Key Points:
- Twenty years of experimental data show that biomass production in ponderosa pine forests is controlled by interactions between climate and soil resources
- Fertilization and understory suppression reduce competition for water and nutrients and increase productivity of pine plantations beyond expected limits
- Tree ring isotope data show that physiological acclimation to climate variability diverges depending on edaphic properties and management history

Supporting Information:
- Supporting Information S1

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(continued)

Two Decades of Experimental Manipulation Reveal Potential for Enhanced Biomass Accumulation and Water Use Efficiency in Ponderosa Pine Plantations Across Climate Gradients

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Abstract In this study, we report 20 years of data from three ponderosa pine plantations in northern California. Our sites span a natural gradient of forest productivity where climate variability and edaphic conditions delineate marked differences in baseline productivity (approximately threefold). Experimental herbicide application and fertilization significantly reduced competition and improved tree growth by 1.4- to 2.2-fold across sites. At the site of lowest productivity, where soils are poorly developed and water limiting, tree growth increased strongly in response to understory suppression. Small but significant improvements in tree growth were observed in response to understory suppression at the moderate-productivity site. At the site of highest productivity, where climate is favorable and soils well developed, fertilization increased productivity to a greater extent than did understory suppression. In most cases, the effect of understory suppression and fertilization caused an unexpected growth release, exceeding the anticipated maximum productivity by >5 m of additional height and 60–100% more basal area. At the site of highest productivity, however, understory suppression caused a weak increase on late-season growth compared to fertilization alone, suggesting a beneficial effect of understory vegetation on long-term growth at that site. Tree ring cellulose carbon isotopes indicate a negative relationship between intrinsic water use efficiency (iWUE) and tree growth in control stands, which shifted to a positive relationship as both iWUE and tree growth increased in response to management. Cellulose oxygen isotope ratios ($\delta^{18}O$) were positively correlated with iWUE and negatively correlated with vapor pressure deficit across sites, but $\delta^{18}O$ was not a strong predictor of tree growth.

Plain Language Summary This study is the culminating effort of a 20-year experiment on the effects of climate variability and management in California's ponderosa pine plantations. Pine trees were grown in three different climatic and edaphic zones treated with herbicide to reduce competition from understory plants and/or fertilizer to stimulate growth. We found that management increased tree growth and, in most but not all cases, the combination of understory suppression and fertilization stimulated productivity beyond the expected growth potential of each site. In addition, we observed interesting differences between treatments according to soil and a climate conditions of each site. Wet sites have the most productive forests overall, but they also respond less strongly to management than do dry sites of low productivity, where understory suppression and fertilization were most effective in increasing tree growth and water use efficiency. These results provide a road map for enhancing carbon accumulation and water use efficiency through adaptive management of soil-plant-atmosphere interactions in planted forests and will help modeling efforts aimed at mitigating the impacts of climate change on montane forest landscapes.

1. Introduction

Accumulating observational evidence suggests that the availability of soil resources regulate the impact of climate variability on temperate forest ecosystems (Dietrich et al., 2016; Fernández-Martínez et al., 2014; Gómez-Guerrero et al., 2013; Maxwell et al., 2018). Few studies, however, have experimentally tested the long-term effect of competition for soil resources in forests across climatic stress gradients. To address

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this limitation, we studied ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) plantations as a model system to quantify the impact of competition for water and nutrients under contrasting climatic scenarios. Ponderosa pine is broadly distributed across North America (Little, 1971) and is the most commonly planted tree species in Northern California (Powers & Ferrell, 1996). Along with other dominant conifers, ponderosa pine populations have been increasingly threatened by climatic and land use change (Young et al., 2017). Throughout the region, planted ponderosa pine forests are a major component of working landscapes, where the use of "stand improvement" practices to attenuate resource limitation is commonly achieved through the use of herbicide and fertilization. These management practices have long been used during the establishment of forest stands, when young trees are thought to face strong competition for water and/or nutrients with understory plant communities, which have long been shown to limit growth and lead to tree mortality at shrub densities as low as 20% (Oliver, 1984). However, many uncertainties still surround the effectiveness of traditional management practices on ponderosa pine stands under increasing climatic stress.

The Mediterranean climate of northern California produces seasonal precipitation, primarily during the winter, where trees and forest ecosystems experience water stress during most of the growing season (Franco-Vizcaino et al., 2002; Turner, 1991). Thus, as the soil desiccates and transpiration is increasingly suppressed into the growing season, water soluble nutrients also become limiting as they must be acquired via mass flow and diffusion to the root surface. As a result, the physiological response of trees to water availability (e.g., changes in stomatal conductance and water use efficiency) is inherently connected to nutrient limitation (Lambers et al., 2008). As temperatures continue to rise and precipitation becomes more variable throughout the region, it is important to understand these interacting processes because water availability could limit the efficacy of competitor removal with herbicide and fertilization management strategies that are commonly designed to improve nutrient availability (Zhang et al., 2013). This study seeks to characterize the long-term effect of standard forestry practices on the growth and physiological response of ponderosa pine trees to spatial and temporal climate variability.

Three experimental plantations with identical layouts, controls, and treatments were selected for this study. They span a variety of temperature and precipitation regimes (as well as edaphic properties) where stands were established in the 1980s and sampled in 2007 using standard dendrochronological techniques. To understand how climate variation interacts with soil resources and management with respect to tree growth and stand productivity, tree ring and environmental data were combined with isotopic records of tree ring cellulose. Specifically, stable isotope ratios of carbon and oxygen were used to gain insight into physiological mechanisms driving tree growth response to climate and management. As in previous studies of this kind (Maseyk et al., 2011), we used carbon isotope ratios ($\delta^{13}C$) of tree ring cellulose as a proxy for intrinsic water use efficiency (iWUE). According to well-known factors affecting carbon isotope fractionation (defined mathematically in equations (1)–(3) of the methods), any environmental stress that leads to a reduction in stomatal conductance (e.g., low water availability) will also impact the photosynthetic uptake of CO_2, thus shifting the efficiency of carbon uptake by photosynthesis per unit of water transpired (iWUE). When coupled with analyses of oxygen isotope ratios ($\delta^{18}O$) cellulose $\delta^{13}C$ can be used to infer the dominant physiological driver of iWUE variation (Brooks & Mitchell, 2011; Roden & Farquhar, 2012). This is possible because a decrease in stomatal conductance (g_s) causes a change in transpiration rates leading to isotopic enrichment of $\delta^{18}O$ in leaf water. Thus, whenever concerted changes in $\delta^{18}O$ and $\delta^{13}C$ ratios occur, variation in iWUE can be interpreted as variation in water availability as the primary control on productivity compared to, for example, nutrient limitation of photosynthesis (Maxwell et al., 2014; Sparks & Ehleringer, 1997).

Tree ring $\delta^{18}O$ ratios also depend on source water values which vary widely over time and space with changes in rainfall, temperature, and vapor pressure deficit (VPD; Cernusak et al., 2018; Edwards et al., 1996). Thus, developing physiological interpretations of $\delta^{18}O$ data collected across multiple sites are often unfeasible. To address this issue, here we compare $\delta^{18}O$ data from co-located control and treatment stands as additional evidence for interpreting iWUE acclimation to differences in water availability in response to management using local baselines to control for climate-induced tree ring $\delta^{18}O$ variation, as suggested in previous studies (Silva et al., 2015; Silva & Horwath, 2013; Sternberg, 2009). Accordingly, our analysis combines dendrochronological and isotopic data with climatic variables to quantify the effects of competitor

Table 1
Climate Data Calculated Based on the Years 1986–2008

Site characteristics	Elkhorn	Whitmore	Feather Falls
Elevation (m)	1,545	756	1,246
SI_{50} (m)	17	23	30
Province	Klamath	Cascade	Sierra
Planted	1988	1986	1988
Initial status	Plantation	Brushfield	Natural stand
Soil great group[a]	Dystroxerept	Haplohumult	Haploxeralf
MAP (mm)[b]	1,035	1,080	1,990
MAT (°C)[b]	11.0	14.8	12.5
VPD (hPa)[b]	14.4	21.47	16.8

Note. SI_{50} = Site Index, growth potential for 50 years of growth; MAP = mean annual precipitation; MAT = mean annual temperature; VPD = vapor pressure deficit.
[a]Data from McFarlane et al., 2009.   [b]Data from PRISM climate group.

removal and/or fertilization experiments on tree and stand productivity as well as their physiological basis. Although ponderosa pine has been studied extensively across its range to assess variation in iWUE (Soulé & Knapp, 2011), and growth response to stand density (McDowell et al., 2010), seasonal rainfall dynamics (Roden & Ehleringer, 2007), and elevation (Adams & Kolb, 2005; McDowell et al., 2010), recent changes in climate and unexpected pine population collapse show that further investigation is necessary.

2. Materials and Methods

2.1. Study Sites

We used sites from the Garden of Eden study, which were established to determine the effects of silvicultural treatments over a range of plantation sites typifying ponderosa pine growth in northern California (Powers & Ferrell, 1996). At each site, 24 contiguous 0.04 ha plots were established and hand planted, in the spring of 1986 or 1988, at a 2.4-m square spacing (1,680 trees/hectare) from converted brush fields or natural stands (see Tables 1 and A1 for details), consisting of two levels of four factors (2 × 4) with three replications. This study focused on the core treatments that controlled understory vegetation (repeated herbicide application) and soil fertility (repeated application of N, P, K, Ca, Mg, S, Zn, Cu, and B). Herbicide was applied annually to suppress understory vegetation in the form of glyphosate, hexazione, and triclopyr according to manufacturer recommendations that are specific to soil type. Fertilizer were applied at planting and to stimulate growth in years 3, 5, and 7 at an exponential rate to match increasing demand, the exact application rates are supplied in Table A1. The combination of these treatments and control stands (adjacent tree plantations with no further treatment) was also included in the study. Establishment and further treatment details for the experimental plantation sites are available in Powers and Ferrell (1996). Among the study areas, we selected three sites located <140 km apart, which represent a broad range of productivity (Table 1). Productivity was assessed by site index (50-year base) estimated from heights and ages of dominant trees in bordering stands (Powers & Oliver, 1978). Soil depth plays an important role in the variation of site water availability with a moderately deep Dystroxerept at Elkhorn Ridge (ER), the least productive site with low water holding capacity, and the lowest soil organic matter content in the upper profile (0-30 cm). Whitmore (WH) and Feather Falls (FF), the intermediate and highest productivity sites, have deep Haplohumults or Haploxeralfs, respectively, with greater water holding capacity and soil organic matter contents than at ER.
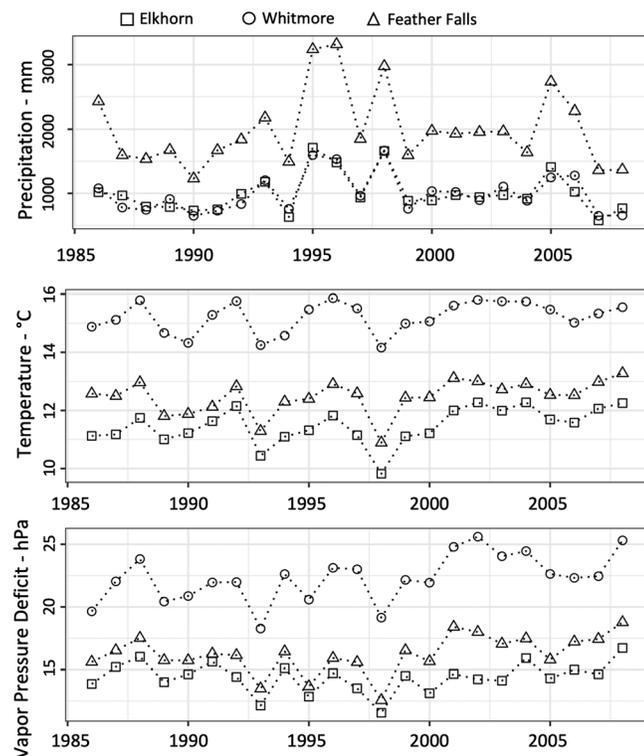
3. Climatic Data

Mean annual precipitation, mean annual temperature, and mean annual maximum vapor pressure deficit were extracted from raster data provided by the PRISM climate group (Table 1 and Figure 1; PRISM Climate Group, 2004). PRISM climate data were available at monthly time steps for the entire experimental period, where monthly values were averaged to generate mean annual values for each site. Polygons of each site were used to define grid cells from which climate data were extracted and weighted to account for grid cells that were only partially incorporated. Annual precipitation varies broadly across sites from a low of 577 mm in 2007 at ER to >3,000 mm in 1995 and 1996 at FF. Site index values and rainfall follow the same sequence with ER the driest site (1,035-mm mean annual precipitation—MAP), followed by

Figure 1. Mean annual precipitation (mm), mean annual temperature (°C), and mean monthly vapor pressure deficit maxima for the duration of the experiment (1986–2007). Analysis of isotopic ratios in tree ring cellulose began when tree reach reproductive maturity (1994), and ended at the time of tree harvest (2008) with the last year omitted because the harvested trees were felled in the spring or early summer and did not represent an entire growth season.

WH (~1,080 mm) and FF (1,990 mm). Site mean annual temperatures are warmest at WH (14.8 °C) and coolest at ER (11.0 °C), with FF in between (12.5 °C). Climate conditions varied significantly across the region during the isotopic record (1994–2007) with considerable interannual variation (Figure 1). Mean annual maximum VPD, a metric of evaporative demand, or water stress of a site was also extracted from PRISM data, which shows a different trend, with ER as the lowest (14.4 hPa) and WH the highest (21.5 hPa) indicating greatest climatic water stress at the WH site. Annual variation in climate help illustrate interactions between treatments and periods considered "wet" or "dry," though discrepancies between the SI_{50} and VPD trends indicate that other factors may control to the productivity gradient. As all stands reached canopy closure, environmental conditions were cool and wet (1995–1998, nominally the "wet period") followed by 6 years of average to dry conditions (1999–2005, nominally the "dry period"). The last few years of the tree ring record (2005–2006) were wet followed by the driest year of the study (2007).

4. Sample Collection and Analysis

For estimating the total productivity of the plantations, all trees were measured at managed and control stands for all sites. For dendrochronological and isotopic analysis an equal number of trees representing small, intermediate, and large diameter at breast height classes were selected and felled from three replicated plots totaling nine trees harvested per treatment at each site. A sample wood disk was cut from the bole of each tree, ~10 cm above the ground to ensure all growth rings were retained. Samples were oven dried at 70°C until they reached a consistent mass. A representative block, ~5-cm wide centered on the pith, was cut from each sample disk and sanded for growth ring measurements with 2–3 additional slices (<10-mm thick) cut to provide biomass for cellulose extraction and subsequent carbon and oxygen isotope analysis. Prior to isotopic measurements, wood samples were ground to <0.5 mm and pure alpha cellulose was isolated using standard extraction methods (Brendel et al., 2000).

Earlywood (EW), latewood (LW), and total (TW) annual ring widths were measured in two directions, along the primary axis, from the pith to the edge. All measurements were generated with a tree ring analysis system (WinDENDRO[TM] 2002), with 0.001-mm accuracy, and averaged. In most cases, 21 individual growth rings could be identified but the early growth in smallest trees often appeared as a continuous mass over the first few years. EW and LW growth rings were distinguishable after year 5 in all trees. Basal area increment (BAI) was calculated using average radial increments, assuming circular geometry. Biomass samples were excised from multiple points in a particular annual growth ring, composited and chopped to <2-mm pieces. Isotopic measurements were made on 1–2 mg of sample with a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer for δ^{13}C measurements and a Hekatech HT Oxygen Analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer for δ^{18}O measurements at the University of California Davis Stable Isotope Facility. All values are expressed as a ratio to their respective standards in ‰ (per mil)—PeeDee belemnite for δ^{13}C ratios and Vienna Standard Mean Ocean Water for δ^{18}O ratios. In all cases measurement precision was better than 0.1‰ as determined from repeated measures of internal quality standards and from replicate samples.

Carbon and oxygen stable isotope analyses of annual tree growth rings provide an integrated measure of physiological responses to management practices and environmental processes that can be transferred across broad spatial and temporal scales (Barbour, 2007; Brooks & Coulombe, 2009; McDowell et al., 2003). To account for this, variation associated with decreasing atmospheric $^{13}CO_2$ abundance ($\delta^{13}C_{air}$) over time due to fossil fuel emissions was removed from the $\delta^{13}C_{plant}$ values by calculating the atmosphere-to-plant isotope discrimination Δ^{13}C each year using equation (1) (Farquhar et al., 1982).

$$\Delta^{13}C = \left(\delta^{13}C_a - \delta^{13}C_p\right) / \left(1 + \frac{\delta^{13}C_p}{1,000}\right), \tag{1}$$

$\delta^{13}C_{air}$ values were obtained (McCarroll & Loader, 2004) and extrapolated for years exceeding those reported. Calculated Δ^{13}C values was then used to estimate iWUE (A/g_s) using the following two equations:

Table 2
Summary Statistics of Experimental Data Over 20 Years Averaged by Treatments and Compared Within Site

Site	Treatment	Basal area (m²/ha)	Early wood (mm)	Late wood (mm)	Height (m)	iWUE (μmol/mol)	δ¹⁸O (‰)
Elkhorn Ridge	C	180b	117b	8.2c	12.4c	102.2a	26.2a
	F	375ab	236ab	17.1b	18b	98.2ab	26.4a
	H	366ab	222ab	20.3a	18.1b	93.9b	26.1a
	HF	476a	304a	20.6a	23.1a	99.7ab	25.7a
Whitmore	C	246b	142b	14.2c	17.6c	98.5ab	27.2a
	F	396b	231ab	24.8b	23.5b	99.5a	27.0ab
	H	409b	249ab	23b	23.4b	96.4ab	26.8ab
	HF	677a	354a	30a	29.2a	93.1b	26.2b
Feather Falls	C	531c	358c	24.4b	33.7c	89.0a	25.0a
	F	833a	518a	47.5a	39.6a	84.5a	25.1a
	H	597b	373b	32.3ab	35.4b	79.0b	24.2b
	HF	856a	563a	29.7ab	38.4a	86.9a	25.5a

Note. Letters represent significant differences determined using repeated measures analysis of variance for the duration of the experiment (1986–2007); $\alpha = 0.05$; $n = 9$ trees per treatment. Treatment labels represent experimental stands selected as control (C), fertilizer application (F), herbicide application (H), and fertilizer plus herbicide application (HF).

$$\Delta^{13}C = a + (b-a)\frac{c_i}{c_a} \qquad (2)$$

$$iWUE = \frac{A}{gs} = \frac{c_a\left(1-\frac{c_i}{c_a}\right)}{1.53} \qquad (3)$$

where a is fractionation resulting from diffusion (4.4‰), b is the fractionation associated with carboxylation by Rubisco (~27‰), and C_i/C_a is the ratio of [CO_2] inside the leaf to [CO_2] in the atmosphere.

5. Statistical Analysis

All statistical analyses and data visualization were performed in the R statistical computing environment (R Team Core, 2015). Repeated measures analysis of variance (ANOVA) was used to assess significant differences in tree growth response and isotopic composition of wood cellulose to treatment over time at each site. Comparisons of multiple mean values between sites and between treatments within site were made using Tukey's honestly significant difference post hoc test, as identified by different letters denoting significant differences. This approach was also used to compare environmental variables between sites. Two-way ANOVA tests with interaction terms were used to assess the significance of treatments and sites, and their interaction. As these data were nonnormal, a generalized linear mixed effects model with penalized quasi-likelihood criteria were used (glmmPQL function in MASS package) with random intercepts to control for tree, site, and interannual variability. In all cases, statistical analyses were performed for each site and treatment using response data normalized relative to controls; that is, (treat − control)/control. Data are presented for all measured variables either in the main text or appendices used to generate a correlation table including all significant linear (positive or negative) relationships between climatic, physiological, and growth variables. The entire data set can be found in the supporting information or downloaded from a permanent online repository at https://scholarsbank.uoregon.edu.

6. Results

6.1. Growth Response to Treatments

Repeated application of herbicide and fertilizer significantly enhanced tree growth with respect to diameter and height at all sites (Table 2). Clear divergences in cumulative growth relative to control stands were observed from year 6 onward (Figure 2), with baseline site productivity reflecting differences in climate and soils across the three sites. In absolute terms, average tree growth rates in control stands increased as a function of increasing precipitation and soil development from Elkhorn Ridge to Whitmore and FF (Tables 1 and 2). In proportional terms, the greatest positive effect of herbicide and fertilizer application
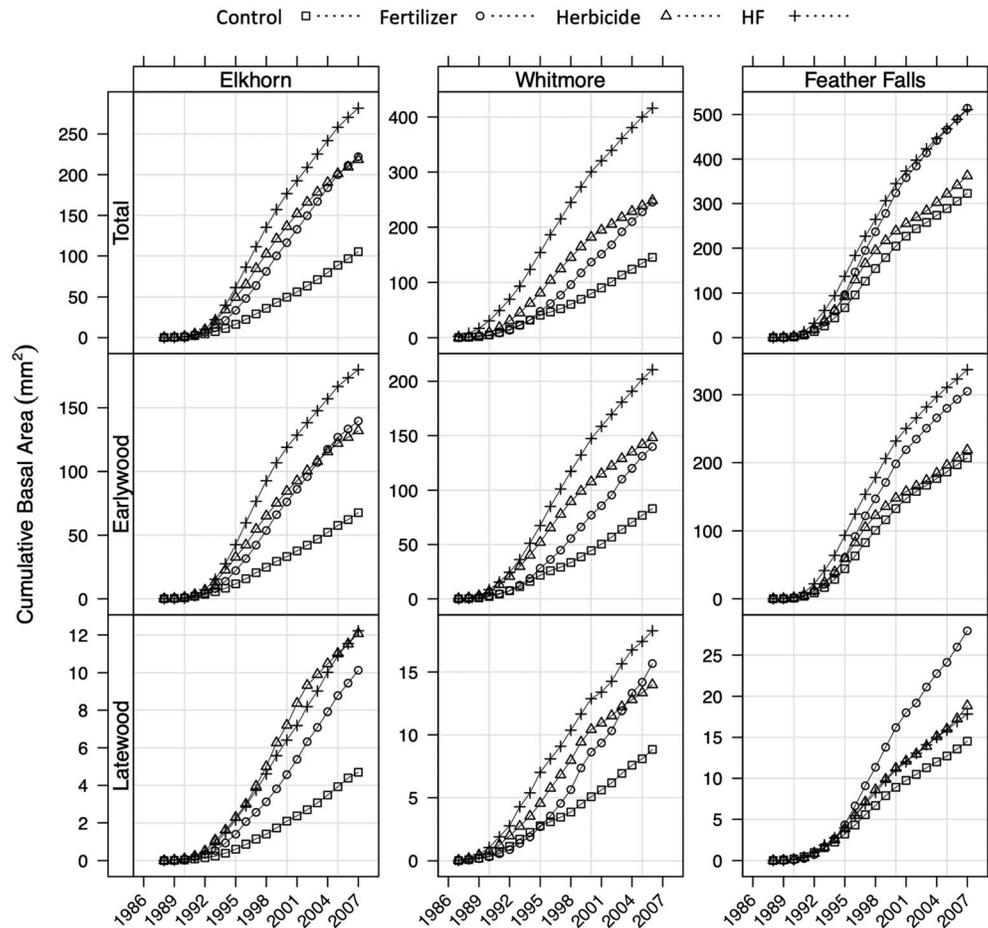
Figure 2. Cumulative basal area increments for all sites and treatments (control, fertilized, herbicide, and HF; herbicide plus fertilization). Each value represents the annual mean of nine trees at each stand. Trees were selected from the entire range of stem diameters with a small, medium, and large tree taken from each replicate plot. Note that differences in baseline productivity reflect site-specific climatic and edaphic conditions (Table 1), but treatments improved tree growth in all cases.

on tree growth was observed at the least productive site (ER), with a small but statistically significant positive effect of both treatments on tree growth at the most productive site (FF; Tables 1 and 2). On average, cumulative BAI of trees under managed stands increased by a factor of 2.2 at ER, 2 at WH, and 1.4 at FF relative to control stands (Figure 2). After 20 years, the combined effect of herbicide and fertilization enhanced BAI growth by >2.6-fold ($p < 0.001$) and 10–12 m of additional height compared to controls. Fertilized treatments with or without herbicide applied in combination had similar effects on BAI and tree height, with slightly greater early wood growth under herbicide plus fertilizer application (Table 2). In combination with fertilization, understory suppression promoted a significant increase in late season growth at ER and WH, while fertilization alone caused a 60–70% increase in late wood at FF. These results reveal strong differences between annual and early wood BAI growth across sites and treatments, with no significant interactions ($p = 0.15$ and 0.06) found between them, but with significant interaction between site and treatment effects on late wood growth and tree height ($p < 0.004$; Table 3).

6.2. Intrinsic Water Use Efficiency

Annually resolved estimates of iWUE derived from tree ring carbon isotopes varied significantly over time, with significant interactions between sites and treatment (Table 3; $p < 0.001$). On average, control stands at the driest site (ER) supported trees with the highest iWUE (102.2 μmol/mol), whereas significantly lower values were at more productive plantations WH (98.5 μmol/mol) and at FF (89 μmol/mol). In most cases, iWUE decreased significantly in response to herbicide or fertilizer application, with a notable exception at

Table 3

Analysis of Variance Testing the Significance of Site, Treatment, and Their Interactive Effect on Tree Growth (Expressed as Basal Areal Increments—BAI) and Physiological Metrics (Carbon and Oxygen Isotope Ratios) for the Duration of the Experiment (1986–2007)

Metric	Predictor	DF	Sum square error	Mean square error	F	P
Annual BAI	Site	2	226	113.2	36.2	<0.0001
	Treatment	2	23	41.5	13.2	<0.0001
	Site:treatment	4	81	5.3	1.7	0.15
	Residuals	1074	3,363	3.1		
Early wood BAI	Site	2	127.6	63.8	22.0	<0.0001
	Treatment	2	80.4	40.2	13.9	<0.0001
	Site:treatment	4	26.3	6.6	2.3	0.059
	Residuals	1074	3,106.5	2.9		
Late wood BAI	Site	2	455.4	227.7	26.0	<0.0001
	Treatment	2	103.9	51.9	5.9	0.003
	Site:treatment	4	136.2	34.1	3.9	0.004
	Residuals	1020	8,916.6	8.7		
iWUE (annual cellulose)	Site	2	0.35	0.18	39.2	<0.0001
	Treatment	2	0.43	0.22	48.0	<0.0001
	Site:treatment	4	0.53	0.13	30.0	<0.0001
	Residuals	1074	4.8	0.0045		
$\delta^{18}O$ (annual cellulose)	Site	2	0.048	0.024	16.5	<0.0001
	Treatment	2	0.058	0.029	19.9	<0.0001
	Site:treatment	4	0.20	0.049	33.3	<0.0001
	Residuals	1074	1.6	0.0015		

Note. The effect of site and treatment on tree growth are significant in all cases ($\alpha = 0.05$; $n = 9$ trees per treatment), but interactions among these predictors are only significant for late wood growth, and isotopic data. This implies that physiological acclimation to climate variability reflect interactions between treatment and site-specific edaphic properties.

the intermediate productivity site (WH), where fertilized trees had higher iWUE than control trees (Table 2). When the entire range of iWUE measurements ($n = 168$) is normalized by subtraction and division relative to controls at each site (Figure 3), it is apparent that no significant changes in iWUE occurred in response to herbicide or fertilizer application at the most productive and wettest site (FF). In contrast, the same analysis shows that iWUE increased significantly in response to herbicide plus fertilization in ER, whereas WH stands had the most increase in iWUE caused by fertilization (Figure 3). The normalized iWUE data also showed large temporal variation (>20% in some cases; supporting information Figure S1), reflecting a weak but significant correlation with fluctuations in climate and VPD (Figure 4).

6.3. Cellulose $\delta^{18}O$ Isotope Ratios

Tree ring cellulose $\delta^{18}O$ ratios were significantly different across sites, with responses to treatment observed in a couple of cases; that is, a significant decline in cellulose $\delta^{18}O$ (~1‰ relative to control) in herbicide-treated stands at the wettest site and in response to herbicide plus fertilization under intermediate precipitation (Table 2). As expected, control stands at the wettest site yielded samples with the lowest tree ring cellulose $\delta^{18}O$ ratios, (~25‰ on average). Significantly higher average $\delta^{18}O$ ratios were observed at ER and WH (26.2 and 27.2‰, respectively). Unlike variation in iWUE, when the entire range of cellulose $\delta^{18}O$ measurements is normalized by subtraction and division relative to controls, herbicide-treated plots are the only ones to cause changes in baseline $\delta^{18}O$ with significant differences observed only at WH (Figure 3). The normalized $\delta^{18}O$ data showed low temporal variation over most of 20 years of observation in relation to iWUE (<10% in most cases; supporting information Figure S1), yet a significant positive relationship was observed between $\delta^{18}O$ and iWUE (Figure 4).

6.4. Relationship Between Stable Isotope Data

Across sites, the largest temporal change in iWUE inferred from cellulose carbon isotope ratios occurred in the wettest years, when tree ring cellulose also had the lowest $\delta^{18}O$ values (1999 and 2006 at WH and FF; Figures A1 and A2). This indicates that favorable climatic conditions of a single year influence all trees independently of treatment and site. Interannual variation in $\delta^{18}O$ values was similar across sites (coefficient of variation 5–6%), but the narrowest annual variation (2006; 2.2‰) and broadest annual variation (1995;
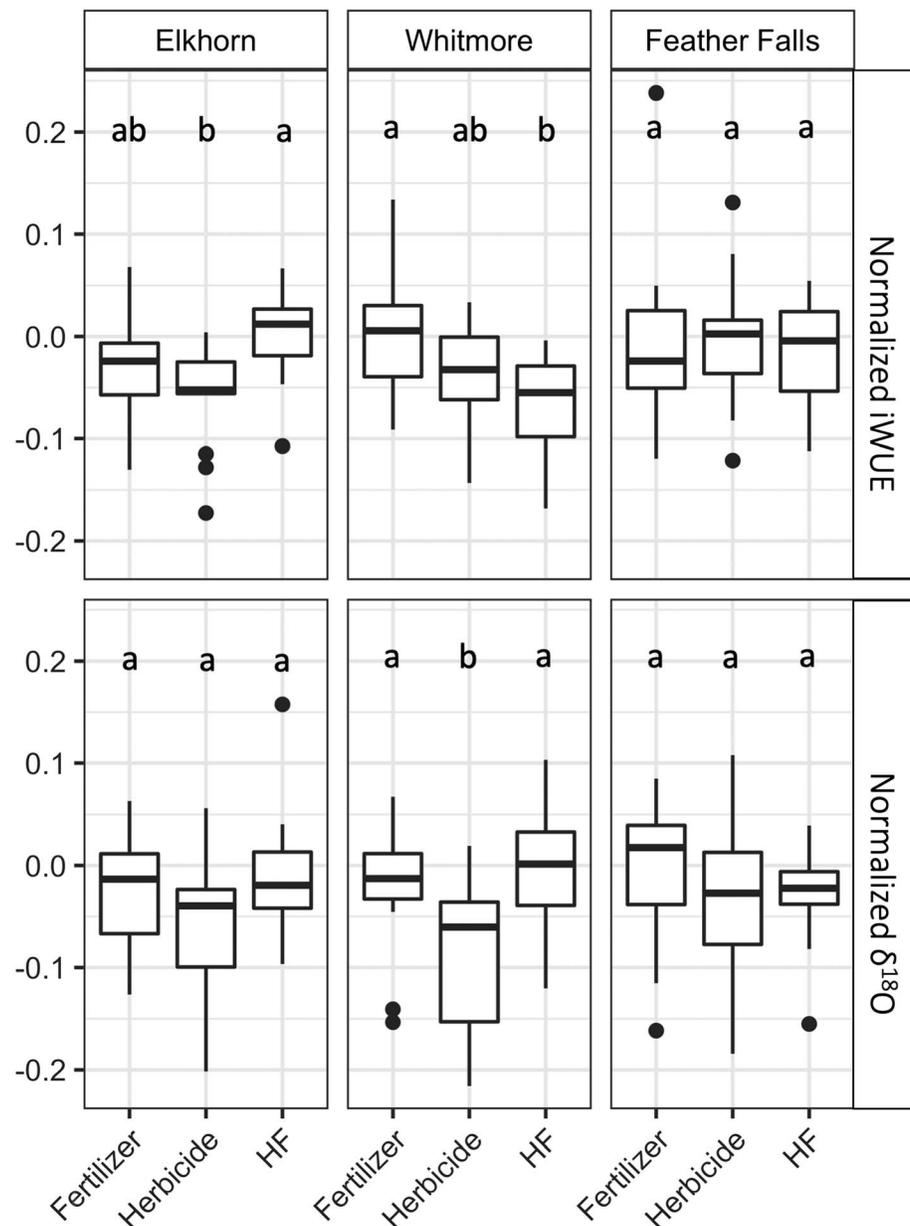
Figure 3. Mean values of tree ring cellulose $\delta^{18}O$ and $\delta^{13}C$-derived intrinsic water use efficiency (iWUE) normalized across sites and treatments for the duration of the experiment (1986–2007). Normalization is achieved by subtracting mean values of the control within a year from each treatment value, and dividing by the control mean. Thus, control values are shown as 0 and significant differences from the control are noted with asterisks above each individual treatment (Tukey HSD test, $\alpha = 0.95$).

6.3‰) were recorded at the wettest site (Tables S2). Across sites, cool wet years coincided with significant declines in tree ring $\delta^{18}O$ ratios, compared to baseline conditions; for example, in 1999 and 2006 at FF and in 1999 at WH. Tree ring $\delta^{18}O$ ratios did not change significantly at WH in the cool and wet 2006 conditions, although this did lead to this site's second lowest annual value. Similarly, the lowest annual values at ER were also produced during wet and cool conditions in 1998 and 1999 at that site.

Despite divergent tree ring carbon and oxygen isotope ratios with respect to overall variability and sensitivity to treatment (described above), we found a significant positive relationship between $\delta^{18}O$ and iWUE when controlling for site-specific baselines; that is, normalized isotopic data (Figure 4). Furthermore, convergences emerged when raw isotope data were separated by sites and treatments. In Figure 5, a significant
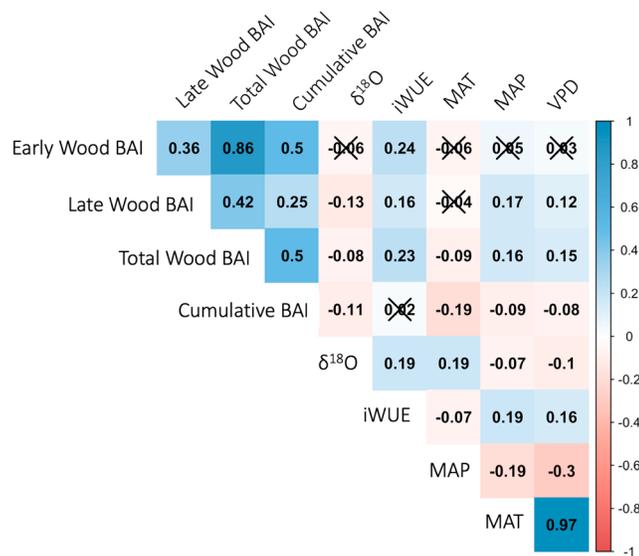
Figure 4. Pearson correlation table prepared using tree ring and climate data normalized for the duration of the experiment (1986–2007). Red and blue cells indicate negative and positive relationships, respectively. Cells containing X symbols represent nonsignificant correlations ($p > 0.05$). BAI = basal areal increments; iWUE = intrinsic water use efficiency; MAT = mean annual temperatures; MAP = mean annual precipitation.

positive relationship is apparent between $\delta^{18}O$ and iWUE values, with consistently lower values recorded at FF than at any other site. The connection between $\delta^{18}O$ and iWUE data, characterized by a strong separation between wet and dry sites, strengthened in stands under herbicide application and fertilization ($p < 0.001$), reflected in significant coefficients of determination ($R^2 = 0.24$ in controls and $R^2 = 0.42$ and 0.55 in herbicide and fertilized treatments, respectively; Figure 5). By contrast, the relationship between $\delta^{18}O$ and iWUE values disappeared under herbicide plus fertilization ($R^2 = 0.03$ $p = 0.31$), where 10 to 20% increases in iWUE relative to controls were decoupled from variation in precipitation regimes (recorded in tree ring $\delta^{18}O$ values).

7. Discussion

Over the course of 20 years, we measured the effect of climate and water or nutrient limitation on three ponderosa pine plantations in Northern California. The main results of this experiment are summarized here as deviations from baseline productivity (i.e., co-located control stands) in response to understory suppression and fertilization treatments. Our experimental sites span a broad range of climatic and edaphic conditions where baseline tree growth and stand productivity vary approximately threefold (Figure 2). Across the entire productivity gradient, we found that the suppression of understory vegetation or fertilization significantly increased tree growth rates and stand-level productivity relative to controls. In most cases, the synergistic effect of understory removal plus fertilization caused a 5- to 12-m increase in tree height and a 60–100% increase in basal area. This positive response in productivity exceeds the anticipated maximum productivity of each site, set on the basis of climatic and edaphic conditions at the beginning of the experiment (Robert F Powers & Reynolds, 1999). We also found significant interactions between treatment and site conditions affecting growth patterns. Specifically, the degree to which water or nutrient availability limited tree growth varies depending on soil properties at each site. For example, the change in cumulative basal area and height for trees under herbicide plus fertilization indicates that productivity is primarily limited by water at sites where soils are poorly developed (i.e., Elkhorn; inceptisols), whereas water and nutrients colimit productivity at dry sites where well-developed soils occur (i.e., Withmore; ultisols), and nutrient limitation is the most important factor limiting productivity at the wettest site where baseline productivity is highest (i.e., Feather Falls; Table 1). This result is consistent with recent findings from Northern California forests, where iWUE has been shown to reflect interactions between climate variability and stage of soil development across different parent material (Maxwell et al., 2018).

One notable manifestation of site-treatment interactions is the weak response of late wood production at FF under herbicide application compared to fertilized stands. At that site, the positive effect of fertilization on late-season tree growth was much stronger than that of herbicide application even when herbicide and fertilizers were combined (Figure 2 and Table 2). This response is consistent with recent observations in other ponderosa pine forests in the same region (Qiao et al., 2014), where the presence of understory species has been shown to improve litter decomposition and accumulation of carbon and nitrogen in mineral soils relative to stands where understory removal or suppression took place. It is important to note that the beneficial effect of understory presence on carbon and nitrogen cycling described by those authors was most apparent in occluded (physically protected and biologically formed) soil aggregates after 10 years of experimental work. Our results provide further evidence in support of the notion that biological diversity can in the long run, depending on site conditions, be more beneficial for sustained forest productivity than the effect of fertilization during the establishment of monodominant stands. This finding is also in agreement with experimental evidence from other forest biomes showing that functional diversity of understory species and their microbial symbionts can have lasting benefits for the fixation of new and recycling of existing soil nitrogen pools by dominant tree species (e.g., Bomfim et al., 2019; Winsome et al., 2014).
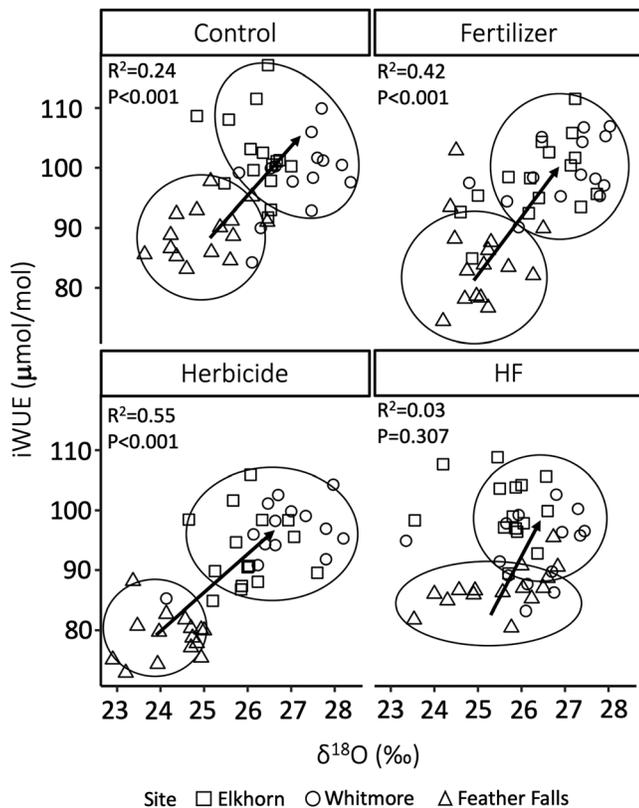
Figure 5. Two-dimensional plots of $\delta^{18}O$ and intrinsic water use efficiency (iWUE) of ponderosa pine trees by treatment and sites represented as shapes. Across all treatments there is distinct grouping of Feather Falls (bottom left corner), showing significant differences in physiological performance relative to drier sites (Whitmore and Elkhorn Ridge) where iWUE highest, which indicates low stomatal conductance across all treatments (Scheidegger et al., 2000). The direction of increased stomatal regulation (decreased conductance), most pronounced effect in Herbicide plots, is indicated by arrows between clustered $\delta^{18}O$ and iWUE values.

In unmanaged forests, we often see a negative relationship between iWUE and tree growth, which arise from a fundamental tradeoff between resource use efficiency and productivity (Gomez-Guerrero et al., 2013; Peñuelas et al., 2011; Silva & Anand, 2013). Here, we found evidence of such a tradeoff in control stands, but not in managed stands. For example, the most efficient trees with respect to water use were at the least productive site; that is, Elkhorn control stands were on average ~10% more efficient than trees growing at the most productive FF stands (Figure 5). The effect of treatment changed the relationship between iWUE and tree growth by reducing water stress and iWUE relative to controls (up to 6% on average; Figure 3), leading to a positive correlation between iWUE and annual tree growth across sites (Figure 4). Crucially, the removal of understory vegetation combined with fertilization at the least productive site simultaneously increased iWUE and caused an acceleration of tree growth. By contrast, fertilization increased both iWUE and productivity in intermediate productivity stands, and iWUE was unresponsive to understory removal at the wettest and most productive site (FF). At that site, the combination of herbicide and fertilization had significant but small effects on basal area increments relative to drier stands that responded more strongly to understory removal. We thus conclude that competitor removal amounted to an overall increase in productivity, which could be interpreted as an effective extension of the growing season (Wei et al., 2014), a response that is most pronounced at sites where water is most limiting.

After 20 years of experimental data, we found fluctuations in iWUE of the same magnitude and direction as those observed in unmanaged Mediterranean landscapes, where low water availability maintains elevated iWUE (Maseyk et al., 2011). This is consistent with the notion that tree growth in Mediterranean systems is limited by low diffusion of CO_2 into the leaf as stomatal conductance (g_s) downregulates leaf gas exchange, thereby constraining photosynthetic rates (A; Andreu-Hayles et al., 2011; Dietrich et al., 2016; Gómez-Guerrero et al., 2013). When normalized growth responses (i.e., management-induced shifts in iWUE relative to control) are compared, we see a positive relationship between efficiency and productivity (Figure 4), which is diagnostic of CO_2-induced stimulation of photosynthesis (Silva & Anand, 2013). This interpretation is also supported by cellulose $\delta^{18}O$ values, which generally did not respond to treatment (Figure 3), but decreased across sites with increasing VPD (Figure 4). This result is in agreement with findings by Ulrich et al. (2019), which show that decreasing $\delta^{18}O$ values within a site, where source water and climate are similar, can be interpreted as a direct response to differences in transpiration. Consistent with this interpretation, the strongest impact of management on tree ring cellulose-^{18}O in our experiment was observed for understory suppression and fertilization combined, which caused a convergence in iWUE and $\delta^{18}O$ values across sites (Figure 5). The photosynthetic stimulation benefits of that treatment were clear, as it caused a 10 to 20 μmol/mol increase in iWUE and at the same time produced an unexpected growth release during most of the growing season, effectively decoupling A from downregulation of g_s. As discussed above, this response was less pronounced at the wettest site, where neither isotopic metrics nor late wood production responded strongly to herbicide application, separating FF (with low iWUE and $\delta^{18}O$) from dry sites (with high iWUE and $\delta^{18}O$) in all treatments but understory suppression plus fertilization (Figure 5).

Carbon dioxide enrichment experiments have long established that tree species respond to rising atmospheric CO_2 by growing faster and transpiring less, leading to greater shifts in efficiency compared to any other functional type (Ainsworth & Long, 2005). In natural forests, however, dendrochronological and isotopic studies of dominant tree species have repeatedly shown that soil resources constrain tree growth response to rising atmospheric CO_2 (Giguère-Croteau et al., 2019; Linares & Camarero, 2011; Peñuelas

et al., 2011). In environments where CO_2 levels have risen in concert with increasing soil water and nutrient availability, tree growth stimulation can be sustained from decades to centuries (e.g., Correa-Díaz et al., 2019; Silva et al., 2016). By diminishing the effect of resource limitation and accounting for differences between treated and control stands, our data show how CO_2 stimulation of tree growth might be sustained in managed forests despite significant edaphic and climatic variability. This realization leads us to two important conclusions: (i) trees grow more efficiently with respect to soil resources under management—while at the same time surpassing site-specific limits to productivity—rather than exhibiting signs of progressive resource limitation commonly observed in unmanaged forests; and (ii) iWUE and $\delta^{18}O$ values were more often than not stable over time and lower in treated than in control stands despite a 10% rise in atmospheric CO_2 over the course of the experiment across all sites (Figures A1 and A2). Taken together, our data indicate that the physiological performance of trees and their influence on forest productivity depend on site-specific conditions as well as management history, which can modulate the sensitivity of trees to climatic and atmospheric change. These findings provide a roadmap for increasing biomass production through adaptive management to optimize carbon sequestration and water or nutrient conservation under climatic stress.

Appendix A

Background experimental information, raw isotope data, and time series are presented here to supplement the main text.

Table A1
Nutrient Application Rates for Fertilized Sites Since Planting in 1986, Adapted From Powers and Ferrell (1996)

Nutrient	At planting	End of year 2	End of year 4	End of year 6	Sum for6 years
N	15.6	46.6	213.7	798.7	1074.6
P	7.9	23.2	103.4	395.2	529.7
K	7.7	23.2	109.6	399.4	539.9
Ca	10.1	23.6	118.6	264	416.3
Mg	5.5	16.8	61.7	137.2	221.2
S	5.2	28.3	16	62.4	111.9
Zn	1.1	3.2	14	55.1	73.4
Cu	0.5	1.6	6.8	26.9	35.8
B	0.5	1.6	6.8	26.8	35.7

Table A2
Intrinsic Water Use Efficiency (iWUE) and Cellulose $\delta^{18}O$ Values Averaged Across All Treatments by Site and Year

	Elkhorn		Whitmore		Feather Falls	
Year	iWUE (μmol/mol)	$\delta^{18}O$ (‰)	iWUE (μmol/mol)	$\delta^{18}O$ (‰)	iWUE (μmol/mol)	$\delta^{18}O$ (‰)
1994	95.7 (9.5)	25.7 (1.3)	99.5 (8.3)	27.1 (1.9)	91.9 (11.0)	24.4 (1.4)
1995	96.6 (10.5)	25.79 (1.9)	99.4 (7.2)	26.3 (2.1)	91.5 (10.6)	24.7 (2.0)
1996	100.2 (12.5)	25.6 (1.3)	93.1 (11.1)	27.1 (1.7)	85.6 (11.4)	24.9 (1.8)
1997	98.0 (9.6)	26.3 (1.5)	97.7 (10.4)	27.5 (0.8)	86.8 (10.3)	25.4 (1.5)
1998	96.1 (12.0)	25.5 (1.5)	98.0 (5.8)	27.0 (1.0)	83.6 (10.1)	24.7 (1.0)
1999	98.9 (10.7)	25.7 (1.4)	90.8 (5.5)	25 (1.8)	80.3 (9.8)	23.9 (1.1)
2000	97.9 (11.1)	26.3 (1.4)	101.7 (9.0)	27.6 (1.0)	85.1 (11.3)	25.6 (1.0)
2001	94.6 (10.0)	26.2 (1.1)	98.1 (8.5)	26.7(1.1)	82.2 (12.1)	24.4 (0.7)
2002	104.4 (11.3)	26.6 (0.9)	100.2 (11.6)	26.6 (1.4)	87.8 (10.7)	25.5 (1.2)
2003	99.2 (10.6)	26.7 (0.9)	96.7 (11.3)	27.5 (1.3)	82.1 (10.1)	25.6 (1.0)
2004	101.9 (10.0)	26.6 (1.4)	94.3 (11.6)	26.9(1.8)	82.2 (9.6)	25.0 (1.1)
2005	94.6 (11.3	25.9 (1.3)	98.6 (9.7)	27.4 (1.2)	84.7 (8.3)	25.2 (1.1)
2006	95.2 (14.1)	26.0 (1.1)	92.3 (10.6)	25.9 (1.4)	81.7 (8.1)	23.9 (0.8)
2007	96.2 (11.0)	26.4 (1.1)	98.3 (14.0)	26.9 (1.4)	82.7 (7.6)	25.45 (1.5)
2008	108.2 (12.8)	26.3 (0.8)			84.7 (8.0)	25.6 (0.7)

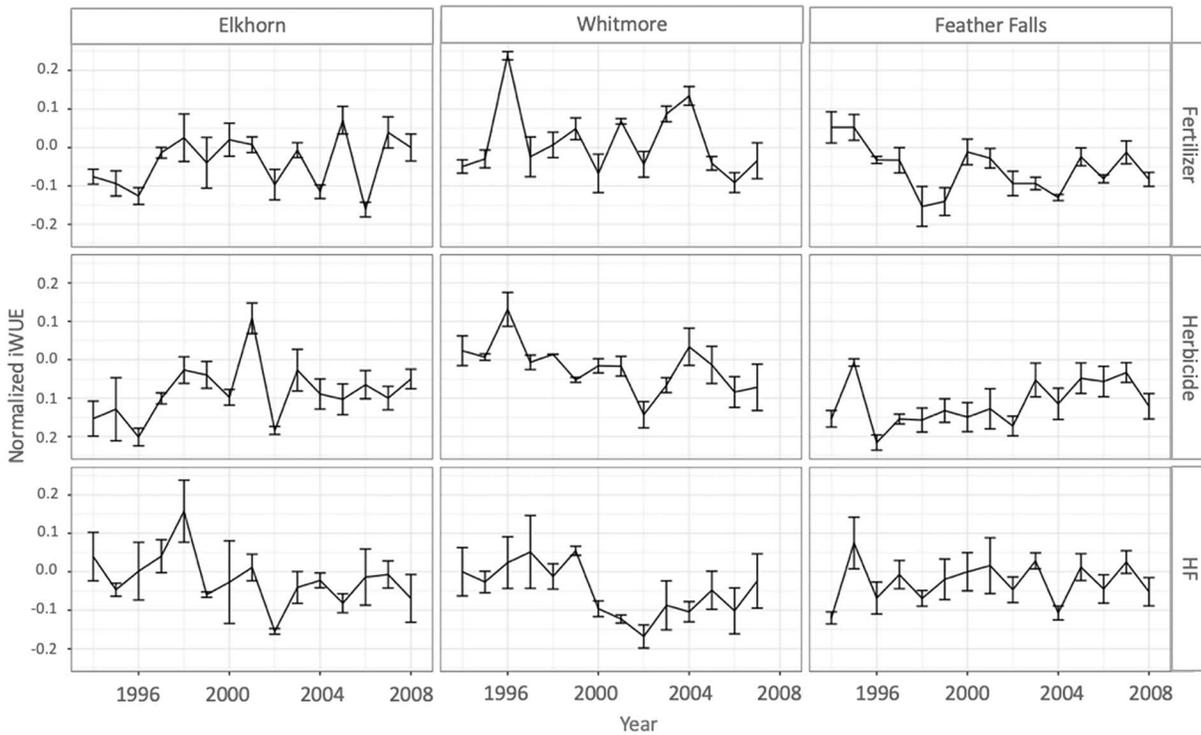**Figure A1.** Average intrinsic water use efficiency (iWUE) normalized by subtraction and division relative to control trees ([treat − control]/control). Error bars represent standard deviations ($n = 9$ per treatment at each site).

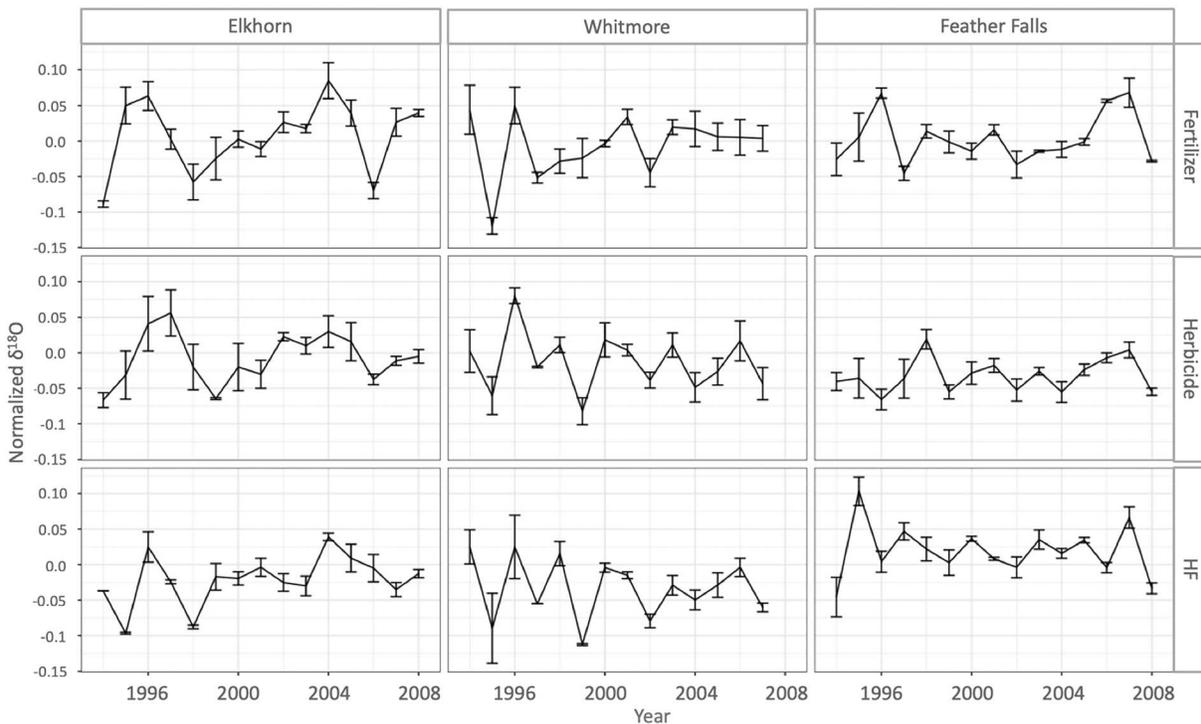**Figure A2.** Tree ring cellulose $\delta^{18}O$ values normalized by subtraction and division relative to control trees ([treat − control]/control). Error bars represent standard deviations, $n = 9$ per treatment at each site.

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