

Changing growth response to wildfire in old-growth ponderosa pine trees in montane forests of north central Idaho

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Abstract

North American fire-adapted forests are experiencing changes in fire frequency and climate. These novel conditions may alter postwildfire responses of fire-adapted trees that survive fires, a topic that has received little attention. Historical, frequent, low-intensity wildfire in many fire-adapted forests is generally thought to have a positive effect on the growth and vigor of trees that survive fires. Whether such positive effects can persist under current and future climate conditions is not known. Here, we evaluate long-term responses to recurrent 20th-century fires in ponderosa pine, a fire-adapted tree species, in unlogged forests in north central Idaho. We also examine short-term responses to individual 20th-century fires and evaluate whether these responses have changed over time and whether potential variability relates to climate variables and time since last fire. Growth responses were assessed by comparing tree-ring measurements from trees in stands burned repeatedly during the 20th century at roughly the historical fire frequency with trees in paired control stands that had not burned for at least 70 years. Contrary to expectations, only one site showed significant increases in long-term growth responses in burned stands compared with control stands. Short-term responses showed a trend of increasing negative effects of wildfire (reduced diameter growth in the burned stand compared with the control stand) in recent years that had drier winters and springs. There was no effect of time since the previous fire on growth responses to fire. The possible relationships of novel climate conditions with negative tree growth responses in trees that survive fire are discussed. A trend of negative growth responses to wildfire in old-growth forests could have important ramifications for forest productivity and carbon balance under future climate scenarios.

Keywords: climate change, fire, growth, ponderosa pine

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Introduction

North American fire-adapted forests are experiencing changes in fire frequency and climate. In addition to potential effects on fire activity (Running, 2006; Westerling *et al.*, 2006; Morgan *et al.*, 2008), these novel conditions may also alter postwildfire responses of fire-adapted trees that survive fires. Changes in tree growth responses to recent wildfire have received little attention, but could have important ecosystem effects.

Ponderosa pine forests are a widespread fire-adapted forest type that range across western North America. Historical, frequent, low-intensity wildfire in many ponderosa pine forests has generally been considered to have a positive effect on the growth and vigor of ponderosa pine trees that survive after fire (Covington & Sackett, 1986, 1992; Donner & Running, 1986; Agee,

1993; Baird *et al.*, 1999; Stone *et al.*, 1999; Gundale *et al.*, 2005). Active fire suppression policies during the 20th century, however, have led to a decrease of fire frequency in many of these forests. This is also true for mixed-species ponderosa pine forests in the inland northwest that have historically longer fire intervals. The relative lack of frequent fire in these forests has created high stand densities and fuel loads, a possible cause of increasing numbers of uncharacteristically high-severity wildfires in recent years (Arno & Allison-Bunnell, 2002; Miller *et al.*, 2009) that are more likely to harm residual trees (Raymond & Peterson, 2005; Strom & Fulé, 2007). Adding to the potential effects of increasing fuels in many forests is evidence that recent fire activity may also be strongly linked to changing climatic conditions (Westerling *et al.*, 2006). Historically, years with large numbers of fires across western North America were warmer and drier than normal, while years when no fires burned were cooler and wetter (Heyerdahl *et al.*, 2008a). Consistent with this, in the 20th century, years with higher summer temperatures

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and earlier snowmelt had greater numbers of fires, and fires burned longer under these conditions (Running, 2006; Westerling *et al.*, 2006; Morgan *et al.*, 2008). Warmer and drier climatic conditions are therefore a likely cause of increasing fire activity since 1980 (Westerling *et al.*, 2006). Although there is uncertainty about whether higher fire intensities and severities are associated with these changes (Keane *et al.*, 2008), it is probable that stand and climatic conditions that produce larger, longer, and more numerous fires across landscapes also produce fires that are hotter and more destructive to trees and forests (Lavery & Williams, 2000; Keane *et al.*, 2002; Ryan, 2002; Hood *et al.*, 2007; Miller *et al.*, 2009). In addition, warmer and drier conditions may create soil moisture deficits that could weaken trees and decrease resilience to fire even if fire intensity (heat experienced by the tree during fire) is not changed.

These potentially novel environmental changes may alter the net effect of wildfire on individual tree growth, even in fire-adapted species. Ponderosa pine has thick bark and self-pruning branches that protect mature trees from fires. Relatively frequent fire in these forests is thought to promote vigorous growth by limiting competition with smaller trees for important resources (Covington & Sackett, 1986, 1992; Donner & Running, 1986; Agee, 1993; Baird *et al.*, 1999; Stone *et al.*, 1999; Gundale *et al.*, 2005). Positive tree responses have been reported in treatments that reduce density via thinning (Feeney *et al.*, 1998; Kolb *et al.*, 1998; Latham & Tappeiner, 2002; Sala *et al.*, 2005; Ritchie *et al.*, 2008), burning (Weaver, 1967), or combined thin and burn treatments (Fulé *et al.*, 2005; Zausen *et al.*, 2005). However, fire can also harm trees directly (Hood *et al.*, 2007), reduce N in the soil (Grier, 1975; Landsberg *et al.*, 1984; Monleon *et al.*, 1997; Wright & Hart, 1997; DeLuca & Zouhar, 2000), or impair below-ground biotic communities responsible for nutrient cycling (Neary *et al.*, 1999). Not surprisingly, treatments that include fire have sometimes produced net negative effects on trees (Landsberg *et al.*, 1984; Busse *et al.*, 1996; Maloney *et al.*, 2008) or lower benefits compared with thin-only treatments (Ritchie *et al.*, 2008). An important question is whether novel climate or changes in fire frequency or severity will alter the balance of positive vs. negative effects of individual fires on tree growth.

The effects of recurrent fire on fire-adapted trees are complex and difficult to study. Studies after single fires are insufficient because the integrated long-term effects of multiple recurrent fires may be different from the sum of short-term responses to individual fires. For example, recurrent fires that individually harm surviving trees may benefit these same trees over the longer term by reducing competition. Experimental treatments

also may not mimic unmanipulated wildfire in unmanaged forests and before-and-after studies usually lack unmanipulated control stands, weakening inferences. Comparing stands burned under natural (unmanipulated) conditions with nearby unburned stands is usually infeasible because of the rarity of natural pairing that would control for other environmental differences between stands that would affect tree responses. Furthermore, growth responses driven by competitive release may be biased in second growth forests where stands are likely to be more dense (Naficy *et al.*, 2010) and more even-aged. These limitations (prescribed fire instead of natural fire, lack of paired control stands, and lack of research in unlogged forests) mean that current knowledge of tree growth responses to fire may be incomplete, especially for old-growth forests. The rare studies that have been conducted in unlogged stands either used prescribed fire treatment (Fulé *et al.*, 2005) or did not use paired burned and unburned stands (Sutherland, 1983). Importantly, we know of no study in unlogged forests that measured separate repeated short-term responses to recurring natural wildfires and integrated long-term responses to multiple fires using paired burned and control stands.

Whether novel conditions are altering responses to wildfire in fire-adapted forests is a question of potentially great importance. If tree growth responses to wildfire are changing, ecosystem processes such as productivity and carbon sequestration rates of forests may be affected. Old growth forests can store and continue to sequester carbon over many years (Carey *et al.*, 2001; Luysaert *et al.*, 2008); however, forests across the west are currently experiencing increases in background mortality rates, most likely because of drier climatic conditions (Van Mantgem *et al.*, 2009). There is some evidence that fire severity may affect growth in surviving trees (Mutch & Swetnam, 1995) but whether current climate trends are affecting tree physiology or fire activity to the point of reducing tree growth after fire is not clear. Negative responses to fires under novel conditions could have ramifications both commercially and ecologically for forests. The relative importance of climate change vs. increases in stand density and fuel loads in determining fire responses is a critical distinction for forest management in this context.

In this study, we asked the following questions: (i) How do long-term ponderosa pine growth responses to multiple fires in burned stands compare with growth responses in unburned control stands? (ii) Have short-term (5- and 10-year) growth responses to individual fires changed over the course of the 20th century? (iii) To what extent do climate variables associated with fire activity (temperature and precipitation) and variables associated with increasing fuels (time since fire)

contribute to temporal variability of short-term responses to fire? We used tree-ring measurements to assess both long- and short-term ponderosa pine growth responses to wildfire by comparing trees in paired burned and unburned stands in unlogged forests of northern Idaho. The unlogged status of our sites ensures no confounding effects of prior logging on tree responses to wildfire (Naficy *et al.*, 2010).

Materials and methods

Site selection

In 2003, a total of seven remote study sites were located in unlogged, low- to mid-elevation ponderosa pine/Douglas-fir forests within or on the periphery of wilderness areas in Idaho (see Deluca & Sala, 2006; Keeling *et al.*, 2006, for site selection details). From these sites, four were chosen for this study (Fig. S1). At each site, a stand that burned multiple times was compared with a nearby paired control stand that remained unburned during the same time period. Control stands had not experienced fire for at least 70 years. During the same time period, burned stands experienced one, two, or four wildfires (depending on the site) at intervals ranging from 6 to 58 years (mean = 34 years) with the most recent fire between 12 and 17 years before sampling. Fire histories for all stands were based on U.S. Forest Service fire maps, field reconnaissance, and on-site fire scar analyses (see Deluca & Sala, 2006; Keeling *et al.*, 2006; Keeling *et al.*, in press for more detailed methods on fire histories). Although some physiographic differences between stands existed, on average there were no systematic physiographic differences between control and burned stands from each site across the entire study (paired *t*-tests comparing slope, aspect, and elevation, $P > 0.05$; see Table S1 for environmental data and fire history information). We cannot determine whether fires were actively suppressed even in these remote areas, therefore the terms 'repeatedly burned', 'unburned', or 'control' are not meant to suggest effects because of human management decisions. The fire return intervals in our burned stands are within the historical (i.e., pre-1900) range, which can be more than 25 years for mixed ponderosa pine forests in the northwest region (Arno, 1980; Arno & Allison-Bunnell, 2002; Heyerdahl *et al.*, 2008b).

Data collection

In June and July 2004, an access route across each stand was chosen. Access routes were stratified into equal distances and points along the route were generated randomly within each stratified length. The nearest mature ponderosa pine tree to each point was selected for sampling. At least 10 mature trees were sampled in each stand. In 2006 and 2007, additional trees were sampled at two sites, Mackay Bar (MB) and Bullion Ridge (BR). At each tree, elevation, aspect, slope, GPS coordinates, and tree diameter at breast height (DBH) were recorded. Increment borers were used to extract two cores from each tree and tree diameter at coring height was recorded. The two

cores were taken from opposite sides of the tree, perpendicular to the direction of the slope. Cores were taken at approximately 50 cm height from the ground. Coring heights were recorded for each core. Four bark depth measurements were taken at coring height using a standard forester's bark gauge. Cross-sections at ground level of three ponderosa pine seedlings were taken in each stand for use in estimating ages of trees at coring height. Heights of each seedling were recorded.

Sample preparation and cross-dating

Cores were glued onto wooden core mounts and sanded until rings could easily be distinguished with a binocular microscope. Rings were counted and years were provisionally marked starting at the outermost ring and counting inward toward the innermost ring. The two cores from each tree were visually cross-dated against each other (Stokes & Smiley, 1996) and against a time series of reconstructed Palmer Drought Severity Index (PDSI; http://www.ncdc.noaa.gov/paleo/drought/drght_pdsi.html) for the region. Relatively narrow and wide rings, rings with notable latewood, suspected false or missing rings, and years of growth suppression or release, were recorded and used as an aid in cross-dating of all cores (Yamaguchi, 1991). Rings from all cores were then measured to the nearest 0.001 mm using a Velmex measuring station. The program COFECHA was used to verify the dating accuracy and as an aid in determining missing and false rings which were then checked and corrected by eye on the cores (Holmes, 1983). Tree-ring series were successfully dated for all trees at all sites with the exception of two trees at MC. These two trees were excluded from analyses.

Age estimation

Once cores were cross-dated, the year of the inner-most ring established a minimum estimate of tree age. However, because very few cores intersected the pith of the tree and because trees could not be cored at exactly ground height, it was necessary to add pith and height corrections to the date of the innermost ring to estimate age more accurately. For height corrections, seedling cross-sections were sanded and rings were counted. Height of each seedling was divided by age to compute growth rates (cm year^{-1}) for each seedling and growth rates were compared using two-way ANOVA with site and burned status (burned vs. unburned) as factors. Seedling growth rates did not differ by site or burn status, therefore, all seedlings were pooled and a mean growth rate (cm year^{-1}) was calculated. For each tree, coring height was divided by the mean growth rate to estimate the years to coring height. To estimate the number of rings to pith two methods were employed. Where the geometry of the inner three rings was easily measured, the distance to the pith was calculated from the height and length of the last incomplete ring and this distance was divided by the average of the three inner rings to estimate the number of missing rings to the pith (Duncan, 1989). On some cores, the use of transparent concentric circles was used to make the same estimate (Applequist, 1958).

Calculation of basal area increments

The radius of each tree was calculated by dividing the measured diameter at coring height by 2 and subtracting the average bark depth. Annual radial growth increments were converted to proportions of the total radius (Bakker, 2005) and then converted to annual basal area increments (BAIs) by assuming circular basal area with the pith at the center. Annual BAIs were averaged for the two cores from each tree.

Long-term growth responses to multiple fires

To assess long-term growth responses at each site, we first determined a comparison period, the period during which lack of fire was affecting the control stand (unburned for at least 70 years) and recurrent wildfire was affecting the respective paired burned stand, and a precomparison period, when both stands experienced the same fire exposure. The boundary between precomparison and comparison periods was the year of the earliest 20th-century fire which affected the burned stand but not the control stand. For one site, Moose Creek (MC), this boundary was the year of the first recorded 20th century fire in the burned stands. For two sites, MB and BR, this boundary was the second recorded fire in the burned stand, as both stands experienced the first fire recorded. Long-term growth responses were not computed for the fourth site, Twenty-three Mile (TW), because only a 1992 fire was unique to the burned stand and the comparison period was only 12 years. At MB and BR, the number of years in the comparison period was used to determine the length of the precomparison period. At MC, because the comparison period was much longer and trees were younger, the years 1900–1909 were used as the precomparison period for both stands. As precomparison and comparison periods are the same for each set of paired stands, climatic effects on paired stands were also controlled.

For each tree, the average BAI in the comparison period was divided by its average precomparison period BAI to produce standardized growth values for each tree. Values >1 and <1 represent positive and negative growth responses, respectively. By standardizing growth of each tree, environmental differences between stands that might confound growth differences between stands were controlled. Standardized growth values for each tree were averaged to produce mean standardized growth for each stand. Growth responses at each site were then expressed as: (mean standardized BAI burned stand/mean standardized BAI control stand) $- 1$. By subtracting 1, growth responses are adjusted so that positive values for growth responses indicate higher growth responses, negative values indicate lower growth responses, and a value of 0 indicates no growth response in burned stands compared with the control stands.

Short-term growth responses to individual fires

Five- and 10-year periods, prior to and subsequent to the year of fires affecting the burned stand were used to calculate standardized growth differences (mean BAI after fire year/mean

BAI before fire year) analogous to the long-term standardized growth calculations described before. Site responses were again expressed as: (mean standardized BAI burned stand/mean standardized BAI control stand) $- 1$.

Controlling for age-related growth effects

Growth responses to wildfire may be confounded with age-related effects on growth if sampled trees are in different stages of age-related growth or if significant age differences exist between comparison groups. We minimized potential confounding effects of age as follows: inspection of individual tree growth curves (annual BAI plotted as a time series) at our sites showed that BAI generally increased during early stages of tree ontogeny and then stabilized, usually between ages 50 and 100. Based on these observations, we chose the conservative criterion of only using trees at MB and BR that were at least 100 years old at the beginning of the comparison period. At MC and TW, we included trees that were younger than 100 years old at the time of the comparison period, but only after inspecting the individual growth curves for each tree and ensuring that age-related growth had stabilized for the time period analyzed. Based on these observations, one particularly young tree at MC was excluded from all analyses. Two very old trees from the burned stand at MB were also removed to ensure that average ages between paired stands were similar. There were no significant differences in mean ages between trees in control and burned stands for most tests, with the exception of the long-term response analysis at MC and short-term analyses for 1910 and 1934 at MC. However, the mean age difference between trees for these analyses at MC were not great (mean age control = 192, mean age unburned = 225) and inspection of individual growth curves ensured that all trees analyzed were beyond the period of increasing growth in the early part of the growth curve. Mean tree ages and ranges are recorded in Tables 1 and 2. In addition, correlation analyses showed no significant relationships between tree ages at and 5- and 10-year growth responses to fires for trees older than 100 years (results not shown).

Temporal trends and effects of climatic conditions and time-since-fire

Five- and 10-year growth responses to individual fires for each site and fire year were calculated as described before and plotted in a time series. We tested whether climatic variables that generally influence the size, duration, and number of regional fires were correlated with tree growth responses after fire. Dry winters and warm springs and summers are the general characteristics of years with increased fire activity in this region (Westerling *et al.*, 2006; Morgan *et al.*, 2008; Heyerdahl *et al.*, 2008a). Monthly precipitation and temperature data were obtained for the north-central mountain region of Idaho from NOAA divisional climate data (available online at: ¹). Temperature and precipitation data were converted to anomalies by subtracting each monthly value from the long-term mean. We

¹www7.ncdc.noaa.gov/CDO/CDODivisionalSelect.jsp

Table 1 Long-term growth responses to multiple fires

Site	MC		BR		MB	
	Control	Burned	Control	Burned	Control	Burned
Fires since 1880	None	1910, 1934, 1981, 1987	1914	1914, 1944, 1992	1919	1919, 1960, 1987
Precomparison period	1901–1910	1901–1910	1886–1944	1886–1944	1918–1960	1918–1960
Comparison period	1911–2003	1911–2003	1945–2003	1945–2003	1961–2003	1961–2003
Mean tree age (range)	191 (161–215)	225 (167–282)	330 (287–372)	341 (270–427)	320 (158–355)	344 (188–454)
Growth response (CI), <i>n</i>	0.77 (0.16), <i>n</i> = 9	1.69 (0.56), <i>n</i> = 8	0.76 (0.55), <i>n</i> = 8	0.84 (0.11), <i>n</i> = 17	1.34 (0.20), <i>n</i> = 10	1.21 (0.06), <i>n</i> = 21

Growth responses were calculated as mean of individual tree BAI during comparison period/BAI during precomparison period. Growth response values >1 and <1 represent increases or decreases in basal area growth, respectively, in the comparison period compared with the precomparison period (see 'Materials and methods'). Significant differences ($P < 0.05$) between control and burned stands within sites are given in **bold**. BAI, basal area increment. CI, confidence interval.

Table 2 Short-term growth responses to individual fires

Stand	Control		Burned		Control		Burned	
	Control	Burned	Control	Burned	Control	Burned	Control	Burned
Site of fire/year		MC/1910		MC/1934		MC/1944		BR/1944
Mean tree age (range)	191 (161–215)	225 (167–282)	191 (161–215)	225 (105–282)	330 (287–372)	341 (270–427)	330 (287–372)	341 (270–427)
5-year growth response (CI), <i>n</i>	1.03 (0.06), <i>n</i> = 9	1.19 (0.14), <i>n</i> = 8	0.88 (0.09), <i>n</i> = 9	1.04 (0.20), <i>n</i> = 8	0.95 (0.08), <i>n</i> = 8	0.86 (0.08), <i>n</i> = 17	0.95 (0.08), <i>n</i> = 8	0.86 (0.08), <i>n</i> = 17
10-year growth response (CI), <i>n</i>	0.99 (0.09), <i>n</i> = 9	1.17 (0.12), <i>n</i> = 8	0.87 (0.07), <i>n</i> = 9	1.14 (0.24), <i>n</i> = 9	1.20 (0.14), <i>n</i> = 8	1.05 (0.09), <i>n</i> = 17	1.20 (0.14), <i>n</i> = 8	1.05 (0.09), <i>n</i> = 17
Site of fire/year		MB/1960		MC/1981		MB/1987		MB/1987
Mean tree age (range)	320 (158–355)	344 (188–454)	192 (161–215)	212 (105–282)	250 (143–355)	312 (141–454)	250 (143–355)	312 (141–454)
5-year growth response (CI), <i>n</i>	1.00 (0.11), <i>n</i> = 10	0.96 (0.08), <i>n</i> = 21	0.83 (0.06), <i>n</i> = 9	0.87 (0.06), <i>n</i> = 9	0.74 (0.08), <i>n</i> = 17	0.49 (0.08), <i>n</i> = 25	0.74 (0.08), <i>n</i> = 17	0.49 (0.08), <i>n</i> = 25
10-year growth response (CI), <i>n</i>	1.03 (0.10), <i>n</i> = 10	1.07 (0.12), <i>n</i> = 21	NA	NA	0.79 (0.11), <i>n</i> = 17	0.57 (0.07), <i>n</i> = 25	0.79 (0.11), <i>n</i> = 17	0.57 (0.07), <i>n</i> = 25
Site of fire/year		MC/1987		BR/1992		TW/1992		TW/1992
Mean tree age (range)	192 (161–215)	212 (105–282)	260 (142–372)	255 (134–427)	181 (165–205)	168 (156–189)	181 (165–205)	168 (156–189)
5-year growth response (CI), <i>n</i>	0.93 (0.13), <i>n</i> = 9	0.69 (0.15), <i>n</i> = 9	1.81 (0.55), <i>n</i> = 13	1.27 (0.13), <i>n</i> = 31	1.10 (0.14), <i>n</i> = 10	1.10 (0.11), <i>n</i> = 10	1.10 (0.14), <i>n</i> = 10	1.10 (0.11), <i>n</i> = 10
10-year growth response (CI), <i>n</i>	1.00 (0.26), <i>n</i> = 9	0.69 (0.12), <i>n</i> = 9	1.65 (0.50), <i>n</i> = 13	1.11 (0.13), <i>n</i> = 31	1.05 (0.15), <i>n</i> = 10	0.95 (0.14), <i>n</i> = 10	1.05 (0.15), <i>n</i> = 10	0.95 (0.14), <i>n</i> = 10

Growth responses were calculated as mean of individual tree basal area increments (BAIs) after fire/before fire. Growth response values >1 and <1 represent increases or decreases in basal area growth, respectively, after fire compared with before fire (see 'Materials and methods'). Responses using 5 years and 10 years before and after periods are shown. Significant differences ($P < 0.05$) between control and burned stands for individual fire events are given in **bold**. CI, confidence interval; NA, not applicable.

used simple linear regression to test for significant relationships between 5- and 10-year growth responses to fire and seasonal temperature anomaly, precipitation anomaly, and PDSI for the following seasonal periods prior to each fire: winter (December–February), spring (March–May), summer (June–August), winter–spring (December–May), spring–summer (March–August), and winter–summer (December–August). Growth responses were also plotted against time-since-fire, which was computed as the number of years since the previous fire, and the relationship was tested using simple linear regression.

Statistical analysis

Statistical tests were carried out using the software SPSS 16.0 (IBM, Poughkeepsie, NY, USA). All growth response and age data were tested for normality and homogeneity of variance using Kolmogorov–Smirnov and Levene’s tests, respectively. Five- and 10-year growth response data that failed tests of normality or homogeneity were transformed using square-root or log transformations. If variance could not be stabilized by transformation, a Kruskal–Wallis nonparametric test was employed. We used one-way ANOVA analyses for both long- and short-term responses to fire with stand (control vs. burned) as the main factor and analyzed trees in the age ranges described before (see ‘Controlling for age-related effects’). Relationships between 10-year growth responses to fire and prefire seasonal climate variables and time since fire were tested using simple linear regression.

Results

Long-term growth responses

At one site (MC), there was a significant positive long-term growth response in the burned stand (Table 1). There were nonsignificant long-term growth responses at BR and MC (Table 1).

Short-term growth responses

Short-term growth responses varied depending on fire event (Table 2 and Fig. 1). There were significant positive growth responses to fire at MC in 1910 and 1934. Ten-year responses were slightly stronger than 5-year responses. There were significant negative growth responses at MB in 1987, MC in 1987, and at BR in 1992. Again, 10-year responses were stronger than 5-year responses. Responses for the four other fires analyzed were not significant. Ten-year responses for the 1981 fire at MC were not computed because a subsequent fire occurred less than 10 years later.

Temporal trends, climate, and time-since-fire effects

There was a significant trend of more negative growth responses to fire in more recent years. The trend was

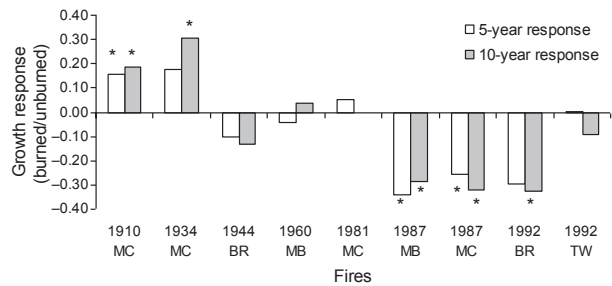


Fig. 1 Ponderosa pine average short-term growth responses to individual fires for nine fire events at four sites. Growth responses to fire were computed as: (mean standardized BAI burned stand/mean standardized BAI unburned stand) – 1. Five-year responses are in white and ten-year responses are in gray. Bars with an * are statistically significant responses (ANOVA, $P \leq 0.05$). Mean standardized BAI, confidence intervals, and sample sizes used to calculate short-term responses are in Table 2. BAI indicates basal area increment.

stronger for 10-year growth responses (Fig. 2a; $R^2 = 0.68$, $P = 0.011$) than for 5-year responses (Fig. 2b; $R^2 = 0.49$, $P = 0.036$). Owing to the stronger trend in

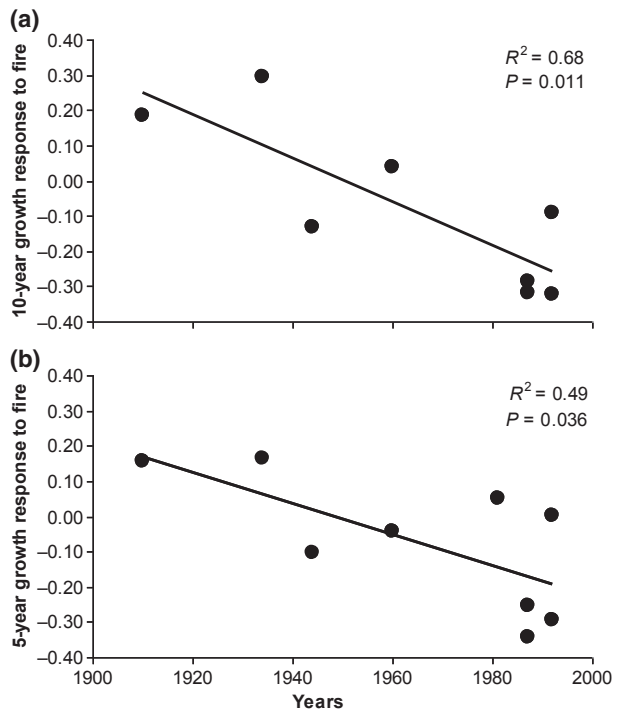


Fig. 2 Ponderosa pine mean growth responses to fire plotted against year of fire. Growth responses to fire were computed as: (mean standardized BAI burned stand/mean standardized BAI unburned stand) – 1. (a) Ten-year growth responses to fire for eight fire events; (b) 5-year growth responses to fire for nine fire events. BAI indicates basal area increment.

10-year growth responses to fire, we focused our climate regression analyses on the 10-year responses. Lower winter (December–February) precipitation was significantly correlated with negative growth responses to fire in recent years (Fig. 3a; $R^2 = 0.852$, $P = 0.001$). Winter (December–February) temperature anomalies were not significantly correlated with growth responses to fire (Fig. 3b; $R^2 = 0.012$, $P = 0.794$), although the lack of significance was primarily because of exceptionally warm winter temperatures in 1934, a year with positive growth responses to fire. Despite the lack of significant overall correlation with temperature, recent years with negative growth responses to fire all had anomalously warm winter temperatures. Winter PDSI was significantly correlated with growth responses to fire (Fig. 3c; $R^2 = 0.742$, $P = 0.006$). There was no significant relationship between time since previous fire and growth response to fire (Fig. 3d; $R^2 = 0.060$, $P = 0.874$).

The same patterns between growth response to fire and both precipitation and PDSI were observed for winter–spring (December–May) although correlations were not significant for spring alone. Winter–spring (December–May) precipitation was significant ($R^2 = 0.828$, $P = 0.002$; results not shown) while spring (March–May) precipitation alone was not significant ($R^2 = 0.071$, $P = 0.523$; results not shown) and winter–spring PDSI was significant ($R^2 = 0.596$, $P = 0.025$; results not shown) while spring PDSI alone was not significant ($R^2 = 0.311$, $P = 0.151$; results not shown). There were no significant relationships between growth responses to fire and seasonal climate variables that included summer months although the four most recent fire years with negative growth responses to fire had anomalously low summer PDSI values (results not shown).

Discussion

Although the long-term sustainability of ponderosa pine forests is known to depend on relatively frequent fire, our results show that both short-term (5–10 years) responses to single fires and longer-term (70–94 years) responses to multiple fires are not always positive. Furthermore, recent fires caused negative growth responses, a trend associated with increasing winter drought. While recent increases in fire activity on the landscape have been associated with changing climate (Westerling *et al.*, 2006), to our knowledge this is the first study to show lack of consistent positive long-term effects of fire on tree growth in a fire-adapted species, and to suggest a climate-driven negative effect of recent fires on individual surviving trees. In a related study where we measured needle chemistry and morphology, recent diameter growth, and variables related to water

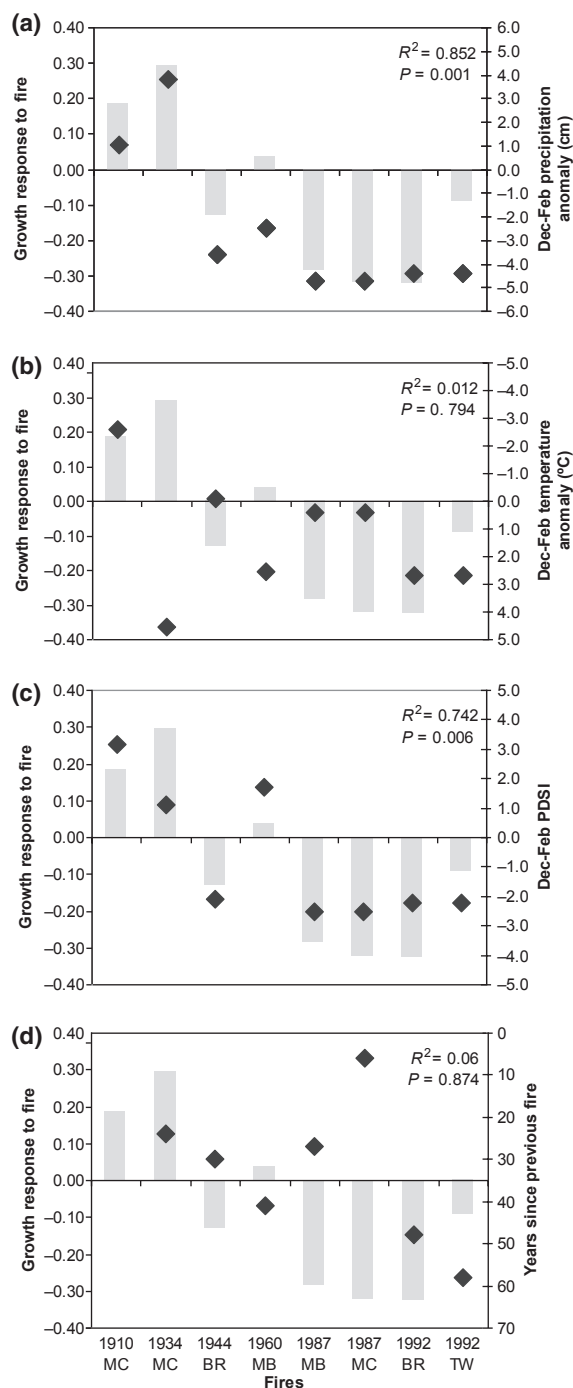


Fig. 3 Correlation of mean growth response to fire with climate variables and time since fire. Growth responses to fire are shown as gray bars in every panel and were computed as: (mean standardized BAI burned stand/mean standardized BAI unburned stand) – 1. Climate variables and time since fire are plotted as diamonds in each panel as follows: (a) winter (December–February) precipitation anomalies; (b) winter temperature anomalies; (c) winter Palmer Drought Severity Index (PDSI); and (d) time since previous fire. BAI indicates basal area increment.

balance, we found that trees in the higher density, unburned stands at our sites were not more physiologically stressed than those in the repeatedly burned stands (Keeling *et al.*, in press). This suggests that lack of fire may be less detrimental to dominant ponderosa pine trees in uneven-aged forests than previously thought. The findings we report here add the interesting possibility that modern wildfires may adversely affect trees. Collectively, our studies suggest that potential negative effects of modern fires may offset benefits associated with frequent fire, even in a fire-adapted species such as ponderosa pine. While further research at broader spatial scales with higher sample sizes is needed to corroborate our findings, a unique strength of our approach is that tree responses to natural wildfire were assessed by comparing repeatedly burned stands with paired unburned control stands in forests that lack the potential confounding effects of prior logging.

Recent fires appear to be more detrimental to tree growth than fires earlier in the 20th century (Figs 1 and 2) at these sites. In fact, the only fires to produce significant positive growth responses were the two earliest fires we studied, 1910 and 1934 at MC. Fires in the mid-century at BR and MB produced nonsignificant and neutral growth responses, while responses to recent fires at all four sites were negative. These results are consistent with evidence suggesting that high severity fire is increasing in portions of the western United States (Holden *et al.*, 2007; Miller *et al.*, 2009). However, while results are based on comparative responses in trees in paired burned and unburned stands, the relatively small number of fires analyzed in this work cautions against drawing broad conclusions about how widespread this trend may be. It could also be that the pattern we document is partly driven by two early fires at one site only (MC). However, the trend is apparent to a lesser degree at MB and BR, and the relatively strong negative responses to recent fires at all four sites are remarkable in itself.

Long-term growth responses need not be consistent with short-term responses to fire, because the mechanisms affecting growth are different in both cases. For long-term growth responses to fire, the main mechanism is maintenance of low density stands and reduced competition. For short-term growth responses, the most important mechanism is probably direct damage from the fire. It is possible that trees may suffer direct short-term negative effects of fire and still benefit from lower competition over the long-run. However, in our study only one site, MC, showed a significant positive long-term response to fire (Table 1). The positive long-term growth response at MC could be interpreted to suggest that a greater number of fires are more likely to produce long-term growth benefits for trees as MC was

also the site with the greatest number of fires (4) in the burned stand during the comparison period. However, the two early fires at MC were the only fires across the entire study to produce significant positive short-term growth responses in the burned stand. Therefore, the long-term positive growth response at MC is likely to be the result of positive effects of the two early fires rather than the sheer number of fires.

The late century negative growth responses to fire were significantly correlated with anomalously lower winter (Fig. 3a) and winter through spring (results not shown) precipitation and higher winter through spring drought severity index (PDSI; Fig. 3c). In general, recent fire years that produced negative growth responses also had higher winter–spring temperatures, although these relationships were not statistically significant (Fig. 3b). Dry conditions during the winter and spring preceding the fire season have been shown to be correlated with increases in area burned in the Idaho Rockies (Westerling *et al.*, 2003) and in Yellowstone National Park (Balling *et al.*, 1992). The implication of these studies is that warmer and drier conditions generate fires that burn larger areas, probably in part because of higher fire intensities. Interestingly, in our study, adverse effects on growth in surviving old ponderosa pine trees were associated with increasing winter drought but not with summer climate variables. This suggests that soil moisture recharge during winter, which influences subsequent duration and extent of water stress, has a relatively strong influence on the ability of individual trees to cope with fire. If corroborated by future research, these results are important given recent trends of reduced snowpack (Mote *et al.*, 2005).

Our findings raise interesting questions for future research into climate-related mechanisms that may drive negative growth responses to fire. Although we do not have direct evidence that the recent fires we studied were of higher intensity or severity than earlier fires at our study sites, a climate-driven increase in fire severity is plausible given the hotter, drier conditions that are occurring across the mountain west, the increases in fire activity (Westerling, 2006), and documented increases in fire severity in other western regions (Miller *et al.*, 2009). Even without increases in fire activity, winter drought and low soil moisture recharge may put physiological stress on trees that could increase damage to trees from fires or reduce resilience to the effects of fire. Therefore, two plausible climate-driven mechanisms (more intense fires, physiological stress from drought) could explain the correlation between warmer, drier winters and springs, and negative tree growth responses to recent wildfire at these sites.

Factors other than climate could also drive adverse growth responses to fire in trees. Fire responses at our sites were not as strongly associated with time since previous fire (Fig. 3d) suggesting that fuel build up between fires during the 20th century may not be as strong a driver of negative growth responses to fire as changing climatic conditions at these sites. However, because we lack fire history data in paired stands before 1880, we cannot compare growth responses to fires in earlier periods with the growth responses we measured in this study. It is possible that long-term fuel build up beginning as early as the 18th century may be interacting with climate change to drive negative responses during the late 20th century. Fire frequency data at MB, where a fire-scar study was conducted (Heyerdahl *et al.*, 2008b), shows that fire frequency has greatly decreased in the 20th century compared with earlier centuries. Therefore, fuel build-up could be a long-term phenomenon. Another plausible prediction for higher-intensity wildfire in recent times that does not invoke climate change or fuel build-up is the possibility that late 20th century fire-suppression practices were able to suppress low-intensity fires such that more modern fires are biased toward higher intensity (Keane *et al.*, 2002).

To our knowledge, this study is the first to report a trend of negative tree growth responses to modern fires in a fire-adapted trees species with a possible link to climate change. Climate projections for the interior west predict increased drought (Westerling *et al.*, 2006), declining winter snowpack (Mote *et al.*, 2005), and increasing temperatures (IPCC, 2007). If replicated across larger regions than studied here, an association between changing climate and negative tree growth responses could have important implications for ecosystem processes. Recent research has found that mortality rates are increasing in forests across the western United States, most likely because of water deficits resulting from warmer, drier conditions (Van Mantgem *et al.*, 2009). Such widespread mortality increases will dampen rates of carbon uptake and storage in western forests. Our results point to the possibility that this reduction in carbon uptake and storage could be exacerbated if growth rates decline in trees that survive fires because of the negative effects of novel climate conditions on growth responses to fire.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Fig. S1. Study area and site locations (RoNR, River of No Return).

Table S1. Physiographic data and mean stand densities for control and burned stands within four sites. Values in parentheses are standard deviations. Different letters are significant differences ($P < 0.05$).

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