REGIONAL AND WATERSHED-SCALE COHERENCE IN THE STABLE-OXYGEN AND CARBON ISOTOPE RATIO TIME SERIES IN TREE RINGS OF COAST REDWOOD (*SEQUOIA SEMPERVIRENS*)

JOHN S. RODEN^{1*}, JAMES A. JOHNSTONE^{2,3}, and TODD E. DAWSON²

¹Department of Biology, Southern Oregon University, Ashland, OR, 97520, USA

²Department of Integrative Biology, University of California, Berkeley, CA, 97420, USA

ABSTRACT

Coast redwood (*Sequoia sempervirens*) ecosystems are strongly influenced by the presence of summer marine fog, and variation in fog frequency is closely linked to climate variation in the NE Pacific region. Because oxygen isotope composition ($\delta^{18}\text{O}$) of organic matter records distinct water sources (e.g. summertime fog vs. winter precipitation) and carbon isotopes ($\delta^{13}\text{C}$) are typically sensitive to humidity and water status, it then follows that inter-annual variation in tree-ring isotope ratios, which are coherent across multiple sites, should preserve a potentially powerful proxy for climate reconstruction. Here we present an analysis of a 50-year time series for both $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values from subdivided tree rings obtained from multiple redwood trees at multiple sites. Within-site and between-site correlations were highly significant ($p < 0.01$) for the $\delta^{18}\text{O}$ time series indicating a regionally coherent common forcing of $\delta^{18}\text{O}$ fractionation. Within-site and between-site correlation coefficients were lower for the $\delta^{13}\text{C}$ than for the $\delta^{18}\text{O}$ time series although most were still significant (at least to $p < 0.05$). The hypothesized reason for the differences in the correlation is that carbon isotope discrimination is more sensitive to microenvironmental and tree-level physiological variation than is $\delta^{18}\text{O}$ fractionation. Stable-isotope variation in tree-ring cellulose was similar between slope, gully and riparian micro-habitats within a single watershed, implying that minor topographic variation when sampling should not be a major concern. These results indicate that stable-isotope time series from redwood tree rings are strongly influenced by regional climate drivers and potentially valuable proxies for Pacific coastal climate variability.

Keywords: Annual rings, $\delta^{18}\text{O}$, $\delta^{13}\text{C}$, cellulose, inter-annual variation, latewood.

INTRODUCTION

Coast redwood (*Sequoia sempervirens* D. Don) ecosystems are limited to a long (ca. 750 km) and narrow (e.g. within 50 km of the Pacific Ocean) region of central and northern California that experiences heavy marine fog during summer (Oberlander 1956). By frequently saturating the canopy atmosphere, fog has strong effects on redwood transpiration rates, as shown by short-term physiological monitoring (Burgess and Dawson 2004; Ewing *et al.* 2009; Johnstone

and Dawson 2010). Dawson (1998) estimated that mature redwood forests obtain between 22–46% of their yearly water input from fog drip, which can further affect tree water balance (Azevedo and Morgan 1974; Huntley *et al.* 1997; Simonin *et al.* 2009). Redwood tree crowns and forest canopies can effectively strip moisture from fog (Azevedo and Morgan 1974; Burgess and Dawson 2004) where it can either drip into the surrounding soils or be retained and taken up directly through plant leaves (Burgess and Dawson 2004). Climate variations that alter either the fraction of fog water utilized by plants or the frequency and intensity of fog events can impact redwood forest hydrologic processes. In fact, Johnstone and Dawson (2010) have shown that inter-annual variability of summer fog frequency displays

³Present address: Joint Institute for the Study of the Atmosphere and Ocean, University of Washington, Seattle, WA, 98105, USA.

*Corresponding author: rodenj@sou.edu; Telephone 541-552-6798; Fax 541-552-6415

coherence across the length of the coast redwood region. Moreover, summer fog frequency is related to a variety of interacting climatic factors, such as the summertime maximum temperature difference between coastal and inland locations, the coastal inversion strength, North Pacific sea surface temperatures, the magnitude of coastal alongshore winds, and therefore the marine upwelling system of the California Current. If the coastal ocean-atmosphere system is modified, then the frequency of summertime fog events that influence redwood trees should change as well (Johnstone and Dawson 2010). In turn, if wintertime precipitation inputs increase or decline, then the fractional importance of fog as a water source will be oppositely affected. During a drier-than-normal year, Dawson (1998) found that redwood trees became more dependent on fog water inputs as other water sources became exhausted.

The stable-oxygen and hydrogen isotope compositions ($\delta^{18}\text{O}$ and $\delta^2\text{H}$) of meteoric water, fog and tree sap are valuable tools for assessing hydrologic inputs as fog, which is isotopically distinct from rainfall (Gonfiantini and Longinelli 1962; Aravena *et al.* 1989; Ingraham and Matthews 1995; Dawson 1998). Through a series of known fractionation events, $\delta^{18}\text{O}$ (and $\delta^2\text{H}$) variation derived from hydrologic inputs is incorporated into the organic matter that makes up tree rings (Yapp and Epstein 1982; White *et al.* 1994; Roden and Ehleringer 1999b; Roden *et al.* 2000; Treydte *et al.* 2006; Gessler *et al.* 2009). Tree-ring cellulose $\delta^{18}\text{O}$ values can be modified by variation in atmospheric humidity and the unique isotope values it possesses, by vapor pressure deficit and therefore the magnitude of leaf evaporative enrichment associated with transpiration (Edwards and Fritz 1986; Roden and Ehleringer 1999a; Wright and Leavitt 2006; Kahmen *et al.* 2008), by variation in source water (Wright *et al.* 1999; Roden and Ehleringer 1999b, 2007) and by post-photosynthetic but pre-biosynthetic factors shown to dampen the original isotope values of sucrose made at the leaf-level before it becomes incorporated into tree-ring cellulose (Brandes *et al.* 2006). Carbon isotope ratios ($\delta^{13}\text{C}$) in tree-ring cellulose have been used to study historical variations in plant water status, temperature, solar

radiation and vapor pressure deficit (Saurer *et al.* 1995; Stewart *et al.* 1995; Hemming *et al.* 1998; Schleser *et al.* 1999; Barbour *et al.* 2002; Leavitt *et al.* 2002; Young *et al.* 2010). The mechanistic foundations for variation in cellulose $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ are now fairly well established (Farquhar *et al.* 1982, 1989; Roden *et al.* 2000; Barbour *et al.* 2004). Thus, absolutely dated time series of $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ variation in redwood tree rings have the potential to provide valuable historical records of climate variation and fog water utilization.

Previously, we found that redwood tree rings exhibit substantial intra-annual variation in both $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ (>3 and 2‰, respectively, Roden *et al.* 2009). The latewood portion of the ring produced the most enriched (in ^{18}O) cellulose whereas the most depleted $\delta^{18}\text{O}$ values were found in the center of the ring. We termed this location “middlewood” as a positional designator (rather than a seasonal one) so as not to confuse it with earlywood. Earlywood spans a large portion of the annual ring, and it is not isotopically uniform (Barbour *et al.* 2002; Poussart *et al.* 2004; Roden *et al.* 2009). A number of studies have confirmed that the first cells produced in spring (initial earlywood) have isotope values related to the previous summer’s environment and thus may represent a mixture of environmental conditions (Ogle and McCormac 1994; Hill *et al.* 1995; Kagawa *et al.* 2005, 2006). For redwood, Roden *et al.* (2009) speculated that the dip in $\delta^{18}\text{O}$ in the middlewood portion of the annual growth ring represents the time when stored carbohydrates from the previous year have been fully exhausted and thus represents the truest spring environmental signal. Although not as consistent in their patterns, $\delta^{13}\text{C}$ also showed significant intra-annual variation in redwood (Roden *et al.* 2009, see also Loader *et al.* 1995; Schleser *et al.* 1999; Warren *et al.* 2001). Thus when sampling longer chronologies, we chose to sample the two portions of the annual ring that produced the greatest intra-annual differences (latewood and middlewood).

Before inter-annual variation in $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ time series of redwood tree rings can be interpreted as proxies for regional climate variability, we must clarify whether such variation is spatially coherent and at what scale. If inter-

annual isotopic variation is not coherent between trees at the same site, then these signals would be of limited use as proxies for any environmental factor. Physiological differences between trees can influence isotopic fractionation, and their ability to dampen climate signals may be an important limitation of this technique. If, however, they are coherent locally but not regionally then climate drivers are likely to be related to microclimate rather than larger scale meteorological patterns (Leavitt *et al.* 2002). These questions require significant replication of trees and sites and analysis of a long enough time series to be able to assess the viability of this system for paleoclimatic reconstruction. Analyzing many years of annual growth rings on a few trees may not provide the information necessary to indicate that those signals represent anything more than microclimatic variation. Within-site and between-site coherence in the stable-isotope variation in tree-ring time series have been reported for other species (Leavitt and Long 1988, 1989; McCarroll and Pawellek 2001; Roden and Ehleringer 2007). In addition, it is important to determine if specific locations at any site are more sensitive to climate variation than others. For example, organic matter $\delta^{18}\text{O}$ values are primarily influenced by source water $\delta^{18}\text{O}$ variation of meteoric waters (Roden and Ehleringer 1999b; Robertson *et al.* 2001). However, if a tree obtains most of its water from a perennial stream because of its location in the riparian zone, then it may not be sensitive to changes in meteoric water $\delta^{18}\text{O}$. Because fog water is captured as it moves across the landscape, it is important to determine if geographic features (*e.g.* slope, aspect) influence uptake of this hydrologic resource. All of these considerations are necessary to develop sampling strategies for optimizing the potential of long-term tree-ring time series to serve as valuable proxies for past climate variation.

Annual differences in hydrologic inputs and environmental conditions are potential drivers of inter-annual variability in cellulose $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ for redwood tree rings (Roden *et al.* 2009). The objective of this study was to determine if there is coherence in the latewood and middlewood

variation of $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ in redwood tree-ring cellulose over the last 50 years between replicate trees at multiple sites. A further objective was to determine if differences in tree location associated with geographic features within a single watershed produce differences in $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values. We hypothesize that (1) redwood trees will display significant coherence in inter-annual $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ time series between trees at a single site and between trees at distant sites, implying that regional climate drivers may impact isotopic fractionation, and (2) local climate drivers or common forcing are more important than geographic influences producing consistent patterns of $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ variation within a watershed.

METHODS

Site Locations, Descriptions and Sampling

From 2002–2003, a minimum of four coast redwood trees (*Sequoia sempervirens* [D. Don] Endl.) were sampled from four sites in Northern California (Figure 1). The most southerly site was the Sonoma site that is a Save-the-Redwood-League reserve called “Grove of the Old Trees” near Santa Rosa, CA (38°24.0'N 122°59.5'W, elevation 220 m a.s.l. with relatively flat topography). Progressing northward, trees were also sampled at the Arcata Community Forest near Arcata, CA (40°52.5'N 124°4.1'W, elevation 158 m, on a gentle slope; in addition, a transect was sampled across an open slope to gully transition at this site), at Prairie Creek near Klamath, CA (41°27.4'N 124°2.8'W, elevation 207 m, situated on a slope facing the ocean), and Jedediah Smith near Hiouchi, CA (41°47.3'N 124°4.6'W, elevation 42 m, with flat topography). Both Prairie Creek and Jedediah Smith sites are part of the Redwood State and National Park system. These sites span a 300-km latitudinal range of classic redwood habitat. All trees sampled were between 55 and 94 cm in diameter and would be classified as canopy subdominants. Trees were cored to obtain approximately the last 50 years of tree rings and because trees were not cored to the center, pith ages were not obtained and juvenile wood was not sampled. Four cores (12 mm diameter) were obtained from

Figure 1. Site map showing the distribution of coast redwood ecosystems and sampling locations (open triangles; from north to south, Jedediah Smith, Prairie Creek, Arcata and Sonoma).

the four cardinal directions at breast height for each tree.

Sample Processing

The four cores from each tree were compared and examined for ring anomalies, and the estimated year (by ring counting) was marked with pinholes. Annual growth increments were measured to the nearest 0.01 mm on all cores on a micrometer stage. The ring-width time series were used for within-tree and between-tree crossdating using the COFECHA program (Holmes 1983; Grissino-Mayer 2001; Roden 2008). Because of the short chronology length, a 20-year spline length (without autoregressive modeling) and a 30-year segment length with a 15-year overlap was utilized. The critical correlation coefficient (99% confidence) for a 30-year segment length was

0.4226. All other default options in COFECHA (e.g. log transformations) were used for all runs. In general, if a tree could not be reliably crossdated with others at the site (or if the four within-tree cores could not be crossdated) the tree was not used for isotope analysis, reducing the number of samples from each site by 1 or 2 trees. Past research considered crossdating coast redwood to be problematic because of extensive ring anomalies (e.g. ring wedging, false latewood bands (Brown and Swetnam 1994)). However, ring anomalies are more prevalent in very large trees whereas these smaller trees were still rapidly growing and producing large rings (up to 10 mm wide), creating few ring-counting problems. The mesic environment of coastal California did produce complacent growth, which made crossdating less than ideal.

An initial study (Roden *et al.* 2009) subdivided redwood tree rings into 10 equal segments and found a consistent pattern in intra-annual variation in $\delta^{18}\text{O}$ with the most enriched (in ^{18}O) values found in the latewood portion (and in the initial earlywood formation of the next year) of the annual ring. The most depleted $\delta^{18}\text{O}$ values occurred in the central portion of the ring. Although this portion is a component of earlywood, Roden *et al.* (2009) used the term “middlewood” to clarify that only the central part of the ring was sampled and not the entire earlywood fraction. Middlewood is a positional designator not a seasonal one because growth rates vary throughout the year. Thus, two portions of each ring were sampled in this study, the latewood (representing summer conditions with the potential for fog water inputs to impact the cellulose isotope ratios) and middlewood (representing spring conditions and the winter/spring recharge period when soil moisture is highest and the water is largely from cold winter storms). Each ring was subdivided into approximately four slivers using a scalpel under a 20 $\times$ dissecting microscope. The latewood sample comprised a thin section within the region of visually dense cells and just inside the ring boundary. The middlewood sample comprised a thin section from the center of the ring and within the less dense earlywood portion. Other portions of the ring (e.g. the initial

earlywood) were discarded. The thickness of each section depended on ring width, and because most ring widths were fairly large (from 2 to 10 mm), subdividing only became problematic with the occasional very narrow ring. The two subdivisions from each core obtained from the four cardinal directions on each tree were pooled, dried at 70°C for 48 h and ground to a fine powder with a ball mill (Wig-L-Bug, Crescent, Elgin, Ill, USA).

Cellulose Extraction

The detailed description of cellulose extraction procedures is given in Roden *et al.* (2009). The procedure is modified from Leavitt and Danzer (1993; see also Gaudinski *et al.* 2005 for a methods comparison). Briefly, resins were extracted from the dried wood samples using organic solvents in a Soxhlet apparatus. Soluble sugars were extracted by boiling in water. Samples were “bleached” using a strong sodium chlorite/acetic acid solution to remove lignin and other N-containing compounds. The resulting holocellulose was converted to α -cellulose in a strong NaOH solution. The α -cellulose was dried at 70°C for 48 h.

Analysis of Stable-Carbon and Oxygen Isotope Ratios

As above, a description of isotope analysis procedures can be found in Roden *et al.* (2009). All isotope measurements were performed at the Center for Stable Isotope Biogeochemistry at the University of California, Berkeley. To measure cellulose $\delta^{18}\text{O}$ a pyrolysis method (at 1,130°C) modified from Farquhar *et al.* (1997) was utilized. From 0.9 to 1.1 mg of α -cellulose was analyzed for $\delta^{18}\text{O}$ with a Thermo-Finnigan Delta Plus XL mass spectrometer (Bremen Germany). The system was calibrated with IAEA C₃ cellulose at an oxygen isotope value of 32.2‰ ($\delta^{18}\text{O}$, VSMOW). Long-term average and external precision for the quality control IAEA V9 cotton cellulose is 28.62‰ ($\delta^{18}\text{O}$ SMOW) with a standard deviation of 0.20‰ (n = 96). Values are expressed in standard “delta notation” as $\delta = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1,000$ in units of per mil (‰) or parts per thousand

where R is the ratio of the rare (^{18}O) to common (^{16}O) isotope.

For $\delta^{13}\text{C}$ measurements, approximately 1 mg of α -cellulose was loaded into tin capsules and combusted on an elemental analyzer (Carlo-Erba Model NS-1500, Milan, Italy) coupled to a PDZ Europa (20/20) isotope ratio mass spectrometer (Crewe, UK). Long-term average and external precision for the quality control α -cellulose standards for $\delta^{13}\text{C}$ was 0.17‰ with a standard deviation of 0.07‰ (n > 2,000; years 2003–2007).

Statistical Analysis of Time Series

Pearson’s correlation coefficients for each time-series comparison and analysis of variance (Univariate GLM) for transect comparisons were calculated using SPSS statistical software (version 15). In addition, because the COFECHA program (Holmes 1983; Grissino-Mayer 2001) was specifically developed to handle time-series correlations between multiple tree-ring data sets, we also ran our isotope time-series data through the COFECHA program (see above for details). We also calculated the expressed population signal (EPS, Briffa and Jones 1990; Robertson *et al.* 1997) as an estimate of signal strength. $\text{EPS} = (t \times r) \div ((t \times r) + (1 - r))$, where t is the number of time series associated with r , which is the mean inter-series correlation coefficient.

RESULTS

Within-Site Coherence

For both latewood and middlewood records, redwood trees growing at each site produced $\delta^{18}\text{O}$ time series that were significantly correlated with each other ($p < 0.01$, Table 1). Not only were these time series coherent between trees at each site, but the absolute values were also quite similar. Although some years were more variable, the range in $\delta^{18}\text{O}$ values for any year was often much less than 1‰ (Figure 2). Maximum inter-annual variation in $\delta^{18}\text{O}$ was between 2 and 3‰ for both latewood and middlewood segments at each site (Figure 2; data not shown for other sites). The expressed population signal statistic (EPS, Table 1) attempts to quantify the strength

Table 1. Summary statistics from between-tree isotope chronologies as derived from the COFECHA program. Also included is the expressed population signal for each between-tree comparison. The analysis was performed using time-series data from three to four trees from each site. Significant correlations are indicated by asterisks: **p < 0.01; and *p < 0.05.

	Mean Measurement (‰)	Mean Correlation	Mean sensitivity	Auto- Correlation	Expressed Population Signal
Sonoma site (1954–2002)					
δ ¹⁸ O latewood	31.7	0.669**	0.030	0.112	0.890
δ ¹³ C latewood	−23.9	0.570**	0.028	0.451	0.841
Δ ¹³ C latewood	16.6	0.624**	0.041	0.211	0.869
δ ¹⁸ O middlewood	30.9	0.702**	0.026	0.182	0.904
δ ¹³ C middlewood	−24.1	0.492**	0.015	0.655	0.795
Δ ¹³ C middlewood	16.8	0.482**	0.021	0.426	0.788
Arcata site (1962–2004)					
δ ¹⁸ O latewood	28.4	0.760**	0.016	0.421	0.905
δ ¹³ C latewood	−23.6	0.540**	0.013	0.506	0.779
Δ ¹³ C latewood	16.1	0.538**	0.019	0.453	0.777
δ ¹⁸ O middlewood	27.0	0.732**	0.017	0.276	0.891
δ ¹³ C middlewood	−23.5	0.415*	0.010	0.727	0.680
Δ ¹³ C middlewood	16.1	0.373*	0.015	0.461	0.641
Prairie Creek site (1953–2003)					
δ ¹⁸ O latewood	27.8	0.747**	0.020	0.121	0.922
δ ¹³ C latewood	−25.1	0.264	0.013	0.726	0.589
Δ ¹³ C latewood	17.8	0.262	0.018	0.413	0.587
δ ¹⁸ O middlewood	27.3	0.628**	0.016	0.129	0.871
δ ¹³ C middlewood	−24.9	0.269	0.013	0.743	0.595
Δ ¹³ C middlewood	17.7	0.246	0.018	0.428	0.566
Jed Smith site (1952–2003)					
δ ¹⁸ O latewood	28.8	0.770**	0.022	0.147	0.909
δ ¹³ C latewood	−24.4	0.625**	0.018	0.378	0.833
Δ ¹³ C latewood	17.2	0.622**	0.026	0.435	0.832
δ ¹⁸ O middlewood	28.5	0.735**	0.022	0.031	0.893
δ ¹³ C middlewood	−24.6	0.381*	0.039	0.331	0.649
Δ ¹³ C middlewood	17.3	0.469**	0.018	0.626	0.726

of common forcing and can be used to indicate the number of replicate time series required to obtain adequate climate signals. Although a specific significance value for EPS is not available, some have suggested (Wigley *et al.* 1984; Robertson *et al.* 1997) that an EPS exceeding 0.85 indicates an acceptable level of chronology confidence. EPS results indicate that three to four trees were sufficient to produce a strong common variance (implying common forcing) for all within-site comparisons of δ¹⁸O time series.

Within-site comparisons of δ¹³C time series produced lower correlations than δ¹⁸O time series (Table 1). Many within-site δ¹³C correlations were still statistically significant (at least to p < 0.05), except those from the Prairie Creek site. Although some within-site δ¹³C time series produced EPS

values close to or exceeding 0.85, in general EPS values were lower for δ¹³C than δ¹⁸O time series (Table 1). It is unclear why the Prairie Creek site did not produce coherent time series. The power of the COFECHA program is in detecting dating errors by breaking the series into segments and testing if better correlations result if the sequences are moved in relation to the mean series. Although the program flagged some odd years for the Prairie Creek data set, there was no clear benefit of shifting years and thus we assumed that each series was correctly dated. A latewood δ¹³C time series from the Sonoma site produced significant within-site correlations (Figure 3A), whereas a middlewood time series from Prairie Creek (Figure 3B) did not. Within-year variation in δ¹³C values appear greater than for δ¹⁸O variation, with

Figure 2. Latewood (A) and middlewood (B) $\delta^{18}\text{O}$ time series for tree-ring cellulose in three replicate redwood trees from the Jedediah Smith site. Both latewood and middlewood series were significantly correlated ($p < 0.01$, see Table 1).

many years producing a between-tree range of $\delta^{13}\text{C}$ values up to 2‰ (Figure 3). Maximum inter-annual variation in $\delta^{13}\text{C}$ was between 1 and 3‰ for both latewood and middlewood segments at each site (Figure 3; data not shown for other sites).

Many $\delta^{13}\text{C}$ time series produced lower-frequency trends (Figure 3B) that were likely associated with changing concentration and $\delta^{13}\text{C}$ values of atmospheric CO_2 (Francey *et al.* 1999; McCarroll *et al.* 2009). To correct for this we calculated $\Delta^{13}\text{C}$ values for all time series: $\Delta^{13}\text{C} = (\delta^{13}\text{C}_{\text{source}} - \delta^{13}\text{C}_{\text{product}}) / (1 + \delta^{13}\text{C}_{\text{product}})$, where source is atmospheric CO_2 and product in this case is cellulose (Farquhar *et al.* 1982). On occasion, using $\Delta^{13}\text{C}$ rather than $\delta^{13}\text{C}$ produced higher correlation coefficients, but often the differences were minimal (Table 1). This is likely because the COFECHA program removes nearly all low-

Figure 3. Latewood $\delta^{13}\text{C}$ time series for tree-ring cellulose in four replicate redwood trees at the Sonoma site (A) and middlewood from the Prairie Creek site (B). The time series were significantly correlated ($p < 0.01$, see Table 1) for the Sonoma site but not for the Prairie Creek site.

frequency trends via spline fitting, autoregressive modeling and log transformations (Grissino-Mayer 2001) and $\Delta^{13}\text{C}$ simply eliminates the trend using a different technique. Significant correlations result if Prairie Creek $\delta^{13}\text{C}$ time series are analyzed with standard correlation analysis (not detrended or corrected for changes in $\delta^{13}\text{C}$ of atmospheric CO_2). This demonstrates the importance of correcting for low-frequency trends when determining coherence between isotope time series.

Watershed Coherence

The correlations above were performed on 3 to 4 trees per site, with each tree being in close proximity to the others (within 100 m). To test for larger scale site variation, we measured 24 trees along a transect within one watershed at the Arcata site. Generating 50 years worth of isotope data on each tree would have been time consuming and expensive, thus we decided to focus on only

Figure 4. Middlewood and latewood carbon and oxygen stable isotope composition of tree-ring cellulose from 1999 and 2004 from 24 redwood trees within a single watershed at the Arcata site. The bars represent ± 1 standard deviation for the mean values for each tree-ring subdivision and year.

two years (1999, 2004) that have been shown to produce very different latewood and middlewood values for $\delta^{18}\text{O}$. Three distinct environments were tested along the transect: (1) trees on an open slope above the riparian gully, (2) trees within the gully but away from the stream, and (3) trees in close proximity to the stream (riparian). Although the $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ measurements were variable at each position, distinctions between the two years and between latewood and middlewood were generally maintained (Figure 4). Analysis of variance showed no significant differences between positions (data not shown) indicating that “noise” in the results as seen in Figure 4 was similar for each micro-site. There were no significant differences between the slope, gully and riparian locations for any measurements of $\delta^{13}\text{C}$ or for latewood $\delta^{18}\text{O}$ (Table 2). The only significant

differences between tree locations were for middlewood $\delta^{18}\text{O}$. Trees located in the gully, regardless of proximity to the stream, produced middlewood that was more enriched (in ^{18}O) than trees located on the slope above the gully (Table 2).

Between-Site Coherence

The latewood and middlewood $\delta^{18}\text{O}$ time-series data (using mean values for each site) produced significant correlations between all four sites ($p < 0.01$, Table 3). In addition, the time-series difference between latewood and middlewood $\delta^{18}\text{O}$ was also significantly correlated ($p < 0.01$). These data indicate a strong coherence of factors that influence $\delta^{18}\text{O}$ variation in trees separated by over 300 km. This tight coherence was observed despite significant differences in absolute $\delta^{18}\text{O}$ values between sites. In general the more southerly (Sonoma) and inland (Jed Smith) sites produced more enriched (in ^{18}O) values as compared to the more northerly and coastal sites (Prairie Creek and Arcata) for both latewood and middlewood (Figure 5). The high EPS values (Table 3) for between-site $\delta^{18}\text{O}$ time series indicate adequate signal strength and the potential for common climate forcing for redwood trees at these regional scales.

The analysis for $\delta^{13}\text{C}$ coherence, however, is not as conclusive. Latewood $\delta^{13}\text{C}$ time series were significantly correlated ($p < 0.05$), but middlewood was not (Table 3). These analyses were also performed on $\Delta^{13}\text{C}$ values, but because this had no effect on the conclusions, the results are not presented (the COFECHA program already de-

Table 2. Mean and standard deviation (in parentheses) values for the stable isotope ratios of oxygen and carbon in tree-ring cellulose of coast redwood in a single watershed at the Arcata site. Significant differences ($p < 0.01$) between tree positions (within the column) are indicated with asterisks.

	Middlewood 1999	Latewood 1999	Middlewood 2004	Latewood 2004
$\delta^{18}\text{O}_{\text{cellulose}}$ (‰, VSMOW)				
Slope (n = 7)	26.15 ** (0.31)	28.89 (0.40)	26.59 ** (0.45)	27.81 (0.33)
Gully (n = 10)	26.72 (0.40)	28.75 (0.49)	27.17 (0.38)	27.93 (0.55)
Riparian (n = 7)	26.90 (0.41)	28.69 (0.33)	27.50 (0.60)	28.04 (0.53)
$\delta^{13}\text{C}_{\text{cellulose}}$ (‰, PDB)				
Slope (n = 7)	−24.86 (0.51)	−23.94 (0.98)	−24.71 (0.85)	−24.38 (0.97)
Gully (n = 9)	−25.17 (1.05)	−24.44 (0.69)	−25.29 (0.73)	−24.43 (0.81)
Riparian (n = 6)	−25.18 (0.88)	−24.78 (0.66)	−24.99 (0.72)	−25.05 (0.56)

Table 3. Summary statistics from between-site, isotope chronologies as derived from the COFECHA program. Also included is the expressed population signal for each between-site comparison. The analysis was performed on mean ($n = 3$ to 4 trees) stable isotope values derived for each site. Significant correlations are indicated by asterisks: ** $p < 0.01$; and * $p < 0.05$.

	Mean Correlation	Mean Sensitivity	Auto-Correlation	Expressed Population Signal
All sites (1952–2003)				
$\delta^{18}\text{O}$ latewood	0.635**	0.019	0.565	0.874
$\delta^{13}\text{C}$ latewood	0.367*	0.015	0.618	0.699
$\delta^{18}\text{O}$ middlewood	0.604**	0.017	0.122	0.859
$\delta^{13}\text{C}$ middlewood	0.283	0.011	0.628	0.612
$\delta^{18}\text{O}$ latewood–middlewood	0.633**	0.240	0.125	0.873
$\delta^{13}\text{C}$ latewood–middlewood	0.404*	0.206	0.128	0.731
Northern sites only (1952–2003)				
$\delta^{13}\text{C}$ latewood	0.509**	0.012	0.656	0.757
$\delta^{13}\text{C}$ middlewood	0.345	0.011	0.598	0.612

trends the data, see above). The EPS values were also lower for $\delta^{13}\text{C}$ than for $\delta^{18}\text{O}$ time series between sites. If we excluded the most southerly and most distant site (Sonoma is 250 km south of Arcata) from the analysis, correlation coefficients were improved (Table 3), indicating that environmental forcing of tree-ring $\delta^{13}\text{C}$ variation may not be as regionally coherent as that for $\delta^{18}\text{O}$ variation. In addition, variability in absolute $\delta^{13}\text{C}$ values in tree-ring cellulose does not seem to be related to particular site locations. The Prairie Creek and Arcata sites are both coastal and within 70 km of each other and yet their $\delta^{13}\text{C}$ values are the most widely separated of the four sites (Figure 6). The absolute amount of carbon isotope discrimination may be a function of local microclimate, whereas inter-annual variability may be influenced by regional climate drivers.

DISCUSSION

In order for tree-ring isotope chronologies to serve as proxies for climate reconstruction, significant inter-annual variation and coherence in that variation between trees must be established. Isotopic time series that are relatively uniform are analogous to complacent growth for ring-width studies in that little useable information can be extracted (Fritts 1976; Schweingruber 1987; Cook and Kairiukstis 1989). Dendrochronologists therefore often recommend sampling from stressful sites as they are likely to produce sensitive ring-

width chronologies (Schweingruber 1987; Stokes and Smiley 1996). Redwood ecosystems would not be considered a particularly stressful environment as evidenced by lush undergrowth and majestic trees, and indeed redwood ring-width time series are relatively complacent (Roden 2008). However, stable-isotope time series produced substantial inter-annual variation (maximum from 2 to 4‰) indicating sensitivity to common forcing. The contrast between what ring widths cannot tell us and what tree-ring isotope ratios can tell us demonstrates the power of using stable-isotope analysis in dendroclimatology. That is, species and habitats that might be avoided from a ring-width perspective have the potential to provide valuable information using isotope variation. Ancient redwood trees could provide millennial scale tree-ring records, however crossdating cores from ancient trees could be problematic as they contain ring anomalies (Brown and Swetnam 1994). Extending ring-width or isotope time series into the distant past would require sampling entire slabs of downed redwood trees (or archival material) where multiple radii can be measured and ring anomalies followed around the circumference.

Our results also demonstrate that isotope time series satisfy the other requirement for use in dendroclimatology, that of coherence. Coherence between ring-width time series is at the heart of dating and chronology generation (Schweingruber 1987; Stokes and Smiley 1996). It is also critical

Figure 5. Mean (within site) latewood (A) and middlewood (B) $\delta^{18}\text{O}$ time series for tree-ring cellulose from redwood trees located at four sites. Both series were significantly correlated ($p < 0.01$, see Table 3).

for using ring widths for climate reconstruction as it is assumed that trees growing in close proximity ought to be influenced by the same environmental forcing (Fritts 1976; Cook and Kairiukstis 1989). The same is true for isotope time series and many studies have shown within-site and even between-site coherence in the stable-isotope variation in tree-ring time series (Leavitt and Long 1988, 1989; Leavitt *et al.* 1985; McCarroll and Pawellek 2001; Ramesh *et al.* 1985; Roden and Ehleringer 2007). Within-site coherence is to be expected, but it should not be assumed, as microenvironmental differences could have stronger influences than

larger-scale climate. Although some of the within-site correlations from this study were quite good ($r > 0.7$), they were far from perfect, indicating that individual tree microenvironments differ in how they produce “noise” in the correlations. In addition, isotope values are the result of not only environmental inputs but also within-plant fractionation events that can be influenced by plant anatomical and physiological attributes (*e.g.* stomatal conductance, Farquhar *et al.* 1982, 1989; Gessler *et al.* 2009). Within-site correlations of $\delta^{13}\text{C}$ time series may have been lower (and for the Prairie Creek site not significant) than for $\delta^{18}\text{O}$

Figure 6. Mean (within site) latewood (A) and middlewood (B) $\Delta^{13}\text{C}$ time series for tree-ring cellulose from redwood trees located at four sites. The latewood $\Delta^{13}\text{C}$ time series were significantly correlated ($p < 0.05$, see Table 3).

time series because carbon isotope fractionation is highly dependent on physiological attributes (e.g. photosynthetic rates and stomatal conductance). The lower values of EPS for $\delta^{13}\text{C}$ comparisons also indicate less confidence regarding common forcing for $\delta^{13}\text{C}$ than for $\delta^{18}\text{O}$ time series. Because our investigations did not focus on decoupling environmental from physiological impacts on the isotope ratios in the tree rings we investigated, we cannot address these issues here.

Our results also indicated that using statistical programs that detrend long-term variation is more important for testing coherence of carbon than for oxygen isotope time series. Correlation coefficients did not change much for $\delta^{18}\text{O}$ time series whether they were detrended (using COFECHA) or not. However, $\delta^{13}\text{C}$ time series can produce erroneous correlations unless corrected for changes in $\delta^{13}\text{C}$ of atmospheric CO_2 ($\Delta^{13}\text{C}$, see also McCarroll *et al.* 2009) or a program that eliminates low-frequency variation is utilized (e.g. COFECHA, Grissino-Mayer 2001). Thus, long

$\delta^{18}\text{O}$ time series that have not been detrended (and $\delta^{13}\text{C}$ if changes in atmospheric CO_2 are accounted for) from ancient redwood slabs have the potential to capture climate information at all temporal frequencies.

The strength of coherence did not substantially differ between latewood and middlewood for $\delta^{18}\text{O}$ time series. However, middlewood $\delta^{13}\text{C}$ time-series correlations were consistently lower than latewood $\delta^{13}\text{C}$ time series (Table 1). Roden *et al.* (2009) speculated that middlewood might be laid down in mid- to late-spring and may represent the clearest isotopic signatures for spring conditions because initial earlywood ring production can have substantial carry-over effects via the utilization of the previous year's carbohydrate from storage (Kagawa *et al.* 2005, 2006). It is possible that summer environmental conditions exert a stronger influence on carbon isotope fractionation than during spring when other factors (physiological) could play a more important role.

A novel feature of this study was to test isotopic variation in many trees along a transect in a single watershed. Isotope dendroclimatology studies that use locations with significant topographic features and potential geographic modification of environmental inputs (e.g. fog movement, drip, and ceiling height may be affected by orographic features) would benefit from developing sampling strategies based on such information. Our results suggest that topographic features do not significantly affect tree-ring cellulose $\delta^{13}\text{C}$ or latewood $\delta^{18}\text{O}$ values. However, middlewood $\delta^{18}\text{O}$ values were higher if the trees were located in the gully than if they were located on a slope above the gully. Whether this difference represents the incorporation of oxygen from a more enriched water source or is the result of increased evaporative enrichment in the gully is unknown at this time.

Significant correlations between latewood and middlewood $\delta^{18}\text{O}$ time series from four distinct sites that span a distance of over 300 km suggests that regional climate forcing influences the isotopic composition of redwood tree rings. This forcing may be related to conditions that modify annual hydrologic inputs that are isotopically distinct (i.e. precipitation *versus* fog, Aravena

et al. 1989; Ingraham and Matthews 1995; Dawson 1998) or that modify isotopic fractionation within the tree (*e.g.* humidity effects on leaf evaporative enrichment, Lipp *et al.* 1996; Roden and Ehleringer 1999b). The strong coherence of between-site $\delta^{18}\text{O}$ time series highlights their potential as proxy records that can be used for paleo-climate reconstruction. Other studies have also found coherence in isotope time series for multiple sites (Leavitt and Long 1988, 1989; Leavitt *et al.* 1985; McCarroll and Pawellek 2001; Roden *et al.* 2009).

The lower between-site correlations for $\delta^{13}\text{C}$ indicate that climate forcing may not be as regionally coherent for $\delta^{13}\text{C}$ as for $\delta^{18}\text{O}$ time series. Carbon isotope fractionation is primarily dependent on chloroplast $[\text{CO}_2]$ that is influenced by leaf-level supply (stomatal and mesophyll conductance) and demand (photosynthesis) functions (Farquhar *et al.* 1982; O'Leary *et al.* 1992). Regional climate factors such as fog frequency and intensity can influence $\delta^{13}\text{C}$ fractionation by increasing supply (via greater stomatal opening under high humidity) and reducing demand (lower light reduces photosynthesis). However, such simple climate drivers will be complicated by other factors and by microclimatic variation that can occur across sites and even within a single tree. For example, drought could modify stomatal set points, and changes in canopy position (tree fall gap) would influence light penetration. The idea that $\delta^{13}\text{C}$ values may be more dependent on micro-site variation than $\delta^{18}\text{O}$ values is also supported by the observation that absolute $\delta^{13}\text{C}$ values differed widely between proximate sites. Roden *et al.* (2009) also found absolute $\delta^{13}\text{C}$ values differed widely even between trees at the same site. Although absolute isotope values are not as critical as coherence in patterns of inter-annual variation for climate reconstruction, these differences imply that climate drivers impose variation onto a baseline level of isotope fractionation that depends on microclimate and tree physiological properties. Between-site correlations were improved if the furthest site (Sonoma) was excluded from the analysis, suggesting that sub-regional climate variations may be important for isotopic values within far northern California.

Thus, in order to effectively use $\delta^{13}\text{C}$ time series for climate reconstruction, replication is essential.

Significant correlations were also observed for the difference between latewood and middlewood isotope time series (Table 3). We have shown previously (Roden *et al.* 2009) that tree rings of redwood possess substantial intra-annual variability and coherent seasonal changes in $\delta^{18}\text{O}$ and to a lesser extent $\delta^{13}\text{C}$. For specific years these differences in $\delta^{18}\text{O}$ from spring to summer can be as high as 4‰ or as low as 0‰, and coherence between replicate trees within a site and between distant sites argues strongly that this variation is associated with regional climate forcing and may be another valuable proxy for climate reconstruction.

In Figure 7 the mean (relative) $\delta^{18}\text{O}$ values for all sites were plotted for latewood, middlewood and their difference to present a general 50-year pattern of isotopic variation. The latewood–middlewood results are absolute rather than relative values as they are already corrected for site differences in their formulation. Particular years containing significant excursions in either latewood, middlewood or their difference are marked with vertical lines to highlight inter-annual variability (Figure 7). For example, the difference between latewood and middlewood for 1983 and 1984 were identical and nearly 0‰, but latewood and middlewood $\delta^{18}\text{O}$ values for those years were quite different. Both 1970 and 1999 produced large differences between latewood and middlewood, but the cause in 1970 was highly enriched $\delta^{18}\text{O}$ in the latewood portion whereas in 1999 it was highly depleted $\delta^{18}\text{O}$ in the middlewood portion (Figure 7). This analysis demonstrates that seasonally resolved isotopic data has the potential to tease out interesting inter-annual differences that would be obscured if only the entire ring is analyzed. Such data provide the opportunity for a comparison between spring and summer climate variables to understand the driving force(s) for $\delta^{18}\text{O}$ (and $\delta^{13}\text{C}$) variation.

It is beyond the scope of this paper to present a detailed analysis of potential climate drivers for isotopic variation in redwood tree-ring cellulose. However, a number of climate features appear correlated with stable-isotope variation in red-

Figure 7. Mean (all sites) latewood–middlewood (A), relative latewood (B) and relative middlewood (C) $\delta^{18}\text{O}$ time series for tree-ring cellulose from redwood trees. Absolute values and deviations for latewood and middlewood $\delta^{18}\text{O}$ differed between sites, and so they were transformed to relative values (mean = 0) for statistical calculations. Time series are of mean values of the four sites and error bars indicate standard error. Vertical lines highlight years with significant excursions.

wood tree rings and show promise for climate reconstruction (Johnstone 2008). Precipitation, fog, atmospheric pressure, air temperature maximums and ocean temperature variation are all part of an integrated set of climate drivers (see Johnstone and Dawson (2010) for a full explanation) and thus isotope time series in redwood tree rings have the potential to capture this climate variation if appropriately applied.

In conclusion, strong within-site and between-site coherence in $\delta^{18}\text{O}$ time series for all segments (latewood, middlewood, and the difference between latewood and middlewood) indicates that common forcing of isotope fractionation in redwood tree rings is regionally coherent and not representative of local conditions only. Although redwood trees could provide long chronologies,

they have been underutilized by dendrochronologists because of issues with crossdating and climatic interpretation of ring-width variation. This is the first study to demonstrate that, by using stable-isotope analysis of tree rings, redwood trees have the potential to provide valuable proxy information about climate from this important region. Although significant correlations for $\delta^{13}\text{C}$ time series imply that regional climate information can be extracted from such records, they are also more influenced by local environmental conditions and potentially individual tree physiological traits. Thus, replication of $\Delta^{13}\text{C}$ time series would be required to improve the accuracy of climate reconstructions. Although site topographic factors were found to have minimal effects on regional climate forcing of redwood tree-ring isotopic composition, large differences in tree position (slope, aspect, proximity to streams *etc.*) should still be avoided as microsite differences may add some noise to the data.

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