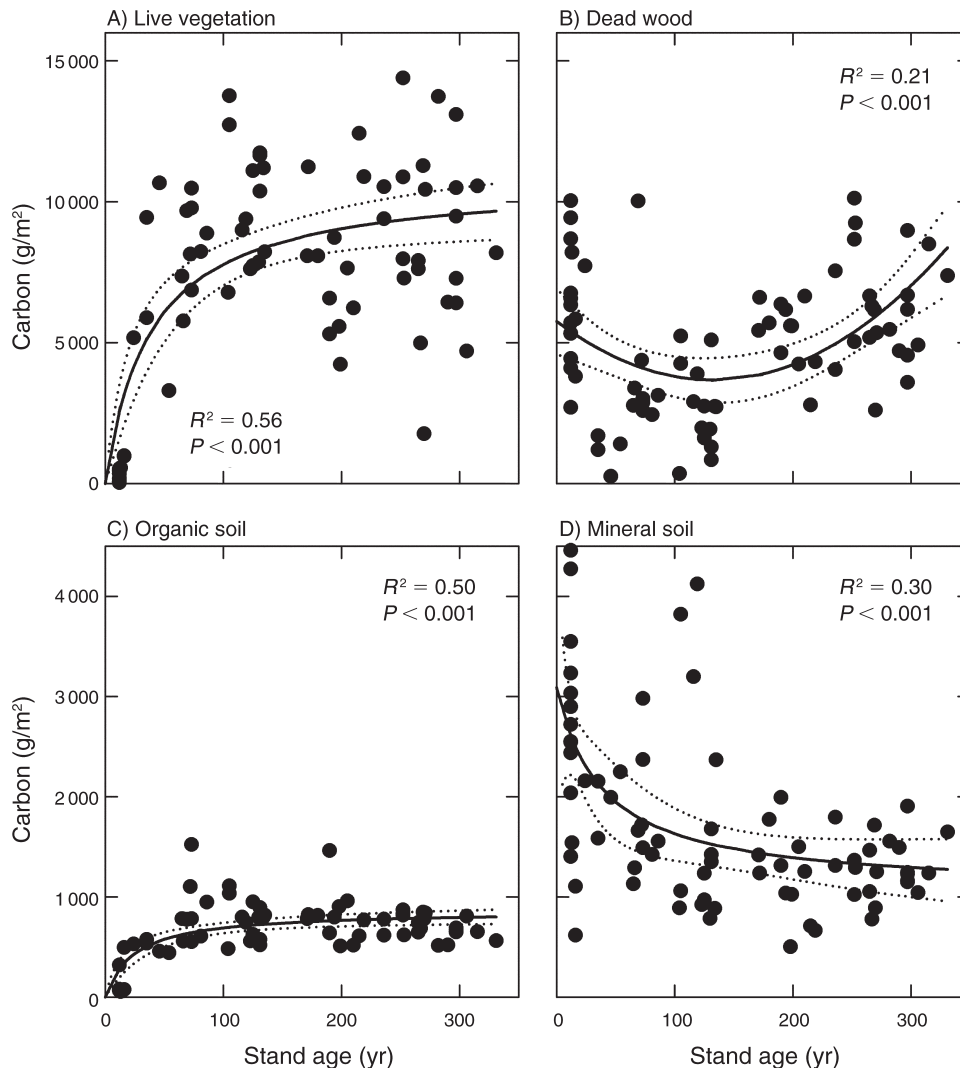
FIG. 2. Carbon pools (g C/m^2) vary with stand age (years), with different patterns for different components: (A) Live vegetation C = (Age × 10 800)/(Age + 38.9); (B) Dead wood C = 5760 − 31.50 × Age + 0.119 × Age^2; (C) Organic soil C = (Age × 859)/(Age + 24.6); and (D) 0–30 cm Mineral soil C = 3090 − ([Age × 2030]/[Age + 39.0]). Error bounds (dotted lines) are 95% confidence intervals for the mean prediction, estimated by SAS Proc NLIN.

(−) and basal area (+), and a multiple linear regression with age, basal area, and relative tree density had an estimated R^2 of 0.76 (standard error of the estimate [SEE] = 2.03 kg C/m^2).

Carbon in dead wood averaged 4900 ± 277 g C/m^2 (mean ± SE), ranging from 260 to 10 100 g C/m^2, with higher variability than live biomass in the youngest forests. Dead-wood C was highly variable and followed a second-order polynomial with increasing stand age (R^2 = 0.21, $P < 0.001$), with the minimum at 125 years after stand-replacing wildfire (Fig. 2B). Residuals from this equation did not correlate with basal area or relative tree density. Down wood contained the most C in the dead-wood pool (65%; 3200 ± 185 g C/m^2), with standing dead wood containing 23% (1214 ± 131 g C/m^2), and root collars 12% (513 ± 32 g C/ m^2). Dead-wood C was

found mostly in down wood in all aged stands; standing dead wood decreased in importance for C storage with stand age (R^2 = 0.17, $P < 0.001$). Carbon in dead wood averaged 36% of total ecosystem C for all stands, ranging from 2% in a sparse stand <50 years old to nearly 80% in a recently burned stand.

Soil C pools

Organic soil C averaged 632 ± 34 g C/m^2 (mean ± SE), ranged from 56 to 1520 g C/m^2, and varied with stand age (R^2 = 0.50, $P < 0.001$), fitting a Michaelis-Menton function and reaching its maximum after 150 years, and recovering half the maximum in 25 years (Fig. 2C). Organic soil C averaged only 4.4% of total ecosystem C (much less than that found in boreal forests [Kasischke and Johnstone 2005]), ranging from
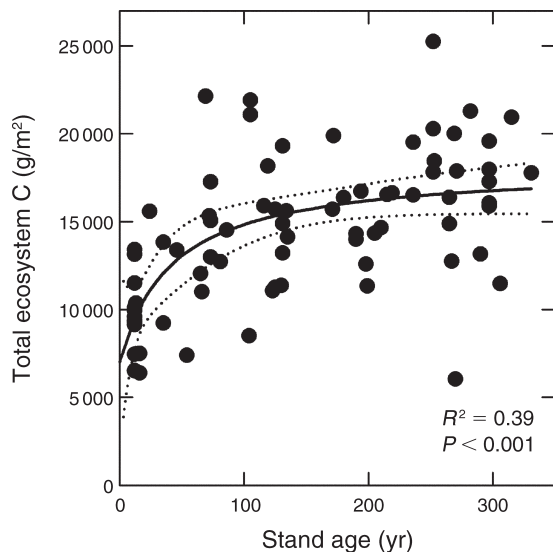
FIG. 3. Total ecosystem carbon increases with stand age (years), but 90% of the increase occurs before age 100 years. Ecosystem C (g C/m^2) = 7020 + ([Age × 11 100]/[Age + 42.4]). After age 70, a linear regression of ecosystem C was not significant ($P = 0.43$). Error bounds (dotted lines) are 95% confidence intervals for the mean prediction, estimated by SAS Proc NLIN.

<1% in a recently burned stand to 13% in a stand >250 years old. Residuals from the nonlinear equation were correlated with basal area (+), but not relative tree density.

Carbon in 0–30 cm mineral soil averaged 1720 ± 100 g C/m^2, ranged from 502 to 4460 g C/m^2, and declined with stand age, with all of the decline occurring in stands <150 years old ($R^2 = 0.30$, $P < 0.001$; Fig. 2D). Mineral soil C averaged 14% of total ecosystem C, ranging from 200 years old to nearly 44% in a 12-yr-old stand. Stand age explained 30% of the variation in mineral soil C across the chronosequence, and the residuals were not correlated with basal area or relative tree density.

Ecosystem C and NECB

Ecosystem C, estimated by summing all of the above C pools, increased with stand age following a Michaelis-Menton function (Fig. 3; $R^2 = 0.39$, $P < 0.001$). For stands older than 70 years, ecosystem C did not vary with stand age ($P = 0.43$). Net ecosystem carbon balance (NECB), estimated as the derivative of the function of ecosystem C and stand age, declined monotonically from 160 g C·m^{-2}·yr^{-1} at age 12 to 5 g C·m^{-2}·yr^{-1} at age 250 (Fig. 4). Ecosystem C recovered quickly relative to the historical disturbance interval, with ecosystem C reaching 80% of that at age 250 by 50 years after the fire and 90% of that at age 250 by 100 years after fire. Ecosystem C varied from 6.0 kg C/m^2 in a 270-year-old stand with high mountain beetle mortality to 25.2 kg C/m^2 in a 252-year old stand and averaged 14.4 ± 0.5) kg C/m^2 for all stands. Residuals from the nonlinear

equation were correlated with both relative tree density (–) and basal area (+), and a multiple linear regression with age, basal area and relative tree density had an R^2 of 0.57 (SEE = 2.88) kg C/m^2.

Variability of C pools

The coefficient of variation (CV) for ecosystem carbon within an age class was low and consistent among age classes (15–30%). CV for total live C was highest in the <25 yr age class (77%), but similar for the other age classes (21–36%). For total dead C, CV was highest for the 40–70 yr and 80–130 yr age classes (46–68%) and similar for the others (20–33%). Variability for organic soil C declined with stand age from a CV of 81% for stands 250 yr old. Mineral soil C was more variable among age classes, with CV of 22% in the >250-yr-old stands to 63% in the 80–130 yr old stands.

ANPP and LAI relationships with stand age and density

Tree aboveground net primary productivity (ANPP) increased from near zero the year after the 1988 fires to 60–160 g C·m^{-2}·yr^{-1} at age 12 (Litton et al. 2004), peaked at 620–980 g C·m^{-2}·yr^{-1} for stands 24–46 years old, and then decreased with stand age for stands >60 years old to a minimum of ~150 g C·m^{-2}·yr^{-1} (Fig. 5A). Both wood and leaf production declined for stands >60 years old ($P < 0.02$), but >90% of the decline in ANPP was from a decline in wood production. We did not estimate ANPP of saplings (trees <4 cm in diameter at 1.4 m) after age 16, but sapling LAI averaged only 2.1% of tree + sapling LAI for stands 40–130 years old and 7–10% for stands >170 years old, so sapling ANPP would have little effect on the pattern shown in Fig. 5A. Projected LAI of trees and saplings averaged 2.65 ± 0.14
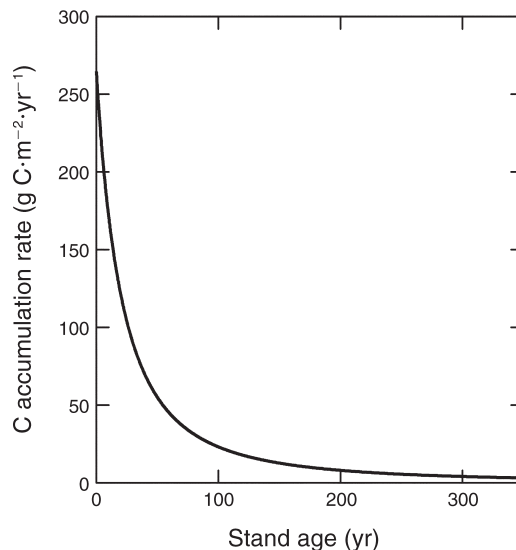

FIG. 4. Carbon accumulation rate decreases with increasing stand age. Carbon accumulation rate was calculated as the derivative of the function used to model total ecosystem C (C accumulation rate = 11 100 × 42.4/(42.4 + Age^2).
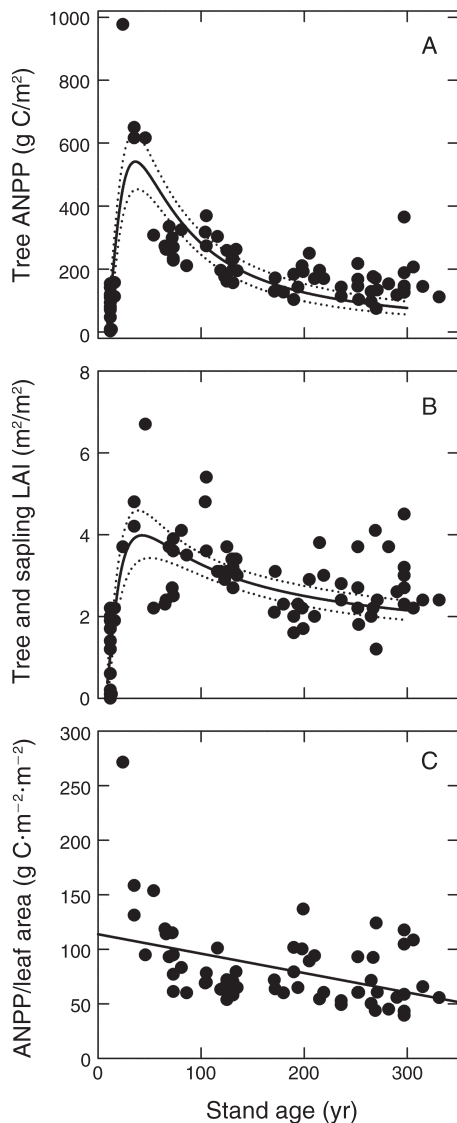
FIG. 5. (A) Tree aboveground net primary productivity (ANPP; in g C/m^2) and (B) leaf area (expressed as LAI; in m^2/m^2) peak early in the life of a lodgepole pine stand and then gradually decline with stand age. Tree ANPP includes sapling ANPP only for stands <17 yr old. The decline in (A) ANPP with age for stands older than 16 years is related to both the decline in (B) leaf area and a decline in (C) growth efficiency or ANPP/leaf area. For Age ≥12,

$$\text{Tree ANPP} = (0.1788\text{Age})^{\left[(0.00285\text{Age})^{-0.5349}\right]}$$

($R^2 = 0.53$, $P < 0.01$);

$$\text{Tree + Sapling LAI} = (0.0846\text{Age})^{\left[(0.0213\text{Age})^{-0.7769}\right]}$$

($R^2 = 0.49$, $P < 0.01$). Error bounds (dotted lines) are 95% confidence intervals for the mean prediction, estimated by SAS Proc NLIN.

m^2/m^2 (mean ± SE) and ranged from 0.04 in a very sparse, recently burned stand to 6.7 m^2/m^2 for a 46-yr-old stand. Tree + sapling LAI had the same pattern as ANPP: a rise to a peak at about age 50 and then a slow decline after age 50 (Fig. 5B). The CV for LAI within age classes decreased from 76% for stands <25 years old to 20–35% for the rest of the chronosequence. LAI was related to relative tree density (quadratic equation, $R^2 = 0.36$), with the highest LAI in stands with relative tree density between 0.4 and 0.6 and linearly related to stand basal area ($R^2 = 0.59$). Tree ANPP (plus sapling ANPP of stands aged 12–16 years) was strongly and linearly related to tree LAI and LAI for saplings aged 12–16 years (Fig. 6). The decline in ANPP for stands >60 years old was related to both a decline in LAI and a decline in ANPP/leaf area (i.e., growth efficiency) ($R^2 = 0.19$) over the same period (Fig. 5B and C).

Chronosequence evaluation

Our evaluation showed that stands <25 years old in our chronosequence were a representative sample of the landscape burned in 1988 because basal area (a proxy for biomass and carbon) of live trees killed by the 1988 fires was similar for stands <25 years old in our chronosequence and random locations across the burned landscape (Fig. 7A). The prefire basal area of chronosequence stands <25 years old was 48% less than the basal area of live trees in older chronosequence stands >100 years old ($P < 0.001$) and 38% less than random older stands on the unburned landscape ($P = 0.003$; Fig. 7B). This analysis suggests chronosequence stands <25 years old may underestimate C storage and storage trajectory for the forest that burned in 1988. Basal area of live trees in older chronosequence stands did not differ from the randomly sampled older stands
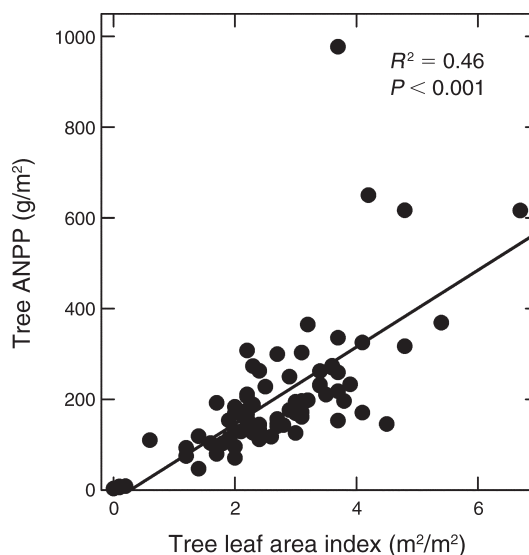

FIG. 6. Aboveground net primary productivity (ANPP) is closely related to stand leaf-area index (LAI). Tree ANPP includes sapling ANPP only for stands <17 years old.
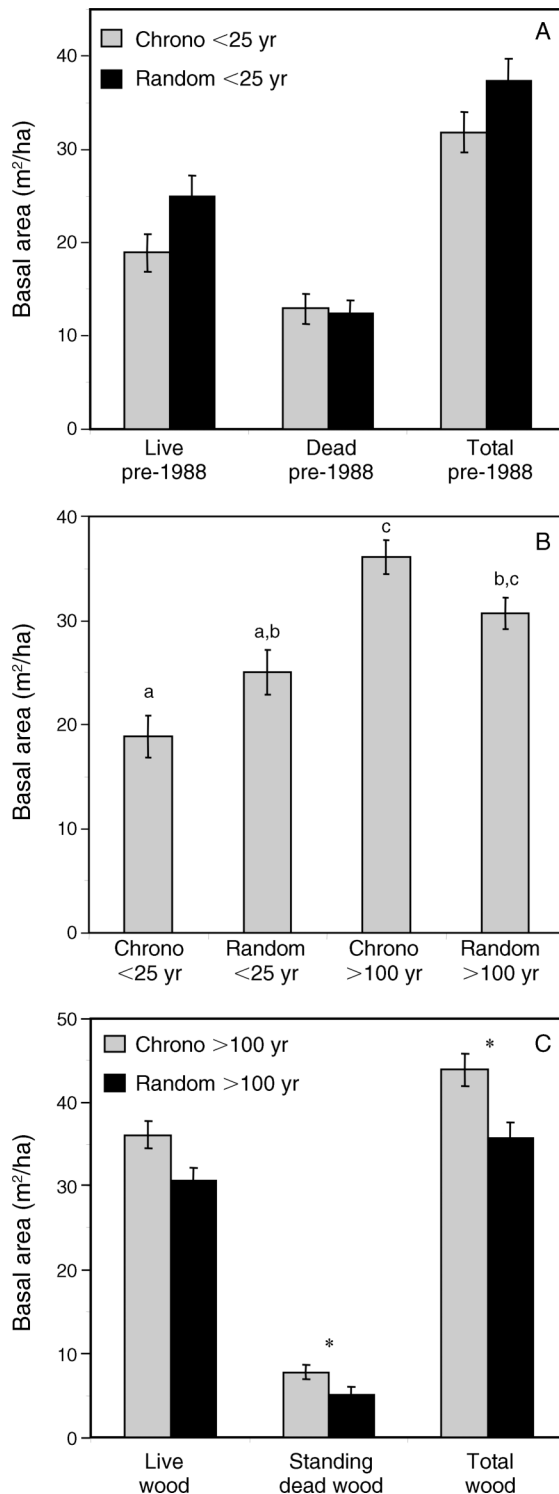
FIG. 7. Basal area in chronosequence stands compared to a random sample of the landscape in: (A) wood live and dead before the last fire in stands <25 years old; (B) live wood only for stands >100 years old and prefire live wood for stands <25 years old; and (C) live wood and standing dead wood in stands >100 years old. In panel (B) comparisons sharing a common lowercase letter are not significantly different; in panel (C) those marked with an asterisk (*) are significantly

on the unburned landscape ($P = 0.15$). Basal area of dead trees and total basal area prior to 1988 in the stands <25 years old in our chronosequence were similar to that of the rest of the burned landscape (Fig. 7A). Total basal area was 18% higher in our older chronosequence stands compared to random older stands on the landscape ($P = 0.023$), suggesting that older stands in the chronosequence may overestimate biomass and carbon for the Yellowstone National Park landscape (Fig. 7C).

DISCUSSION

Postfire recovery of C pools

Recovery of 80% of total ecosystem C within the first 50 years after a stand-replacing fire shows that landscape C is well buffered for historical fire regimes of 150–300 years (Romme 1982, Millspaugh et al. 2000), and that stands were historically likely to recover most or all of the C lost to combustion and mortality decomposition between stand-replacing fire events. The rate of C recovery and the size of the C pools are similar to other studies of forest C in the subalpine forests of the Rocky Mountains, although the C recovery rate is somewhat faster (Arthur and Fahey 1992, Kueppers and Harte 2005, Kashian et al. 2006, Bradford et al. 2008).

Ecosystem C accumulation declines with stand age as wood growth declines, but remains positive throughout the chronosequence. For stand age >70 yr, net ecosystem carbon balance (NECB) is not statistically different from zero. The lack of continued carbon accumulation in these older lodgepole pine forests contradicts other studies identifying older forests as important carbon sinks (e.g., Carey et al. 2001, Luyssaert et al. 2008). Note that the "global average" from flux studies for older forests of 240 g $C·m^{-2}·yr^{-1}$ (Luyssaert et al. 2008) is 48 times higher than the 5 g $C·m^{-2}·yr^{-1}$ for the NECB from our lodgepole pine chronosequence using the Michaelis-Menton fit.

Regeneration time exerts strong control on C recovery (McKinley et al. 2011), and seed release from serotinous cones after fire and subsequent rapid regeneration therefore promotes the recovery of C stocks for lodgepole pine forests. Recovery of C stocks would be slower on a landscape dominated by non-serotinous tree species. For example, Rothstein et al. (2004) documented maximum NECB (estimated as net ecosystem production, NEP) at 16 years for serotinous jack pine (*Pinus banksiana* Lamb.) ecosystems in Michigan compared to 50 years for non-serotinous Scots pine (*Pinus sylvestris* L.) ecosystems in a similar climate (Wirth et al. 2002). On the Yellowstone National Park (YNP) landscape, variability in cone serotiny for lodge-

different ($P < 0.05$). Data are means ± SE. Chronosequence stands likely underestimated biomass in young stands and overestimated biomass in older stands.

pole pine (Schoennagel et al. 2003, Tinker et al. 1994) may affect the recovery of C stocks following stand-replacing fires. Schoennagel et al. (2003) showed that cone serotiny is low at high elevations and in young stands at low elevations in Yellowstone, implying that postfire re-establishment of these stands will be slower or less successful than from older stands at low elevations.

NECB in the chronosequence was never negative, in contrast to theory summarized in Chapin et al. (2002), Kashian et al. (2006), and Goulden et al. (2010) for NEP. Eddy flux measurements for a variety of chronosequences recovering from disturbance showed that NEP is negative immediately after disturbance and slowly increases to a positive value over time (Amiro et al. 2010). Recovery of positive NECB generally occurs within 10 years of a disturbance and the small window of negative NECB releases relatively little of the ecosystem's C (Amiro et al. 2010, Goulden et al. 2010); our sampling started at age 12 and likely missed any negative NECB. The theoretical decrease in NEP comes from decomposition increasing over time after disturbance faster than aboveground productivity and C storage. Although some chronosequence studies have shown an initial decrease in NECB (e.g., Bond-Lamberty et al. 2004), the lack of an initial decrease in our study suggests that the large pool of organic matter killed by the disturbance is decomposing very slowly in this system, in part because of standing dead trees and fallen trees not in contact with the ground that do not decompose (Harmon et al. 2005).

The rapid recovery of ecosystem carbon (90% within 100 years) relative to the mean fire interval of 150–300 years is mostly driven by accumulation in live vegetation (a gain of 7780 g C/m^2 in 100 years, mostly from wood net primary productivity [NPP]), which greatly exceeded the decomposition of dead wood (a loss of 1960 g C/m^2 in 100 years). Carbon in live vegetation followed the typical pattern of rapid C accumulation early in the life of the stand followed by a slowing accumulation in maturing stands (Pearson et al. 1987) and is similar to patterns of biomass in younger stands and stands aged 15–100 years reported by Ryan and Waring (1992) and Smith and Resh (1999). Carbon in dead vegetation matched predictions of a "U-shaped" pattern with stand age, perhaps more closely than documented by any other study. This pattern is created by high initial amounts of fire-killed biomass immediately after the disturbance, a reduction of dead wood to a minimum in middle stand ages when this wood has decayed with only small dead-wood inputs from the re-established forest, and a final increase due to mortality of mature trees (Spies et al. 1988, Sturtevant et al. 1997, Martin et al. 2005, Brassard and Chen 2006). Variability of dead wood C within an age class was similar to the variability of other pools, but very little of the variability could be explained with stand age, tree density, or live basal area. This lack of explanatory power suggests that the forests that burned to create the legacy of dead wood in these stands were very heterogeneous (for younger stands) and that mortality processes within stands are also heterogeneous (for older stands).

Carbon storage and recovery in a warming climate

Marked changes in the fire regimes of subalpine forests will occur if climate change progresses as predicted in the Rocky Mountains (Westerling et al. 2006, 2011). For the YNP landscape to lose C under an altered fire regime, the new interval between stand-replacing fires would need to be less than the C recovery time (<50 years, Kashian et al. 2006, Smithwick et al. 2010). An analysis by Smithwick et al. (2011) showed that the mean fire interval would need to be less than 50 years to reduce landscape C by more than 25%. Westerling et al. (2011) showed that such changes are likely in the next 40 years given the warming that has already occurred in the northern Rocky Mountains and projected changes in climate. After 2050, fire rotations (the time to burn an area equal to the landscape area) for the YNP landscape are predicted to be <30 years (Westerling et al. 2011). Such large changes in the fire regime and climate are likely to also impact regeneration and fire severity, potentially converting forests into grasslands and greatly reducing C storage (Kashian et al. 2006). Significant reductions in fire interval could also create a younger landscape characterized by forests with higher C uptake and denser regeneration, but model analysis by Smithwick et al. (2010) suggests that these factors are unlikely to counter the C-lowering effects of more frequent fire. A conservative, rough estimate for C loss under a fire rotation of 30 years, using the chronosequence NECB relationship, is 30% of ecosystem C at age 250 (4.9 kg C/m^2), or more if regeneration fails. Thus, while C storage on the historic YNP landscape was largely shaped by postfire recovery of C pools under the historical fire regime, more frequent fire and the ability of lodgepole pine to regenerate under a new fire regime and climate are likely to be the primary drivers of future C storage.

Soil carbon

The decline of mineral soil C in the first 150 years was surprising and not countered by an increase in C in the organic horizons. After 100 years, 0–30 cm depth mineral soil lost 1460 g C/m^2 while the O horizon gained 689 g C/m^2. One explanation for the decline in mineral soil C with forest development is the concomitant decline in ANPP. Smith and Resh (1999) found that belowground C flux in lodgepole pine declined as ANPP declined with forest age. If the same decline in belowground flux occurred for this study, C in the mineral horizons might decline if decomposition exceeded inputs. Total soil C (organic and mineral) was unrelated to aboveground litterfall inputs ($P = 0.19$). Turnover time for organic horizon N increased with stand age for the same chronosequence (Smithwick et al. 2009), but the turnover rate for carbon in this study did

not ($P = 0.21$). The high variability in the mineral soil C for the stands that burned in 1988 might be caused by variation in the presence of charcoal in the soil (DeLuca and Aplet 2008). Although postfire decomposition of the organic soil has been shown to be important for C storage in boreal forests (O'Neill et al. 2002, 2003), organic soil C sampled from 12–16 year old stands was very low, indicating that the stand-replacing fires combusted most of the organic soil in this ecosystem. The higher C in the mineral horizons of younger stands suggests that the fire did not remove C from these horizons (Harden et al. 2000, Wirth et al. 2002). Our inability to adequately explain the decline of mineral soil C in this study suggests either that soil C is controlled by factors we were unable to adequately address in this study (e.g., variation in fire severity across the landscape), or that chronosequences are not powerful enough to discern important patterns of very slowly changing C storage in mineral soils.

Changes in ANPP and LAI with stand age

The decline in ANPP with increasing stand age for stands aged >25 years old (Fig. 5), was similar to that found for lodgepole pine in other studies (Pearson et al. 1987, Ryan and Waring 1992, Smith and Resh 1999) and similar in pattern to other tree species (Gower et al. 1996, Ryan et al. 1997, 2004, Drake et al. 2011). Part of the decline in ANPP was promoted by a decline in leaf area, but part was also related to a decline in ANPP/leaf area (growth efficiency). The mechanism promoting this decline in efficiency remains elusive, but it has not been caused by respiration (Ryan and Waring 1992, Ryan et al. 2004, Drake et al. 2011) or declining nutrition (Ryan et al. 2004) and the decline has been accompanied or perhaps caused by reduced photosynthesis (Ryan et al. 2004, Drake et al. 2010), perhaps because of hydraulic limitation (Ryan and Yoder 1997) or sink limitation (Ryan et al. 2006, Sala and Hoch 2009). In this study, the decline in growth efficiency with stand age suggests that either photosynthesis per unit of leaf area declined with stand age, or partitioning of photosynthesis to other sinks increased with stand age, or both (Ryan et al. 2010). The decline in leaf area with stand age after a peak was similar to that in other lodgepole pine chronosequences (Ryan and Waring 1992, Smith and Resh 1999). For all three chronosequences, nitrogen availability increased with forest age (Ryan and Waring 1992, Olsson et al. 1997, Smithwick et al. 2009), so declining nitrogen availability cannot be responsible for the declines in LAI or ANPP. Declining availability of other nutrients (such as P or K) might influence declining ANPP or LAI for lodgepole pine on poor soils, but data supporting this hypothesis are limited (Binkley et al. 1995).

Tree ANPP was closely related to leaf area for all stands. NPP is often related to LAI because of the link between leaf area, photosynthesis, and light absorption (Chapin et al. 2002), and this link is the basis of many forest growth models. In our present study the decline in ANPP/leaf area (growth efficiency) with forest age (Fig. 5C) shows that ANPP can vary for a given LAI, depending on forest age, as suggested previously for this system by Kashian et al. (2005a). ANPP, tree density, and LAI are closely related for saplings in stands derived from the 1988 fires in YNP (Reed et al. 1999, Turner et al. 2004).

Importance of structure for C storage

Structure is very important for C in young stands developing after the 1988 fires in YNP. Relative differences in sapling density—which varied over five orders of magnitude (Kashian et al. 2004, Turner et al. 2004)—are associated with spatial heterogeneity in forest productivity (Reed et al. 1999, Turner et al. 2004), nitrogen dynamics and allocation (Metzger et al. 2008, Turner et al. 2009), refugia from ungulate browsing (Forester et al. 2007), and the spatial distribution of downed wood (Tinker and Knight 2000). Litton et al. (2004) found that ecosystem C was constant across burned areas of contrasting sapling density in YNP, but individual C pools such as live biomass and organic soil C varied with sapling density.

Our chronosequence shows that tree density becomes less important for C storage after canopy closure, and stand age and basal area become more important. In stands <25 years old, tree density is a proxy for site occupancy by trees and for LAI so that the correlation of ANPP and LAI is not surprising. Most sites in older stands are at maximum LAI, perhaps depending more on disturbance, self-thinning, and their particular history than on tree density. Our present study contrasts with the modeling exercise of Kashian et al. (2006), which suggested that C storage at the landscape scale for YNP was more sensitive to changes in tree density than to changes in stand age, because stands with sparse regeneration would be slow to accumulate C. Our chronosequence instead suggests that postfire recovery of leaf area—related to but not directly correlated with tree density—is critical to recovery of ecosystem C.

Kashian et al. (2006) speculated that the ability of a postfire stand to regenerate and develop into a mature stand that mirrors its prefire C—stand replacement—is critical to net C storage over the length of the mean fire interval. Our data suggest that strict stand replacement is unlikely. In stands <40 years old, where fire-killed trees were still present and reconstruction of prefire basal area was possible, regeneration after the 1988 fires decreased as basal area of the trees that were alive before the 1988 fire increased ($R^2 = 0.28$). Regeneration also decreased as the basal area of standing or down dead wood prior to the fire minus any combustion losses increased ($R^2 = 0.45$). In other words, older stands with higher basal area yielded lower regeneration when burned than did younger stands with lower basal area. The variability in both live and dead biomass in the chronosequence also suggests that stands do not replace

TABLE 4. Preliminary results comparing the average amount of carbon stocks in various components for six stands aged 134–262 years at the time of outbreak unaffected by a mountain pine beetle outbreak and six stands of the same age affected by a mountain pine beetle outbreak 25–30 years ago.

Forest stands	Aboveground C (g C/m^2)*	Dead-wood C (g C/m^2)*	Belowground C (g C/m^2)	Forest floor C (g C/m^2)*	Total C (g/m^2)	Tree ANPP (g C·m^{-2}·yr^{-1})
No beetles	10 432	5180	1493	756	17 859	200
Beetles	8 265	6879	1404	911	17 459	200

* $P < 0.05$.

themselves, or at least not exactly. Unfortunately, prefire structure and fire severity are very difficult to identify, and are major weaknesses of this and other chronosequences in fire-prone landscapes in terms of estimating changes in dead C (Wang et al. 2003, Irvine et al. 2007). Fire severity, in particular, may have important impacts on patterns of postfire succession and C accumulation (Chapin et al. 2002) that we were unable to address with the chronosequence approach.

Are chronosequences effective?

A chronosequence assumes that stands vary only in age (Jenny 1941), but makes no assumption about how well the chronosequence represents the sampling area. As such, unreplicated chronosequences have been criticized as misleading (Turvey and Smethurst 1989, Yanai et al. 2000, Johnson and Myanishi 2008). We assert that replicating chronosequences across a landscape, where possible, strengthens the inference that may be derived from chronosequence studies, so long as there is evidence to suggest that the sampled stands are representative of the landscape.

Random sampling revealed that our chronosequence represented the landscape well. However, the data show that the notion of a single chronosequence or even three chronosequences organized by trends in tree density through time cannot capture all of the variability in C on the landscape. The chronosequence was likely to underestimate C in recently burned stands because prefire live basal area (and thus postfire dead wood) was lower compared to the greater landscape, and overestimate C in older stands because basal area is higher compared to the greater landscape. We also expected the chronosequence to show less increase in ecosystem C with stand age (a higher value immediately after the fire and a lower final value).

A major uncertainty in our chronosequence was the discrepancy between the amount of total C in the youngest compared to the oldest stands in the chronosequence. Mean C in our stands 250 years old (see Appendix A). This difference might be partially explained by C loss to combustion, which may be much higher than the 8% estimated by Tinker and Knight (2000), who made their estimates based on relatively large dead wood in an older stand. Many of the stands that burned in 1988 in YNP were younger and likely had much smaller dead wood that may have completely combusted; in these cases, combustion would have been

higher than 8%. The stands >25 years old in our chronosequence were mostly from higher elevations on the Yellowstone subalpine plateaus, where live biomass and dead wood may be higher with less frequent fire and beetle outbreaks and slower decomposition of dead wood.

Sample replication improved the models of ecosystem C. The amount of replication necessary in any field study depends on the strength of the signal relative to the variability present. For our study, a >50% random subsample of the chronosequence was required to reliably recover the nonlinear equation coefficients for ecosystem C—which has an inherently strong signal— compared to a simple linear regression. Replication is clearly necessary when using chronosequences to characterize landscape variability in ecosystem C with stand age.

Potential C storage response to mountain pine beetle outbreaks

Tree mortality following mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreaks can alter forest C storage by affecting the same C pools examined in this study. We examined a subset of the older stands in our chronosequence to determine the impact of mountain pine beetle on ecosystem C 25–30 years after an outbreak by comparing C pools and fluxes for six stands in each group ranging from 134 through 262 years old. Ecosystem C did not differ between the two groups, but the beetle-attacked stand had more dead wood and organic soil C, and less live biomass, than the stands without the mountain pine beetle attack (Table 4). Mortality in the previous beetle outbreak in YNP in the 1970s and 80s (~25% of the lodgepole pine biomass; Romme et al. 1986) appears to be substantially lower than that of the current outbreak elsewhere in western North America, where >70% of the basal area (linearly related to volume) of lodgepole pine was killed by the beetle outbreak in Colorado (Collins et al. 2011). Given that insect outbreaks are second only to wildfires as the largest source of tree mortality in western North America (Samman and Logan 2000), further research into insect outbreak effects on forest carbon storage is certainly warranted.

Conclusions

Natural variability is important for understanding the carbon cycle in fire-prone landscapes, even when the

dominant vegetation type is monospecific and its structure appears relatively simple compared to other forest types. Ecosystem C and the components that comprise it all varied with stand age for our 77-stand chronosequence, and stand age was the dominant control. Stand structure was also important for explaining variability in ecosystem C, live C, and organic soil C. Tree growth, not decomposition of dead wood, controlled the recovery of C after fire, and recovery of C was rapid compared to the historical fire interval. A fire interval of <50 years would remove more than 25% of the ecosystem C over the long term, and projected changes in climate for the next 40 years suggest reductions in frequency that would easily meet this criterion. Therefore, climate-change-induced increases in fire will almost certainly lower ecosystem C, if climate changes as predicted. Though imperfect, replicated chronosequences remain the only way to study recovery from disturbance in slow-growth forests and to capture landscape variability in forest age, stand history, regeneration, fire effects, and disturbance. Forest chronosequence studies should therefore remain an important part of future research to understand variability in patterns of carbon dynamics during forest stand development.

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Supplemental Material

Appendix A

A table of carbon pools for lodgepole pine stands of contrasting age and density in Yellowstone National Park (*Ecological Archives* M083-002-A1).

Appendix B

Description of methodology used to develop allometric equations for estimating lodgepole pine biomass (*Ecological Archives* M083-002-A2).

Data Availability

Data associated with this paper have been deposited in Dryad: http://dx.doi.org/10.5061/dryad.1v87f