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Project Title: Do Fuel Treatments Restore Ecosystem Function? Water Use Efficiency Before and After Fire Suppression and Fuels Treatments in Fire-Prone Pine Forests in the Western United States

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Key Findings

- Fuel treatments that include thinning, and thinning and burning are designed to reduce surface fuels, canopy cover, stand density, and canopy base height, which reduce potential for higher severity fire. Both modeling studies and evaluations of wildfires burning into treated and untreated stands demonstrate that fuel treatments are effective at altering fire behavior, particularly thin and burn treatments. Evidence that fuel treatments produce consistent ecological outcomes and restore ecosystem structure or function in forests highly altered by fire suppression are more limited.

- Quantitative comparisons of post-treatment forest characteristics (density, basal area, species composition) with historical data on forest characteristics with an intact fire regime have been used to evaluate fuel treatments as structural restoration, and to guide restoration prescriptions. Recent advances in stable carbon isotope chemistry provide an opportunity to evaluate the effectiveness of fuel treatments in restoring ecosystem function as measured by the carbon-water balance processes in trees that regulate forest productivity. The isotopic composition (discrimination) of cellulose in tree rings is strongly influenced by canopy photosynthesis and stomatal conductance. Thus, post-treatment changes in carbon-water balance derived from carbon isotopes measured in tree rings can be compared to earlier periods to evaluate short-term treatment effects and longer effectiveness in restoring ecosystem function.

- We hypothesized that carbon isotopic discrimination measured in the cellulose of tree rings would increase with treatments reducing intrinsic water use efficiency and that basal area increment would increase too. We also hypothesized that post-treatment intrinsic water use efficiency would be lower than during the pre-fire suppression, or fire suppression period. Fuel treatments that thin stands are likely to increase discrimination and basal area index due to greater site water availability, higher stomatal conductance and less light-canopy competition. A higher rate of increase in stomatal conductance compared to rate of canopy photosynthesis would result in a decrease in intrinsic water use efficiency.

- Treatment effects were studied in fire-prone ponderosa pine forests at two JFSP supported Fire and Fire Surrogate study sites; one near Flagstaff, Arizona, the other near Wenatchee, Washington. Annual temperature and precipitation are similar at both sites but the seasonality of precipitation is different. Winters are wet and summers are dry in Washington, and precipitation is bimodal in Arizona with a winter peak and then a summer peak associated with the North American monsoon. Thin and thin and burn treatments were implemented at each site between 2002 and 2004.

- Intrinsic water use efficiency increased from 1800-2013 at both sites and in control, thin, and thin and burn treatments due to the physiological response of trees to rising atmospheric carbon dioxide. In Arizona, there was also a marked increase in intrinsic water use efficiency over the last 15 years due to increased drying and a long-term drought. There was no long term trend in discrimination at either site apart from a small increase in Washington after 1975. Counter to our hypothesis post treatment intrinsic water use efficiency was not lower than during earlier reference periods. This can be attributed to the combined effect of rising CO2 concentration and a drying trend observed as higher VPD and reduced water availability.

- Climate affected isotopic composition corrected for changing concentration of ^{13}C and carbon dioxide due to fossil fuel combustion and carbon dioxide between 1895 and 2013. Corrected ^{13}C in ponderosa pine tree rings was negatively correlated with PDSI (drought) at both sites,, and positively correlated with spring and summer temperature in Arizona. Vapor pressure deficit was also positively correlated with corrected ^{13}C, in the spring and summer in Arizona. At the Washington site, corrected ^{13}C was negatively correlated to previous Octobe,r and current may precipitation, and previous June and July vapor pressure deficit. Corrected ^{13}C in Washington was also positively correlated to vapor pressure deficit, in the current May.

- Climate between 1895 and 2013 also affected tree growth at both sites. Basal area index was positively correlated with mean annual PDSI indicating growth was higher in moister years. Basal area index was also negatively correlated with temperature and vapor pressure deficit at both sites, with the strongest relationships in current year May-July in Arizona, and January-March in Washington. Monthly precipitation and basal area index were also positively correlated in most months, with a particularly strong correlation in Arizona in the current July.

- Fuel treatments decreased intrinsic water use efficiency relative to the control in Arizona although the differences were not sufficiently large to reach the threshold of statistical significance. Very dry conditions characterized post-treatment climate in Arizona and treatment decreased competition among trees for water. Decreased competition appears to have led to higher stomatal conductance in surviving trees and thus lower intrinsic water use efficiency, even with post-treatment growth increases as measured by basal area index. The treatment response supports our hypothesis of the expected treatment response.

- Fuel treatments increased water use efficiency relative to the control in Washington although the differences were not sufficiently large to reach the threshold of statistical significance. Conditions were relatively moist during the post-treatment period and during the preceding decade. Increasing intrinsic water use efficiency in all stands reflects the response of trees to rising carbon dioxide and perhaps temperature. The increase of intrinsic water use efficiency and indicates that stomatal conductance was not limiting and treatments led to an increase in canopy photosynthesis.

- Fuel treatments at both sites increased tree growth as measured by basal area index. The basal area index response to treatments, overall, supports our hypothesis of treatment effects of growth, although the post-treatment response for thin only was not sufficiently large to reach the threshold of statistical significance.

Introduction

The extent of forest fires in the American West since the mid-1980s has increased risks to lives, property, water quality, biodiversity, species-at-risk, carbon sequestration, forest timber value and other ecosystem services. Although one driver of the increase in fire extent and severity is climate change (Westerling 2016), human agency in the form of a century of fire suppression management, forest harvesting, and increased fuels has significantly contributed to the severity and extent of recent wildfires. This is particularly true in ponderosa pine and mixed conifer forests where frequent low-intensity surface fires prior to fire suppression maintained lower fuels loads (Covington and Moore 1994; Skinner and Chang 1996). Fire suppression has significantly increased surface and canopy fuel loads and fuel continuity across landscapes increasing the potential for severe fire effects in these ecosystems (Weatherspoon and Skinner 1996; Fulé et al. 2004; Hardy 2005; Finney et al. 2005; Agee and Skinner 2005). The potential for severe fire effects from high fuel loads is exacerbated by the success of initial attack that extinguishes most fires. When initial attack fails, usually in combination with extreme fire weather, rough terrain, or simultaneous lightning strikes, fires spread rapidly and become large with large areas of canopy killing fire (North et al. 2012; Harris and Taylor 2015).

The severity of recent wildfires is of considerable concern to fire and resource managers and the public and this has led to shifts in national forest management policy (i.e. Healthy Forest Restoration Act 2003). There is now an increased emphasis on implementing fuel treatments in areas with high fire hazard to reduce the potential for high severity fire (Agee and Skinner 2005; Schmidt et al. 2008). Generally, mechanical and/or burning treatments are designed to reduce surface fuels, canopy cover, and stand density while increasing canopy base height (Scott and Reinhardt 2001; Agee and Skinner 2005). Alteration of these structural variables by treatments is consistent with an objective of altering fire behavior since they strongly influence potential fire intensity and potential for crown fire (Agee and Skinner 2005). Modeling studies (e.g. Finney et al. 2007; Schmidt et al. 2008; 2008; Ager et al. 2010) demonstrate that treatments are effective at reducing fire behavior and fire severity (i.e. tree mortality). Evaluation of the effects of numerous wildfires burning through both treated and untreated forests corroborate the modeling studies and demonstrate that fuel treatments, especially thin and burn, are very effective at reducing fire severity (Kalies and Kent 2016). In contrast, there is limited evidence that fuel treatments produce consistent ecological outcomes (i.e. soil nutrients/water, hydrology, tree mortality, tree carbon-water balance, carbon dynamics, etc.) and restore ecosystem structure or function to a condition more similar to forests with a historic fire regime compared to forests under a fire suppression regime (McIver et al. 2013; Kalies and Kent 2016). A better understanding of the ecological outcomes of fuel treatments is needed to evaluate their potential for restoring ecosystem function in forests highly altered by fire suppression and other Euro-American land use practices (e.g. logging, grazing).

Comparisons of quantitative historical information of reference forest conditions (tree density, tree basal area, tree spatial patterns) in ponderosa pine and mixed conifer forests (e.g. pre fire suppression or pre Euro-American settlement) based on tree ring reconstructions have been used to broadly guide restoration treatments. Treatments reduce potential fire severity and restore selected structural features to conditions similar to forests before fire exclusion (e.g. Fule et al. 1997; Moore et al. 1999; Taylor 2004; Lydersen et al. 2013; Ziegler et al. 2017). Researchers have made important comparisons of ecosystem structural properties (e.g. stand density, basal area, or tree spatial pattern) associated with pre-fire suppression forests (reference), fire suppressed forests (fire suppression), and post-treatment forests (post treatment) (e.g. Fule et al. 1997; Taylor 2004; Korb et al. 2012). These types of studies have been useful in providing quantitative data to guide and evaluate restoration management using both fuel treatments (e.g. Roccaforte et al. 2015) and resource objective wildfires (Collins and Stephens 2007); Huffman et al. 2015). This approach has also been used to identify differences in forest carbon, nitrogen and phosphorous pools in reference, fire suppression, and post treatment forests (e.g. Hurteau et al. 2011; Kaye et al. 2016).

The use of stable carbon isotope from cellulose in tree rings provide the opportunity to use continuous records of intrinsic water use efficiency (*iWUE*): the ratio of carbon gain per unit of water loss as metric to evaluate the effectiveness of fuel treatments in restoring ecosystem function. Stable carbon isotopes ($\delta^{13}C$) in tree rings provide a retrospective measure of inter-annual changes in gas exchange of trees with the atmosphere, and can be measured for any period spanned by the oldest tree on a site (Leavitt 1993). Carbon in trees originates entirely from atmospheric CO_2 which is assimilated through the leaves, and the annual growth rings of the tree contains the isotopic composition of atmospheric carbon during the growing season (McCarroll and Loader 2004). $\delta^{13}C$ in tree rings are valuable for evaluating and comparing post-treatment responses because of the strong dependence of isotopic composition on canopy photosynthesis (A) and stomatal conductance (g_s) (Faruquar et al. 1989; Walcroft et al. 1997;

McDowell et al. 2010). Plants discriminate against heavier ^{13}C compared to lighter ^{12}C during CO_2 uptake from the atmosphere and discrimination against the heavy isotope (^{12}C) ($^{13}\Delta C$) is proportional to the ratio of the CO_2 in the leaf chloroplast and the atmosphere (Seibt et al. 2008). Variation in $^{13}\Delta C$ and *iWUE*, can therefore be attributed to changes in canopy photosynthesis (A) relative to stomatal conductance (g_s) that result from changes in light, nutrient or water availability (e.g. McDowell et al. 2011). Thus, changes in discrimination $^{13}\Delta C$ documented in tree rings after fuel treatments can be compared to earlier periods (reference, fire suppression) to evaluate both short-term treatment effects and the longer-term effectiveness of fuel treatments in restoring ecosystem function as reflected in carbon-water balance processes in forest trees that regulate forest productivity. The use of tree-ring $\delta^{13}C$ to understand tree response to management treatments is well established and factors affecting discrimination (Δ) are fairly well known, but they have not been applied to fuel treatments designed to reduce fire behavior.

Research Objectives and Hypotheses

This project had three objectives. The first objective was to identify variation in discrimination of $\Delta^{13}C$ and intrinsic water use efficiency (*iWUE*) in Ponderosa pine (*Pinus ponderosa*) tree rings from 1800 to 2012 at two Fire and Fire Surrogate study sites (Arizona, Washington). The sites are both dominated by ponderosa pine but have contrasting climatic conditions (see study area description). Since climatic patterns vary at each site we also conducted an analysis of how discrimination (Δ), intrinsic water use efficiency (*iWUE*), and basal area index (*BAI*) a standard measure of annual tree growth, are influenced by climate and disturbance processes that influenced the forests. Our second objective was to compare fuel treatment effects (control, mechanical, mechanical+burn) on tree's physiology by comparing discrimination (Δ), *iWUE*, and *BAI* amongst treatments . Our third objective was to compare discrimination (Δ) and intrinsic water use efficiency (*iWUE*) pre- and post-treatment as a metric of restoration of forest ecosystem function on the two FFE sites.

Our first hypothesis is that $\Delta^{13}C$ will increase after treatment and more so in mechanical+burned stands than mechanical and this will reduce intrinsic water use efficiency (*iWUE*). We also hypothesize that BAI will increase after treatments. Secondly, we hypothesize that post treatment iWUE is lower than during the reference period. Fuel treatments that thin stands are likely to increase carbon isotope discrimination (Δ) and *BAI* due to increases in water availability and greater stomatal conductance. A higher rate of increase in stomatal conductance (g_s) compared to the rate of photosynthesis (A), would result in a decrease of *iWUE*.

Methods

Study area

To evaluate the effects of fuel treatments on ecosystem function we sampled within sites in Arizona and Washington that were part of the national Fire and Fire Surrogate (FFS) study. The FFS study was designed to analyze the ecological impact of different fuel treatment methods (Schwilk et al. 2009). We chose two FFS sites (Figure 1) that both contain stands dominated by ponderosa pine (*Pinus ponderosa*) but that differ climatically.

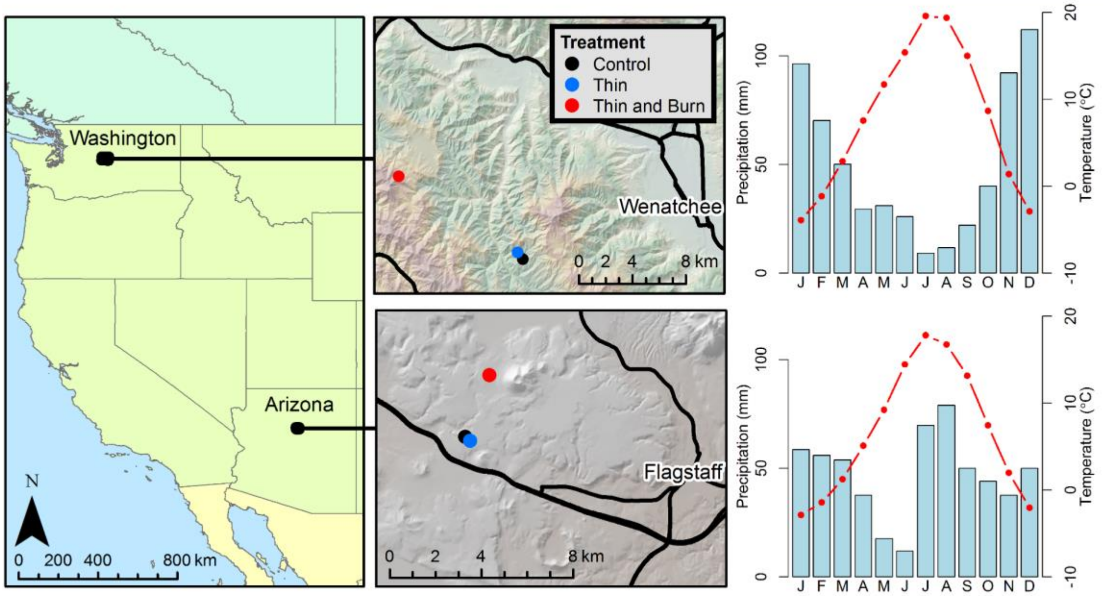

Figure 1. Study site location, treatment site location, and climatic conditions at the Arizona, and Washington national Fire and Fire Surrogates research sites.

The Southwestern Plateau site ("Arizona" site) is located west of Flagstaff, Arizona in the Kaibib and Coconino National Forests and spans 2100 - 2300 m elevation (Converse et al. 2006). The Northeastern Cascades site ("Washington" site) is located between 675 and 1200 m elevation on the eastern slopes of the Cascade Mountains in Okanogan-Wenatchee National Forest in central Washington (Harrod et al. 2009). The Arizona site had a historical fire return interval (FRI) of 2-10 yrs. compared to 10-20 yrs. in Washington (Schwilk et al. 2009). Soils at each site were alfisols and mollisols with similar properties (Boerner et al. 2009). The Arizona treatment units used in this study had minimal topographic relief, and ponderosa pine was the only tree species within the units selected for this study. In contrast the Washington treatment units used in this study had substantial topographic relief (mean slopes ~25-45 %) and were composed of mixture of ponderosa pine and Douglas-fir (*Pseudotsuga menziesii*).

The Arizona and Washington sites experienced similar mean annual precipitation and temperatures but the seasonality of precipitation is different (Figure 1). Mean annual precipitation was 581 mm for the Arizona site and 645 mm for Washington (1981-2010 climate normals from PRISM data, see *Climate analysis*). The Arizona site has a distinct bimodal precipitation pattern that is associated with the southwest monsoon with peaks in July-August and November-March (Adams and Comrie 1997). In contrast the Washington site experiences dry summers and wet winters. Monthly mean temperatures ranging from -2.0°C in December to 17.9°C in July for Arizona and from -3.4°C in December to 19.6°C in August in Washington.

As part of the FFS study (Schwilk et al. 2009) control, thin and thin and burn treatments were replicated three times in Arizona and four times in Washington. One of the replicates per treatment was selected for in both Arizona and Washington, based on accessibility and presence of old (>150 years) ponderosa pines. In the selected thinned units in Arizona, trees had been hand-felled in fall 2002 and slash was placed in small piles by spring 2003 (Converse et al. 2006). The goals of the thinning were to retain large trees and restore stands to pre-settlement forest structure (Converse et al. 2006), in which stands were open with pines growing in small clumps (Cooper 1960, Covington et al. 1997). The thin and burn treatment unit was then burned in fall 2003 (Schwilk et al. 2009). Notably all units at the Arizona FFS site had been pre-commercial thinned in the 30 years preceding treatment (Converse et al. 2006). Because tree limbs and tops were left in the thinned units in Arizona, 1-100 hour surface fuels increased in the thin-only treatment, although thinning still decreased the risk of crown fire by lowering tree density and increasing canopy base height (Stephens et al. 2009). Subsequent burning decreased the quantity of 1-100 hour fuels (8.6 Mg/ha *vs* 15.5 Mg/ha in the thin-only units) which translated into the lowest risk of crown fire among the treatments (Stephens et al. 2009). Forests in this area were subject to extensive grazing and logging beginning shortly after the arrival of the transcontinental railroad in 1882, and fire exclusion since that period resulted in large (more than eightfold) increases in tree density (Fulé et al. 1997).

At the Washington site thinning occurred from fall 2002-spring 2003 with the goal of reducing stand basal area and density while retaining large trees and promoting structural heterogeneity (Harrod et al. 2009). At this much steeper and more topographically complex site (mean slopes of 16-67% amongst all the treatment units, Harrod et al. 2009), merchantable trees were yarded by helicopter, then smaller trees were hand felled and all slash was lopped and scattered (Agee and Lolley 2006, Harrod et al. 2009). Burning occurred in spring 2004, and an early greenup that year led to high live fuel moisture which produced a patchy burn that did not meet objectives for surface fuel reduction (Agee and Lolley 2006). The Washington Thin and Burn unit used in this study was ~400 m higher in elevation than the Control and Thin units (1147 m versus 755 m and 741 m respectively) which likely translated into cooler and more mesic site conditions. The Control and Thin units were dominated by ponderosa pine in 2014 while the Thin and Burn unit contained a more even mix of ponderosa pine and Douglas-fir (Table 1). The Washington site was heavily grazed from 1900-1940, causing a pulse of ponderosa pine regeneration in 1920, and was logged in the 1920s and 1930s before active fire suppression began in the 1930s (Harrod et al. 1999). Similarly to Arizona, these factors resulted in pre-treatment forests that were denser and less spatially aggregated than they were historically (Harrod et al. 1999).

Field sampling

We sampled within our selected treatment units in summer 2014 using one 50 x 50 m plot per treatment unit to characterize vegetation. These plots were located within the units to be in proximity to old ponderosa pines. Within these plots, the diameter at breast height (dbh) of all trees > 5 cm dbh were measured to characterize species composition (Table 1). Cores were taken from canopy dominant or codominant ponderosa pines within 100 m of these field plots except at the Washington Thin unit where lack of old trees led us to expand this boundary to 160 m.

Table 1. Stand density and basal area of live trees > 5 cm dbh at the area used for isotopic sampling within each treatment unit. Data are from one 50 x 50 m plot within each treatment unit. The percentage of each value comprised of ponderosa pine is in parentheses. The Arizona plots contained only ponderosa pine and the Washington plots contained ponderosa pine and Douglas fir.

Site	Treatment	Stem density (stems/ha)	Basal area (m^2/ha)
Arizona	Control	552 (100%)	30.3 (100%)
	Thin	124 (100%)	17.2 (100%)
	Thin and burn	92 (100%)	17.2 (100%)
Washington	Control	156 (97%)	24.1 (97%)
	Thin	100 (88%)	15.6 (83%)
	Thin and burn	64 (44%)	12.2 (60%)

At each treatment unit, a subset of 6-7 trees were sampled for isotopic analysis using a 12 mm increment borer (hereafter the “isotope” increment cores). We sampled three cores from each tree to insure sufficient material for isotopic analyses. In addition, at each site 20 trees were opportunistically cored twice with a 5 mm increment borer to establish a tree ring chronology (hereafter the “chronology” increment cores) to cross-date the isotope increment cores so each ring could be assigned a calendar date of formation.

Sample preparation

The chronology increment cores from each site were prepared for analysis by mounting, sanding and measuring following standard procedures for dendrochronology (Stokes and Smiley 1968). These chronology cores were visually cross-dated with each other, and the series were checked using nearby chronologies downloaded from the International Tree-Ring Data Bank (https://www.ncdc.noaa.gov, 11/11/2014). Ring widths were then measured using a Velmex measuring system (0.001 mm precision). COFECHA (Holmes 1983, Grissino-Mayer 2001) was then used to statistically check the cross-dating of each series. We then standardized each tree ring series from each site using the dplR package in R (Bunn 2008) and built a master chronology to compare the series to the isotope increment cores.

The isotope increment cores were prepared by planing each core with a razor blade and cross-dating the core against the master chronology. Ring widths were measured with a Velmex measuring system. Out of the 6-7 trees originally cored from each treatment unit, five were selected for isotopic analysis (Table S1) based on (1) correlation with the master chronology and (2) number of years represented (older cores were preferred). For further analysis ring width measurements from these isotope cores were converted to basal area increment (BAI, reported in mm^2) (Biondi and Qeadan 2008). The diameter of each tree without bark at a level of 1 ft. (about the level at which trees were cored) was estimated from tree dbh using a linear regression model developed from 220 ponderosa pines in Arizona and New Mexico (Hann 1976). BAI was then calculated with the dplR package in R (Bunn 2008) using these estimated diameters and the ring width series.

After cross-dating and measuring the isotope increment cores, the cores were prepared for isotopic analysis. Individual years from each core were cut using a scalpel, and milled to produce a fine powder. The two increment cores from each tree were pooled to insure an adequate quantity of wood for further analysis. The α-cellulose was extracted from wood samples using the methods elaborated by Green (1963) and modified by Leavitt and Danzer (1993). The α-cellulose samples were weighed into tin capsules and were analyzed at the Yale Analytical and Stable Isotopic Center. Carbon isotope ratios are reported as per mil (‰) enrichment in ^{13}C relative to the Vienna Pee Dee Belemnite (VPDB) international standard. Samples from individual trees (5 trees per treatment unit) were processed for all years from 1999-2013 and for one year per decade for the length of the chronologies (i.e. 1800, 1810, 1820 etc.) in order to assess between tree variability in tree-ring $\delta^{13}C$. Based on this initial analysis one tree in the Washington Control unit with poor correlations with other trees and higher $\delta^{13}C$ compared to the other trees was removed from the analysis, and, the samples for the remaining 29 trees were pooled by treatment and year. The individual tree $\delta^{13}C_{plant}$ values measured in the first round of processing were used to calculate standard error in $\delta^{13}C_{plant}$ and the measures derived from it (see next section).

Calculating Δ and iWUE

Discrimination against ^{13}C ($^{13}\Delta C$) by each tree and intrinsic water use efficiency (*iWUE*) were calculated using the carbon isotope ratios measured in the tree rings ($\delta^{13}C_{plant}$), annual estimates of atmospheric $\delta^{13}C$ ($\delta^{13}C_{atm}$) and annual atmospheric CO_2 concentrations (c_a). Annual values of $\delta^{13}C_{atm}$ were obtained from ice core/firn dataset (Rubino et al. 2013). We fit a 20-year spline to the data and used the spline to generate annual $\delta^{13}C$ values for 1800-1992. For 1993-2013 we averaged values from flask measurements from Mauna Loa and the South Pole, obtained from the National Oceanic and Atmospheric Administration's Earth System Research Laboratory (http://www.esrl.noaa.gov/gmd/dv/data/, 9/1/16). Annual CO_2 concentrations were estimated using a dataset which combines ice core data prior to 1959 (fit with a spline) with a simple average of Mauna Loa and South Pole data from 1959 onward (http://scrippsco2.ucsd.edu/data/atmospheric_co2, 9/1/2016) (Keeling et al. 2001, MacFarling Meure et al. 2006).

Discrimination against ^{13}C was calculated annually using the equation (Farquhar et al. 1982):

$$\Delta = \frac{\delta^{13}C_{atm} - \delta^{13}C_{plant}}{1 + \delta^{13}C_{plant}/1000}$$

To calculate iWUE we first calculated the ratio of intercellular (c_i) to atmospheric (c_a) CO_2 concentrations (Ehleringer and Cerling 1995):

$$\frac{c_i}{c_a} = \frac{\Delta - \mathrm{a}}{b - a}$$

where a is fractionation from diffusion (4.4‰) and b is fractionation during carboxylation (27‰). Then iWUE was calculated following Farquhar and Richards (1984):

$$iWUE = C_a\left(1 - \frac{c_i}{c_a}\right) * 0.625$$

Correcting $\delta^{13}C$ values

Raw δ^{13}C series from tree rings often show a decline since 1850 that inhibits comparison of pre- and post-industrial δ^{13}C values (McCarroll et al. 2009). The first reason for this decline is that atmospheric δ^{13}C ($\delta^{13}C_{atm}$) has declined, largely due to combustion of fossil fuels (McCarroll and Loader 2004). We addressed this trend by subtracting the difference between pre-industrial $\delta^{13}C_{atm}$ and annual $\delta^{13}C_{atm}$.

$$\delta^{13}C_{cor} = \delta^{13}C_{plant} - (\delta^{13}C_{atm} + 6.5)$$

Where $\delta^{13}C_{cor}$ are the corrected δ^{13}C values, $\delta^{13}C_{plant}$ are the raw δ^{13}C values from the tree rings and 6.5 represents the mean preindustrial $\delta^{13}C_{atm}$ level (-6.5 ‰) (Rubino et al. 2013). The second reason for declining post-industrial δ^{13}C is that trees respond physiologically to increasing atmospheric CO_2 levels (McCarroll et al. 2009) (Figure S1). To remove the portion of change in $\delta^{13}C_{cor}$ caused by rising CO_2 we followed the correction procedure of McCarroll et al. (2009) which uses nonlinear regression with two constraints. First, if trees respond passively to rising CO_2 (i.e. no change in stomatal conductance and photosynthetic rate) c_a and c_i will increase such that $c_a - c_i$ remains constant. Second, trees may respond actively to increasing CO_2 such that they maintain constant c_i/c_a ratios, which would mean that the low-frequency trends in $\delta^{13}C_{plant}$ are fully explained by $\delta^{13}C_{atm}$. The correction produces an estimate ($\delta^{13}C_{pin}$) of what annual δ^{13}C values would be under pre-industrial CO_2 concentrations (McCarroll et al. 2009). Therefore, metrics which correct for the Suess effect but not changing CO_2 (e.g. Δ and iWUE) reflect both changes in climate and CO_2 but $\delta^{13}C_{pin}$ may be used to explore trends and variability related to climate alone. Additionally, the corrected $\delta^{13}C_{pin}$ series were used to analyze carbon isotope response to interannual climate variability because unlike the Δ or *iWUE* series they were stationary over time (Figure 2, 3, S2) and therefore reduced the potential for spurious correlations with climate variables.

Climate analysis

To determine the effect of climate on interannual variability in $\delta^{13}C_{pin}$ and tree growth (BAI), we correlated $\delta^{13}C_{pin}$ and BAI with temperature, precipitation, vapor pressure deficit (VPD) and Palmer Drought Severity Index (PDSI). Monthly mean temperature, precipitation and maximum VPD data for the Arizona and Washington sites were obtained for 1895-2015 from the Parameter-elevation Relationships on Independent Slopes Model (PRISM) dataset (Daly et al. 2008) using the interpolation option in the online data explorer to take into account values from surrounding grid cells (http://www.prism.oregonstate.edu/explorer/, 8/25/16). Drought severity was quantified with the Palmer Drought Severity Index (PDSI), using monthly values for 1895-

2013 obtained from the National Oceanic and Atmospheric Administration's National Climatic Data Center (https://www.ncdc.noaa.gov/temp-and-precip/, 2/25/16). In addition we used a gridded reconstruction of annual summer PDSI (Cook et al. 2004) to quantify drought stress from 1800-1894 for the nearest 2.5° x 2.5° gridpoints to the Arizona and Washington sites.

The relationships between the monthly climate variables and annual $\delta^{13}C_{pin}$ and BAI were assessed using correlation function analysis ofthe treeclim package in R (Zang and Biondi 2015) with 0.05 significance thresholds estimated using confidence intervals from 1000 bootstrapped samples. To assess how the relationships changed over time, the correlation function analysis was also performed using a moving window approach of 30 year intervals with a 5 year offset (Biondi and Waikul 2004, Zang and Biondi 2015). For the correlation function analysis, $\delta^{13}C_{pin}$ and BAI values were combined for each site using a simple average of the annual values within each treatment unit.

Analyzing differences among treatments

To visualize whether the treatments affected tree growth (*BAI*) and *iWUE* we first normalized each measure by 10-year pre-treatment means. The mean annual value for each treatment over the 10 years preceding treatment (1992-2001 for Arizona and 1993-2002 for Washington) was calculated and subtracted from mean annual *BAI* and *iWUE* values for 1990-2013. In addition, one-way repeated measures ANOVA with post-hoc Tukey tests were used to test for differences among treatment units in *BAI* and *iWUE* for the 10 years post-treatment. For these tests 10-year pre-treatment means for *BAI* of individual trees were subtracted from post-treatment values. Because we did not calculate individual tree *iWUE* for 1992-1998, pre-treatment means from 1999-2001 for Arizona and 1999-2002 for Washington were used for the ANOVA testing.

Results and Discussion

Long-term responses of Δ*, iWUE, and BAI to climate, atmospheric* CO_2*, and stand development*

The *iWUE* increased at the Arizona and Washington sites from 1800-2013, especially after 1900 and this reflects the physiological response of trees to rising atmospheric CO_2 (Figures 2 and 3). All six treatment units recorded a significant ($p < 0.01$) increase in *iWUE* from 1800-2013 (slope = 0.10-0.18, r = 0.74-0.88) and from 1900-2013 (slope = 0.19-0.29, r = 0.78-0.87). Atmospheric CO_2 (in ppm) and *iWUE* were also significantly positively correlated in all treatment units from 1800-2013 (slope = 0.10-0.18, r = 0.76-0.88). In parallel, Δ did not exhibit any substantial long-term trend apart from a small increase after 1975 at the Washington site (Figure 3). In Washington, the Thin and Burn unit had consistently higher Δ and lower *iWUE* than the other two lower-elevation treatment units (Figure 3) although the gap between the Thin and Thin and Burn treatments narrowed after 1985. The marked increase in iWUE in the last 15 years in Arizona reflects the recent drying trend observed in the southwestern United States.

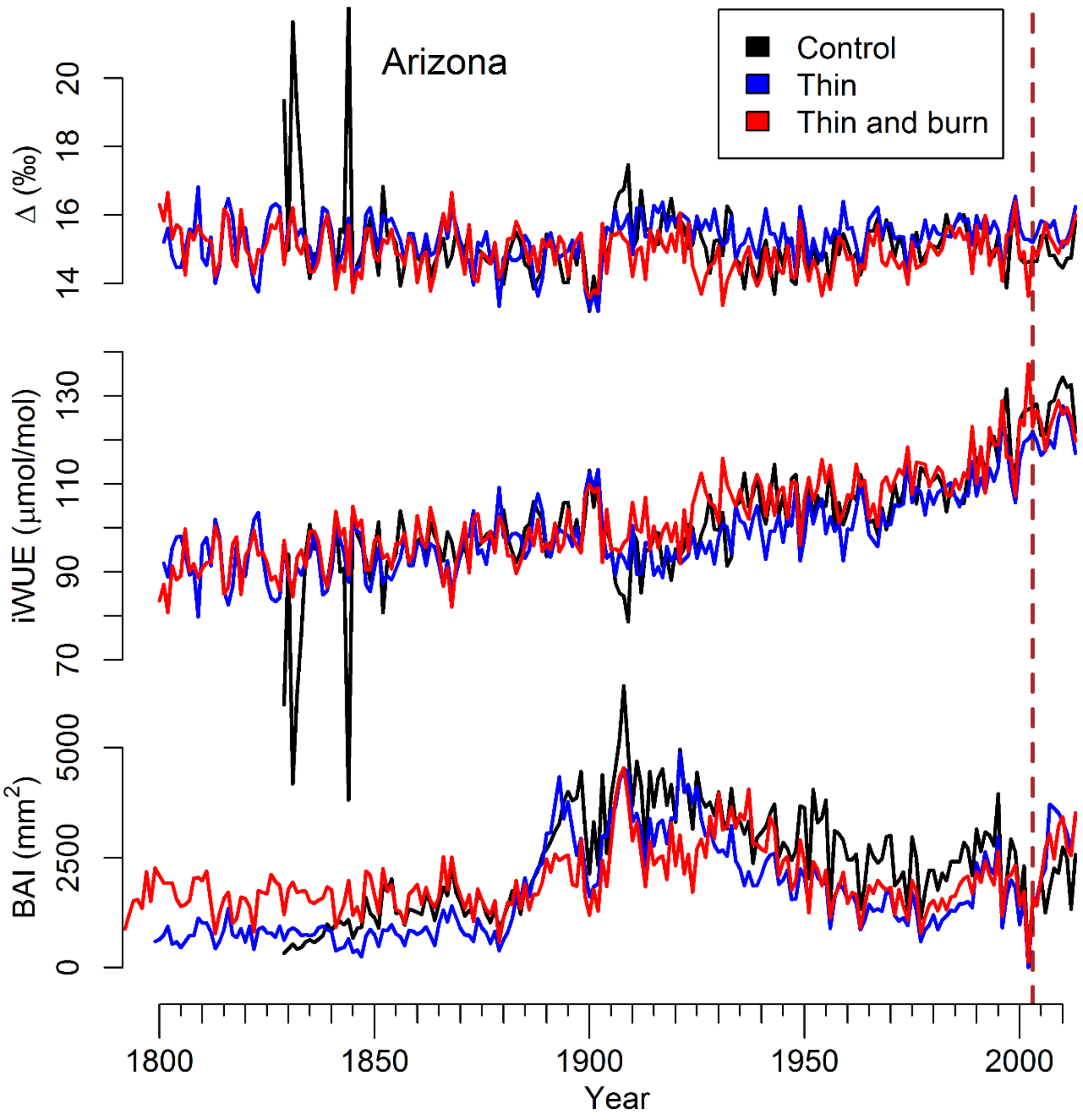

Figure 2. Annual discrimination against ^{13}C (Δ, top), intrinsic water-use efficiency (iWUE, middle) and basal area increment (BAI, bottom) for the three treatment units at the Arizona site. The dashed brown line represents the time of treatment (fall 2002-fall 2003).

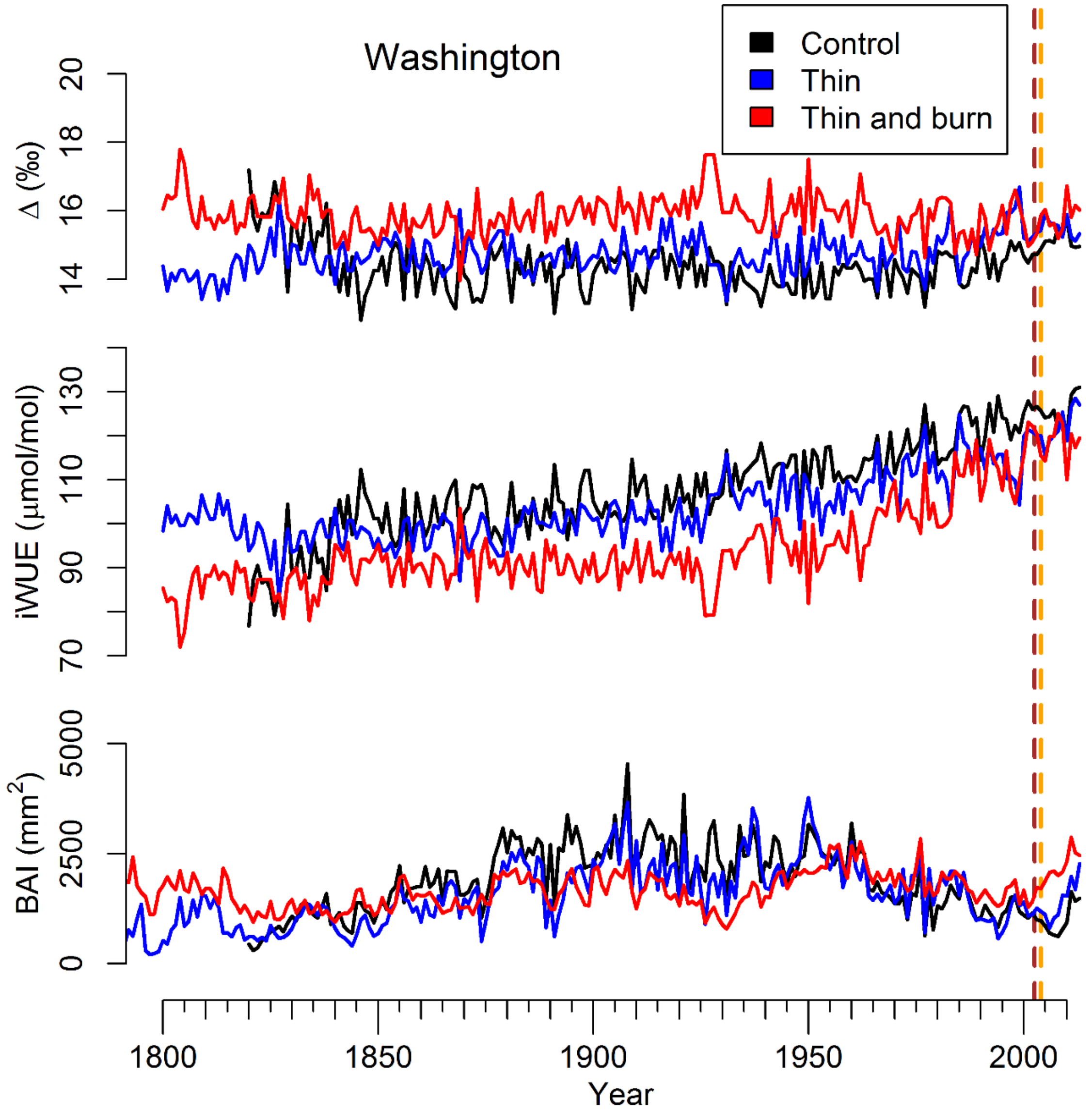

Figure 3. Annual discrimination against ^{13}C (Δ, top), intrinsic water-use efficiency (iWUE, middle) and basal area increment (BAI, bottom) for the three treatment units at the Washington site. The dashed brown and gold lines represent the time of thinning and burning treatments respectively (fall 2002 and spring 2004).

Climate affected $\delta^{13}C_{pin}$ similarly at the Arizona and Washington sites although the magnitude and seasonality varied. At both sites $\delta^{13}C_{pin}$ was negatively correlated with annual PDSI from 1895-2013 ($r = -0.59$ in Arizona, $r = -0.39$ in Washington, $p < 0.01$). In Arizona $\delta^{13}C_{pin}$ was positively ($p < 0.05$) correlated with the current year's May and July temperature as well as the previous year's July temperature (Figure 4). Correlations with precipitation were negative from the previous November to the current May with a particularly strong correlation ($r < -0.4$) with current July precipitation. VPD was positively correlated with Arizona $\delta^{13}C_{pin}$ especially from the current March to the current September. The Washington site had significant negative correlations between $\delta^{13}C_{pin}$ and previous October and current May precipitation. VPD and $\delta^{13}C_{pin}$ were significantly and negatively correlated in the previous June and July and positively correlated in the current May.

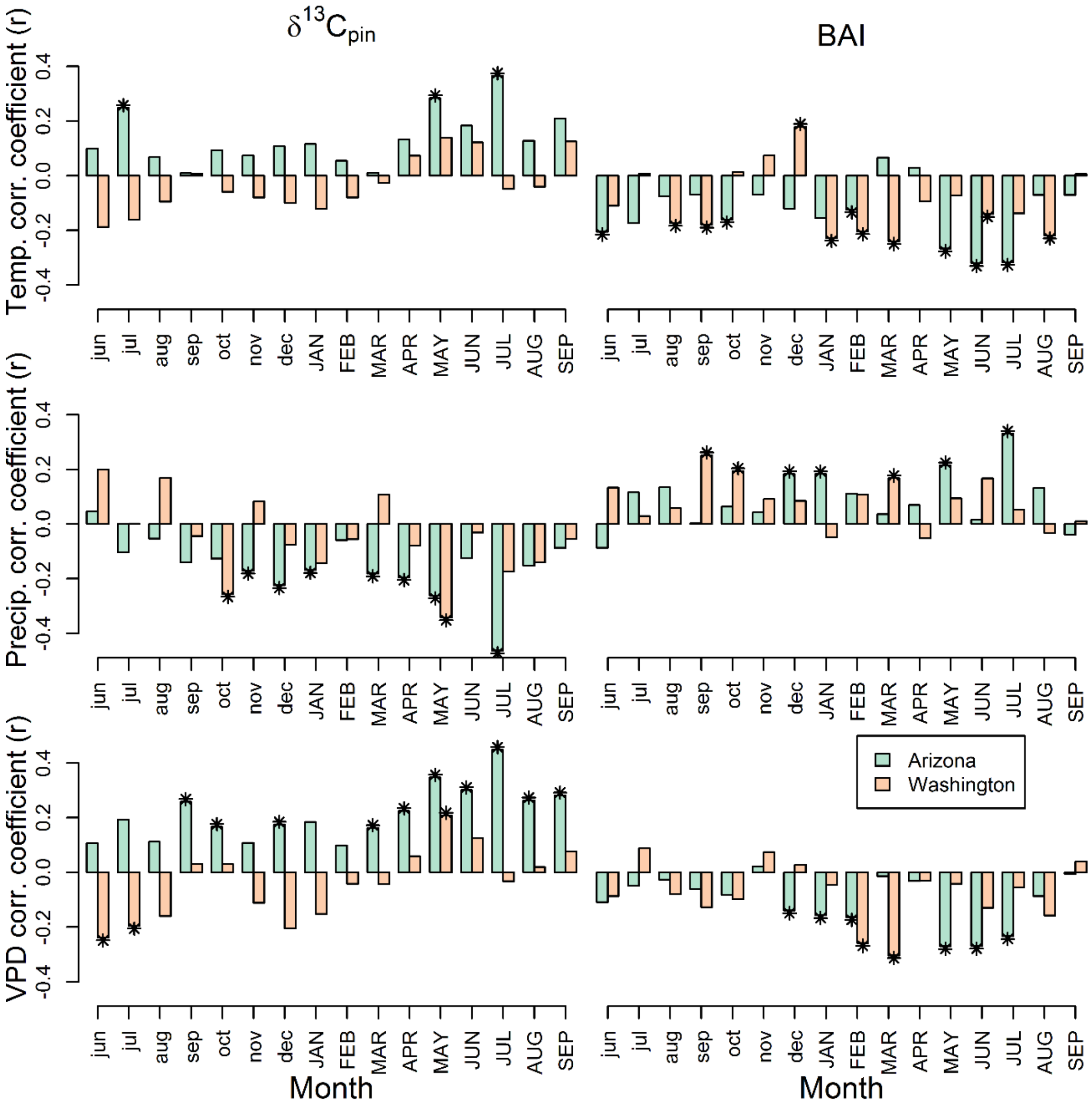

Figure 4. Correlation function analysis showing the response of annual tree ring ^{13}C ratios ($\delta^{13}C_{pin}$, left column), corrected for changing atmospheric $\delta^{13}C$ and CO_2 concentrations, and tree growth (basal area increment, BAI, right column) to monthly mean temperature (top row), total precipitation (middle row) and average maximum vapor pressure deficit values from 1895-2013. Significant ($p < 0.05$) correlations are starred. Upper and lower case lettering indicate the current growth year and the previous year, respectively.

In Arizona, there was a large increase in BAI beginning after 1880, followed by a decrease from about 1925-1980 (Figure 2). The Washington units did not show the same clear pulse in radial growth after 1880 that was observed in Arizona (Figure 3). At both sites, BAI and mean annual PDSI were positively correlated from 1895-2013 ($r = 0.38$ in Arizona, $r = 0.31$ for Washington, $p < 0.01$). BAI was negatively correlated with temperature and VPD at both sites although these relationships were strongest in the current May-July in Arizona and in the winter (January-March) in Washington (Figure 4). Monthly precipitation and BAI tended to be positively correlated at both sites with a particularly strong correlation in Arizona in the current July.

Although iWUE increased from 1800-2013 at both sites, c_i/c_a ratios (and Δ) remained relatively constant. A constant c_i/c_a ratio corresponds to a moderate stomatal control and is characteristic of many tree species in temperate forests. The constant c_i/c_a during the industrial period (an active response to rising CO_2), yields a large increase in $c_a - c_i$ and therefore an increase in iWUE which is consistent with the observed increase in *iWUE* in the Arizona and Washington records (McCarroll et al. 2009; Van de Sleen et al 2014, Frank et al 2015). Some trees, however, have abruptly switched from an active response to a passive response (constant $c_a - c_i$) (Waterhouse et al. 2004, McCarroll et al. 2009, Gagen et al. 2011), causing iWUE to level off despite increasing atmospheric CO_2. This switch is potentially evident in Washington, where c_i/c_a increased after 1985 and the rates of increase in iWUE appeared to slow.

Increasing iWUE since the onset of the industrial period in *ca*. 1850 has been observed in forests worldwide due to rising CO_2 levels from use of fossil fuels (Nock et al. 2010, Frank et al. 2015, Urrutia-Jalabert et al. 2015), including ponderosa pine forests in the western US (Soule and Knapp 2011, 2015). Although iWUE and stem growth (*BAI*) have been found to be positively correlated in ponderosa pine forests (Soule and Knapp 2011, 2015), other research has found that increases in iWUE do not necessarily lead to increased stem growth, especially with increasing temperatures and water stress (Nock et al. 2010, Andreu-Hayles et al. 2011, Lévesque et al. 2014, Urrutia-Jalabert et al. 2015).

In Arizona BAI did not increase with iWUE (Figure 2). Instead variation in BAI tracked stand development processes. The Arizona site is located in an area that was heavily logged following the arrival of the transcontinental railroad in 1882 (Fulé et al. 1997), and this is likely to have greatly reduced competition in the trees that were not removed by logging and were sampled by this study. The large increase in BAI in surviving trees in the late 19th and early 20th century is consistent with a sudden post-logging increase in light and moisture. As post-logging tree establishment increased early in the 20th century, and fire suppression was implemented, stand density and basal area increased to values exceeding those before logging (Fulé et al. 1997). Increasing stand density and competition from *ca*. 1925 to 1975 is likely the cause of the steady decline in BAI over this period. Forests at the Arizona site were pre-commercial thinned in the 30 years before treatment (Converse et al. 2006), and this is evident in the observed BAI increase from 1975-1995 (Figure 2). Other studies of ponderosa pine that found increases of BAI with iWUE (e.g. Soule and Knapp 2011, 2015) selected samples in open forest stands that maximize the influence of climate and rising CO_2 on carbon-water balance which minimized responses to other stand development processes such as competition, disturbance, and succession.

Interannual variability in $\delta^{13}C_{pin}$, or annual $\delta^{13}C$ values under pre-industrial CO_2 concentrations, was influenced by climate, especially in Arizona where drought and higher growing season water demand were associated with higher $\delta^{13}C_{pin}$ (Figure 4). These climate correlations with $\delta^{13}C_{pin}$ were weaker at the Washington site. However, positive correlations with June VPD and temperature and negative correlations with previous October-current February precipitation were stronger over the past 50 years in Washington than in 1900-1960 (Figure 5), suggesting that drought response has become a more important driver of variability in $\delta^{13}C_{pin}$. This temporal variation in the correlation pattern is also evident with BAI (Figure 6).

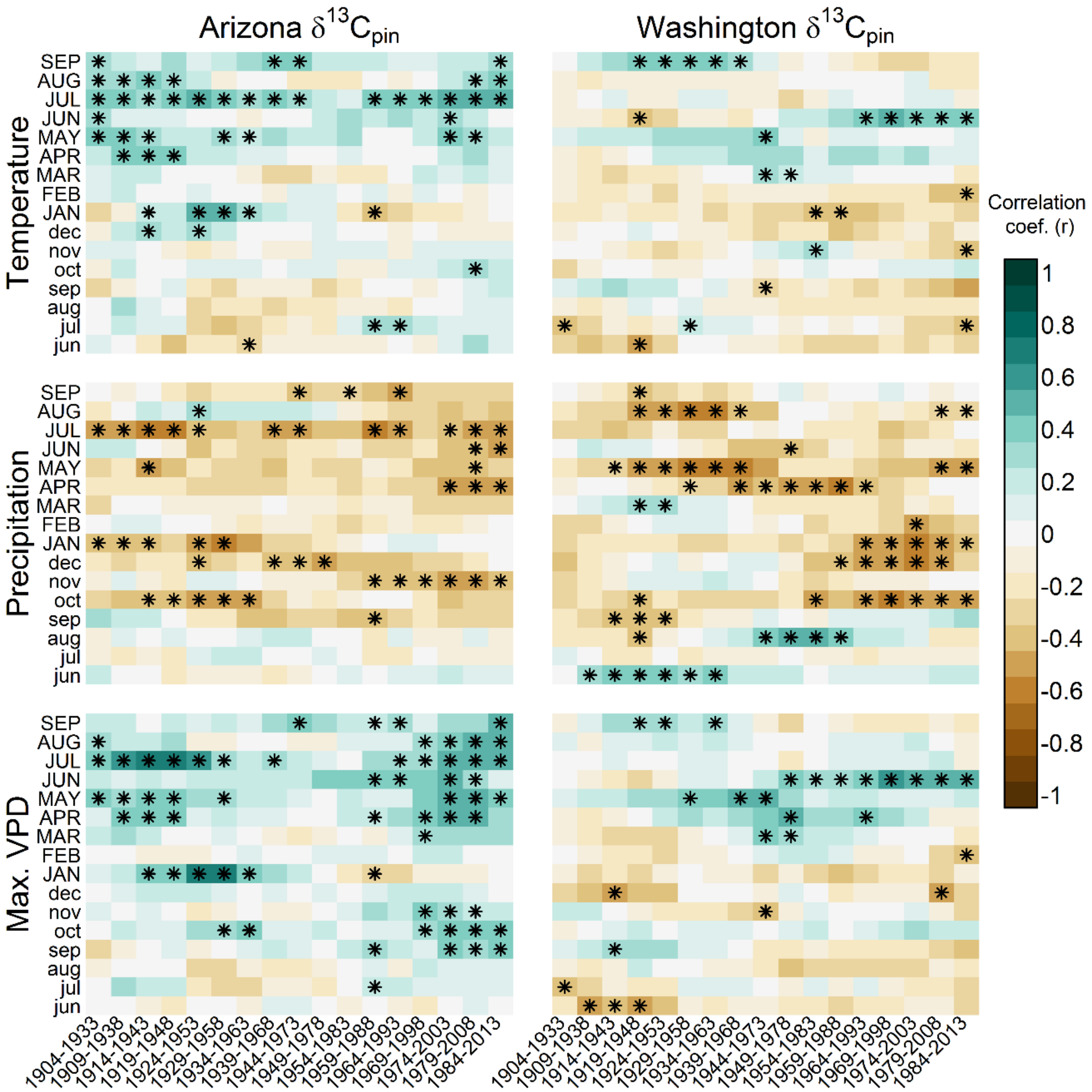

Figure 5. Moving window correlation function analysis showing the relationship over 30 year intervals between annual tree ring ^{13}C ratios ($\delta^{13}C_{pin}$) and three monthly climate variables: mean temperature, total precipitation and maximum vapor pressure deficit (VPD). Colors represent the strength of the correlations over 30 year windows for the Arizona (left column) and Washington

(right column) sites. Significant ($p < 0.05$) correlations are starred. Upper and lower case lettering indicate the current growth year and the previous year, respectively.

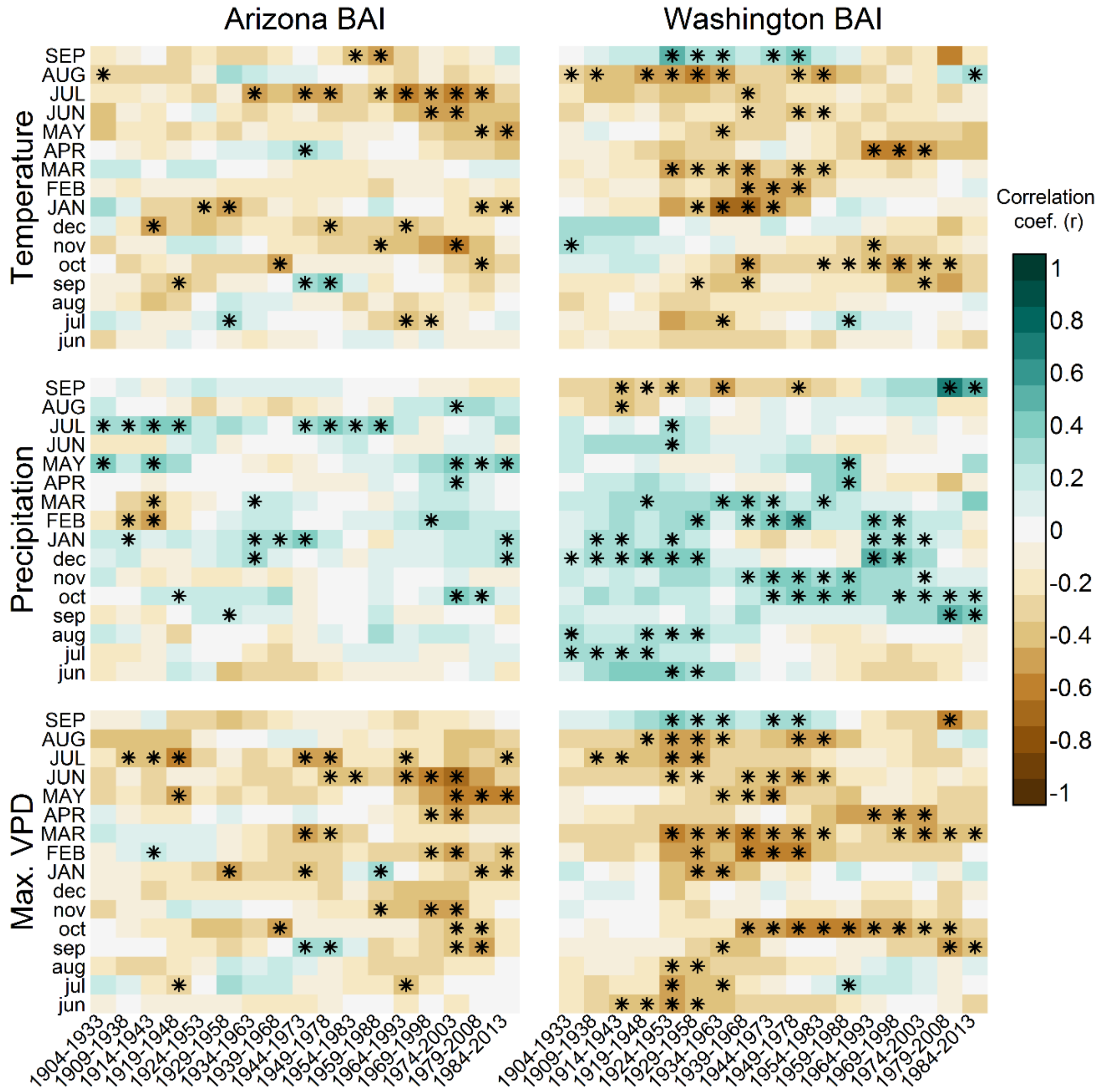

Figure 6. Moving window correlation function analysis showing the relationship over 30 year intervals between tree growth (basal area increment, BAI) and three monthly climate variables: mean temperature, total precipitation and maximum vapor pressure deficit (VPD). Colors represent the strength of the correlations over 30 year windows for the Arizona (left column) and Washington (right column) sites. Significant ($p < 0.05$) correlations are starred. Upper and lower case lettering indicate the current growth year and the previous year, respectively.

The positive relationship between drought intensity (PDSI and VPD) and $\delta^{13}C_{pin}$ is consistent with decreasing stomatal conductance during drought years that would tend to decrease iWUE (increase $\delta^{13}C_{pin}$). A period of increased iWUE and decreased BAI from 1900-1905 in Arizona corresponded with a period of very low (-5,-6) PDSI, and 1905-1910 saw high PDSI, increased BAI and decreased iWUE (Figure 2).

Short-term responses of BAI and iWUE, to fuel treatments

Fuel treatments at both sites influenced tree growth, and hence, rates of live tree carbon sequestration. Thinning and thinning and burning caused an increase in BAI (Figures 7 and 8) between the Control and Thin and Burn units in Washington site ($p < 0.01$, ANOVA and post-hoc Tukey test) and a nearly significant response ($p = 0.06$) between the Thin and Control sites in Arizona. The BAI response to treatments, overall, supports our hypothesis of treatment effects (thin and burn), but the post-treatment response for thin only was not sufficiently large to reach the threshold of statistical significance. Radial growth increases after restoration treatments that reduce density and basal area are common in ponderosa pine forests but specific response can vary by site, stand history, and tree age (e.g. Skov et al. 2005).

An analysis of carbon stocks at a number of the FFS network sites showed that thinning or thinning and burning reduced vegetation carbon by ~30 Mg/ha and that fire reduced forest floor carbon storage by ~1-7 Mg/ha (Boerner et al. 2008). These carbon losses were offset by enhanced uptake of ~12 Mg/ha carbon in first 1-3 years following treatment, although the two sites used in this study were not resampled >1 year post-treatment in the network analysis (Boerner et al. 2008). Similarly, eddy covariance measurements of carbon and water flux in an Arizona ponderosa pine forest showed that thinning reduced the strength of the carbon sink for two years, and then it strengthened compared to values in an undisturbed stand due to reduced competition for water (Dore et al. 2012). The post-treatment BAI increases at both study sites supports work that shows that increased productivity in surviving trees partially offsets carbon losses from thinning and burning, and is consistent with observed increases in BAI following thinning in other studies despite a lack of significant change in iWUE (Fernandez-de-Una et al. 2016). Moreover, thinning helps protect trees from drought-induced mortality by increasing g, reducing the risk of hydraulic failure and carbon starvation (McDowell and Allen 2015). Prescribed fire treatments and low stand density have been found to reduce drought-induced mortality at least in California mixed-conifer forests (Van Mantgem et al. 2016).

An analysis of potential tree mortality and emissions from six western FFS sites found that in most cases, thinning and thinning and burning reduced estimated tree mortality and emissions from wildfire. At the Arizona site, treatment however did not affect the potential for carbon loss from wildfire (Stephens et al. 2012). Similarly, treated and untreated units at the Washington site did not show significant differences in estimated basal area survival after wildfire (Agee and

Lolley 2006), suggesting that treatment at both sites may not have successfully mitigated risk of severe wildfire. Severe wildfire which converts ponderosa pine stands to grassland has been shown to result in a large and persistent carbon source as opposed to thinning stands, after which carbon sink strength recovers in ~4 years (Dore et al. 2012).

Fuel treatments decreased iWUE relative to the Control unit in Arizona but increased iWUE in Washington (Figures 7 and 8), although the differences between treatments were not statistically significant.

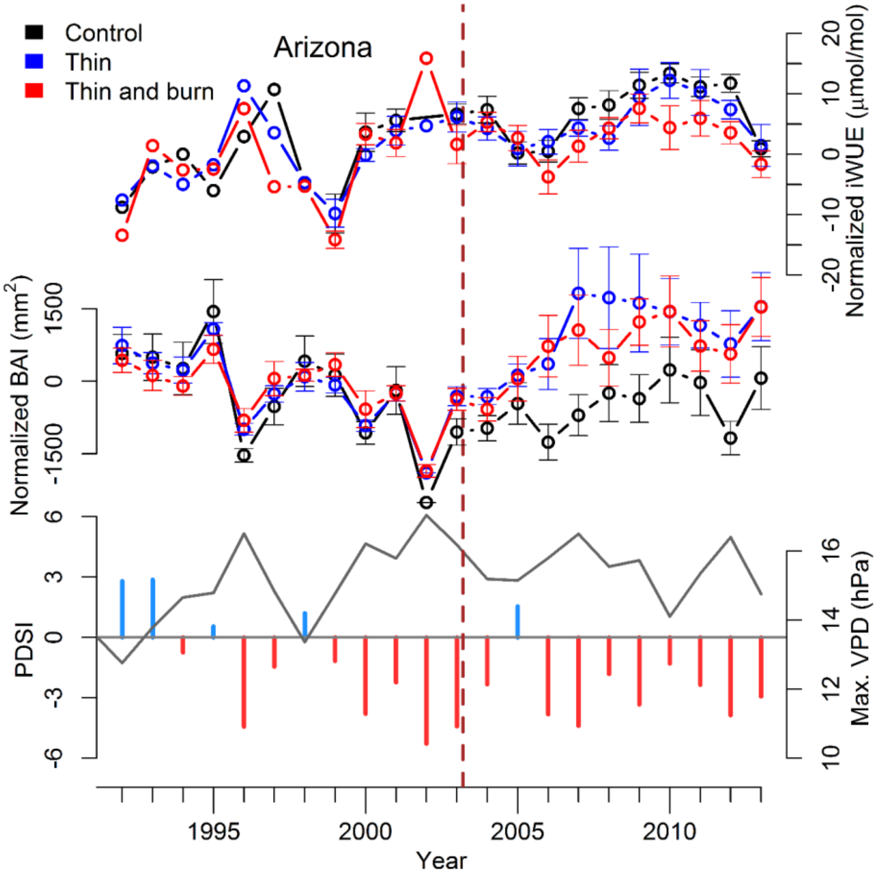

Figure 7. Intrinsic water use efficiency (iWUE) and basal area increment (BAI) in each treatment unit (Control, Thin, and Thin and Burn) at the Arizona site. Values for iWUE and BAI are normalized to 1992-2001 means for each treatment unit. Bars represent ±SE for years in which individual tree values (n = 5 per treatment unit) were measured. Annual Palmer Drought Severity Index values for the region are shown at the bottom (blue and red bars) along with average maximum vapor pressure deficit (gray line). Thinning occurred in fall 2002 and burning in fall 2003, represented by the dashed line.

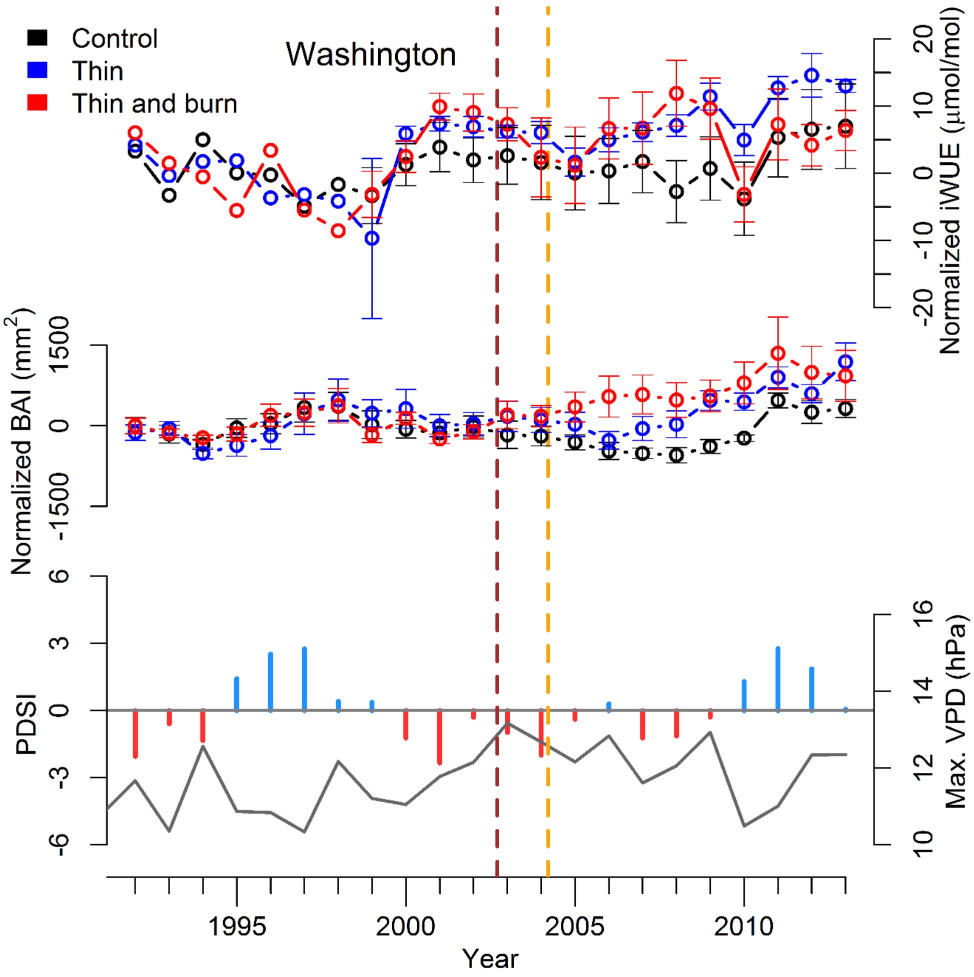

Figure 8. Intrinsic water use efficiency (iWUE) and basal area increment (BAI) in each treatment unit (Control, Thin and Thin and Burn) at the Washington site. Values for iWUE and BAI are normalized to 1993-2002 means for each treatment unit. Bars represent ±SE for years in which individual tree values (n = 5 per treatment unit) were measured. Annual Palmer Drought Severity Index values for the region are shown at the bottom (blue and red bars) along with average maximum vapor pressure deficit (gray line). Thinning occurred in fall 2002 (dashed brown line) and burning in spring 2004 (dashed yellow line).

These contrasting treatment responses at the two sites likely reflect climatic conditions before and after treatment. At the Arizona site, the period 2000-2013 was characterized by very dry conditions represented by low PDSI and high maximum VPD (Figure 5). These years are part of a prolonged drought across the southwestern US (Dai 2013), which was extremely severe in 2002, caused increased water stress and triggered tree mortality across the region (Breshears et al. 2005, 2009, Williams et al. 2010, Ganey and Vojta 2011). The large response of iWUE to the in 1997-1998 to a wet El Nino demonstrates considerable sensitivity of trees at the Arizona site to moisture (Fiure 5). At the water-stressed Arizona site, treatment decreased competition among plants for water, and seems to have led to higher stomatal conductance (g_s) in the surviving trees and thus lower iWUE despite increased radial growth (Figure 5). Thus, treatments lower iWUE mean values. The control stand which does not include treatments effects, and thus represent the tree's physiological response to atmospheric CO_2 and climate show the highest iWUE. Increase in iWUE reflects increasing drought stress. Both treatments display lower iWUE compared to the control indicating that treatment led reduced stress via increased water availability. The treatment effect on iWUE was strongest for the first 3-5 years and most persistent in the thin and burn treatment perhaps due to both increase water availability, and an increase in nutrients from thinning and burning (e.g. Sanchez-Meador et al. 2017). Carbon isotopic discrimination is mainly controlled by stomatal conductance, driven by VPD and soil moisture. The higher iWUE observed in the control site results from stomatal limitation on iWUE and subsequent reduction of photosynthetic assimilation and growth despite increasing $CO_{2.}$ Lower iWUE in the treatment stands results from reduced stomatal limitation (g_s) via reduced competition and higher photosynthetic assimilation than in the control sites. Treatments did not change isotopic discrimination during the post treatment years, indicating that growth was caused by an increase in A and g_s. Overall, there was a reduction in iWUE in treated stands in Arizona which supports our hypothesis of treatment effects, but the treatment response was not sufficiently large to reach the threshold of statistical significance.

In comparison, iWUE prior to treatment at Washington varied among sites due to differences in elevation. All sites experienced relatively moist conditions (higher PDSI, lower maximum VPD) in the 10 years before and after treatment (Figure 6). The increasing trend in iWUE in all stands reflect the physiological response of trees to rising CO_2 in the atmosphere and perhaps temperature affecting photosynthetic capacity. In Washington, iWUE and isotopic discrimination increased in post treatment years. Compared to the Arizona site, growth at the Washington site was less water-limited. Decreased competition for water and nutrients due to thinning and thinning and burning led to increases in canopy photosynthesis (A) rather than g_s which increased iWUE.

The observed decrease in iWUE following treatment in Arizona agrees with previous work on tree carbon-water balance responses to forest management in ponderosa pine forests of Arizona. Thinning has been found to increase Δ in Arizona ponderosa pine stands in the 12 years following thinning, and Δ was negatively correlated with stand basal area (McDowell et al. 2006). From 13-40 years, an effect on Δ was not apparent but the leaf area to sapwood area ratio was negatively correlated with basal area, indicating that trees adapted structurally to thinning in the long term (McDowell et al. 2006). Thinning also increased Δ and decreased iWUE in dry (annual precipitation of 360 mm/yr) ponderosa pine forests in Oregon (McDowell et al. 2003). On the other hand, in wetter forests, thinning treatments have been linked to increases in iWUE, for example in planted pine and fir forests in Spain (1089 mm/yr. precipitation) (Navarro-Cerrillo et al. 2016) and in Douglas-fir forests in British Columbia, Canada (1160 mm/yr.) (Brooks and Mitchell 2011). In Douglas-fir stands in Oregon (1417-1968 mm/yr.) thinning either increased (one unit) or did not significantly change (two units) iWUE (Ruzicka et al. 2017). Fernandez-de-Una et al. (2016) argue that significant differences in iWUE due to treatments are not a general case but are tied to systems strongly limited by one factor (e.g. water, light or nutrients) such that treatment differentially affects either A or g instead of both in tandem. The different treatment responses to treatments in Arizona and Washington support this perspective.

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Supplemental Figures and Tables

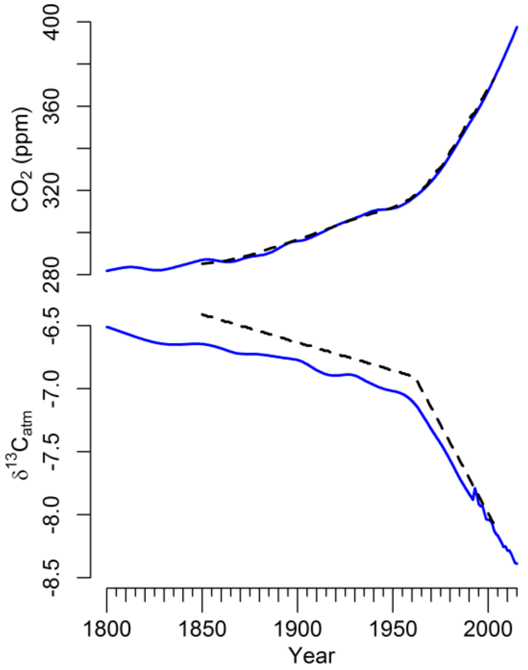

Figure S1: A comparison of annual atmospheric CO_2 concentrations (top) and atmospheric $\delta^{13}C$ (bottom) generated for this study for 1800-2013 (blue lines) with values reported by McCarroll and Loader (2004) (dashed black lines).

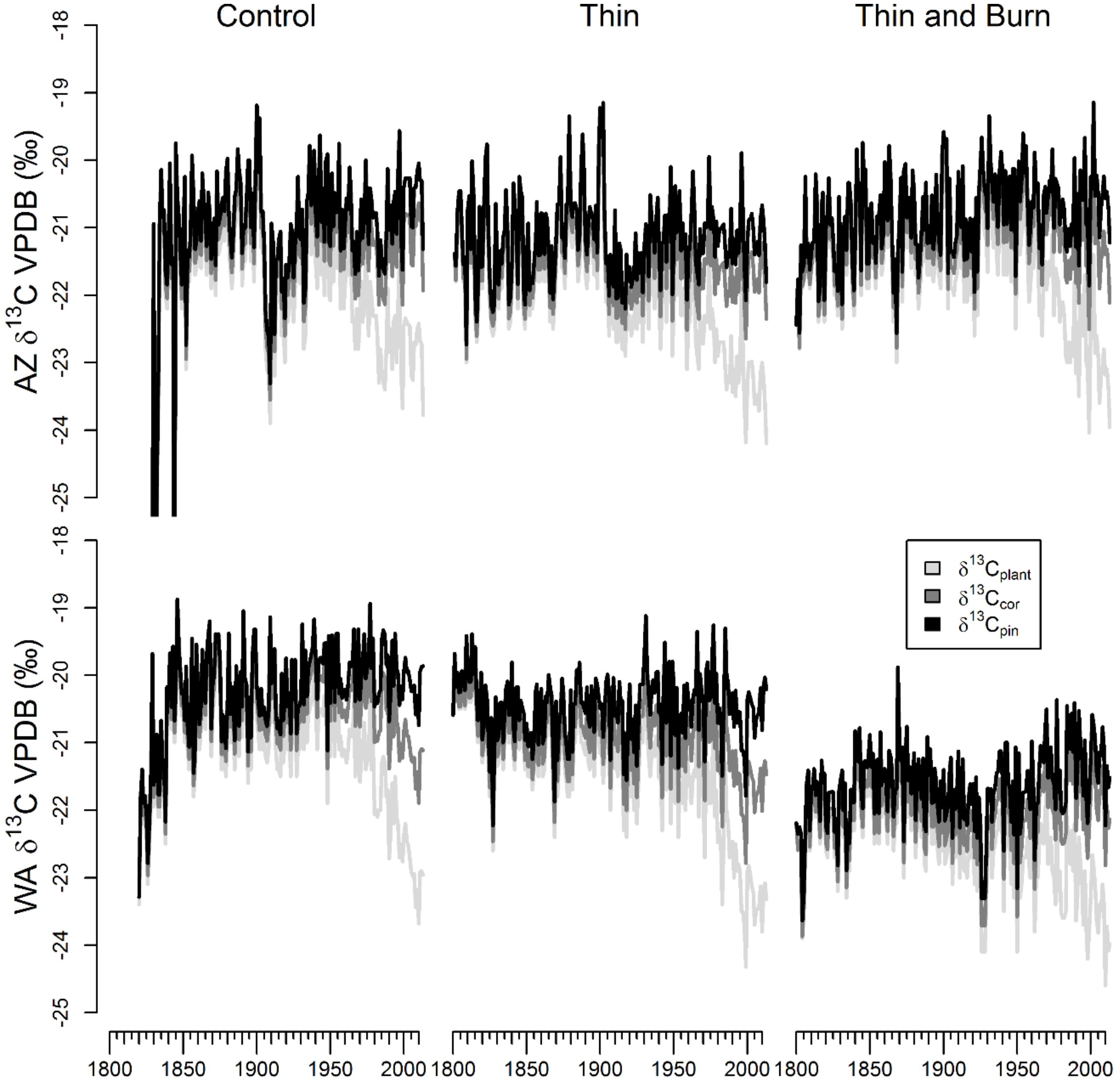

Figure S2. Results of correcting tree ring carbon isotope ratio time series ($\delta^{13}C_{plant}$, light gray) for changes in atmospheric $\delta^{13}C$ since 1800 ($\delta^{13}C_{cor}$, dark gray) and additionally for trees' physiological response to changing atmospheric CO_2 concentrations ($\delta^{13}C_{pin}$, black). The top row shows series for each treatment unit (Control, Thin, Thin and Burn) at the Arizona site and the bottom row shows the series from the Washington site.

Table S1. Increment cores used for isotopic analysis at the Arizona and Washington sites. Within each treatment unit two cores each from five trees were used except for the Washington Control site where only four trees were used. The master chronologies with which each series was compared were built from smaller-diameter increment cores taken from 20 trees at each site. In Arizona 28 of 30 cores were missing a ring in 2002, a year of severe drought in the southwestern US. In Washington 3 cores had years since 1990 omitted due to thin and/or missing rings between 1990 and 2013. Years before 1800 were not used for analysis.

Site	Treatment	Tree	Core	Earliest ring	Correlation with master	Notes
AZ	Control	2	A	1847	0.69	2002 absent
		2	B	1860	0.71	2002 absent
		3	A	1855	0.69	2002 absent
		3	B	1854	0.7	2002 absent
		4	A	1855	0.54	2002 absent
		4	B	1845	0.58	2002 absent
		5	A	1854	0.7	2002 absent
		5	B	1829	0.68	2002 absent
		6	A	1843	0.68	2002 absent
		6	B	1844	0.76	2002 absent
	Thin	1	A	1826	0.7	2002 absent
		1	B	1814	0.68	2002 absent
		2	A	1844	0.73	2002 absent
		2	B	1877	0.69	
		4	A	1802	0.52	2002, 1880, 1879, 1878 absent
		4	B	1835	0.65	2002 absent
		5	B	1859	0.71	2002 absent
		5	C	1841	0.68	2002 absent
		6	A	1799	0.71	2002 absent
		6	C	1824	0.58	2002 absent
	Thin and Burn	2	A	1802	0.7	2002 absent
		2	B	1812	0.76	2002 absent
		3	A	1832	0.81	2002 absent
		3	C	1820	0.8	2002 absent
		4	A	1788	0.73	2002 absent
		4	B	1810	0.65	2002 absent
		5	A	1801	0.72	2002 absent
		5	B	1878	0.7	
		7	A	1825	0.81	2002 absent
		7	B	1830	0.73	2002 absent
WA	Control	1	A	1818	0.43	
		1	C	1836	0.41	not used 2001-2013
		3	A	1838	0.46	
		3	B	1854	0.43	
		4	A	1820	0.42	
		4	C	1820	0.38	

	6	A	1823	0.45	
	6	B	1835	0.42	
Thin	1	A	1813	0.32	
	1	B	1887	0.36	1994-2013 not used
	3	A	1821	0.26	2000-2013 not used
	3	B	1860	0.44	
	4	A	1825	0.39	
	4	B	1820	0.33	
	6	A	1764	0.39	Only 1870-2013 used
	6	B	1755	0.26	
	7	A	1832	0.41	
	7	B	1825	0.47	
Thin and Burn	1	A	1754	0.49	1847-1850 not used
	1	B	1733	0.44	
	2	A	1822	0.51	
	2	B	1826	0.44	
	3	A	1817	0.5	
	3	C	1844	0.46	
	4	A	1812	0.5	
	4	B	1800	0.49	
	5	A	1673	0.38	
	5	B	1726	0.36	

Table S3 Deliverables for the project.

Deliverable Type	**Description**	**Delivery Dates**
Conference	Taylor, A.H., Belmecheri, S., Harris, L. Do fuel treatments restore ecosystem function? Response of water use efficiency to fuels treatments in an Arizona ponderosa pine forest as measured by tree ring δC_{13}, Tucson, AZ	12/1/2016
Conference	Taylor, A.H., Belmecheri, S., Harris, L. Do fuel treatments restore ecosystem function? Response of water use efficiency to fuels treatments in Arizona and Washington ponderosa pine forest as measured by tree ring δC_{13}, American Geophyscial Union, San Francisco, CA	12/14/2016
Data set	Time series of tree ring widths; Time series of δC_{13} isotope measurements in control, thin, and thin and burn sites in Arizona and Washington. These data sets have been quality checked and will be archived in the International Tree Ring Data Bank hosted by NOAA-NCDC	Within 12 months post project or acceptance of publication, whichever comes first
non-referred publication	Do Fuel Treatments restore ecosystem function? Water use efficiency before and after fire suppression and fuels treatments in fire-prone pine forests in the western United States. Research Brief for Southwest and Northwest Fire Science Consortia	4/30/2017
draft manuscript	The effects of fuel treatments on water use efficiency in ponderosa pine forests	9/30/2017
Draft manuscript	Variable response of radial growth and water use efficience in ponderosa pine forests in the northwest and southwest United States	9/30/2017

Research Brief: Do fuel treatments restore ecosystem function? Water use efficiency before and after fire suppression and fuels treatments in fire-prone pine forests in the western United States. Alan Taylor, Soumaya Belmecheri, Lucas Harris, Department of Geography, The Pennsylvania State University (JFSP Project 13-1-04-22)

Fuel treatments, including mechanical thinning and prescribed fire, have become an increasingly important management tool in dry forests of the western US. One goal of these treatments is to reduce the risk of high-severity wildfires. However, the broader goal is to restore ecosystems to a state in which fires once again regulate forest structure and function.

A key question when treating fuels is whether or not these treatments restore ecosystem function. What makes this question challenging to answer is that we lack information on how forests functioned before Euro-American settlement. Establishing a quantitative measure of how dry forests functioned in the past under an intact fire regime would allow us to evaluate how effective fuel treatments are today in restoring forests.

Carbon isotopes in tree rings offer a way to compare ecosystem function in the 1800s to ecosystem function today. Tree rings are valuable because they provide information at annual resolution, and variability can be measured by analyzing multiple trees. Although ring widths alone provide valuable information about how trees have responded to past changes in climate and disturbances, isotopes in tree rings provide additional information on carbon-water balance that relates to ecosystem function.

Carbon isotopic fractionation happens in plants during photosynthesis. Plants take in carbon dioxide (CO_2) for photosynthesis through pores- at the leaf surface called stomata, and they open and close their stomata in response to environmental conditions (such as drought, high temperature). While opening stomata allows plants to take in more CO_2 and assimilate more carbon, water is also lost when the stomata are open. If humidity is low and soil moisture is low, plants will tend to keep their stomata closed to conserve water. In moister conditions stomata tend to be open to maximize carbon assimilation. Stomatal conductance, which reflects this tradeoff between carbon and water, is a major determinant of carbon isotopic fractionation in plants.

The ratio of $^{12}C/^{13}C$ in a tree ring reflects isotopic fractionation during photosynthesis in that growth year. By measuring this ratio and correcting for atmospheric CO_2 concentrations a measure called intrinsic water use efficiency (iWUE) can be derived. iWUE is the ratio of photosynthetic assimilation A (or carbon gained by the plant) and stomatal conductance, or how much water the plant lost through its stomata, g. By calculating iWUE from tree rings we can get a measure of how well the tree is functioning in response to environmental change. By measuring multiple trees, we can obtain a measure of ecosystem function for every year and characterize the variability within the ecosystem.

We calculated iWUE from tree ring carbon isotopes for the past 200 years in ponderosa pine stands in Arizona and Washington. Although the two sites differ in terms of climate, both sites burned frequently and at low severity in the past. The sites were heavily grazed and logged in the late 1800s and early 1900s, and experienced a long period of fire suppression after the early 1900s. These stands received fuel treatments 15 years ago as part of an earlier study, so that some stands were mechanically thinned, some were thinned and then burned and some were left untreated. In 2014, we collected cores from fifteen trees each in Arizona and Washington, five trees within each treatment (control, thin and thin and burn). Calculating iWUE from these ponderosa pine stands lets us answer two questions:

1) *How did ecosystem function change over the past two centuries in these forests?* We expected that water use efficiency rose from 1800-2013 due to increased atmospheric CO_2, but also expected iWUE to change after logging and fire suppression and to vary year to year in response to drought stress.

2) *Have the fuel treatments in these forests restored ecosystem function?* Because fuel treatments should reduce competition and recycle nutrients we anticipated that the fuel treatments would increase productivity, as measured by growth. We expected both A and g to increase after treatment, and A/g to decrease in drought-stressed forests where less competition for water after treatment leads to increased g relative to A.

Change from 1800-2013

We found that iWUE increased from 1800-2013 and especially from 1900-2013 at both study sites. These increases closely tracked rising atmospheric CO_2 levels. Similar CO_2-driven increases in iWUE have been observed since 1800 in forests worldwide, sometimes resulting in increased tree growth. iWUE also varied year-to-year at our sites in response to drought, increasing during dry years when closing of stomata decreased g.

Tree growth at our sites did not increase in tandem with iWUE. Instead, growth increased in Arizona from 1880-1910, a period of intense grazing and logging in the area during which surviving trees would be expected to grow faster due to reduced competition. Growth declined from 1920-1980 during a period of fire suppression and increasing tree density, which meant increased competition among trees for water and nutrients. Growth was less variable at our Washington site but did decline from 1950-2000, which was also a period of fire suppression and increasing forest density.

Effects of fuel treatments

At both sites treated units had increased growth (as measured by basal area increment, or BAI) relative to the control units in the ten years following treatment. However, iWUE responded in opposite ways at the sites. In Arizona iWUE decreased slightly in treated stands relative to the control, and in Washington iWUE increased relative to the control.

These divergent treatment responses likely reflect differences in what was limiting tree growth at each site. The southwestern US experienced severe and widespread drought from 2000-2013. Under such dry conditions pines in treated units likely responded to increased availability of water after treatment, meaning that g increased more than A and A/g, or iWUE, decreased. In contrast, the Washington site experienced moister, cooler conditions after treatment and therefore pines at that site were likely less moisture limited. In this case, the pines likely responded primarily to increased light and nutrients instead of water and therefore A would be expected to increase more than g, meaning increased iWUE as we observed in Washington.

Our work shows that fuel treatments had a positive effect on productivity of canopy trees at both sites, but through different primary mechanisms: increased water availability at the drought-stressed Arizona site and increased light and nutrients at the moister Washington site. In both sites, treatments reduced competitions and the effect of environmental stressors on tree's physiology.

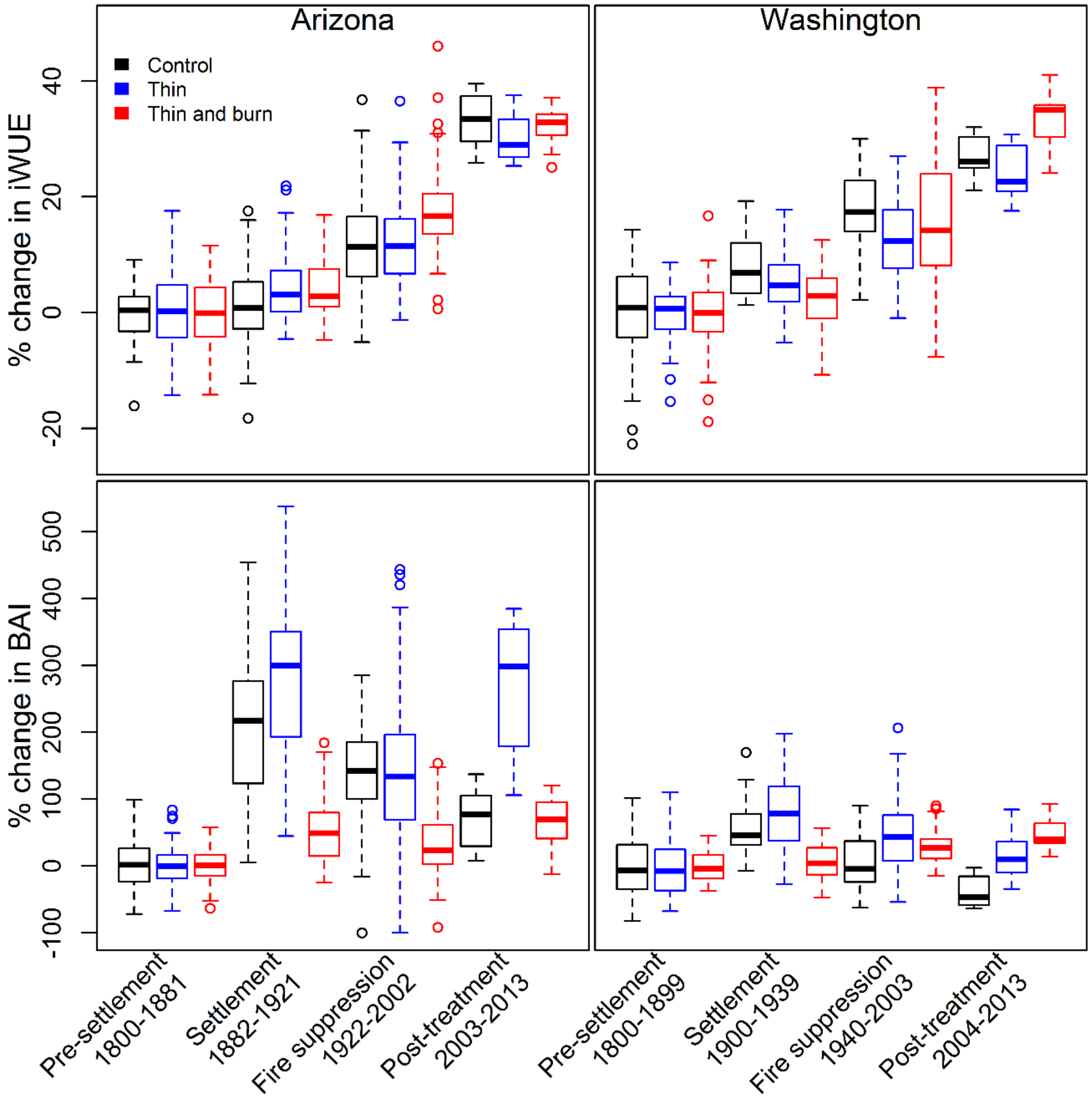

Figure 1. Percent change in intrinsic water use efficiency (iWUE, top) and tree growth (basal area increment, bottom) at the Arizona and Washington study sites in relation to pre-Euro-American settlement values (i.e. means from "Pre-settlement" years).

Figure 2. Collecting tree cores for carbon isotope analysis in the Arizona Fire and Fire Surrogate study site near Flaggstaff, Arizona in May 2014.