An Investigation of the Physiologic Response of Ponderosa Pines to An Extreme Summer Precipitation Event with Stable Carbon Isotopes

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Abstract

In recent decades, a great deal of research has sought to define growing season and water source for ponderosa pine forests around the United States using stable carbon isotopic composition. These studies have focused primarily on developing models from multi-year datasets or environmental transects. We used stable carbon isotopic composition ($\partial^{13}C$) found in annual growth ring cellulose to examine seasonal precipitation's importance to growth, and better understand how an individual extreme precipitation event might be utilized for growth in ponderosa pine trees in Colorado's Front Range foothills. Spring precipitation, winter relative humidity, and summer relative humidity were all significantly correlated to $\partial^{13}C$ in latewood cellulose. Earlywood cellulose $\partial^{13}C$ was most correlated to combined winter and spring precipitation, and spring and summer relative humidity. The thousand year rain event that occurred in the study area in September 2013 did not manifest in isotopic values from 2013 growth rings, but the 2014 growth rings showed evidence of greater than expected water availability based on precipitation data. We suspect that water from the storm was stored at depth, and drawn upon by ponderosa pines through the 2014 growing season.

Background

Ponderosa pine, or *Pinus ponderosa* var *scopulorum (Engelm.)* forests are one of the dominant ecosystem types in the semi-arid foothills of Colorado's Front Range. Because these forests are seasonally water limited, they may be especially vulnerable to climate change and changing precipitation regimes (Thomas et al. 2009). Understanding the dynamics of *P. ponderosa* growth and water usage is crucial for anticipating how to manage these forests, which cover around 2.5 million acres of Colorado and share water resources with many of the most populated areas of the state (CSFS 2008).

Tree rings can provide an excellent record of the growth dynamics in trees, especially in conjunction with local climate data. Trees in temperate climates (including *P. ponderosa*) produce discrete annual rings, such that factors that control growth can be examined on an annual scale. The effects of climate conditions, including drought severity, temperature, and seasonal precipitation, on tree rings have been studied for decades (Stahle and Cleaveland 1988; Cook et al. 1987; Perkins and Swetnam 1996). The width of a tree ring indicates how much growth occurred in the vascular cambium of a tree within one year, so climate conditions such as water availability are represented in tree rings because they affect growth rate. Growth rates often change over the course of the year, resulting in distinct sections of individual annual ring. *P. ponderosa* rings are comprised of an earlywood component, built early in the growing season (spring) and a latewood component, built later in the growing season (early summer). Separating these components can allow for sub-annual resolution.

Stable carbon isotope compositions of annual tree rings have proven useful in assessing water availability and drought stress in trees (Adams and Kolb 2004; Roden et al.

2005; Sparks and Ehleringer 1997), and, more specifically, in exploring the seasonality of *P. ponderosa* growth and water usage (Leavitt et al. 2002; Roden and Ehleringer 2007). Cellulose, the primary component of wood tissue, in each latewood ring is built with carbon fixed that year (Jaggi et al. 2002). The isotopic composition of that carbon has the potential to act as a proxy for environmental factors like precipitation, relative humidity (RH), and temperature. Earlywood can contain some carbon fixed and stored from the previous season, but still provides a valuable indication of early season conditions (Jaggi et al. 2002). Carbon, once fixed in cellulose, is stable and its isotopic ratios do not change (Loader 2004). As a result, tree ring cellulose can record trees' response to climate conditions throughout the lifetime of the tree (Loader 2004).

Studies have correlated ∂^{13}C values in latewood with year round precipitation and summer monsoon precipitation (Leavitt et al. 2002; Roden and Ehleringer 2007, Barnard et al. 2012). However, analysis of ^{18}O (which provides information about water source due to the unique isotopic values of different spatial and temporal sources) in latewood cellulose and water sources suggest that *P. ponderosa* in the Western US predominately utilize winter water for growth year-round, and that the impacts of summer precipitation are limited to reducing vapor pressure deficit and water vapor lost through stomata by increasing water use efficiency (Kerhoulas et al. 2017; Kerhoulas et al. 2013; Koch and Mullin 2010). It is worth noting that studies performed in the Southwest (Arizona, New Mexico) are influenced by more consistent monsoonal precipitation than the site of this study, which is dominated by spring moisture, while Arizona can receive up to 70% of its annual precipitation during the summer monsoon (Roden and Ehleringer 2007

In coming years, the water resources on which *P. ponderosa* rely are likely to undergo changes. Rising temperatures due to climate change will likely result in less winter precipitation, earlier snowmelt, and more summer precipitation in much of the Western US, including the Colorado Front Range (Knowles 2006; Clow 2010). In addition, extreme precipitation events have increased in all US regions in recent decades, and are expected to continue to do so (National Climate Assessment 2014). While water accumulated during extreme snowfall events remains in storage until snowmelt, extreme rain events are associated with rapid runoff and flooding. In order to improve the understanding of how *P. ponderosa* will be impacted by a changing climate, it will be important to understand not only the seasonality of their growth, but also if and how they respond to increasing summer precipitation and extreme rain events. Such water sources may become increasingly important in a future climate regime with drier winters.

In September of 2013, more than 40cm of rain fell in eight days in Boulder County, CO. This 1,000-year rainfall event provided an excellent opportunity to examine the ecohydrological impacts of an extreme late-summer precipitation event on *P. ponderosa* forests. The extent to which trees are able to utilize moisture from such an event, and for how long following the event remains unclear. In this study, we measured stable carbon isotopes in tree rings to better understand the physiological response of *P. ponderosa* to the 2013 heavy rainfall. We focused on *P. ponderosa* in a single headwater catchment. In doing so, we created a record of carbon isotope composition, a proxy for physiologic response to water availability at annual and sub-annual timescales. In conjunction with extensive precipitation records, these data allowed us to (1) evaluate the relationship between climate conditions such as relative humidity and precipitation timing/quantity, and carbon discrimination, and (2) gain unique insight into the magnitude and duration of the physiologic response of *P. ponderosa* to an extreme late-summer precipitation event. We hypothesize that $\partial^{13}C$ of ring cellulose will be more negative, and indicate greater water available for growth, in years with wetter growing seasons, and that, following the 2013 rain event, it will remain more depleted than would be expected without the rain event through the 2014 growing season because subsurface storage of rainwater through the winter will increase water available for growth in the following year.

Stable Carbon Isotopes and Water Use Efficiency

Carbon in cellulose is fixed during photosynthesis from atmospheric CO_2 that enters leaves through pores called stomata. The stable isotopic composition ($\partial^{13}C$) of atmospheric CO_2 is approximately -8‰, calculated in parts per thousand based on an international standard, as follows.

$$\partial^{13}C = ([^{13}C/^{12}C]_{sample}/[^{13}C/^{12}C]_{standard} - 1) * 1000‰$$

C3 plants (including conifers) preferentially fix ^{12}C once CO_2 enters the leaf in a process called fractionation due to carboxylation. Fractionation due to carboxylation is the result of an enzymatic preference for ^{12}C over ^{13}C. Photosynthetic products are therefore depleted in ^{13}C, typically with a $\partial^{13}C$ of around -20‰ to -30‰ (Loader 2004). The rate of fractionation that occurs during photosynthesis is constant, and total depletion in ^{13}C is primarily controlled by the $\partial^{13}C$ of CO_2 within the leaf (Loader 2004). This internal $\partial^{13}C$ of CO_2 is a result of the rate of photosynthesis compared to rate of diffusion of CO_2 through stomata. When stomata are open and there is a high internal CO_2 concentration, there is greater discrimination against ^{13}C than when stomata are restricted and internal CO_2 concentrations are low, and more enriched in ^{13}C.

H_2O molecules are smaller than CO_2 molecules, so water vapor also escapes through stomata. Therefore, the primary reason plants reduce their stomatal conductance is to reduce moisture loss. When water availability is low, stomatal conductance is decreased, reducing both CO_2 concentrations in leaves and discrimination against ^{13}C during carbon fixation. Thus, in times of limited water availability, carbon fixed by the tree into sugars and eventually cellulose should have higher $\partial^{13}C$ values than in times of abundant water.

The reduction of stomatal conductance increases the intrinsic water use efficiency (WUE), or ratio of the rate of photosynthesis to stomatal conductance. High WUE is an acclimatization to conditions with lower water availability compared to demand. At higher WUE, more CO_2 is fixed per amount of water lost from the leaf through the stomata. Decreases stomatal conductance leads to lower internal CO_2 concentrations, which leads to an enrichment in ^{13}C. The result is lower overall discrimination against ^{13}C associated with greater WUE. Plant tissues built under conditions with low water availability compared to transpiration rates (water vapor lost during photosynthesis) are less depleted in ^{13}C (have less negative $\partial^{13}C$) due to higher WUE during photosynthesis (Adams and Kolb 2004). Changes in WUE as a response to environmental conditions can depend on several factors including species and topography (Adams et al. 2014).

Methods

Site Description

Samples were collected in Betasso Preserve, a study area in the Boulder Creek Critical Zone Observatory (CZO). Betasso is a tributary catchment to Boulder Creek, located in lower Boulder Canyon. Its elevation ranges from 1810 to 2024m above sea level and receives an average of 476mm of precipitation per year, about 32% of which falls as snow (Cowie 2010). Betasso represents the foothills ecosystem type, with forest composed primarily of pure *P. ponderosa*, and mixed P. ponderosa and *Pseudotsuga menziesii* stands.

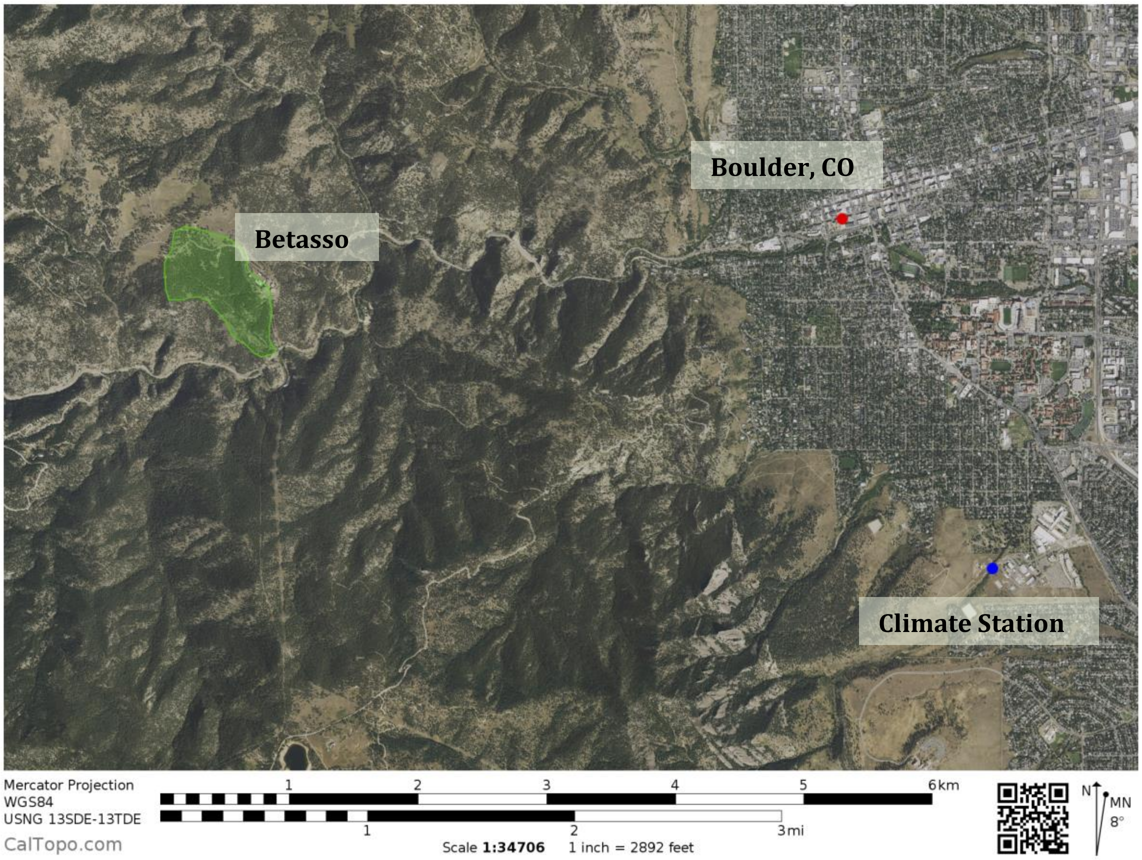

Figure 1: Map of study area and climate station. *Caltopo 2017*

Precipitation, Relative Humidity, and Groundwater

Precipitation and relative humidity (RH) data were acquired from High Plain Regional Climate Center site BOULDER, CO (elevation= 1672 meters, Figure 1). For correlation analysis with latewood ∂^{13}C, precipitation and RH were broken up by seasonal timing into water year (October-September), winter (October-March), spring (March-June), monsoonal summer (July-September), and combined winter and spring (October-June). We were interested in the importance of combined winter and spring precipitation because snow can contribute to precipitation totals throughout both seasons.

Because we were interested in how water may be stored between seasons, we examined groundwater data from long-term datasets maintained by the Boulder Creek CZO (Anderson and Rock 2017). Depth to water was measured using a datalogging pressure transducer in the groundwater well in Betasso.

Dendrochronology

Sample cores were collected in May 2015 from five trees. Two cores were collected at chest height (approximately 1.4m above ground surface) on opposite sides of each tree with a 12mm diameter increment borer. Cores were allowed to air dry, then were lightly sanded to improve visibility of rings and scanned to produce high-resolution color images. Ring widths were measured with WINDENDRO dendrochronology software. All cores were visually cross-dated using a master chronology developed from *P. ponderosa* of the central Front Range (Veblen et al. 2000). Specifically, 2012, 2006, and 2002 were used as marker years. Earlywood and latewood for each year were identified visually based on differing wood color and density, and cut from the core separately, using a dissecting scope and an EXACTO knife or microtome when possible. Individual samples from the two cores from each tree were combined together to increase sample mass and minimize the impact of any variability caused by differential growth within the tree such that, in total, two samples were produced from each tree for each year, one of earlywood, and one of latewood.

Stable Carbon Isotope Composition

We extracted holocellulose from whole wood samples for stable isotope analysis using methods adapted from Leavitt and Danzer (1993). Holocellulose is a preferred material in stable isotope analysis of tree rings because the carbon it contains is immobile and confined to the ring built in the year during which that carbon was fixed, while whole wood contains a variety of compounds, some of which are highly mobile (Loader 2004). Samples were run through a Soxhlet extraction process using 2:1 toluene to ethanol, then using only ethanol to remove resins and other non-polar compounds. Boiling samples in water removed water-soluble compounds, and bleaching samples in an acidic sodium chlorite solution removed lignin, leaving only holocellulose.

We weighed and analyzed the samples in two separate batches. Earlywood and latewood samples for years 2010-2015 from the Betasso plot were run on a continuous flow stable isotope mass spectrometer in the University of Wyoming Stable Isotope Facility. Samples of 2005-2009 growth rings were run at the CU Boulder Earth Systems Stable Isotope Lab using a Thermo Delta V mass spectrometer with continuous flow. Stable isotope values of a subset of samples analyzed at both facilities were significantly different ($p<0.01$), with the mean of the differences equaling 0.65‰. A basic offset correction of +0.65‰ was applied to data acquired from the University of Wyoming Stable Isotope Facility (years 2010-2015).

Data Analysis

All analyses were performed using statistical analysis code in R. Trees had different mean stable isotope compositions, likely due to variations in water usage associated with size or dominance (Barnard et al. 2012, Kerhoulas et al. 2013). Additionally, sample values from the same tree could not be considered independent. Therefore, correlations of isotopic composition as a function of environmental conditions were determined based on linear mixed effects models. Mixed effects model add a random intercept for a sample identity such as ‘tree’ (tree 1, tree 2, etc) that is recognized to affect the independent variable in a consistent way. For each environmental variable analyzed, a system of regressions were found in which the fit line of each tree was allowed to have a different intercept, but retain the same slope. Correlation statistics were then found based on this shared slope. Differences in Akaike’s information criterion (ΔAIC) were used to measure relative quality of models, with low ΔAIC indicating higher model quality. Models with ΔAIC of less than 2 were considered to be of equal quality. ΔAIC were determined separately for RH and precipitation models due to the differing sample sizes.

Results

Total annual precipitation for water year 2013 (847mm) was well above the mean of water years examined (mean=542mm, sd=114mm), but growing season precipitation (March-June) for the same year (232mm) was slightly below the average (mean=239mm, standard deviation, or sd=81mm). Conversely, annual precipitation for the 2014 water year (589mm) was slightly above average, while precipitation during the growing season of 2014 (223mm) was below average (mean=239mm, sd=81mm).

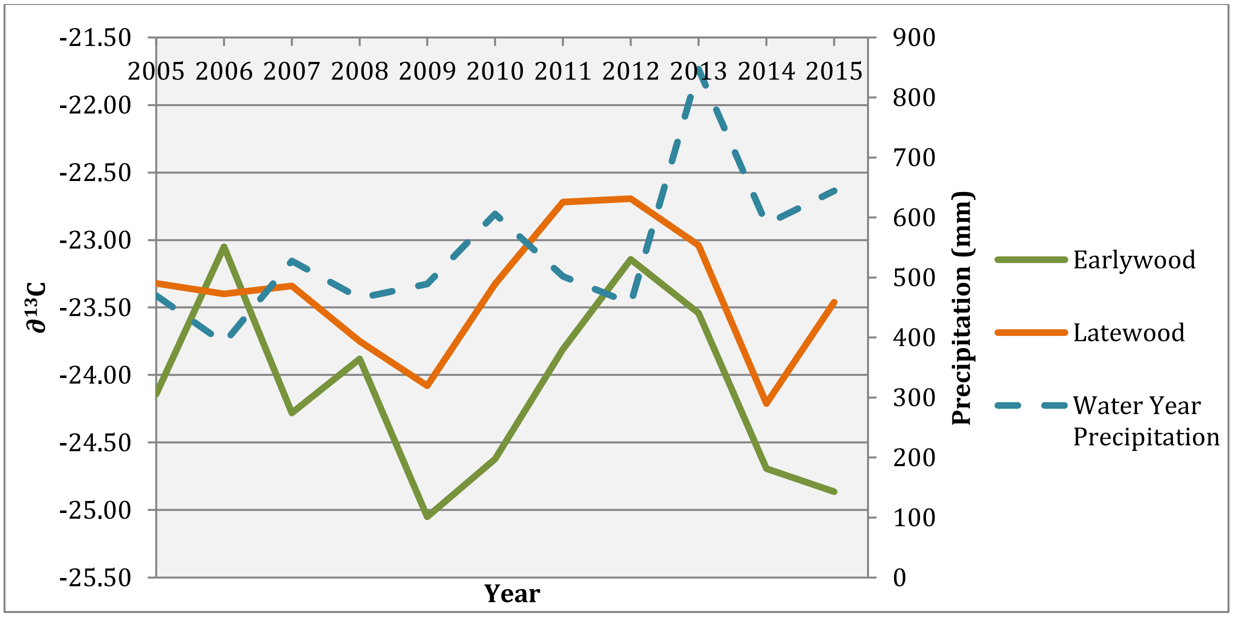

Figure 2: Time series of total water year precipitation and average earlywood and latewood isotopic composition for years 2005 through 2015 from Betasso.

At the Betasso groundwater well location, depth to groundwater is typically at its maximum, around 2700 cm, in March, prior to spring snowmelt. Immediately following the 1000-year rain event in 2013, the water table rose over 200 cm, and the water table remained elevated by 50 cm to 100 cm through the 2014 growing season.

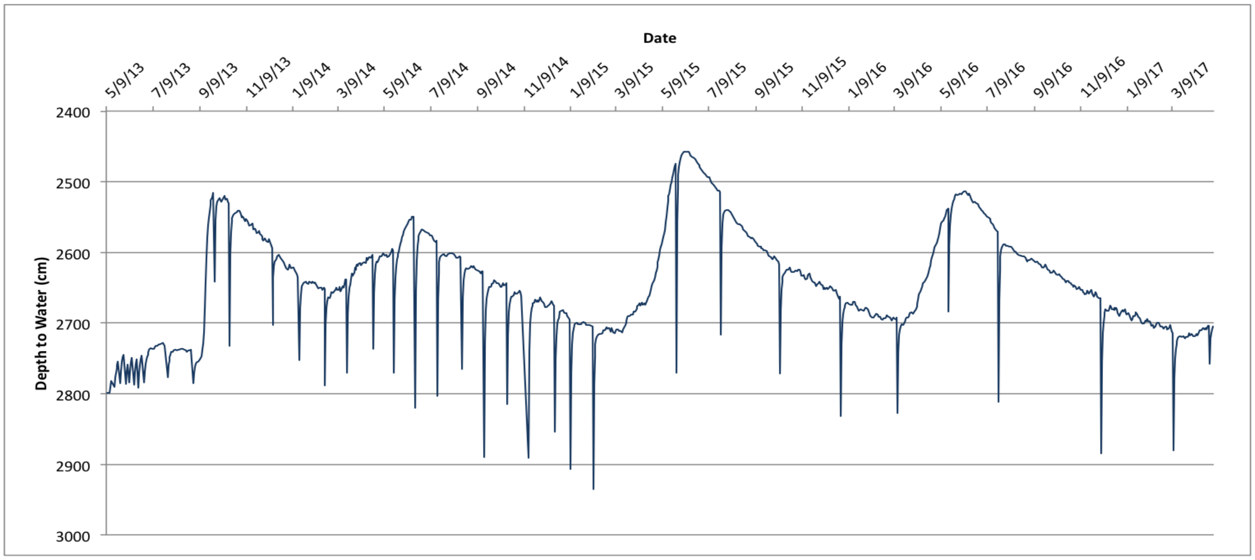

Figure 3: Time series of depth to water (cm) in Betasso. Intermittent large spikes are the result of the well being pumped down for sampling, and are not representative of the depth to groundwater.

Mean earlywood ∂¹³C was more negative than latewood ∂¹³C ($p<0.01$). ∂¹³C in 2013 growth rings did respond to the rain event in Septtember 2013. Neither earlywood nor latewood ∂¹³C from 2013 (averaged across trees) were notably negative, suggesting no sizable increase in water available for growth during the 2013 growing season. The second lowest mean ∂¹³C value in the earlywood time series and the lowest mean ∂¹³C value in the latewood time series are associated with the 2014 water year.

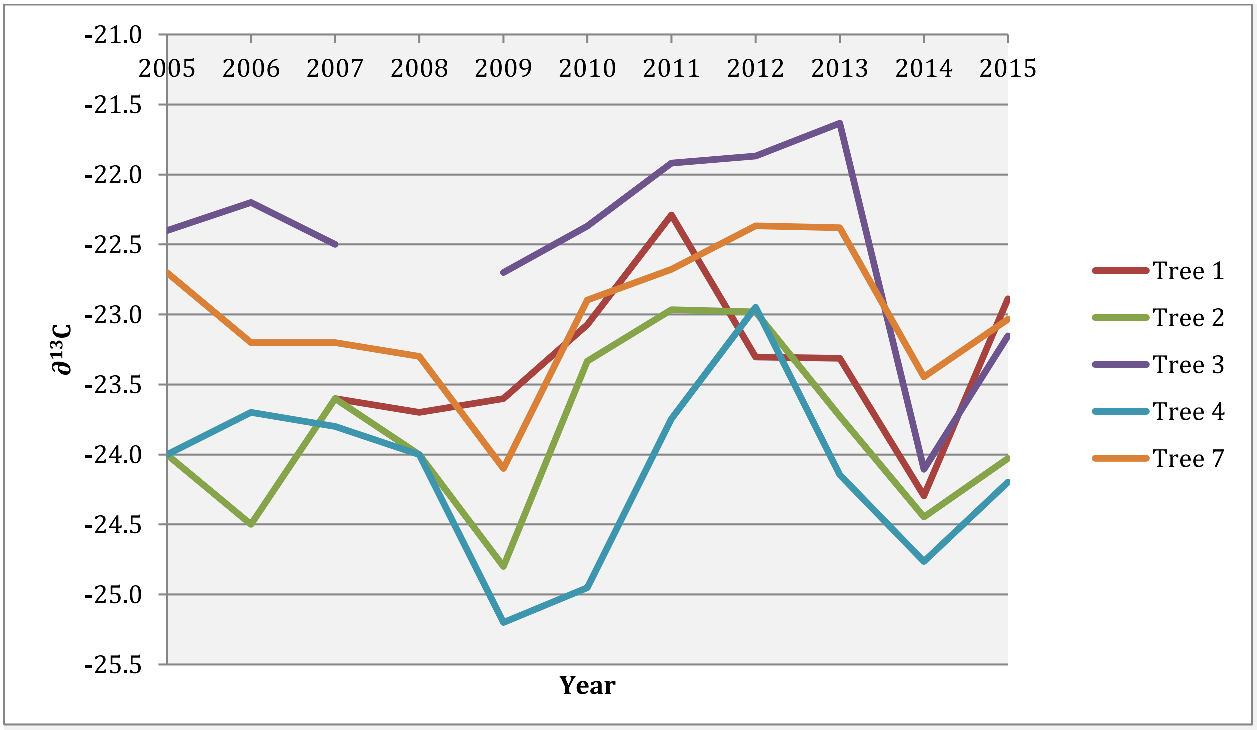

Figure 4: Time series of latewood isotopic composition for individual trees in Betasso

Of the precipitation periods tested, Betasso latewood ∂¹³C was only significantly correlated to spring precipitation, falling between March and June ($p=0.02$). Significant correlation was also found for winter ($p=0.019$) and summer ($p=0.026$) average RH. While earlywood ∂¹³C was not directly correlated with winter precipitation falling between October and March ($p=0.06$), the strongest models tested for precipitation were for the combined total of winter and spring precipitation ($p<0.01$). Earlywood $\partial^{13}C$ was also significantly correlated with precipitation and average RH for spring and summer. However, despite having a sufficiently low p-value, the ΔAIC for the relationship between earlywood $\partial^{13}C$ and summer precipitation is >10, indicating that this model is poor and lacks statistical support.

	Latewood		**Earlywood**	
Variable	P-Values	ΔAIC	P-Values	ΔAIC
WY PPT	0.88	0	0.23	27.56
Oct-Jun PPT	0.06	2.47	0*	0
Oct-Mar PPT	0.64	4.68	0.06	30.26
Mar-Jun PPT	0.02*	0.18	0*	5.86
Jul-Sep PPT	0.15	4.54	0.01*	29.5
Avg RH Oct-Jun	0.06	2.49	0*	4.54
Avg RH Oct-Mar	0.02*	0	0*	0
Avg RH Mar-Jun	0.13	4.59	0*	11.47
Avg RH Jul-Sep	0.03*	0.61	0.60	24.33

Table 1: P-values and ΔAIC values for liner mixed effects models of latewood $\partial^{13}C$ and earlywood $\partial^{13}C$ as a function of seasonal precipitation and average total RH. *Denotes significance at the $p<0.05$ level.

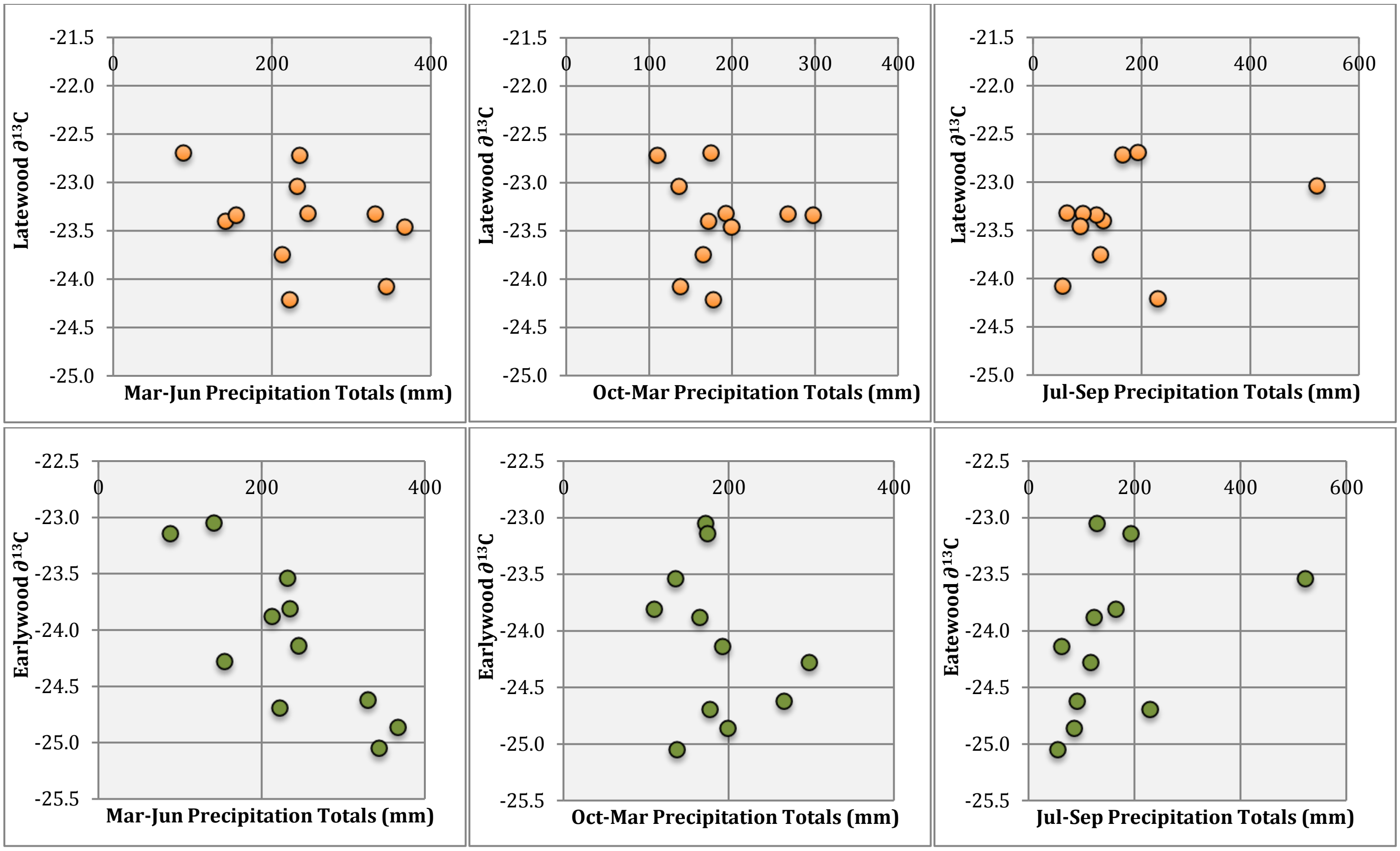

Figure 5: Mean latewood (orange) and earlywood (green) isotopic composition as a function of precipitation periods representing spring, winter and summer precipitation.

Residuals were plotted from models relating latewood ∂^{13}C to spring precipitation and earlywood ∂^{13}C to winter and spring precipitation. All residuals were relatively close to zero, with the exception of 2014 earlywood and latewood. These residuals had the largest absolute values observed. The residual for 2014 earlywood was -0.74 and 2.3 standard deviations from the mean of residual absolute values for earlywood. The 2014 latewood was -0.88, and 2.4 standard deviations from the mean of residual absolute values for latewood.

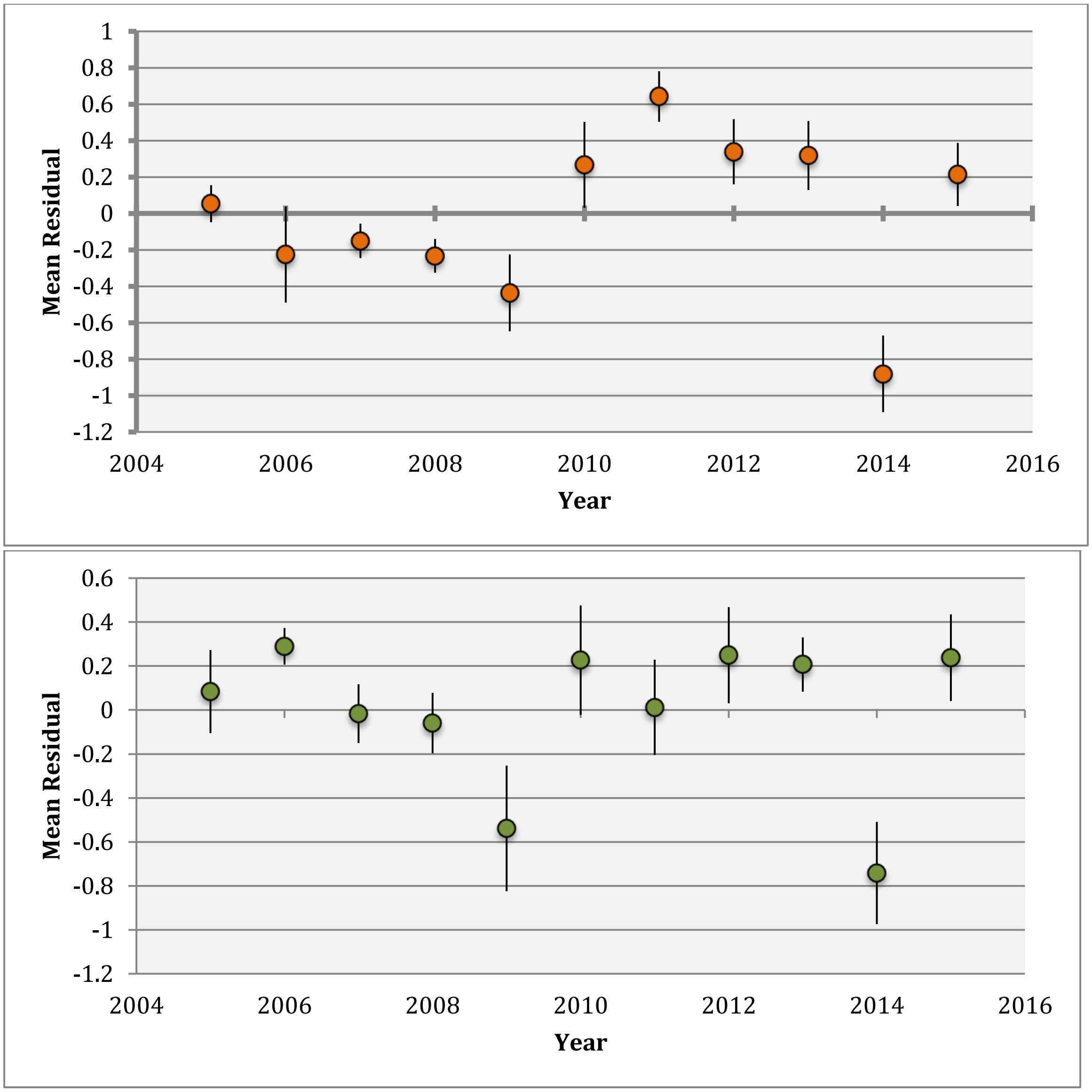

Figure 6: Mean residuals by year from a liner mixed effects model of Betasso latewood as a function of March through June precipitation (orange) and earlywood as a function of October through March (green).

Discussion

We confirmed that stable carbon isotope composition of earlywood and latewood from tree ring chronologies can act as a proxy for some environmental conditions. Spring precipitation was predictive of ∂^{13}C in both earlywood and latewood. Winter precipitation alone was not predictive, but winter and spring combined were the strongest correlation measured for earlywood ∂^{13}C. No other published studies were found that relate latewood

∂^{13}C to spring precipitation, but studies have found ring widths in the Colorado Front Range to correlate positively with spring precipitation (Adams et al. 2014; Veblen et al. 2000). Unlike other studies, we found no correlation between latewood ∂^{13}C and water year precipitation or summer precipitation (Leavitt et al. 2002; Roden and Ehleringer 2007; Barnard et al. 2012), nor did we find evidence of a correlation between winter precipitation and latewood ∂^{13}C, as was suggested by Kerhoulas et al. (2017).

Winter precipitation falling between October and March may not be as important for latewood growth in *P. ponderosa* in the Front Range at the elevation of Betasso, because such areas rarely hold a snowpack throughout the winter. In Boulder, CO, December, January, and February, are the driest months of the year, while April and May are the wettest, and still receive much of their precipitation as snow. While precipitation falling during the winter months is not a good predictor of growth, this does not mean that snow itself is unimportant, because much of the snowfall in the study site occurs in spring, rather than winter. Trees may not utilize winter precipitation for growth simply because it contributes a small fraction of the water available during the growing season to trees when compared to spring precipitation.

Interestingly, while neither winter nor summer precipitation were adequate predictors of ∂^{13}C in latewood, winter RH and summer RH were significantly correlated to latewood ∂^{13}C. As was suggested by Kerhoulas et al. (2017), the importance of summer RH may be attributable to the lowered vapor pressure deficit and higher water use efficiency associated with higher RH. In higher RH conditions, a smaller vapor pressure gradient between the leaf interior and the surrounding atmosphere decreases diffusion of water vapor from the leaf into the air, minimizing water loss. The physiological response of the plant is a reduction in WUE, so, much like decreased water availability, high vapor pressure deficits results in decreased stomatal conductance (McDowell et al. 2008), and increases ∂^{13}C. Overall, these findings suggest that while spring precipitation is a more important predictor for late season *P. ponderosa* growth than summer precipitation, the growing season may extend well into the summer.

The primary focus of this study, the extreme precipitation event in September 2013, occurred well outside the spring water season. Given this, it is unsurprising that we did not find clear isotopic evidence of increased water availability until the 2014 growing season. 2013 latewood isotopic composition (-23.04) was less negative than the mean (mean= -23.39), which is the opposite of what would be expected if growth continued into September as there was very high water availability during the 2013 flood. Carbon in latewood and earlywood formed during the 2014 growing season were the most, and second most, respectively, depleted of the years studied. ∂^{13}C in earlywood and latewood were also more negative than would be expected based on linear mixed effects models for ∂^{13}C and spring precipitation, with largest residuals observed for said models. Based on this evidence, we suspect that some water from the extreme September 2013 precipitation event was stored through the winter and into the 2014 growing season when *P. ponderosa* trees were able to utilize it for growth.

Hydrological data suggest that water from the September, 2013 event may have been stored at depth. Water tables rose in Betasso by amounts similar to those seen during spring snowmelt. Importantly, the water table remained higher than would be expected without the September precipitation event through the following growing season. In porous soils *P. ponderosa* typically root to depths of greater that 2 m, with roots observed at depths up to 12 m in fractured bedrock (Oliver and Ryker 1990). The depth from which *P. ponderosa* draw water for growth is not entirely clear and likely site dependent, but Brooks et al. (2002) found in a Pacific Northwest ponderosa pine forest that only 18-30% of summer soil moisture depletion in the upper 2m of soil occurred in the upper 60cm. Groundwater depths at the Betasso well exceeded these depths, but the well is located higher in the catchment than the sampled plot, where depth to groundwater may have been smaller. Without more direct measurement, it remains unclear whether the sampled trees could have had access to groundwater.

Conclusion

Stable carbon isotopic analysis suggests that the extreme summer precipitation event in September 2013 resulted in increased water availability the following year for ponderosa pine trees in the catchment sampled in this study. Latewood built in 2013 did not have anomalously negative ∂^{13}C, as growth likely ceased before September, but latewood from 2014 did. In general, summer precipitation like the 2013 event was not predictive of latewood ∂^{13}C for that year, as spring precipitation was the dominant water source for *P. ponderosa* growth. This suggests that moisture received in September is not utilized for growth in these trees, unless an event is sizable enough to be stored as deep soil moisture of recharge groundwater until the following growing season. Based on these findings, a shift towards more summer precipitation and less winter and spring precipitation may result in less water available to ponderosa pines for growth, unless the summer precipitation events are sufficiently intense to induce deep infiltration and increase storage through the following growing season.

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