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Radial Growth Rate Responses of Western Juniper (*Juniperus occidentalis Hook.*) to Atmospheric and Climatic Changes: A Longitudinal Study from Central Oregon, USA

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Abstract: *Research Highlights:* In this longitudinal study, we explore the impacts of changing atmospheric composition and increasing aridity on the radial growth rates of western juniper (WJ; *Juniperus occidentalis Hook*). Since we sampled from study locations with minimal human agency, we can partially control for confounding influences on radial growth (e.g., grazing and logging) and better isolate the relationships between radial growth and climatic conditions. *Background and Objectives:* Our primary objective is to determine if carbon dioxide (CO_2) enrichment continues to be a primary driving force for a tree species positively affected by increasing CO_2 levels circa the late 1990s. *Materials and Methods:* We collected data from mature WJ trees on four minimally disturbed study sites in central Oregon and compared standardized radial growth rates to climatic conditions from 1905–2017 using correlation, moving-interval correlation, and regression techniques. *Results:* We found the primary climate driver of radial growth for WJ is antecedent moisture over a period of several months prior to and including the current growing season. Further, the moving-interval correlations revealed that these relationships are highly stable through time. Despite a trend toward increasing aridity manifested through significant increases in maximum temperatures during the summer growing season, WJ radial growth post-1960 exceeds growth pre-1960, especially during drought years. Our results support prior conclusions that increasing atmospheric CO_2 increases water-use efficiency for this semiarid species, which allows the trees to continue to grow during climatic periods negatively associated with radial growth. *Conclusions:* Recent studies have shown that semiarid ecosystems are important for understanding global variations in carbon uptake from the atmosphere. As WJ woodlands cover an extensive region in western North America and have undergone rapid expansion during the 20th and 21st centuries, they may become an increasingly important carbon sink.

Keywords: western juniper; radial growth rates; carbon dioxide enrichment; aridity; summer warming; Oregon

1. Introduction

Western juniper (*Juniperus occidentalis Hook*; WJ) is a dominant tree in semiarid (<~50 cm annual precipitation) portions of the interior Pacific northwestern United States. The current range is roughly 3.6 million hectares [1], mostly in central Oregon east of the Cascade Mountains, but extends to portions of five western states (CA, OR, NV, WA, ID). The encroachment of WJ into ecosystems dominated by sagebrush (*Artemesia* spp.) has been examined for over 50 years [2–7]. As encroachment continues into the 21st century [8–10], changes in the form and function of WJ/sagebrush ecosystems are evolving. Potential negative aspects of WJ encroachment include less soil moisture for grasses and shrubs, an increase in erosion, reduced herbaceous cover, decreased species diversity, decreased streamflow, and an increase in exposed ground [11–13]. However, some of these conclusions may not be operative [14]. The principal positive aspect of WJ encroachment relates to potential gains in carbon sequestration with a greater density of WJ trees. Globally, the largest vegetation sinks for carbon are in tropical ecosystems, but semiarid ecosystems have substantive control over the interannual variability of carbon and have become increasingly important through time [15]. Similarly, the interannual variability in global carbon uptake is directly linked to an increase in semiarid vegetation, largely in Australia [16]. Campbell et al. [10] examined the specific consequences of juniper encroachment on carbon uptake and found that the carbon sequestration component related specifically to WJ encroachment is small relative to growth. That said, WJ growth rates are steady, and the spatial potential for continued WJ expansion is large enough that continued encroachment "can have a significant impact on continental carbon stocks, even when the changes per unit area are small relative to other terrestrial carbon fluxes" due to increasing biomass ([10], p. 230).

Multiple synergistic factors have been implicated in WJ encroachment, including grazing, fire suppression, increasing seed supply, favorable climatic conditions, and carbon dioxide enrichment [3,5–7,17,18]. An early pulse of WJ expansion occurred in the late 19th century and was concurrent with an extended period of favorable climate conditions [19]. Increased livestock grazing in the late 19th and early 20th century likely stimulated expansion by a combination of reducing herbaceous cover needed to sustain fires and an increase in shrub cover favorable for juvenile WJ development [19]. With 20th century fire suppression efforts the intervals between large, stand-replacing fires increased [19]. As the density and cover of WJ increased, there has been an increasing seed rain, such that more juniper promotes more juniper [7]. Through repeat vegetation sampling [20] and then using dendroecological techniques [21], the potential role of carbon dioxide enrichment in WJ encroachment was explored. The basic premise of this theory is that increasing levels of atmospheric CO_2 cause increasing water-use efficiency, allowing for a potentially longer growing season and less negative impacts on WJ radial growth rates during drought periods [22–25].

In the last two decades (1998–2017), climatic conditions in central Oregon (Climate Division 7; CD7) have become warmer and drier during the western juniper growing season. Maximum temperatures in May–June were above the long-term (1905–2017) average during 70% of the years, averaging 0.64 degrees C above average during these decades. June values of the Palmer Drought Severity index (PDSI; [26]), which measures soil moisture based on precipitation and temperature conditions and is a primary determinant of radial growth for western juniper, averaged −0.92 (−1.0 is "abnormally dry" [27]) for the 20-year period, and 45% of those years were in the "moderate drought" range (−2.0 to −2.9) or worse. In a synthesis of projected climate changes from 35 general circulation models for Oregon's Columbia River Basin, Rupp et al. [28] report that these vectors will likely continue, with increases of summer temperature of 18%–24% and decreases in summer precipitation of 4%–10% relative to the baseline period of 1979–1990. Similar vectors have been reported for the overall climate of the state of Oregon [29].

Using tree-ring data collected in the late 1990s, Knapp et al. [21] concluded that CO_2 enrichment was likely a substantive driving force for WJ expansion because expansion occurred on sites where the other driving forces (e.g., livestock grazing) were absent, and was occurring in the late 20th century during a period of unfavorable climatic conditions for WJ growth. Given that the data collected for the dendro-based investigation of the possible influence of increasing atmospheric CO_2 on WJ was collected two decades ago [21], our study objective is to examine if either a CO_2-fertilization effect remains operative or an acclimatization process occurred. Since we conducted our original sampling principally at federally designated Research Natural Areas, the study sites remain intact and have largely not been affected directly by anthropogenic forces such as fire suppression, logging, and grazing.

Thus, we present a longitudinal study to assess what type of growth effect an additional 14% (360 ppmv in 1998, 410 ppmv estimated in 2018) of atmospheric CO_2 has had on these trees despite two decades of increasing aridity. We also assess if elevated CO_2 can ameliorate the effects of increasing aridity on this tree species, which is a key component of a broad area of research associated with the effects atmospheric CO_2 enrichment [23,24,30,31].

2. Materials and Methods

2.1. Field Sampling

In September 2018, we recollected samples from live, mature WJ trees at four sites in central Oregon (Figure 1) from which we had developed tree-ring chronologies during 1996–1999 (Horse Ridge Research Natural Area, HRR; The Island Research Natural Area, IRR; Powell Butte Research Natural Area, PBR; [21]), and 2006 (Quarry Study Site, QRJ; [32]) All the sites are open canopy, minimally disturbed WJ woodlands, and three of the sites (HRR, IRR, PBR) are recognized as areas of ecological importance by their designation as Research Natural Areas [33]. At each site, we collected a minimum of two core samples from 20–30 trees using a selective sampling strategy and Haglof 5.03 mm diameter increment borers. All of the trees we sampled were in in clear open-canopy locations (i.e., no overlap of an individual tree canopy with another tree), and we avoided sampling trees where the radial growth patterns may have been compromised by lightning strikes, pathogens such as dwarf mistletoe (*Arceuthobium* spp.), or fires that produced significant fire scars. As with any tree-ring study based on sampling of live trees only, the potential for a non-quantifiable type of bias (i.e., "slow-grower survivorship bias") ([34], p. 6832]) exists within our sampling framework. As we had existing chronologies for each site, we combined samples from the two chronologies to create a new chronology extending through 2017. Whenever the 2018 collection site overlapped with the original collection site, we used only one core per tree in the chronology from the early sample and only one from the 2018 sample, thus assuring that no more than two core samples from any individual tree were included. Since we mixed tree-ring samples from different eras of fieldwork (c.f., [21,32]), it was necessary to exclude some samples from inclusion in the chronology. When we had to choose between including an A, B (or sometimes C) core from an individual tree, we generally retained the sample with the highest individual interseries correlation (thus, in closest agreement with the remaining samples in the chronology). However, in some cases, we retained a given sample with a lower interseries correlation if it contained a longer record. Overall, we followed a similar strategy as our prior work ([21], p. 95) in that we sought to include "the cores with the clearest ring structure (to facilitate crossdating and measurement) and longest sequences (providing greater comparative analysis)".

Our selection of western juniper is based on several criteria. First, western juniper woodlands occur within semiarid environments [35] where the effects of increasing aridity may make them among the first species to be affected by the changing environmental conditions in the Pacific Northwest. Second, the species is considered dendroclimatically important as it exhibits clear annual growth rings and strong interannual ring-width variability (relating to environmental sensitivity). Third, research has suggested that older trees are particularly sensitive to environmental change such as rising atmospheric CO_2 [36–38], and our study sites are comprised of many old-growth trees exceeding 300 years of age. Finally, our prior work (e.g., [21,24,32]) has demonstrated that climate/radial growth responses can be modeled with a single variable—June PDSI. Thus, the ability to examine the effects of other factors when radial growth exceeds that predicted by climate alone is simplified.

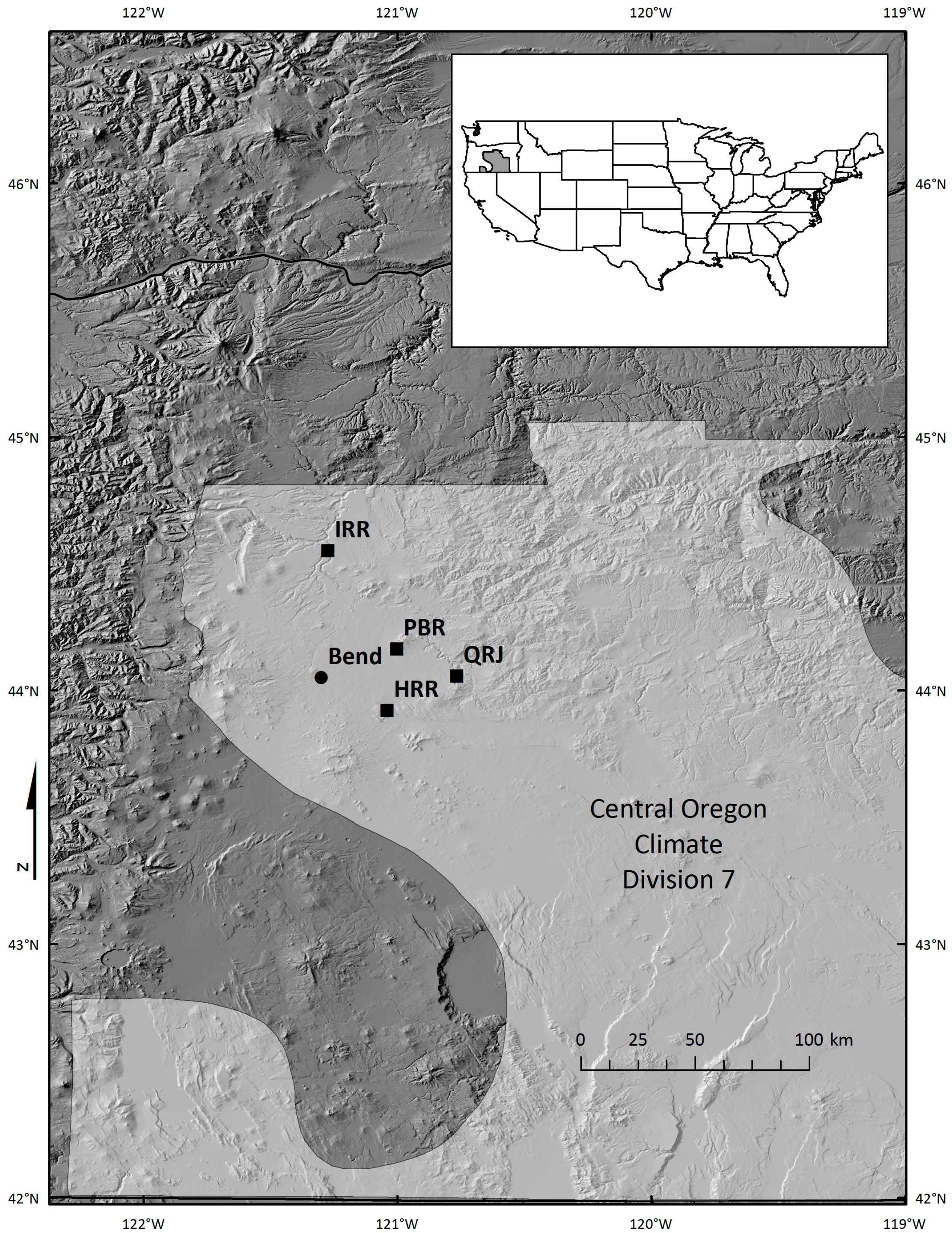


Figure 1. Locations of the four study sites and boundaries for Oregon Climatic Division 7.

2.2. Laboratory Processing and Chronology Development

We sanded each sample until the cellular structure was clear and then crossdated the samples using the list method [39] with the original chronology providing signature growth years (low or high) until at least the mid-1990s. We measured the samples collected in 2018 using the computer program WINDENDRO [40]. We combined the older and newer samples and checked the accuracy of our crossdating using COFECHA [41]. For dendroecological research, WJ is an excellent species to work with as it typically produces both high interseries correlation and mean sensitivity. We used the program ARSTAN [42] to standardize the new chronologies. We experimented with different standardization techniques and found that the negative exponential option with the standard chronology produced virtually identical annual growth values as the other techniques (e.g., cubic spline, Appendix 1). As negative exponential was the technique we had used in previous work with this species [21,24,32], our selection of negative exponential also allows for more direct comparisons between this project and prior work. In addition to the individual chronologies, we created a regional chronology (hereafter COMBO) combining all the samples from the four sites.

2.3. Statistical Analyses

We examined climate/growth relationships using data from Oregon Climate Division 7 (Figure 1). Specifically, we examined relationships between radial growth from the four sites plus COMBO and precipitation, minimum, average, and maximum temperature, and the PDSI using Pearson correlation. Although these data extend to 1895, Keim [43] has demonstrated that the early portion of the record is impacted by a lack of stations, so we began our analyses in 1905 and they extend through 2017, which is the last year of complete radial growth for our samples. We examined monthly relationships from October of the prior year through September of the current year. We also created and analyzed relationships from several multi-month variables (e.g., average temperature June–August). From these initial correlation analyses, we learned that the strongest climate/growth relationships existed with the regional-average chronology (COMBO), so we used COMBO exclusively for the remaining analyses.

After identifying the precipitation, temperature, and PDSI climatic variables most strongly associated with radial growth, we developed bivariate and multivariate linear regression models for COMBO. We used stepwise regression to determine which variable or combination of variables would produce a model that is logical, statistically valid, and offers a high degree of explanatory power. As PDSI is a water balance-based measure of drought severity that includes impacts of both precipitation and temperature, we could only examine it using bivariate models. We examined standardized residuals from each model for autocorrelation using Pearson correlation between the residuals and time. For growth/climate models, the presence of temporal autocorrelation has been used as an indicator in which some additional exogenous factor (e.g., CO_2) is affecting radial growth [21,44,45]. As one of the objectives of this study is to address the potential for a continuing influence of atmospheric CO_2 enrichment on radial growth, we added CO_2 as an additional predictive variable when autocorrelation was detected with $p < 0.10$.

We tested for long-term (1905–2017) and shorter-term (last 50, 30, and 20-year) linear trends in the single month and multi-month precipitation, temperature, and PDSI variables most closely associated with standardized radial growth from the COMBO chronology using Pearson correlation. For the precipitation, temperature, and PDSI variables included in regression models (excluding CO_2), we examined the temporal stability of the growth/climate relationships using a 24-year moving interval analysis procedure and the program Dendoclim2002 [46].

As PDSI incorporates both the supply and demand for moisture and has been shown to be a driving force for WJ growth in this region [32], we used the PDSI variable most strongly related to COMBO (June PDSI) to identify possible changes in radial growth associated with changing climatic conditions in the region or CO_2 enrichment. We first split the data into equal-length early (1905–1960, mean CO_2 306.9 ppmv) and late (1962–2017, mean CO_2 353.5 ppmv) periods. Then, we compared rates of COMBO standardized radial growth using several categories of drought (moisture) severity (e.g., all years early versus late when PDSI < -3.0). We tested for significant ($p < 0.05$) difference in radial growth and PDSI values between early and late periods using a Mann–Whitney U test. We also calculated mean radial growth for COMBO and June PDSI values by pentad and present the temporal patterns.

3. Results

All four tree-ring chronologies had high interseries correlations and mean sensitivity, and there is a high degree of covariance among the four sites (Table 1). At the four study sites and for COMBO, the climatic variable most closely related to standardized radial growth is the total precipitation from

October of the prior year through June of the current year (Table 2). For PDSI, in all cases, we found June to be positively and significantly ($p < 0.01$) associated with standardized radial growth (Table 2). Although the magnitude of these relationships is less than for prior October–June precipitation, in all cases, there was no significant difference ($p > 0.05$) in the two r values based on a Fisher r-to-z transformation test. For temperature, we found that the average maximum temperature of May and June was negatively related to radial growth at three of the study sites, and for COMBO, and maximum June–August temperature was the strongest at IRR (Table 2). While the temperature relationships are much weaker than either precipitation or PDSI, they are moderately strong and significant ($p < 0.05$) and demonstrate that thermal conditions in late spring to early summer play an important role in modulating western juniper radial growth.

Table 1. Study sites chronology information and Pearson r-values between chronologies using standardized radial growth from 1905–2017 (* = significant at $p < 0.01$).

Study Site	#Samples	Interseries Correlation	Mean Sensitivity	Mean Length of Chronology (years)	*r*-Value between Sites (1905–2017)			
					HRR	IRR	QRJ	PBR
HRR	33	0.87	0.59	178.9	-	0.75 *	0.8 *	0.76 *
IRR	32	0.85	0.6	140.9		-	0.68 *	0.71 *
QRJ	30	0.86	0.66	147.2			-	0.8 *
PBR	30	0.8	0.72	169.2				-
COMBO	125	0.78	0.64	159.2				

Table 2. Strongest relationships between standardized radial growth and precipitation, temperature, and Palmer Drought Severity index (PDSI) variables for individual sites and COMBO (* indicates significant relationship at $p < 0.01$).

Site	Precipitation Variable	Pearson *r*-Value
QRJ	prior October to June	0.74 *
HRR	prior October to June	0.68 *
PBR	prior October to June	0.71 *
IRR	prior October to June	0.67 *
COMBO	prior October to June	0.78 *
Site	**Temperature Variable**	**Pearson *r*-Value**
QRJ	May–June maximum	−0.41 *
HRR	May–June maximum	−0.35 *
PBR	May–June maximum	−0.36 *
IRR	June–August maximum	−0.32 *
COMBO	May–June maximum	−0.4 *
Site	**PDSI Variable**	**Pearson *r*-Value**
QRJ	June	0.71 *
HRR	June	0.64 *
PBR	June	0.67 *
IRR	June	0.66 *
COMBO	June	0.74 *

The temporal pattern of climate/growth relationships from October of the prior year to September of the current year further illustrates the interplay of precipitation and moisture on the radial growth of western juniper in the region (Figure 2). For precipitation, there is no singular month that provides anywhere close to the strength of the total precipitation between the prior October and June, with both early winter (i.e., prior December and January) and late spring to early summer (i.e., May) of approximately equal importance. The influence of temperature is not significant until spring, and peaks in June. The combination of a positive influence of moisture supply and negative influence of moisture demand on western juniper radial growth rates is succinctly illustrated by the monthly temporal pattern of the water balance-based PDSI, with a steady increase in *r*-values from October of the prior year, which peak in importance in June of the current growing season.

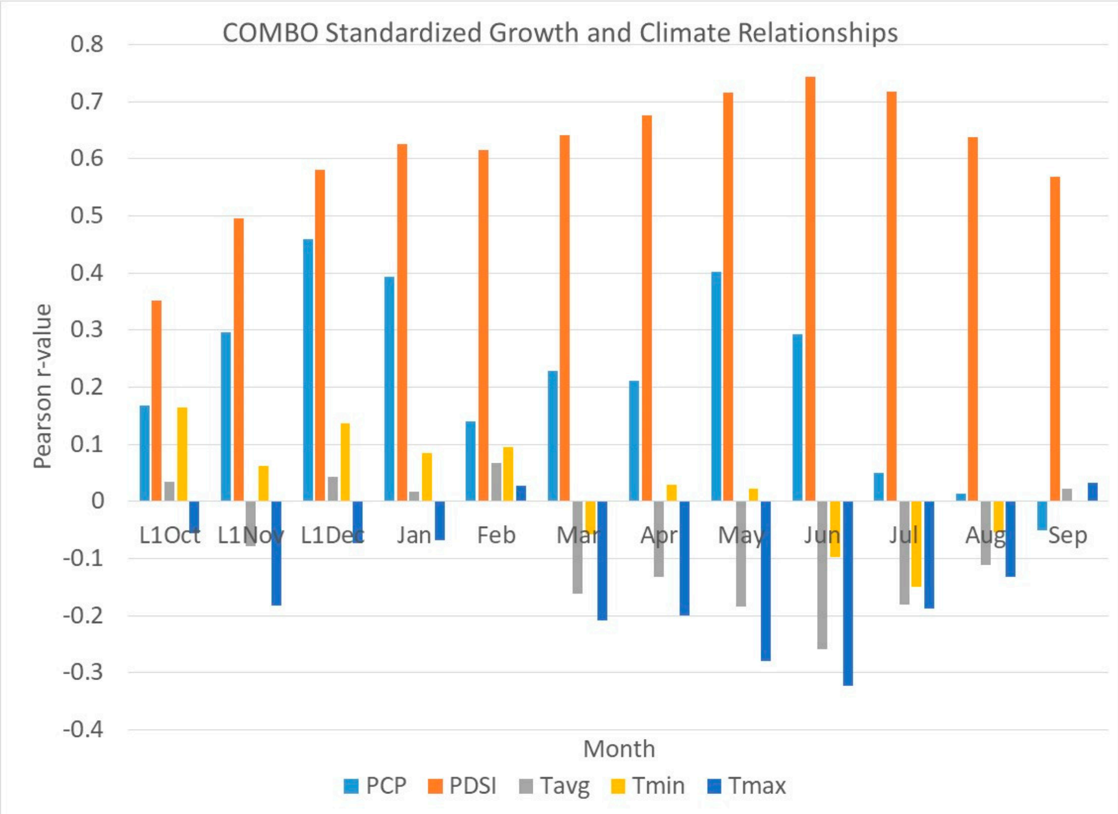


Figure 2. Pearson correlation relationships between COMBO standardized radial growth and monthly climatic conditions from October of the prior year (L1Oct) through September of the current year, 1905–2017. Variables examined included monthly total precipitation, Palmer Drought Severity index (PDSI), and minimum, maximum, and mean air temperature. All climate data from Oregon Climatic Division 7. Statistical significance ($p < 0.05$) begins at approximately +/− −0.20.

The strongest bivariate growth climate model explains 60.1% of the variance in COMBO radial growth using prior October to June precipitation as the explanatory variable (Table 3). Residuals from this model were not temporally autocorrelated. The combined effects of precipitation and temperature are illustrated by a multivariate regression model including both prior October–June precipitation and May–June maximum temperature, which explains 62.5% of the variance in standardized radial growth. Much of the explanatory power for this model is supplied by the positive influence of precipitation, with an R^2 change of 2.4% associated with the addition of the maximum May–June temperature, which negatively affects growth. Residuals from this model were weakly autocorrelated with time ($p < 0.01$). The bivariate model that we created using June PDSI is able to explain 55.4% of the variance in standardized radial growth (Table 3). Residuals from this model were strongly autocorrelated with time ($p < 0.01$). When we added CO_2 as an additional explanatory variable to the June PDSI model, we obtained a statistically valid model with explanatory power of 57.8%, an R^2 change of 2.4%, and the residuals were not temporally autocorrelated ($p > 0.05$).

Table 3. Regression model statistics where standardized radial growth is the dependent variable and the explanatory variables are climatic parameters based on 1905–2017 observations. COMBO is the multi-site measurement of radial growth; O_Jppt is total precipitation (cm) from the prior year October through the current year June; MJTmax is the average of the May–June maximum temperature (°C); JunePDSI is the value of the Palmer Drought Severity Index in June; CO_2 is the annual atmospheric carbon dioxide level (ppmv). Climate variables are from Oregon Climate Division Seven; CO_2 data are from Mauna Loa observations (1958–2017) and ice cores (1905–1957) from the Scripps CO_2 Program (http://scrippsco2.ucsd.edu).

The best bivariate model:
COMBO = −0.651 + (0.046 × O_Jppt) R^2 = 0.60; *p*-Value model *p* = 0.000; *p*-Value O_Jppt *p* = 0.000
The best multivariate model: COMBO = 0.338 + (0.042 × O_Jppt) + (−0.045 × MJTmax) R^2 = 0.63; *p*-Value model *p* = 0.000; *p*-Vlaue O_Jppt *p* = 0.000; *p*-Value MJTmax *p* = 0.01 R^2 change adding in MJTmax = 2.4% Residuals from the model with time: *r* = 0.18, *p* = 0.059
The best PDSI Model: pCOMBO = 0.992 + (0.131 × JunePDSI) R^2 = 0.55; *p*-value model = 0.000; *p*-Value JPDSI = 0.000 Residuals from the model with time: *r* = 0.31, *p* = 0.001
Model with JunePDSI and CO_2: COMBO = 0.200 + (0.135 × JunePDSI) + (0.002 × CO_2) R^2 = 0.58; *p*-Value model = 0.000; *p*-Value JunePDSI = 0.001; *p*-Value CO_2 = 0.013 R^2 change adding CO_2 = 2.4% Residuals from the model with time: *r* = 0.09, *p* = 0.345

There are no significant trends in COMBO radial growth for any of the four time periods examined (Table 4). While COMBO has a positive slope over the full data period (Figure 3), in the last 50, 30 and 20 years, this has switched to a negative slope (Table 4). Long-term (1905–2017) temporal trends for the variables included in the regression models reveal the potential importance of changing climatic conditions on western juniper radial growth (Figure 3). While only the maximum May–June temperature has a significant ($p < 0.05$) long-term trend among the climate variables (Table 4) included in the regression models, it is clearly a driving force for PDSI values that have a weakly negative long-term slope despite a weakly positive upward slope compared to prior October–June precipitation. Long-term trends in CO_2 are strongly upward in a non-linear fashion (Figure 3d). Among the individual monthly variables most strongly related to standardized radial growth (Figure 2), only the June maximum temperature had a significant long-term trend (Table 4). We also examined shorter-term climate changes (i.e., the last 20 years) and found no significant trends, although most variables were trending in the same direction as the long-term (i.e., positive or negative; Table 4). While the primary drivers of radial growth from prior October–June precipitation and/or June PDSI have essentially a flat trend line over the last three and two decades, the May–June temperatures continue to exhibit a positive slope.

For both prior October–June precipitation and June PDSI, the climate/growth relationships are stable through time, with every 24-year window producing significant ($p < 0.05$), positive, and strong correlation values (mean moving interval correlation of 0.8 for prior October–June precipitation and 0.79 for June PSDI (Figure 4). For the May–June maximum temperature, we found significant ($p < 0.05$) negative relationships for every 24-year window through 1963 and after 2001, but several windows with non-significant relationships in the middle decades of the record.

Table 4. Temporal trends (via Pearson *r*-Values) of the COMBO chronology and the climate variables most closely associated with standardized radial growth from the COMBO chronology. (* = significant at $p < 0.01$).

	Full Record (1905–2017)	Last 50 Years (1968–2017)	Last 30 Years (1988–2017)	Last 20 Years (1998–2017)
Variable (COMBO)	0.13	−0.00	−0.01	−0.09
Variable (Single Month)				
Prior December Precipitation	0.16	0.11	0.27	0.37
June PDSI	−0.1	−0.09	−0.03	−0.06
June Maximum Temperature	0.24 *	0.12	0.24	0.17
Variable (Multi-Month)				
Prior October–June Precipitation	0.09	−0.02	−0.01	0.03
May–June Average Max Temp	0.26 *	0.12	0.2	0.23

The comparison of pentadal mean values of COMBO radial growth and June PDSI reveals a generally expected pattern, with growth values above normal (i.e., >1) during wet years (+PDSI) and below normal (i.e., <1) in dry years (–PDSI) through the middle portion of the record (i.e., 1960; Figure 5). However, post-1965, there are four pentads (1965, 1985, 2005, and 2015) that record above normal growth in conjunction with negative PDSI values. In comparing the mean values of COMBO early (1905–1960) versus late (1962–2017), growth was consistently greater in the late period (Table 5). We found the greatest absolute differences during years with extreme drought (PDSI < −3). While this was not statistically significant ($p > 0.05$), the number of years with PDSI < −3 produced a small sample size. For PDSI years < −2, the growth in the later years was significantly different from the early period ($p < 0.05$).

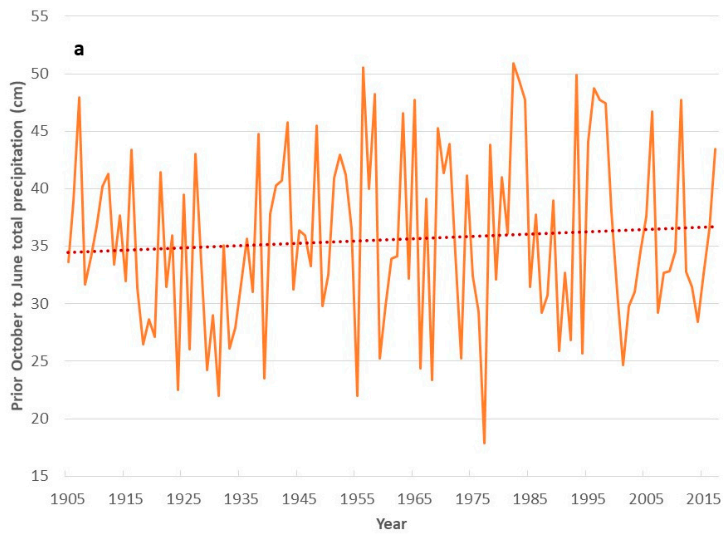
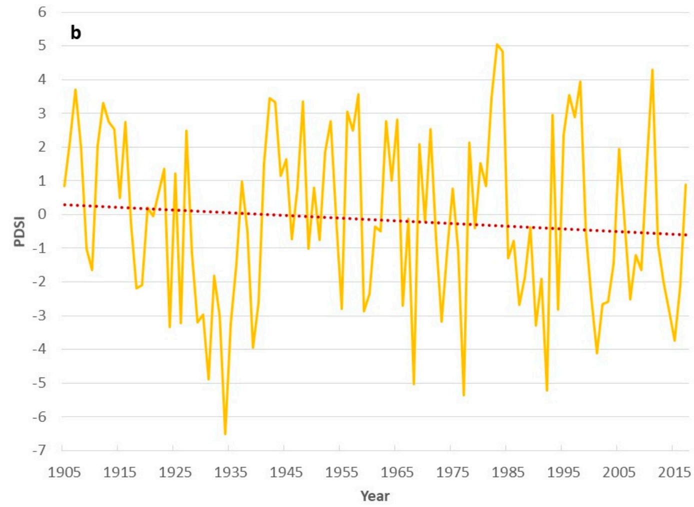
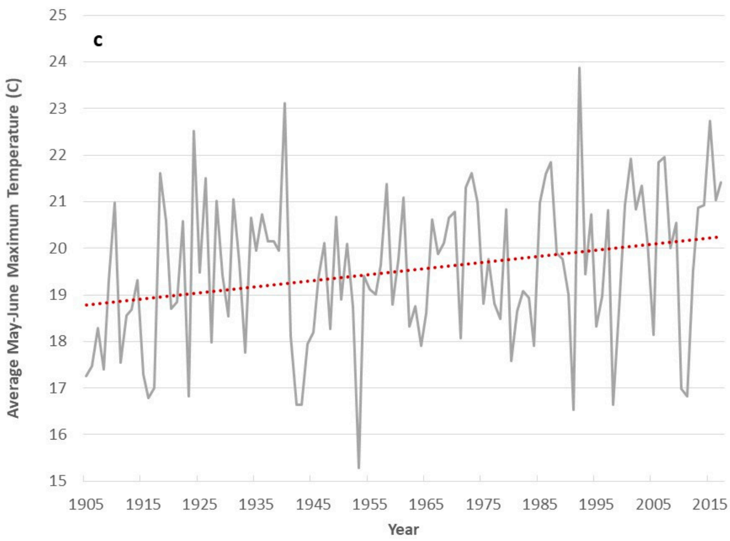
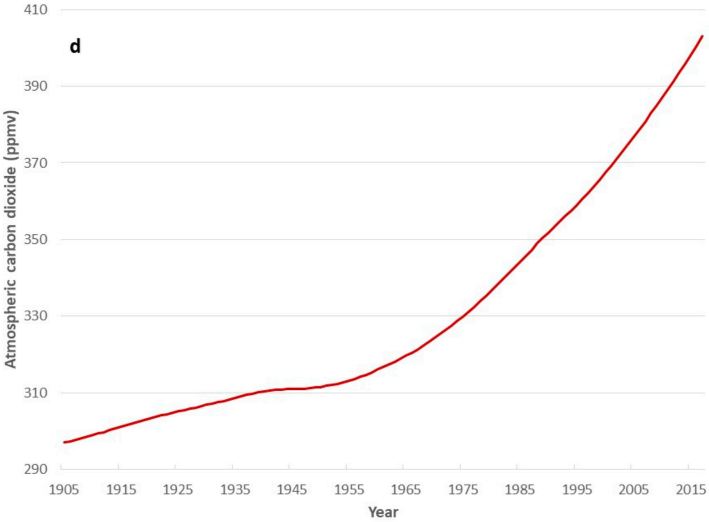


Figure 3. *Cont.*







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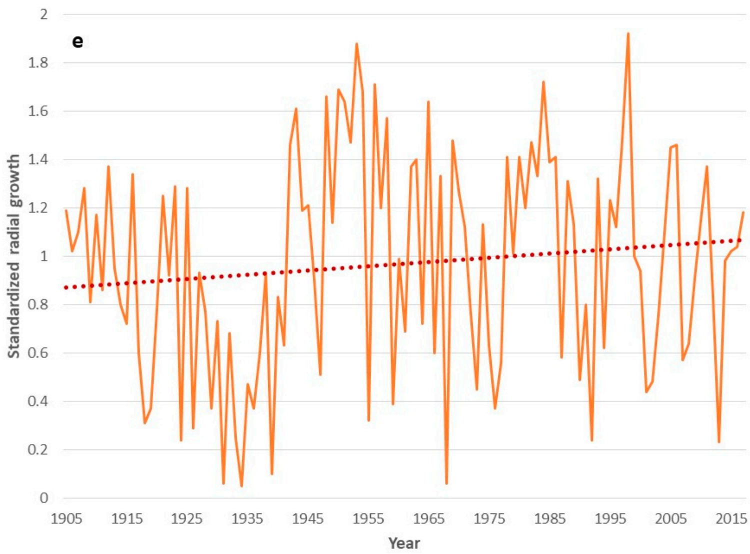

Figure 3. Temporal patterns (1905–2017) for (**a**) prior-year October–June total precipitation (cm), (**b**) June PDSI, (**c**) average maximum temperature (°C) for May–June, (**d**) annual atmospheric CO_2 concentrations (ppmv), and (**e**) standardized radial growth for COMBO.

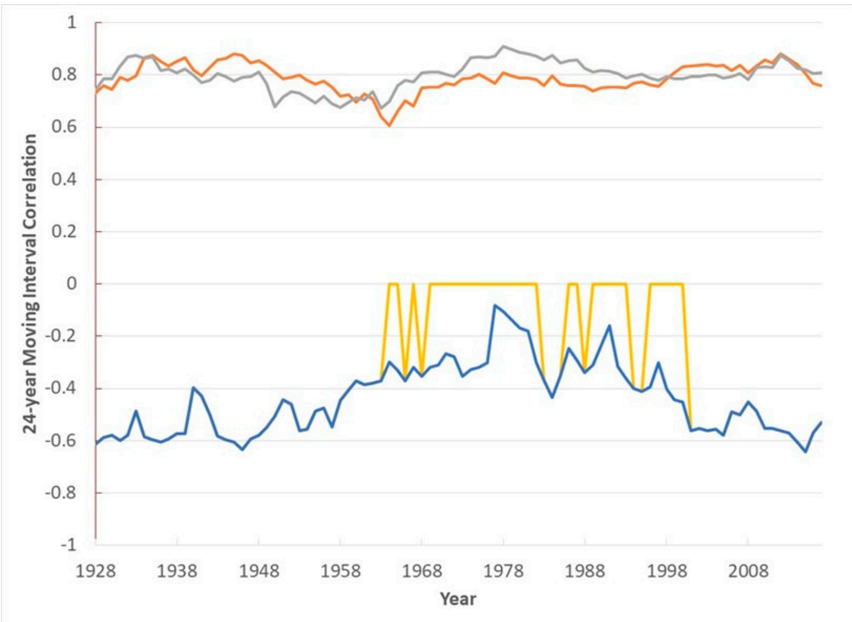

Figure 4. Significant ($p < 0.05$) 24-year moving interval correlation values between COMBO standardized radial growth and prior October–June precipitation (gray line) and June PDSI (orange line). All correlations between COMBO and May–June maximum temperature are shown with a blue line, 24-year windows when those correlations are non-significant ($p > 0.05$) are shown with a gold line.

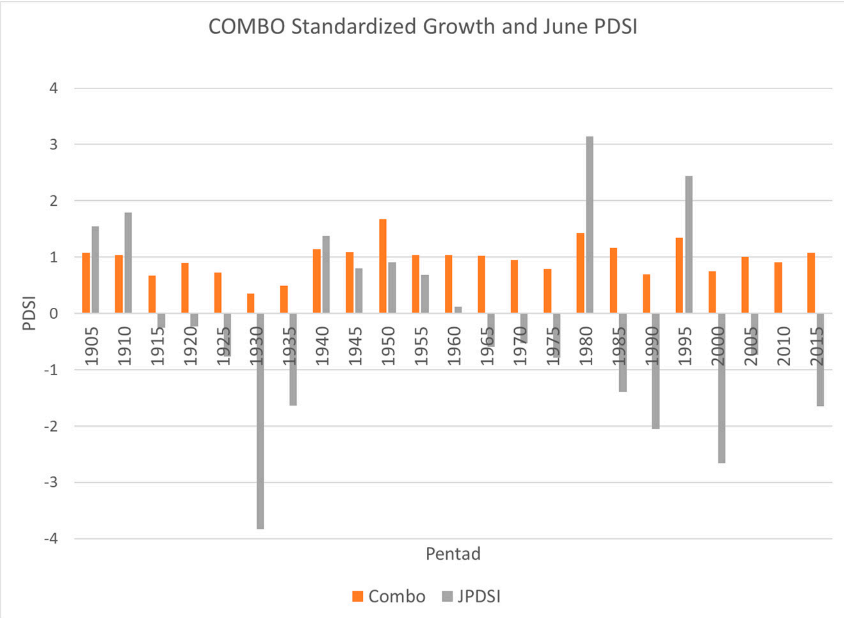

Figure 5. Pentadal values of standardized radial growth for COMBO and June PDSI at Oregon Climatic Division 7. 1905 pentad is 1905–1909, and the final pentad is only three years, 2015–2017.

Table 5. Comparison of COMBO standardized radial growth early (1905–1960) and (late 1962–2017) by June PDSI category (*p*-Values are from a Mann–Whitney U test, with significant ($p < 0.05$) differences boldfaced).

	PDSI < −3		
	PDSI	Growth	# years
EARLY	−3.9	0.23	8
LATE	−4.3	0.47	7
p-Value	0.315	0.132	
	PDSI < −2		
	PDSI	Growth	# years
EARLY	−3.3	0.38	15
LATE	−3.3	0.59	17
p-Value	0.479	**0.034**	
	PDSI < −1		
	PDSI	Growth	# years
EARLY	−2.7	0.51	21
LATE	−2.7	0.71	25
p-Value	1.00	0.236	

4. Discussion

One of the benefits of working in minimally disturbed western juniper woodlands is that radial growth responses to changing climatic conditions or increasing CO_2 should not be masked by other exogenous factors. Events such as grazing, logging, and road building, either operating individually or together, can alter the surrounding environment of trees by affecting the amounts of light, nutrients, and soil–water availability [47]. By sampling on established Research Natural Areas, the potential effects of human activities on radial growth are minimized. Further, each site represents an open-canopy woodland; thus, the trees are not subject to changes in light intensity caused by infilling. While some western juniper trees are host to dwarf mistletoe (*Phoradendron juniperinum*), which could potentially reduce radial growth rates, we did not sample trees with colonies of the parasite plant.

The relationships between prior-year October–June cumulative precipitation and radial growth were all significant ($p < 0.01$) and positive, reflecting the importance of cumulative water supply over several months prior to the peak summer growing season. This result was expected, as Knapp et al. [21] found October–June precipitation to be the variable most strongly associated with the radial growth of western juniper based on chronologies developed within the region in the 1990s and including three of our study sites (HRR, PBR, and IRR). In southern Oregon, Knutson and Pyke [48] also found October–June precipitation to be the most important driver of radial growth at the majority of 17 western juniper study locations. The other climate variable that is strongly related to WJ radial growth is June PDSI. That these two measures are providing similar explanatory power for western juniper radial growth is expected, as the calculation procedures for the PDSI incorporate antecedent moisture conditions over multiple months [26]. Knapp and Soulé [32] also found June PDSI values to be strongly related to WJ radial growth at 11 sites in central Oregon. As we also found significant and negative relationships between radial growth and May–June maximum temperature, years with ample water supplied through precipitation combined with low rates of evapotranspiration will be conducive for radial growth. Conversely, drought years in this region are typically associated with persistent upper-level ridging that both reduces precipitation and leads to above normal temperatures, leading to moisture deficits and low rates of radial growth.

Testing residuals from regression models for temporal autocorrelation is a metric that has been used in prior research to suggest that an important exogenous factor for radial growth (such as CO_2) was not reflected in the model (e.g., [21,44]). For our June PDSI model and our multivariate model with prior October–June precipitation and May–June maximum temperature, the residuals were positively autocorrelated, suggesting that radial growth in the later portion of the record was overpredicted. In exploring the potential impacts of carbon dioxide enrichment on the radial growth of western juniper, Knapp and Soulé [32] showed that CO_2 could be successfully used as a predictor in multiple regression models. Adding CO_2 to both these models produced a small increase in explanatory power (2.4% for both models), which is substantively less than the 14% for WJ trees in the same region but using datasets that ended in 2006 [32]. These findings suggest that while elevated atmospheric CO_2 can ameliorate the effects of increasing aridity, there may be environmental limits (e.g., prolonged drought) in which these benefits become inoperative (e.g., [49]).

We found that the thermal climate during the WJ growing season has become significantly warmer long-term (1905–2017), with a similar magnitude of change (although non-significant) during the last 20 years (Table 4, Figure 3). Conversely, the primary moisture variable impacting WJ growth is positively sloping for all time periods examined, with the strongest trends also occurring during the last 20 years. The impact of the temperature increases is best illustrated by June PDSI, which remains negatively sloping through time despite the increases in moisture. Although temperature is a weaker driving force for WJ radial growth than moisture, the relationship between growth and temperature is consistently negative (Table 2); thus, this aspect of climate change should be impacting WJ radial growth in an increasingly negative fashion. Although the thermal climate of the region has clearly changed, the climate/growth relationships for temperature, precipitation, and PDSI have remained largely stable. For temperature, the moving-interval correlations ranged between approximately −0.3 and −0.6 for all periods (Figure 4), which is a similar range of relationships found for both precipitation and PDSI (i.e., ranging from approximately 0.6 to 0.9). Perhaps the return to significant relationships between temperature and WJ growth from ~1976 onwards (i.e., 24-year moving windows ending in ~2000) is related to increasing temperatures.

In addressing the question if carbon dioxide enrichment continues to be an important driver for the radial growth of WJ, the most compelling evidence comes from our comparisons between radial growth and June PDSI. As previously shown (Table 2), June PDSI is a significant predictor for WJ radial growth. However, in the post-1950s era when atmospheric CO_2 levels have rapidly escalated, several pentads recorded above normal radial growth despite having negative mean PDSI levels, which is an incongruent finding absent some other explanatory causal mechanism. Given that pentadal means could be skewed by individual years that were extremely atypical, we approached the June PDSI-based analyses a second way and found similar results (Table 5). For all three drought categories (i.e., PDSI < −1, −2, and −3), the early period (1905–1960) mean moisture conditions measured by June PDSI were either the same as the late (1962–2017) period or slightly wetter. Yet, in all three categories, the average radial growth post-1962 was greater, and significantly greater in the 17 years falling into the PDSI < −2 category (moderate drought). Since the observed *changes* in climate have not been conducive for enhanced radial growth, a logical conclusion is that some other mechanism is allowing the trees to grow better during drought conditions in the later portion of the record. We posit that in central Oregon, the most logical mechanism is that CO_2 enrichment continues to increase the intrinsic water-use efficiency (iWUE; [50]) of WJ, allowing the trees to grow at relatively faster rates during periods of drought in recent decades when compared to growth experienced during drought periods of the early 20th century. Various studies have linked CO_2 enrichment to increasing radial growth for trees (e.g., [21,30,42,51–55], with increasing rates of iWUE concurrent with atmospheric CO_2 increases [25] continuing to be proffered as a key mechanism in recent work (e.g., [56–58]). However, in a meta-study based on global records from the International Tree Ring Databank, Gedalof and Berg [59] concluded that CO_2 enrichment was the likely primary driving force for the increased radial growth of trees only 20% of the time, and that changes in photosynthesis related to increasing CO_2 were more important than increases in iWUE for growth enhancement. Others have reached similar conclusions, principally that, despite increasing iWUE related to increasing levels of atmospheric CO_2, there have not been commensurate increases in the growth rates of trees (e.g., [49,60,61]). Further, the synergistic reactions of trees to macroenvironmental changes such as warming, increasing aridity, and increasing CO_2 levels (e.g., [38,62,63]) make it difficult to isolate the individual effects of any single driving force on radial growth.

5. Conclusions

This study provided us with an opportunity to conduct a longitudinal study of the driving forces behind WJ radial growth rates in central Oregon. We conclude that in the ~20 years from our initial work on this topic [21], little has changed in terms of the basic climate/growth relationships. Variables that we identified as the primary drivers of radial growth based on tree-ring and climate data ending circa 1998 remain unchanged through 2017. Further, our moving-interval analyses suggest that the climate/growth relationships have remained stable since the early portion of the 20th century. Two of the factors we identify as being drivers of radial growth, temperature and atmospheric carbon dioxide, have experienced significant temporal changes, but one impacts growth negatively (temperature), and the other impacts growth positively. While increasing summer temperatures are making the climate in central Oregon more arid during the growing season for WJ, our results suggest that the trees are not responding in a commensurate fashion. That is, we found that several pentads since the 1960s recorded normal- to slightly above-normal radial growth rates while experiencing drought conditions, and that WJ are growing at faster rates during drought periods post-1960 relative to pre-1960. Thus, in answering the question of whether CO_2 enrichment remains operative, we find evidence that suggests that the answer is yes. With increasing aridity and absent some other logical explanation, it is likely that an increasingly rich CO_2 environment is allowing the trees to outperform growth expectations based on climatic conditions. Given the recent findings that semiarid environments are critical determinants of short-term variance in global carbon storage [6,15,16], and the continued expansion of WJ woodlands into sagebrush-dominated ecosystems [8–10], any continued enhancement of WJ radial growth by CO_2 enrichment should result in increased carbon uptake for a species that is dominant across 3.6 million hectares of the American West.

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