

EXPLORING THE ROLE OF WATER IN TREE GROWTH
AND WHAT TREES CAN TELL US ABOUT THE
HYDROCLIMATE OF THE PAST

by

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CHAPTER ONE

INTRODUCTION

The relationship between climate and tree growth is a well-established and important tenet shaping current, past, and future perspectives of both forest growth dynamics and climate. Indeed, the entire scientific field of dendrochronology and its invaluable contributions to ecological, archeological, and climatological knowledge rest on the premise that climate imparts a common control on growth in trees of a given region via modulation of the most limiting factor or factors for growth (Fritts, 1976). Tree growth dictates not only the structure and function of ecosystems and landscapes worldwide but also exerts a primary control over the global carbon cycle via formation of the largest above ground terrestrial sink for long-term carbon sequestration through the process of xylem tissue formation (xylogenesis)

In arid and semi arid regions worldwide, water is a primary control on tree growth, as highlighted by the strong correlations between tree ring width and regional moisture conditions over annual to centennial time scales (Cook *et al.*, 2007, 2010; Stahle *et al.*, 2016). As trees grow, the spatial and temporal patterns of water availability resulting from climate dynamics at various scales are reflected in the radial growth of trees and ultimately recorded in the annual growth rings that develop in extra-tropical trees around the world. However, the physiological nature of how water actually limits the radial growth of trees remains uncertain (Körner, 2015). This is because physiological mechanisms controlling radial growth are well hidden, occurring *beneath*

the very tissues (phloem) that transport carbohydrates for growth.

Interestingly, factors that control xylem tissue development in non-woody plants, principally xylem water potential (Ψ_x), were relatively well understood in the laboratory as early as the 1980's (Boyer *et al.*, 1985; Nonami & Boyer, 1989, 1990). However, efforts to expand this understanding have been largely overshadowed by a carbon-centric view of plant growth limitation fostered by simultaneous advances in the measurement of leaf-level gas exchange in plants used to understanding the factors that limit photosynthesis (Körner, 2015). As such, few recent studies have focused on the role of Ψ_x in xylem tissue growth and, with a few exceptions (Steppe *et al.*, 2006; Zweifel *et al.*, 2016), fewer still have investigated the process in trees.

Here, we revisit the role of water potential in tree growth control using a field-based approach to exploring the role of soil moisture supply and atmospheric moisture demand on tree water potential and subsequently, growth. We explore how limitation in tree radial growth can be well predicted by local hydrometeorological conditions and associated tree water potentials, and observe that such limitation occurs under conditions that are considerably more mesic than those associated with the onset of photosynthetic limitation resulting from stomatal regulation (Martin *et al.*, 2017). While direct observation of tree xylem growth and growth limitation remains a very challenging problem, our findings provide strong evidence for the role of Ψ_x in the regulation of tree radial growth in dry environments.

An equally challenging obstacle to understanding the linkages between tree growth and water availability is determining where the water that trees use for growth

actually comes from (Harpold *et al.*, 2015). In a general sense, trees source water from soil moisture that is recharged by precipitation. However, precipitation patterns often vary across seasons, and in much of the American West, the primary season for precipitation (winter-spring) and soil moisture recharge (early spring) are somewhat out of phase with the primary season for tree growth (spring-summer) (Pyke, 1972). As such, many western forests are heavily reliant on precipitation that falls prior to the primary growing season for a large portion of total annual growth (Roden & Ehleringer, 2007; Hu *et al.*, 2010; Trujillo *et al.*, 2012). Because one of the most prominent features of observed climate change in the American West has been an advancement in the timing of spring conditions (Cayan *et al.*, 2001; Stewart *et al.*, 2005), developing a better understanding of how the timing of moisture delivery and tree growth relate is an important research goal.

Using a field-based study carried out over three years in western Montana, we quantified the timing and magnitude of moisture delivery to a forest ecosystem, and coupled this to isotope-based observations of where in the soil profile trees sourced water from as well as the seasonal evolution of radial growth. This allowed us to estimate the importance of winter precipitation relative to summer rains for growth in trees over the growing season. This work establishes a baseline understanding of how temporal dynamics of moisture delivery to forests and tree growth relate in time and can help guide our understanding of how ongoing changes to climate conditions may affect tree growth in the future.

The study of tree growth enjoys a broad familiarity amongst the general public

that is often lacking in many technical fields of science in that many people understand, and are fascinated by the patterns of tree growth that are recorded in annual rings. Fewer people however, realize these patterns hold a wealth of information about climate conditions that serve as an invaluable record of annually resolved climate histories that help place current observations in a long-term context (Fritts, 1976). Over the last several decades, tree-rings have been used extensively to reconstruct past climate across much of the American west and have greatly improved our understanding of long-term patterns of temperature, precipitation, snow pack, and streamflow in the region (Stine, 1994; Cook *et al.*, 2004; Woodhouse *et al.*, 2006, 2010; Stahle *et al.*, 2007; Pederson *et al.*, 2011; Anchukaitis *et al.*, 2017). As rising air temperatures and growing populations place increasing demands on existing water supplies efforts to understand long-term patterns of variability in hydroclimate in particular, have been received increased attention across the west in recent years (McCabe & Wolock, 2007; Pederson *et al.*, 2013; Griffin & Anchukaitis, 2014; Woodhouse *et al.*, 2016). However, it is interesting to note that to date, the United State's largest river basin, the Missouri river, has remained largely uncharacterized in this way.

In order to better understand the hydroclimatic dynamics of the Missouri river, we developed a network of tree ring based reconstructions of streamflow spanning 1200 years for every major tributary across the mountain headwaters of the Missouri river. We examined the history of basin-wide drought events evident in the tree ring record in the context of reconstructed temperature and explored how the relationship between temperature and streamflow has changed over time. As a result, it is evident that rising

temperatures create new challenges for water managers and users in the Upper Missouri River Basin that are likely to increase as temperatures warm in the future.

While understanding and utilizing patterns of tree growth in nature is a highly complex and difficult endeavor, it is one that continues to offer many intellectual rewards and is arguably of growing importance as forests around the world are increasingly subjected to the increased stresses of accelerating climatic change (Williams *et al.*, 2013, 2015). To this end, the findings reported here provide an incremental step forward in our understanding of a diverse set of topics pertaining to the growth of trees and the relationship between tree growth and climate.

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CHAPTER TWO

HYDROMETEOROLOGY ORGANIZES INTRA-ANNUAL PATTERNS OF TREE GROWTH ACROSS TIME, SPACE, AND SPECIES IN A MONTANE WATERSHED

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HYDROMETEOROLOGY ORGANIZES INTRA-ANNUAL PATTERNS OF TREE GROWTH ACROSS TIME, SPACE, AND SPECIES IN A MONTANE WATERSHED

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Summary

- Tree radial growth is often systematically limited by water availability, as is evident in tree ring records. However, the physiological nature of observed tree growth limitation is often uncertain outside of the laboratory.
- To further explore the physiology of water limitation, we observed intra-annual growth rates of four conifer species using point dendrometers and microcores, and coupled these data to observations of water potential, soil moisture, and vapor pressure deficit over two years in the Northern Rocky Mountains, USA.
- The onset of growth limitation in four species was well explained by a critical balance between soil moisture supply and atmospheric demand representing relatively mesic conditions, despite the timing of this threshold response varying by up to two months across topographic and elevation gradients, growing locations, and study years.

- Our findings suggest that critical water deficits impeding tissue growth occurred at relatively high water potential values, often occurring when hydrometeorological conditions were relatively wet during the growing season (e.g. early spring in some cases). This suggests that species-specific differences in water use strategies may not necessarily affect tree growth, and that tissue growth may be more directly linked to environmental moisture conditions than might otherwise be expected.

Key words: growth, hydraulic limitation, moisture supply and demand, soil moisture, soil plant atmosphere continuum, tree, water potential, vapor pressure deficit

Introduction

That climate and tree growth are often tightly linked is a well-established and important principle shaping current, paleo, and future perspectives of both forest productivity (via modeling) and climate (via tree-ring based paleo-climate reconstructions). In arid and semi-arid regions worldwide, strong correlations between tree ring width and regional moisture conditions over annual to multi-decadal time periods highlight the role of water as a primary control on tree growth (Cook *et al.*, 2007, 2010; Stahle *et al.*, 2016). Water and plant growth are inextricably linked through transpiration and photosynthesis, with terrestrial productivity often being highly controlled by water availability (Rosenzweig, 1968; Biederman *et al.*, 2016). Trees act as

conduits for moisture transport from Earth's surface to the atmosphere with plants as a whole accounting for up to 64% of global evapotranspiration (Good *et al.*, 2015).

The general effects of climate on tree growth have been understood for centuries; however, the physiological mechanisms controlling radial growth are well hidden, occurring *beneath* the very tissues (phloem) that transport carbohydrates for growth. The tree rings that record this climate-growth relationship form via the process of xylogenesis. This includes cell division, cell expansion, and deposition of cell wall material (Lambers *et al.*, 2008). While cell division does not lead to an appreciable size increase (Green, 1976), cell expansion may account for at least 80% of the size increase ultimately manifested as ring width. Deposition of cell wall material likely accounts for the majority of biomass added, but accounts for little size increase (Cuny *et al.*, 2015). While views on the role of cell division in growth continue to evolve (Beemster *et al.*, 2003), here we focus only on the size increase associated with cambial cell expansion (hereafter simply 'growth') while acknowledging that both cell division and expansion ultimately facilitate growth (Zahner, 1968).

Water limitation can influence radial growth via negative tensions generated in the xylem. General theory holds that newly divided cambial cells expand at a rate proportional to the difference between turgor pressure (Ψ_p , MPa) and the minimum turgor required for cell wall extension (Y , MPa) (Lockhart, 1965), although the process of expansion is further moderated by other factors including cell wall flexibility (Pritchard, 1994), biochemical signaling (Davies & Zhang, 1991), solute production (Michelena & Boyer, 1982), and the supply of water to developing tissues (Boyer *et al.*, 1985). During

transpiration, water is moved upward from the soil and from within-tree storage reservoirs to the atmosphere, with the continuum maintained via capillary forces and cohesion between water molecules as water in the xylem replaces water lost from leaves (Dixon & Joly, 1894; Pickard, 1981; Steppe *et al.*, 2006). This process is counterbalanced by gravity and by resistances within the xylem itself, generating negative hydrostatic pressure (tension) in the xylem stream, termed xylem water potential (Ψ_x). Under conditions of low water availability, the supply of water is likely the most important factor for cell expansion because of its direct role in maintaining Ψ_p greater than Y in cells that are simultaneously expanding due to cell wall loosening. This hypothesis is supported by laboratory observations of immediate cessation of cell expansion in response to decreased Ψ_x even when Ψ_p of expanding cells is fully maintained (Boyer *et al.*, 1985; Nonami & Boyer, 1989, 1990).

In nature, Ψ_x is almost constantly changing due to variations in transpiration (Kaufmann, 1976) and can routinely reach highly negative pressures inducing stomatal regulation of Ψ_x to prevent cavitation (Sperry *et al.*, 1996; Sparks & Black, 1999). Both theory (Boyer & Silk, 2004) and modeling effort (Steppe *et al.*, 2006) suggest a tight linkage between Ψ_x and cambial cell expansion and hence, growth. Mechanistically, Ψ_x should influence growth via the inhibition of cambial cell expansion by negative pressures present in adjacent xylem tissues (low Ψ_x), and evidence suggests that levels of Ψ_x that inhibit cell expansion are substantially less negative than those typically associated with the onset of stomatal regulation (Körner, 2015). This suggests that at least in the early stages of drought, trees may consistently prioritize carbon uptake over

growth by leaving stomata open at the expense of growth (which is inhibited by falling Ψ_x), thus leading to a decoupling of the two processes (Muller *et al.*, 2011).

In this study, we explore how low soil moisture supply and/or high atmospheric demand limits growth rates in four conifer species across a watershed. Furthermore, we explore if the growth response of trees to moisture supply and demand may be predictable and consistent across a range of species and hydrometeorological conditions. We report the findings of a field-based study aimed to address the following objectives:

- To quantify the relationship between radial growth, soil moisture supply, and atmospheric moisture demand.
- To compare our findings to existing evidence for how water potential (Ψ) controls radial growth.
- To determine the consistency of these relationships across environmental gradients and among different tree species.

Materials and Methods

Study design and sampling

This study was conducted over the 2014 and 2015 growing seasons at the Lubrecht Experimental Forest in western Montana, USA, in a mixed coniferous forest of the Northern Rockies. Four sites were selected within smaller sub-catchments of the North Fork Elk Creek watershed to capture hydrometeorological variation from high (c.1750 m ASL) to low (c.1400 m ASL) elevations as well as across North, South, and West facing aspects. Soil types within the study area ranged from gravely loamy sands to gravely sandy loams although soils are heterogeneous even within sites due the

complexity of the mountainous terrain and the variability of soil depths (NRCS, 2017). One site was omitted from the analysis due to severe canopy defoliation by western spruce budworm (*Choristoneura occidentalis*) during both study years. Within each site, we sampled trees representing differing topographic positions; we selected four trees from convergent, hollow locations and four trees from more divergent slope locations (Table 1.1), with tree selection dictated by the proximity to a central data-logger. Tree species sampled included Douglas fir (*Pseudotsuga menziesii* var. *glauca* (Mayr) Franco), ponderosa pine (*Pinus ponderosa* P. & C. Lawson), western larch (*Larix occidentalis* Nutt.), and Engelmann spruce (*Picea engelmannii* Parry ex. Engelm). We measured stem radii using two point dendrometers installed at breast height on each of 24 trees for a total of 48 sensors in the study (see Wang & Sammis, 2008 for dendrometer design and calibration details). Stem radius readings were logged using CR1000 data-loggers (Campbell Scientific Inc., Logan, UT). Central to each topographic grouping of trees, we recorded air temperature and relative humidity with a VP3 temperature and humidity sensor, and soil volumetric water content (VWC_{soil}) at 50 cm depth using 5TE sensors and EM50 data-loggers (Decagon Devices Inc., Pullman, WA).

All trees were sampled for cellular analysis of growth to compare against automated measurements of stem radius from dendrometers. During 2015, a total of 216 microcores were collected at bi-weekly intervals from near the dendrometer on each tree. Microcores were then fixed, embedded in paraffin, and sectioned to a thickness of 8 μm for microscopic analysis of developing cells (Rossi *et al.*, 2006a).

Table 1. Study trees

site	species	topographic position	dbh [cm]
Driest	Douglas fir	hollow	26.20
	Douglas fir	hollow	38.20
	Douglas fir	slope	31.00
	Douglas fir	slope	35.80
	ponderosa pine	hollow	43.00
	ponderosa pine	hollow	56.30
	ponderosa pine	slope	24.40
	ponderosa pine	slope	42.10
Intermediate	Douglas fir	hollow	50.40
	Douglas fir	hollow	56.00
	Douglas fir	slope	32.00
	Douglas fir	slope	36.80
	western larch	hollow	27.60
	western larch	hollow	38.10
	western larch	slope	29.00
	western larch	slope	56.90
Wettest	Douglas fir	hollow	52.50
	Douglas fir	hollow	64.60
	Douglas fir	slope	22.20
	Douglas fir	slope	24.50
	Englemann spruce	hollow	56.50
	Englemann spruce	hollow	67.20
	Englemann spruce	slope	22.10
	Englemann spruce	slope	78.10

In all species except western larch, we measured predawn and midday stem water potential, Ψ_{pre} and Ψ_{mid} (MPa), three times in 2014 (June, July, and August). For each tree, the tip of a sunlit branch was cut with a pole pruner and inserted into a pressure chamber (Model 600, PMS Instrument Co., Albany, OR) (Scholander *et al.*, 1965). Because we did not measure water potentials in western larch, this species was excluded from all analyses incorporating water potential measurements.

Estimation of growth

All analyses were constrained to the ‘growing season’, defined as a period of 140 days beginning May 4th in 2014 and April 15th in 2015. For each year, this time interval visually captured the period of cambial cell expansion in all trees evident from the dendrometer records and supported by observations of xylogenesis using microcores.

We estimated seasonal growth curves from dendrometers in individual trees from all-time daily radius maxima. Growth estimates made at daily maxima generally provide an accurate estimate of growth provided that no underlying water deficit in the tree simultaneously limits stem radius. Of concern was the effect that cumulative tree water deficits could have on the estimation of seasonal growth over time. To address this, we compared growth curves estimated from dendrometers to observations of xylogenesis made using microcores. Because we were only able to collect microcores for half of the 2014 season, this analysis was restricted to the 2015 growing season.

We found stem radii measured from thin sections of microcores (μm) to correlate with radii measured with dendrometers (μm) ($r = 0.89$ and a slope of 1.27 with dendrometers consistently overestimating stem radial increments). This is consistent with the fact that the dendrometers measure newly formed xylem and phloem cells while we quantified only new xylem cells using microcores. We assessed whether cumulative water deficits affected the relationship between dendrometers and microcores over time by comparing the fit of linear and quadratic models relating the two measurements. We reasoned that a linear relationship between dendrometers and microcores reflected a consistent relationship between the measurements, while a curved relationship, caused by

cumulative water deficit in the stem over time, reflected a divergence between the two measurements. In all cases, we found a consistent linear relationship over the growing season. An exception to this was the observation that at the very start of the growing season, some radii increased a small amount before xylogenesis was observed in microcores.

Quantification of moisture supply and demand

Using the half-hourly measurements of air temperature and relative humidity, we quantified the evaporative demand of the atmosphere as vapor pressure deficit, (VPD, kPa):

$$\text{VPD} = e_{(T)} - e_{(T)} * \text{RH} / 100 \quad (\text{Eqn. 1})$$

where $e_{(T)}$ is the saturation vapor pressure at air temperature T (K) and RH (%) is relative humidity. Following (Tetens, 1930) $e_{(T)}$ was calculated as

$$e_{(T)} = 0.6108 * \exp[17.27T / (T+237.3)]. \quad (\text{Eqn. 2})$$

We estimated moisture supply as the volumetric water content of soil (VWC_{soil}) at a depth of 50 cm.

In addition to stomatal regulation, Ψ is strongly controlled by the moisture gradient resulting from the difference between soil moisture supply and atmospheric demand (VPD) (Dixon & Joly, 1894; Scholander *et al.*, 1965). Here we utilize a simple proxy for the combined influence of soil moisture supply and atmospheric demand on the soil-atmosphere system termed the Hydrometeorologic Dryness Index (HDI, $\text{kPa m}^{-3} \text{H}_2\text{O m}^3 \text{soil}$) and defined as:

$$\text{HDI} = \text{VPD} / \text{VWC}_{\text{soil}} \quad (\text{Eqn. 3})$$

Here, VPD captures the atmospheric demand for moisture by quantifying the absolute water concentration difference between the leaf and the atmosphere, with the tree's ability to maintain turgor depending on its moisture supply (soil water). Thus, HDI modifies the demand term (VPD) by dividing it by a measure of soil moisture (VWC_{soil}) to reflect the increasing difficulty for the tree to maintain turgor with decreasing soil moisture.

Previous authors have applied an Ohm's Law approach to link hydrometeorology to plant water relations (e.g. Steppe *et al.*, 2006). In this context, surface to atmosphere flow of water is proportional to a water potential difference between soil and atmosphere divided by the total resistance to flow along the soil-plant-atmosphere continuum. However, data needed to quantify flow, the surface-atmosphere water potential difference, and other resistances present in the flow-path are not trivial to collect, especially in a field study. While HDI does not replace a mechanistic model such as an Ohm's law analogy for quantifying components of the complex soil-plant-atmosphere-system, its component data are relatively easy to collect and serve as a simple proxy for water-flow through the soil-plant-atmosphere continuum. As conditions dry, an increasing atmospheric moisture demand is met by a decreasing soil moisture supply, which leads to an exponential increase in HDI and drives Ψ more negative in trees. It is important to consider that because soil moisture supply is partly a function of soil water retention characteristics in addition to moisture content, observed relationships between Ψ and HDI may be soil-specific. In addition, stomata also act to regulate Ψ and increasingly limit the influence of HDI on Ψ as conditions dry. Because stomatal

responses vary by species, we assessed species-specific relationships between Ψ and HDI.

To provide a general visualization of the topographic and spatial variability of HDI, we related observed soil moisture to the topographic wetness index (TWI) (Beven & Kirkby, 1979), elevation (m), and summer solstice solar insolation (W m^{-2}) (Bird & Hulstrom, 1981; Corripio, 2014) and related VPD to elevation at each of eight micro-meteorological stations in the watershed by multiple/linear regression. We then calculated HDI for each grid cell in the watershed using a ten-meter digital elevation model (Fig. 1.1). Over both growing seasons, modeled VPD, VWC_{soil} , and HDI described an average of 91.0%, 20.0%, and 73.3%, respectively, of the spatial variation in observed values of VPD, VWC_{soil} , and HDI on a daily basis. While the spatial variability in VPD was well explained by elevation alone, the variability in soil moisture present across the complex topography of the study area was more difficult to model.

We categorically defined the three different study sites within the watershed as “dry”, “intermediate”, and “wet” based on the observed seasonal average value of HDI at each site (Fig. 1.2). The driest site was lowest in elevation and faced predominantly south, while the intermediate site was slightly higher in elevation and faced predominantly northwest, and the wettest site was highest in elevation and faced predominantly southwest.

Extraction of low frequency signals from time series data

Both stem radius and HDI time series were extremely noisy over daily intervals as both reflect diurnal swings in microclimatic conditions and weather. While it is unclear

at exactly what frequency the mechanics of growth respond to hydrometeorology, our aim was to generally quantify this response over the course of the growing season. To extract the low frequency features of each time series, we applied a low-pass filter to both HDI and stem radius using a cubic smoothing spline implemented in R (R Core Team, 2013) using package *dplR* (Cook & Kariukstis, 1990; Bunn, 2008).

We filtered stem radii time series with the most flexible spline possible that resulted in a single inflection point in the annual growth curve of each tree. The form of each resulting time series generally approximated the Gompertz function commonly used to fit annual tree growth curves (Zeide, 1993; Rossi *et al.*, 2006b). This process facilitated the calculation of growth rate (stem radius increment, SRI, $\mu\text{m day}^{-1}$) curves with a single local maximum over the growing season (Fig. 1.3). The minimum period necessary to produce a filtered growth curve with a single inflection point ranged from 27 to 119 days over all trees and both study years.

In choosing a low-pass filter to smooth the HDI time series, we sought to match the frequency used to filter stem radii time series. To minimize subjectivity in the process of filtering HDI, we generated 100 different filtered HDI time series with spline periods ranging from 5 to 105 days. This centered the range of periods on the mean period used to filter all radii, which was 55 days, and which we used for further analyses. We then quantified the amount of uncertainty associated with the estimation of HDI resulting from the smoothing process alone (horizontal error bars, Fig. 1.4, d).

Calculation of growth rates (SRI), maximum growth (SRI_{max}), and HDI_{crit}

We quantified growth as the observed stem radius increment (SRI) from filtered stem radius time series where growth is greater than zero only when the maximum stem radius achieved in a given day is greater than the all time previous maximum (Zweifel *et al.*, 2016). In order to estimate daily SRI from growing season stem radius curves, we calculated the discrete derivative of filtered stem radius time series as:

$$SRI = \text{radius}^t - \text{radius}^{t-1} \quad (\text{Eqn. 4})$$

Where, SRI is the change in radius from time $t-1$ to time t in units of $\mu\text{m}/\text{day}$ (Fig. 3a). Because we filtered each stem radius time series to contain only one inflection point, its derivative contained only one local maximum (Fig. 1.3b). We interpreted this maximum value of SRI as the maximum daily growth rate (SRI_{max}) observed during the growing season with all values of SRI following this maximum representing the ‘growth limitation’ phase of the SRI time series.

In order to estimate the hydrometeorological conditions under which the rate of radial growth decreased, we estimated the corresponding HDI value (HDI_{crit}) associated with SRI_{max} by averaging the values of HDI experienced by all trees on the day each tree reached SRI_{max} (Fig. 3). We found that across the landscape and among the four different species, the average HDI_{crit} was $5.72 \text{ kPa m}^{-3} \text{ H}_2\text{O m}^3 \text{ soil} \pm$ a standard error of 0.22. We further evaluated the timing of SRI_{max} (τSRI_{max} , Day of year) and HDI_{crit} (τHDI_{crit} , Day of year) as follows: we defined the day at which each tree reached its maximum growth rate during the season (τSRI_{max}) as the day that tree expressed SRI_{max} and we defined

$\tau\text{HDI}_{\text{crit}}$ as the day that daily average HDI first exceeded a value of $5.72 \text{ kPa m}^{-3} \text{ H}_2\text{O m}^3$ soil (Fig. 3).

Analyses of the $\tau\text{SRI}_{\text{max}}$ vs. $\tau\text{HDI}_{\text{crit}}$ relationship

Exploratory analyses revealed a close relationship in time between $\tau\text{SRI}_{\text{max}}$ and $\tau\text{HDI}_{\text{crit}}$. We tested the strength of this relationship and its dependence on factors such as average site moisture conditions, topography, study year, and species using a linear model. Within this framework, we expected a close relationship between $\tau\text{SRI}_{\text{max}}$ and $\tau\text{HDI}_{\text{crit}}$ to be characterized by a slope coefficient (β_1) close to 1 and a high r^2 . We compared a suite of additive and non-additive models based on the general non-additive form of $\mu\{\tau\text{SRI}_{\text{max}} \mid \tau\text{HDI}_{\text{crit}}\} = \beta_0 + \beta_1 * \tau\text{HDI}_{\text{crit}} + \beta_2 * \text{FACTOR} + \beta_3 * \tau\text{HDI}_{\text{crit}} * \text{FACTOR} + e$, where the mean of $\tau\text{SRI}_{\text{max}}$ given $\tau\text{HDI}_{\text{crit}}$ is explained by the linear combination of $\tau\text{HDI}_{\text{crit}}$, factor, and the interaction of the two. We assessed support for separate estimations of β_1 for different levels of site, topography, study year, and species by comparing additive and non-additive models for each factor using F-tests, and report the variance in $\tau\text{SRI}_{\text{max}}$ explained by $\tau\text{HDI}_{\text{crit}}$ as the squared correlation between $\tau\text{SRI}_{\text{max}}$ and $\tau\text{HDI}_{\text{crit}}$ within individual factor levels as well as the variance explained across all factors.

Assessing the effect of growing season HDI on average daily growth rates.

We explored the cumulative effect of growing season moisture stress on growth by examining the relationship between the proportion of time during the growing season that average daily HDI remained above HDI_{crit} ($\alpha\text{HDI}_{\text{crit}}$) and average seasonal SRI. Comparing absolute growth in trees is difficult due to the number of confounding factors that also influence individual tree radial growth (e.g. ontogeny, genetics, competition,

leaf area, etc.). To compensate for this, we averaged growth rates of trees in each topographic position within each site to amplify site-specific growth signals responding to a common condition of HDI. We also determined the effect of tree size (diameter at breast height, DBH) on the relationship by comparing a non-linear model with and without DBH using a likelihood ratio test (Huet *et al.*, 2004). Finding little evidence for an effect of DBH on radial growth among trees studied, ($p=0.19$, $\lambda=1.71$, d.f.= 1), we regressed these mean growth rates on $\alpha\text{HDI}_{\text{crit}}$ by non-linear-least-squares regression (NLSR) using the ‘nlsLM’ function in R package ‘minpack’ (Elzhov *et al.*, 2016) and verified the goodness of fit by leave-one-out cross-validation. We could not assess how growing conditions of the previous year may have influenced current year growth given the duration of our study (e.g. Zielis *et al.*, 2014). However, the modeled relationship between $\alpha\text{HDI}_{\text{crit}}$ and growth is a good fit for both years despite a considerable increase in $\alpha\text{HDI}_{\text{crit}}$ in 2015. Nonetheless, some errors due to annual carry-over effects on growth may be present in the analysis.

Converting Ψ_{pre} and Ψ_{mid} to Ψ

While we were unable to directly measure Ψ_x , we were able to make branch level measurements of predawn (Ψ_{pre}) and midday (Ψ_{mid}) water potential. We sampled twigs for Ψ_{pre} and Ψ_{mid} from c. 5.5m above the dendrometers in order to estimate a proxy for water potential at the dendrometer (hereafter simply Ψ). One can account for the effect of gravity on Ψ as a decrease of 0.01 MPa in Ψ for each one meter increase in stem height (Scholander *et al.*, 1965). However, additional resistances resulting from the flow of water through xylem can generate larger vertical gradients in Ψ . From a survey of the

literature (Hellkvist *et al.*, 1974; Hinckley *et al.*, 1978; Bauerle *et al.*, 1999; Woodruff *et al.*, 2004) we found considerable variation in Ψ gradients, and in some cases, the variation within a single species exceeded the variation observed among different species. Given this variation, we estimated a mean gradient for converting Ψ_{mid} to Ψ from all available literature estimates (17 in all), multiplied this gradient by 5.5 m, and added this to the observed value of Ψ_{mid} . This mean gradient estimate was equal to 0.0634 ± 0.0143 MPa m⁻¹. The mean value for gradients of Ψ_{pre} from the literature was 0.0046 MPa m⁻¹ lower than that of Ψ_{mid} , thus we used a value of 0.0588 for the gradient of Ψ_{pre} (Bauerle *et al.*, 1999; Woodruff *et al.*, 2004). While these studies suggest that vertical gradients in water potential larger than those expected from gravity alone can exist in trees even during the pre-dawn, theory predicts only the gravitational effect on Ψ should persist when flow in the tree ceases. As we did not quantify flow in the study trees, some error may exist in our estimate of Ψ at times.

Modeling Ψ from HDI and Estimating Ψ_{crit} at $\text{HDI} = \text{HDI}_{\text{crit}}$

In order to explore the mechanistic link between observed growth limitation and hydrometeorology, we estimated seasonal time series of average daily Ψ based on concurrent measurements of HDI. We modeled Ψ from observed HDI by fitting a negative exponential function, by NLSR as described for the modeling of average daily SRI from $\alpha\text{HDI}_{\text{crit}}$. The function form reflected the expected shape of the relationship based on theory (increasing slope of Ψ/HDI with increasing HDI due to increasing stomatal regulation of Ψ). We assessed the goodness of fit for species-specific models via a leave-one-out cross-validation procedure. We assessed the importance of species

differences in the fit of the relationship by comparing the summed log likelihoods from models fit to data subset by species to the full model including data from all species using a likelihood ratio test (Huet *et al.*, 2006).

To estimate Ψ_{crit} , we evaluated the function for each species at a value of $\text{HDI} = \text{HDI}_{\text{crit}}$ and generated 95 percent confidence intervals for the estimates by Monte Carlo simulations using the predictNLS function from R package ‘propagate’ (Spiess, 2014).

Results

Spatiotemporal variability in HDI and its constituent variables

Topographic features and seasonal changes in weather generated considerable variation in the magnitude of HDI within the watershed. Point measurements of HDI ranged from 0 to c.100 during the study, with HDI equal to 0 when relative humidity (RH) equaled 100%. Spatial variation in average growing season HDI modeled from point observations over both study years is shown for the North Fork Elk Creek watershed in Figure 1.1. HDI tended to be higher at lower elevations, on more southerly

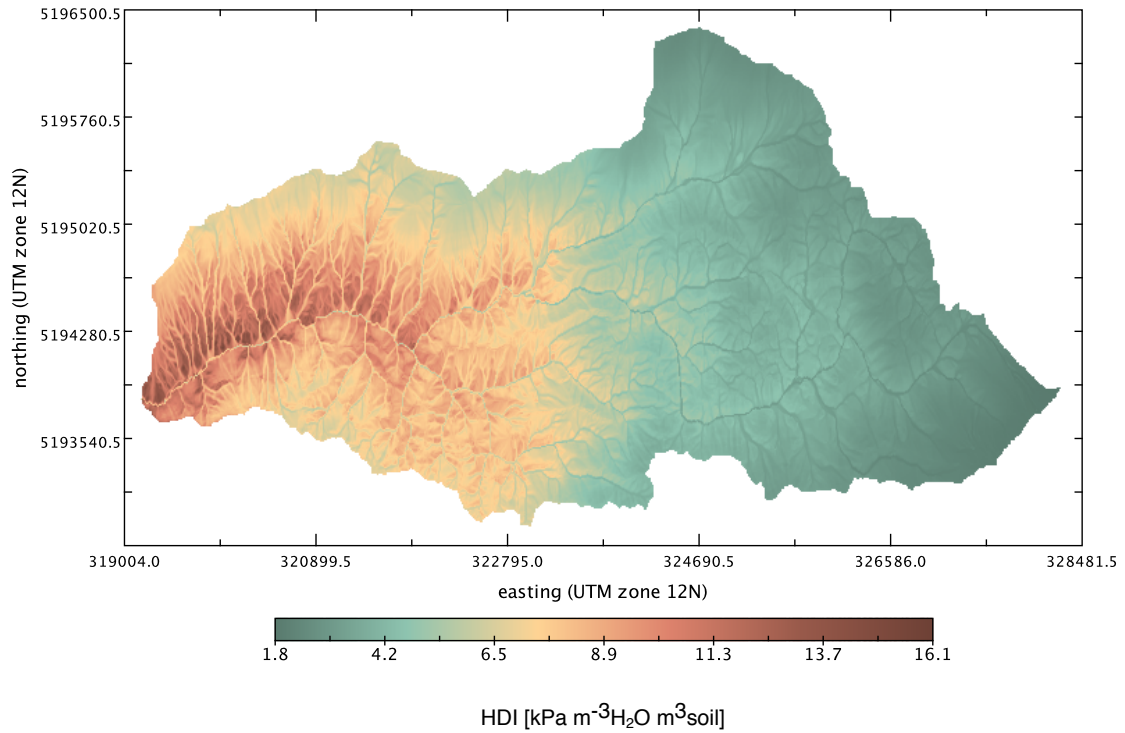


Fig. 1.1. The spatial distribution of the average growing season hydrometeorologic dryness index (HDI) for 2014 and 2015 modeled by multiple linear regression from point observations of soil moisture and vapor pressure deficit in relation to radiation, elevation, and the topographic wetness index (TWI) within the North Fork Elk Creek Watershed.

aspects, and in more divergent topographic positions. HDI was also much higher during the day than at night. The magnitude and temporal distribution of HDI was similar in both study years but the onset of summer-like conditions was delayed by approximately 20 days in 2014 relative to 2015 (Fig. 1.2).

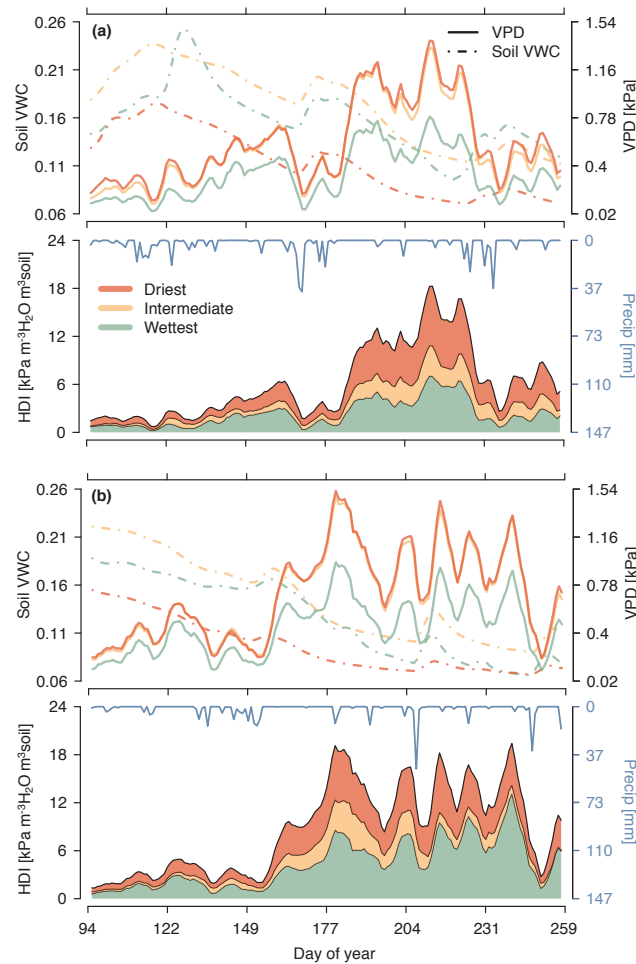


Fig. 1.2. Time series of soil water content (VWC), atmospheric vapor pressure deficit (VPD) and average daily hydrometeorologic dryness index (HDI) at each of the 3 study sites (driest, intermediate, wettest) during the 2014(a) and 2015(b) growing seasons. Rainfall averaged across all sites is also shown on the reversed right axis. For clarity, all data except rainfall are shown as five-day moving averages.

Because HDI is the quotient of two variables, VPD and soil moisture, it is difficult to assess the ecologically meaningful contribution of each variable independently over the course of a growing season, especially since VPD and soil moisture sometimes drive variability in HDI independently, and other (more often) times in concert.

However, in a post-hoc analysis, we held either VPD or soil moisture constant at its observed seasonal mean while assessing average HDI in the watershed at each point observation of the complementary variable. This allowed us to estimate how often VPD or soil moisture alone might drive HDI above HDI_{crit} . In so doing, we estimated that soil moisture levels alone would be enough to surpass the HDI_{crit} threshold 48 percent of the time versus only 32 percent of the time for VPD. This is somewhat counterintuitive as short-term variation in HDI is almost entirely driven by VPD. However, high VPD levels are transient, giving way to high humidity and low temperatures most nights.

Furthermore, because soil moisture changes much more slowly than VPD, it serves to slowly modulate the effect of VPD on HDI over the course of the growing season, driving HDI exponentially higher in response to VPD as soil water evaporates (Fig. 1.5).

The response of growth to HDI, the timing of maximum growth, and the onset of growth limitation

Across a heterogeneous landscape with differing micro-topography, daily growth rates of all four trees species increased sharply in response to increasing daily average HDI, but growth slowed as HDI surpassed a daily average value of approximately 5.72 $kPa\ m^{-3}\ H_2O\ m^3\ soil$. Growth then decreased as conditions dried, to a point where daily

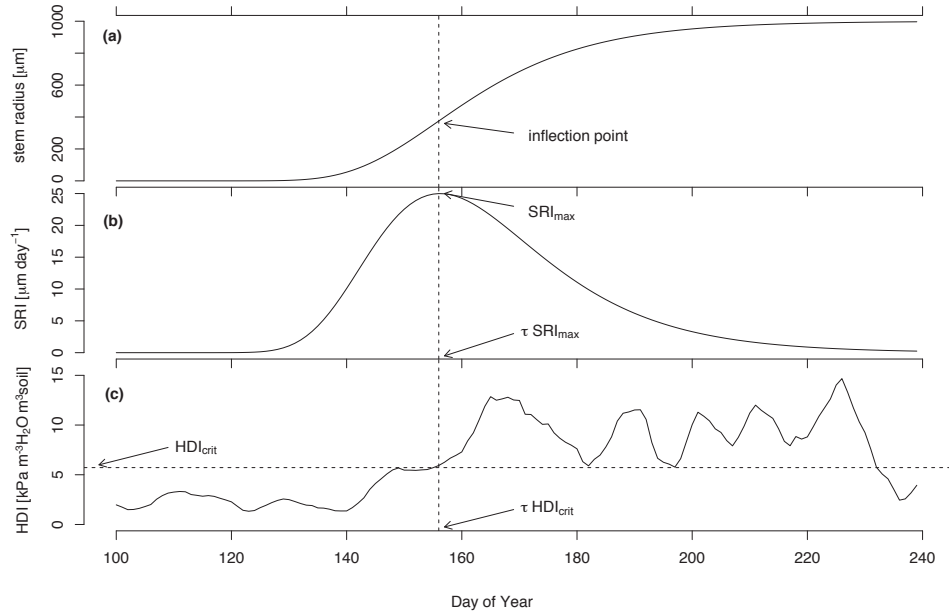


Fig. 1.3. Conceptual diagram showing the relationship between a smoothed annual growth curve (a), its derivative (stem radius increment - SRI) (b), and the hydrometeorologic dryness index (HDI) (c). SRI_{max} = maximum rate of SRI, τ SRI_{max} = day of year when SRI_{max} is reached, and τ HDI_{crit} = day of year when the critical value of HDI (HDI_{crit}) associated with SRI_{max} is reached.

growth approached zero when average daily HDI exceeded $20 \text{ kPa m}^{-3} \text{H}_2\text{O m}^{-3} \text{soil}$. The importance of 5.72 as an HDI threshold value for growth was evident when assessing the timing of peak growth in trees during the growing season. The statistics for the regression analyses of τ SRI_{max} on τ HDI_{crit} are shown in Table 1.2. Even though the day of year of maximum growth rates varied by up to two months in different locations over the two study years, τ HDI_{crit} alone described 73% of the variation in τ SRI_{max} (Fig. 1.4d). We estimated the slope of τ SRI_{max} / τ HDI_{crit} (β_1) at 0.76 ± 0.069 including all trees. We found little evidence that β_1 varied across differences in species, average site moisture condition, topographic position, and study year (F-tests, $\alpha=0.05$, Table 1.2) (Fig.

1.4a,b, and c). In 2015, the mean of $\tau\text{HDI}_{\text{crit}}$ for all trees was 23.2 ± 4.4 days earlier than that of 2014 and similarly, the mean of $\tau\text{SRI}_{\text{max}}$ for all trees was 22.2 ± 3.7 days earlier in 2015 than 2014.

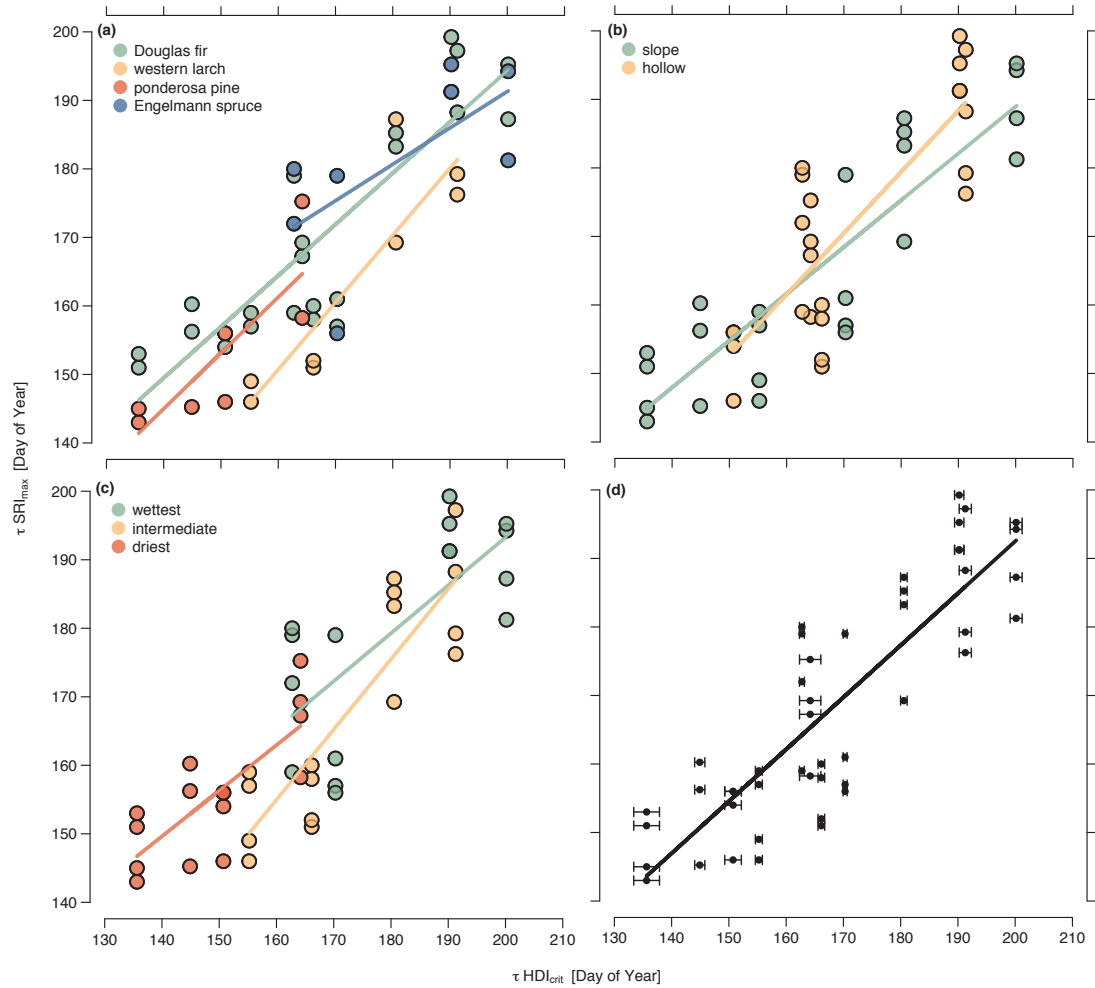


Fig. 1.4. The day of year on which average daily hydrometeorologic dryness index (HDI) first exceeded 5.72 kPa m⁻³ H₂O m³ soil ($\tau\text{HDI}_{\text{crit}}$) vs. the day on which daily growth rates peaked ($\tau\text{SRI}_{\text{max}}$) for all study trees over both years. Color and regression lines depict groups of trees and the fitted line for each group based on species (a), topographic position (b) and site (c). Error bars show two standard errors of the mean for $\tau\text{HDI}_{\text{crit}}$ from the full suite of splines used to filter HDI (d). Species shown include Douglas fir (*Pseudotsuga menziesii* var. *glauca* (Mayr) Franco), ponderosa pine (*Pinus ponderosa* P. & C. Lawson), western larch (*Larix occidentalis* Nutt.), and Engelmann spruce (*Picea engelmannii* Parry ex. Engelm).

When trees were aggregated by site and topographic position, their seasonally averaged mean daily growth rates exhibited a non-linear relationship with the proportion of time that HDI exceeded HDI_{crit} (αHDI_{crit}) (Fig. 1.6). This relationship was approximated by the function:

$$SRI = SRI_{max} - a * e^{(k * \alpha HDI_{crit})} \quad (\text{Eqn. 5})$$

Where SRI_{max} = the estimated average maximum value of SRI for all sites, a is a constant, and k = is the rate constant for SRI_{max} . We estimated a , k , and SRI_{max} to be 0.28 ± 0.36 , 4.48 ± 1.62 , and 18.69 ± 1.06 , respectively.

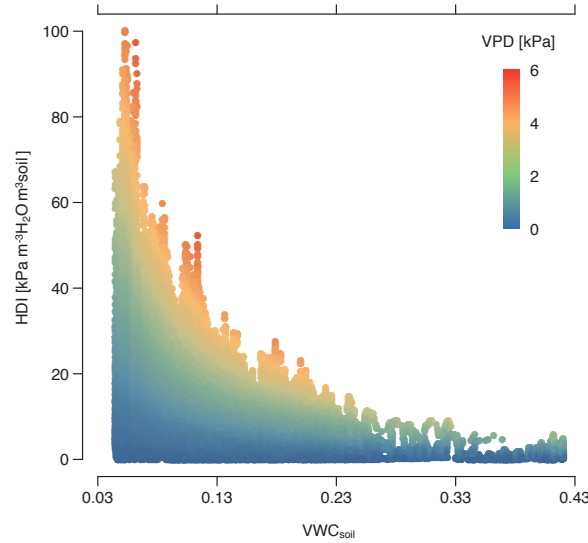


Fig. 1.5. 2014 & 2015 growing season point observations of the hydrometeorologic dryness index (HDI) vs. soil moisture (VWC_{soil}) color coded by vapor pressure deficit (VPD).

We estimated the cross-validation r^2 for the model to be 0.61 using a leave-one-out cross-validation approach. Figure 1.6 shows that the relationship is not linear; growth rates are

relatively unaffected until trees spend approximately half of their time above HDI_{crit} , after which growth rates decline exponentially with a decrease in the estimated time suitable for cell expansion.

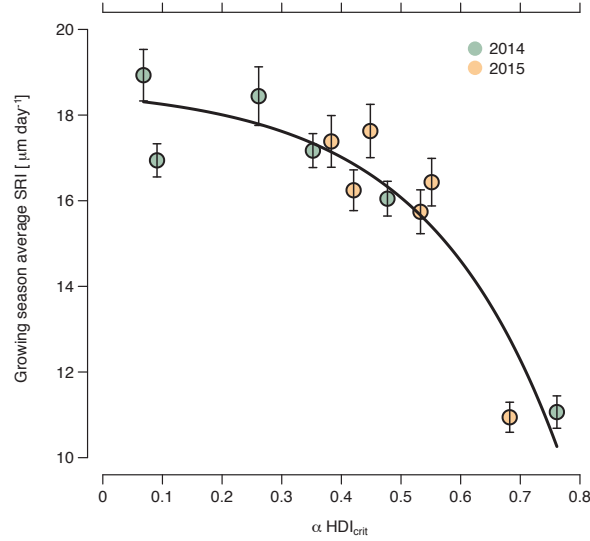


Fig. 1.6. The relationship between the proportion of days during the growing season in which average hydrometeorologic dryness index (HDI) was above its threshold value of $5.72 \text{ kPa m}^{-3} \text{ H}_2\text{O m}^3 \text{ soil}$ (αHDI_{crit}), and the mean daily growth rate (SRI) for each study plot over both years. Error bars depict one standard error of the mean.

The response of Ψ to HDI and species estimates of Ψ_{crit}

Water potential (Ψ) decreased with increasing HDI as approximated by a negative exponential function of the form:

$$\Psi = \Psi_{max} * e^{(-k * HDI)} \quad (\text{Eqn. 6})$$

Where Ψ_{max} is the estimated average maximum value of Ψ for a given species within the range of observed HDI, and k is the rate constant for Ψ . This general relationship between HDI and Ψ shows that as moisture conditions become drier (from either drying

soils or drying atmosphere), trees experience more negative water potentials and water stress. This tendency is inversely asymptotic at higher values of HDI, as is expected due to regulation of Ψ by stomata (Fig. 1.7). The response of Ψ to HDI varied slightly by species ($p=0.002$ from a likelihood ratio test, $\lambda=20.49$, d.f. = 6). Cross validation r^2 from a leave-one-out procedure for species-specific models for Douglas fir, Englemann spruce, and ponderosa pine was 0.71, 0.39, and 0.71 respectively.

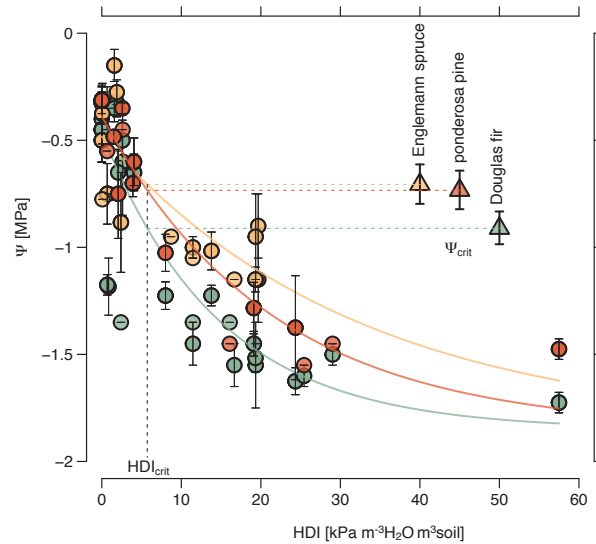


Fig. 1.7. The relationship between the hydrometeorologic dryness index (HDI) and xylem water potential (Ψ) estimated from repeated stem water potential measurements across time and a range of moisture conditions. Circles represent the mean of each species ($n=4$ trees) per sampling from each sampling location with error bars showing 1 standard error of the mean. Triangles represent estimated growth-critical values of Ψ (Ψ_{crit}) for each species with error bars showing 95% confidence intervals for the mean. Solid lines depict the fit of the negative exponential function by non-linear least squares regression. The estimated growth-critical value of the HDI is indicated by the dashed vertical line. Species shown include Douglas fir (*Pseudotsuga menziesii* var. *glauca* (Mayr) Franco), ponderosa pine (*Pinus ponderosa* P. & C. Lawson), and Englemann spruce (*Picea engelmannii* Parry ex. Engelm).

Table 2. Regression analysis and F-test statistics for the estimation of the timing of maximum growth ($\tau\text{SRI}_{\text{max}}$) vs. the timing of the estimated growth threshold value of the Hydrometeorologic Dryness Index ($\tau\text{HDI}_{\text{crit}}$).

Factor ¹	Level	Estimate ²	Std. Error	Df	Res. Df	F	t	Pr. >F	Pr. >t	r ²
$\tau\text{HDI}_{\text{crit}}$: SPECIES				3	39	0.850		0.475		
	Engelmann spruce	0.531	0.192	39			2.770		0.009	0.43
	ponderosa pine	0.814	0.281	39			2.900		0.006	0.69
	Douglas fir	0.747	0.088	39			8.532		<0.001	0.79
$\tau\text{HDI}_{\text{crit}}$: YEAR	western larch	0.980	0.210	39			4.673		<0.001	0.80
				1	43	1.590		0.214		
	2014	0.707	0.099	43			7.173		<0.001	0.74
	2015	0.482	0.149	43			3.232		0.002	0.29
$\tau\text{HDI}_{\text{crit}}$: POSITION				1	43	2.054		0.159		
	hollow	0.894	0.121	43			7.398		<0.001	0.69
	slope	0.683	0.084	43			8.155		<0.001	0.79
$\tau\text{HDI}_{\text{crit}}$: SITE				2	41	1.510		0.233		
	driest	0.666	0.207	41			3.220		0.003	0.61
	intermediate	1.026	0.155	41			3.220		<0.001	0.77
	wettest	0.700	0.142	41			4.923		<0.001	0.53
None ³	all levels	0.759	0.069	45			11.075		<0.001	0.73

¹Interaction terms between $\tau\text{HDI}_{\text{crit}}$ and factors SPECIES, YEAR, POSITION and SITE, for which support was assessed via F-tests.

²Estimated slope of $\tau\text{SRI}_{\text{max}}$ vs. $\tau\text{HDI}_{\text{crit}}$ (β_1) [days] for each factor level given the general non-additive model of form $\mu\{\tau\text{SRI}_{\text{max}}|\tau\text{HDI}_{\text{crit}}\} = \beta_0 + \beta_1 * \tau\text{HDI}_{\text{crit}} + \beta_2 * \text{FACTOR} + \beta_3 * \tau\text{HDI}_{\text{crit}} * \text{FACTOR}$

³Regression statistics for the reduced model $\mu = \{\tau\text{SRI}_{\text{max}}|\tau\text{HDI}_{\text{crit}}\} = \beta_0 + \beta_1 * \tau\text{HDI}_{\text{crit}}$

Statistically significant values are indicated in bold text.

The shape of the relationship for each species determined its individual estimate of Ψ_{crit} by evaluation of Ψ at HDI_{crit} . We estimated Ψ_{crit} based on a common HDI_{crit} value across species because the mean estimate of HDI_{crit} was statistically equivalent for these different species ($\text{HDI}_{\text{crit}} = 5.76 \pm 0.21$, $F=0.143$, d.f.= 2 and 36, $p=0.87$). This suggests that growth limitation in all tree species began in unison in response to hydrometeorological conditions despite species' physiological differences. Species-specific parameter estimates for the relationships as well as estimates for Ψ_{crit} are shown in Table 1.3. Douglas fir exhibited the lowest water potentials across its range of HDI followed by ponderosa pine. Engelmann spruce experienced a more limited range of HDI, which resulted in more uncertainty in the model fit for this species, yet Engelmann spruce maintained the highest potentials of all species across this range (Fig. 1.7).

Table 3. Parameter estimates for the relationship between water potential (Ψ) and the Hydrometeorologic Dryness Index (HDI) .

Species	Parameter	Estimate	Std. Error	Lower 95% C.I.	Upper 95% C.I.
Douglas fir	$\Psi_{\max}$	-0.465	0.048		
	k	0.068	0.008		
	Ψ_{crit}	-0.911		-0.986	-0.832
ponderosa pine	$\Psi_{\max}$	-0.388	0.063		
	k	0.047	0.007		
	Ψ_{crit}	-0.734		-0.823	-0.642
Engelmann spruce	$\Psi_{\max}$	-0.483	0.061		
	k	0.031	0.006		
	Ψ_{crit}	-0.706		-0.797	-0.613

Discussion

In this study, we addressed hydrometeorological controls on *intra*-annual growth dynamics across a complex watershed and among different tree species with different physiological responses to water availability. We found that the onset of growth limitation in trees was tightly controlled by changes in hydrometeorology; specifically, we found that all four conifer species expressed limitation in growth when HDI exceeded $5.72 \text{ kPa m}^{-3} \text{ H}_2\text{O m}^3 \text{ soil}$ (HDI_{crit}) (Fig. 1.4). At a HDI of $5.72 \text{ kPa m}^{-3} \text{ H}_2\text{O m}^3 \text{ soil}$, atmospheric demand combined with soil moisture supply generated moderate hydraulic tension in transpiring trees, resulting in Ψ ranging from -0.71 to -0.91 MPa depending on species (Fig. 1.7). This relationship was established based on real-time measurements of HDI concurrent with Ψ , which varied across the season due to species-specific traits and topographic controls on hydrometeorology. These water potential values represent possible threshold values in which xylem expansion is inhibited, thereby resulting in decreased growth rates. The strong relationship between HDI and growth was consistent across species and at different landscape positions (Fig. 1.4), suggesting that HDI may be

a useful variable for predicting the onset of forest growth limitation both in time and space (Fig. 1.4).

The relationship between radial growth and HDI

We found a strong relationship between radial growth and HDI among all four tree species. Although the range of HDI was larger for species growing in drier landscape positions (e.g. Douglas fir and ponderosa pine) compared to species growing in more mesic landscape positions (e.g. western larch and Engelmann spruce), different species converged on a similar value of HDI_{crit} . Such a finding is surprising, but not unprecedented. For example, in a northern boreal forest, trees from multiple genera were observed to synchronize the timing of maximum growth around the occurrence of the summer solstice when photoperiod was longest (Rossi *et al.*, 2006b).

At the driest locations in the watershed, daily average HDI exceeded HDI_{crit} as early as mid-May and remained above HDI_{crit} for much of the growing season (Fig. 1.2). Radial growth peaked from mid May to early June, which is consistent with other dendrometer-based reports of radial growth phenology in trees from similar elevations and latitudes (Zweifel *et al.*, 2006; Cuny *et al.*, 2015). The time that HDI exceeded HDI_{crit} (τHDI_{crit}) varied by up to two months across the landscape and two study years. However, τHDI_{crit} described 73% of the variation in the timing of peak growth (τSRI_{max}) (Fig. 1.4). In addition, the variables used to calculate HDI (temperature, humidity, and volumetric soil moisture) are predictably influenced by local topography (Beven & Kirkby, 1979; Bonan, 2002) (Fig 1.1.). This suggests that the topographic structure of the landscape may serve to organize patterns of tree growth across a particular region. As

such, combinations of HDI and topographic information such as elevation and curvature may serve as generally applicable tools for understanding the spatial distributions of forest growth dynamics in water-limited systems, and where covariance between topography and other growth-limiting variables is understood. Additionally, analyses of seasonally integrated records of HDI may prove useful for estimating inter-annual variation in growth for both modeling and the development of proxy climate records from tree rings. Of course, in practicality, tree growth is rarely limited by only one factor and interactions among these limiting factors may change seasonally.

If $\tau\text{HDI}_{\text{crit}}$ were the sole factor controlling $\tau\text{SRI}_{\text{max}}$, we would expect $\tau\text{SRI}_{\text{max}}/\tau\text{HDI}_{\text{crit}}$ to equal 1: however, we see that the slope of this relationship is c. 0.76 based on all trees (Table 1.2). Several explanations for this result are plausible. For one, trees growing in the driest locations are likely to begin growth earliest because these sites are also typically the warmest during the day, and temperature is likely the primary control on the initiation of growth in the cold spring climate of the Northern Rockies (Oribe *et al.*, 2003; Rossi *et al.*, 2008). As growth in these trees began as early as April, it is likely that low soil and air temperatures exhibited considerable control over rates of radial growth, especially at night when Ψ conditions are most favorable for growth. In addition, those trees living in the wettest locations (such as those at the wettest site in 2014) did not regularly experience HDI_{crit} until late July. For these trees, other factors such as a decreasing photoperiod may begin to exert considerable control over growth rates later in the season (Rossi *et al.*, 2006b). It is likely that HDI imparts the greatest control over growth in trees when other factors such as temperature and photoperiod are not limiting.

These moderate conditions typify growing conditions for trees at the intermediate wetness site, including western larch, where, although not statistically different from other groupings of trees given our level of replication, $\tau\text{SRI}_{\text{max}}/\tau\text{HDI}_{\text{crit}}$ most closely approached 1 at 0.98 and 1.03 for larch and intermediate site trees respectively (Table 1.2).

It is also important to note that we aimed to quantify the seasonal evolution of a critical level of HDI (and associated Ψ) for growth limitation. As such, we based our analyses on low-pass filtered daily maxima (growth) and daily average (HDI) data. While these variables integrate the high-frequency variability of moisture conditions and stem radius dynamics over long time periods, they do not necessarily represent how the system behaves over short time steps. According to theory, growth likely occurs somewhat opportunistically when VPD and soil moisture facilitate high Ψ (e.g. night-time), leading to alternating periods of growth and zero-growth (Zweifel *et al.*, 2016) and it can be expected that such dynamics underlie the findings presented here.

Water potential (Ψ) controls on radial growth.

While HDI_{crit} and $\tau\text{HDI}_{\text{crit}}$ are strong predictors for peak tree growth, the mechanism by which these variables may influence growth is hypothesized to involve Ψ . The process by which Ψ directly limits growth has been suggested from laboratory results for some time (Boyer, 1970; Hsiao, 1973). However, to date there has been little research devoted to describing this process within actual forest communities or across a range of growing conditions. Steppe *et al.*, 2006, used *Fagus sylvatica* to demonstrate the mechanics of radial tree stem growth as governed by the Lockhart equation

(Lockhart, 1965), which describes the mechanical and hydraulic process of cell expansion. Similarly, (Zweifel *et al.*, 2016) provided evidence for threshold type growth dynamics in multiple temperate forest tree species with their zero-growth model of stem radii. Both approaches considerably improved model simulations of growing stem radius dynamics, providing additional support for the role of Ψ in the radial growth of tree stems via its importance to the Lockhart model of cell expansion (Boyer *et al.*, 1985).

Our estimates of Ψ_{crit} (-0.71 to -0.91 MPa) were similar to levels suggested by (Körner, 2015) to be critical for optimal meristem function (-0.5 to -0.8 MPa). However, absolute values for Ψ estimated from branch level water potential should be interpreted cautiously as some uncertainty results from the estimation of water potential gradients along the flow path from the bole to the branch. We estimated Ψ_{crit} and Ψ in general to be slightly lower in Douglas fir trees than in ponderosa pine or Engelmann spruce, which is consistent with earlier findings that demonstrate lower vulnerability to cavitation in Douglas fir than in ponderosa pine (Stout & Sala, 2003). In the studied watershed, Douglas fir dominates stands and grows across a larger range of moisture conditions than other species, suggesting a competitive advantage. Furthermore, because Douglas fir was able to maintain growth at lower Ψ than co-occurring species, it may be able to acquire more carbon via a lower degree of stomatal regulation without necessarily sacrificing growth in size.

The consistency of the growth response across environmental gradients and among different tree species

Synchrony in the growth response of different tree species to HDI_{crit} is somewhat counterintuitive given the general expectation that tree species are physiologically adapted for a particular moisture range. For example, within the North Fork Elk Creek watershed, ponderosa pine is almost entirely restricted to hot and dry landscape positions, while Engelmann spruce is generally restricted to wet and cool locations. However, despite growing in different moisture habitats, the level of HDI critical for sustained growth, was similar for these two species. Additionally, the predictability of the growth response to HDI was consistent across multiple environmental gradients regardless of species (Table 1.2). This implies that despite the expectation of different species-specific responses to water stress, the role of Ψ in cambial cell expansion may be well conserved, and acts as a unifying feature across a range of species.

The emergent properties of tree growth and water relations reflect an underlying set of important physiological trade-offs, balancing the need to acquire and store carbon, to protect hydraulic function, and to develop and expand new tissues. For trees in dry regions, these needs must be consistently met despite often challenging moisture conditions. While we do not yet fully understand the mechanistic details of how these needs are balanced, the moisture supply and demand framework (in this case HDI) can be a useful tool in predicting the outcomes of this balancing act where a reliable physiological response (such as growth limitation) exists (e.g. Sperry *et al.*, 2016). In the semi-arid system studied, growth was rapid in the short but well-watered conditions of

spring; however, in the dry warm-season, prioritization of carbon assimilation drove xylem tensions higher in transpiring trees. The tradeoff is sensible, as carbon for respiration and the maintenance of hydraulic function represents an immediate requirement for survival (Sevanto *et al.*, 2014). However, growth ultimately shapes a forest and its myriad ecological processes over time, and as such, must remain a fundamental focus in our understanding of the relationship between climate and forest ecosystem function.

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CHAPTER THREE

DIFFERENCES IN THE USE OF WINTER PRECIPITATION
BY CONIFERS ALONG AN ELEVATION GRADIENT
IN THE NORTHERN ROCKIES

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DIFFERENCES IN THE USE OF WINTER PRECIPITATION BY CONIFERS
ALONG AN ELEVATION GRADIENT IN THE NORTHERN ROCKIES

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ABSTRACT

In temperate regions such as the American west, forest trees often exhibit growth sensitivity to climatic conditions of a particular season. For example, annual tree ring growth increments may correlate well with records of winter precipitation but appear unrelated to summer rainfall, suggesting that such trees rely more on winter snows than summer rains. This phenomenon is well documented in tree ring records from across the west but the coarse spatial distribution of tree ring records and the intentionally selective sampling used to develop most tree ring chronologies generally prohibits tree ring based exploration of what drives varying seasonality in forest growth-precipitation interactions. Because both the timing and character of seasonal western climate patterns are expected to change considerably over coming decades, such underlying variation can be expected to influence how different forest trees respond to climate change as a whole, with shifts in seasonality potentially benefitting some trees while challenging others. In a subalpine forest of the Northern Rockies, we tracked tree water use and growth in Douglas fir trees for three years using stable water isotopes while simultaneously quantifying and tracking precipitation inputs to soil moisture across a vertical soil profile. We found that prevailing soil moisture conditions drive variation in effective rooting depth that in turn determines which seasonal precipitation inputs are available to support tree growth and function. In general, trees at lower elevations relied more on winter precipitation sourced from deep soils while trees at higher elevations made better use of summer rains sources from near-surface soil layers, however, over 80% of annual growth was attributed to winter precipitation in both cases. As both the timing of seasons and phase of

precipitation (rain vs. snow) are likely to change considerably across much of the west, such patterns in tree water use are likely to play a role in determining the evolution of forest composition and structure in a warming climate.

INTRODUCTION

Across much of the western U.S., recent decades have been characterized by marked changes to hydroclimate including reduced snowfall (Knowles *et al.*, 2006), declining snowpack (Hamlet *et al.*, 2005; Mote *et al.*, 2005; Pederson *et al.*, 2011) and an earlier onset of spring conditions (Cayan *et al.*, 2001; Stewart *et al.*, 2005). Regionally, annual moisture delivery is generally dominated by inputs from North Pacific winter storms (Pyke, 1972). As such, the observed climate changes tend to limit the amount of water present on the landscape later in summer by routing melt water to streamflow earlier (Regonda *et al.*, 2005) and by reducing snowpack storage of water delivered to the region via winter precipitation (Cayan, 1996). This can have significant consequences for forests that rely on this water for growth and function during the summer growing season (Hu *et al.*, 2010; Trujillo *et al.*, 2012). However, soils also make up an important storage reservoir, either via the integration of winter snows as melt-water (McNamara *et al.*, 2005) or by direct recharge from summer rains (Hamlet *et al.*, 2007).

Trees do not typically make use of precipitation directly but instead pull water from the soil matrix post-infiltration. In fact, a recent body of evidence suggests that soil water used by plants can be functionally separate from that which contributes to groundwater and streamflow (Renée Brooks *et al.*, 2010; Good *et al.*, 2015), but see (McCutcheon *et al.*, 2017). Because of this, soil hydrologic processes considerably affect

the responses of tree growth and function to precipitation inputs. In particular, the water storage capacity of soils and the timing of soil water recharge and depletion ultimately dictate how precipitation (snow or rain) manifests as plant available water (McNamara *et al.*, 2005; Smith *et al.*, 2011).

Across much of the western U.S., peak soil moisture and hence, maximal recharge, typically coincides with the end of snowmelt (Bales *et al.*, 2011; Harpold *et al.*, 2015). However, with the exception of the highest elevations, this maximum supply of moisture is usually out of phase with maximal evaporative and transpiration demand, as potential evapotranspiration (ET) tends to peak in July (Thornthwaite, 1948; Shevenell, 1999), although peak ET can range anywhere from one to three months or more post-melt, depending on location (Dye, 2002). This means that in some cases, forest function and productivity can depend heavily on winter precipitation that is stored in the soil profile (Roden & Ehleringer, 2007; Hu *et al.*, 2010). However, some trees may also rely heavily on direct recharge of soil moisture from summer rains (Roden & Ehleringer, 2007).

Collectively, some of these past studies support the notion that at broad spatial scales, trees depend primarily on precipitation inputs from the dominant mode of precipitation. For example, in a study of ponderosa pines, Roden and Ehleringer (Roden & Ehleringer, 2007) used water isotopes from tree xylem and precipitation to find a strong association between winter precipitation water use in west coast populations vs. monsoon precipitation use in desert southwest populations, reflecting the seasonal distribution of the dominant precipitation type at these locations. However, given that

mountain environments tend to be highly heterogeneous in landscape structure, it remains uncertain if these general patterns in water use hold at finer spatial scales. Recent studies have linked soil moisture storage to fine scale landscape variability such as topography and forest cover (Geroy *et al.*, 2011; Harpold *et al.*, 2015); other studies demonstrate how local microclimate can influence forest productivity (Martin *et al.*, 2017, Hoylman *et al.*, 2018), suggesting that relationships between seasonal precipitation dynamics and forest function should be further organized by landscape characteristics at relatively fine spatial scales.

Given that snowpack is predicted to continue decreasing in the western U.S (Barnett & Pennell, 2004), there is a pressing need to link ecosystem water availability with a mechanistic understanding of how, when, and where trees access that water. Also, because shifts in the timing of seasons are already a major component of observed climate change (Cayan *et al.*, 2001; Stewart *et al.*, 2005), we need to directly link different seasonal modes of precipitation with observations of plant productivity. In mountain ecosystems, these linkages can be difficult to characterize both spatially and temporally because of the high degree of variability in landscape characteristics. The central aim of this study was to quantify the importance of winter precipitation as a water source and how its importance is controlled by landscape characteristics. To address this aim, we asked three questions: 1) Where along the soil depth profile are trees sourcing water from? 2) What proportion of that soil water used is derived from winter precipitation? 3) How do landscape characteristics such as elevation and hillslope topography influence the importance of winter precipitation as a water source for trees?

MATERIALS AND METHODS

Study location

This study took place over two years from the spring of 2014 to the fall of 2015 at the Lubrecht Experimental Forest, a mixed coniferous forest of the Northern Rockies in western Montana, USA. We selected four sites within small sub-catchments of the North Fork Elk Creek watershed to capture topographic variation from high (c. 1750m above sea level (asl)) to low (c. 1400m asl) elevations as well as across north and south facing aspects. Within each site, we sampled trees and soils from differing hillslope positions (referred to hereafter as ‘plots’), representing convergent, hollow locations and more divergent slope locations. Soil types within the study area range from gravely loamy sands to gravely sandy loams, although soils are heterogeneous even within sites as a result of the complexity of the mountainous terrain and the variability of soil depths (NRCS, 2017). Two snow survey telemetry (SNOTEL) stations are located within the experimental forest (Lubrecht Flume station # 604, 1426m, (low elevation) and N Fork Elk Creek station # 657, 1905m, (high elevation)). On average the low elevation SNOTEL receives 514mm of accumulated precipitation while the high elevation SNOTEL receives 664mm across a 30 year normal (1981-2010). The percentage of annual precipitation stored as snowpack averages 27% and 46% for low and high elevations respectively.

Tree xylem, soil, and water isotope sampling

During 2013, 2014, and 2015 we collected over 2000 samples for water isotope analysis from within the North Fork Elk Creek watershed. Within each hillslope plot, we

selected three trees from each species present for xylem water sampling. Beginning as early as the first week in April and continuing every two weeks, we collected xylem tissue from the bole of each tree using an increment borer. Phloem and heartwood tissues were removed from each xylem sample and the sample was placed into 12 mL glass sample vials with PTFE lined caps. Sample vials were further sealed with parafilm, placed in plastic bags, and stored on dry ice before being frozen in laboratory freezers until waters were extracted. The tree species we collected include ponderosa pine (*Pinus ponderosa*), western larch (*Larix occidentalis*), Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta*), and Douglas Fir (*Pseudotsuga menziesii*). Unlike the other species, Douglas fir grow across the entire watershed, for low to high elevation; therefore, we used Douglas fir xylem water isotope as the primary tree species for the analysis partitioning the seasonality of water used by trees. Soil water was also collected at each sampling interval. Two small soil pits were dug in undisturbed soil central to each plot to a depth of 50cm. In general, dense shallow regolith prevented digging to greater depths by hand. Soil samples from depths of 0, 5, 10, 20, 30, and 40 cm were then collected in glass vials from the pit wall and stored in the same way as tree samples until extraction.

Rainwater was collect at the same time that trees were sampled. Rain was collected in Nalgene bottles fitted with a funnel and screen. Mineral oil was poured into the funnel prior to each collection to prevent evaporation of rainwater between samplings. Stream water samples from sites with surface water present in the hollow were collected when rainwater was collected. Water samples were handled in the same

way as tree samples except they were not allowed to freeze prior to analysis. Water samples were kept refrigerated at all times. Snow water was collected within a week of April 1st of each year using a snow sampling tube. A snow core containing the full depth of the existing snowpack was placed into plastic bags, allowed to melt in the laboratory, mixed, and then placed into glass vials to be stored in the same way as rain and stream water.

Extraction of xylem and soil water

Water from xylem and soils was extracted by cryogenic distillation (Ehleringer *et al.*, 2000). Vials were opened, placed in a glass tube, and loaded onto the extraction apparatus to be heated under vacuum at 110 degrees C. The evaporated water was then condensed in the bottom of a separate glass tube by submersion in liquid nitrogen. Samples were heated until no further vapor could be made to condense within the distillation tube by complete submersion of the tube in liquid nitrogen. Condensate from each sample was then thawed in the tubes while sealed with parafilm, mixed, and poured into sample vials to be frozen until analyzed.

Stable isotope analysis

Xylem, soil, and precipitation water samples were analyzed for D/H and ¹⁸O/¹⁶O by cavity ring-down spectroscopy (CRDS) using a Picarro L2120i water analyzer. Stable isotope ratios of hydrogen and oxygen were expressed using δ notation (units of ‰):

$$\delta D = (R_{\text{sample}}/R_{\text{standard}} - 1) / 1000, \quad (1)$$

where R_{sample} and R_{standard} are the molar ratios of D/H of the sample and standard water (V-SMOW), respectively, and similarly for ¹⁸O/¹⁶O. We verified the results from the

isotope analysis using CRDS by sending a subset of 74 xylem and soil water samples to the Center for Stable Isotope Biogeochemistry at UC Berkeley for analysis by isotope-ratio mass spectrometry (IRMS). Values of δD and $\delta^{18}\text{O}$ from CRDS agreed with values of δD and $\delta^{18}\text{O}$ from IRMS with R^2 of 0.99 and 0.94 respectively.

The relationship between the oxygen and hydrogen isotopes is well understood (e.g. Rayleigh distillation), along with the associated equilibrium and fractionation factors. For kinetic fractionation, as in the case of evaporation, there is lower diffusivity for H_2^{18}O molecules. This leads to more, or an enrichment of HDO molecules. Hence, calculations of deuterium excess (d) can be used to evaluate evaporative enrichment using the following equation:

$$d = \delta\text{D} - 8 * \delta^{18}\text{O} \quad (2)$$

Analyses

General methodological approach

In order to quantify how landscape characteristics influence the importance of winter precipitation as a tree water source, we asked two basic questions: (a) what proportion of water in both deep and shallow soils is derived from winter precipitation and (b) where in the soil profile are trees sourcing water from? To address the first question (a), we estimated the contribution of winter precipitation to growing season soil moisture by tracking growing season soil water recharge from summer rains relative to antecedent moisture from winter precipitation. We explicitly quantified how the seasonal makeup of soil moisture evolved over the growing season across a range of soil depths, and examined how these dynamics varied across the landscape. To address the second

question (b), we employed stable isotopes of water from soils and tree xylem to estimate the distribution of tree source water over soil depth as a simple proportion of deep versus shallow soil moisture present in xylem. We examined if this proportion changed over time, and how it varied across the landscape. Considering points a & b above, we then estimated the seasonality of water actually taken up by trees at a given point in time. Finally we coupled daily estimates of winter water use by trees with concurrent measurements of radial growth and literature based estimates of biomass production to quantify the importance of winter precipitation to growth in trees over the summer season.

Quantifying seasonal precipitation inputs and their contribution to soil moisture

We quantified the magnitude of precipitation inputs for each day of the two-year study period and classified them as either snow or rain following the temperature independent approach of Rajagopal & Harpold, (2016). The classification was based on precipitation, snow depth, and snow water equivalent observations from the high and low elevation SNOTEL sites within the study area for water years 2014 and 2015.

In a location central to each topographic grouping of trees, we measured soil volumetric water content at 10, 30, and 50 cm depth using 5TE sensors and EM50 data-loggers (Decagon Devices Inc., Pullman, WA, USA). In addition, to allow the flexibility of aggregating distinct soil layer isotopic signatures into deep and shallow pools, we estimated soil moisture at 0, 5, 20, and 40 cm as well using a quadratic model fit to the soil moisture measured at 10, 30, and 50 cm.

Because we were interested in comparing tree water use in different sites across the landscape, we needed to clearly define the transition between winter and summer seasons in a way that was site specific, since the timing of this transition can vary across gradients such as elevation or aspect. Thus we defined the transition from winter to summer at each topographic location within each site as the last day of snowmelt. To do this, we inferred the presence/absence of snow on the ground from 10 cm soil temperature. The summer season was considered to begin when temperature sensors at 10 cm depth began recording diurnal temperature swings in spring. Because snowpack insulates the ground leading to near-constant soil temperatures until snow melts away, it was easy to visually use the 10 cm depth sensor to pinpoint the exact timing of snowmelt at each study plot. For the purpose of this analysis, the summer season was considered to end on September 1st of each year, the date of the latest xylem water isotope sampling.

To assess how non-winter precipitation (summer rain) contributed to soil moisture following snowmelt, we used a bucket mixing model approach. We assumed that immediately following snowmelt, 100% of the water in the soils was derived from winter snowmelt (α_w). However, as the season progressed and summer precipitation (α_s) began to infiltrate the upper soils, this rain began to mix with the previous snowmelt water in the soils. To account for this mixing, we used the following calculation: summer season soil moisture inputs were quantified on a daily basis under the assumption that the soil moisture pool was made up of 100% winter precipitation on the first day following snowmelt ($t=1$). Subsequent daily increases in Θ observed at each soil depth layer were used to calculate α_s on a given day t as follows:

$$\begin{aligned}
& \text{if } \sum_{i=2}^t (\Theta^i - \Theta^{i-1}) = 0, \text{ then } \alpha_s^t = 0, \text{ else} \\
& \text{if } \sum_{i=2}^t (\Theta^i - \Theta^{i-1}) \leq (\Theta^t - \Theta^{t-1}), \text{ then } \alpha_s^t = \frac{(\Theta^t - \Theta^{t-1})}{\Theta^t}, \text{ else} \\
& \text{if } \Theta^t - \Theta^{t-1} \leq 0, \text{ then } \alpha_s^t = \alpha_s^{t-1}, \text{ else} \\
& \alpha_s^t = \frac{[(\alpha_s^{t-1} \times \Theta^{t-1}) + (\Theta^{t-1} - \Theta^{t-2})]}{\Theta^t}
\end{aligned} \tag{3}$$

where Θ^i is the observed volumetric water content of the soil layer being assessed on the i^{th} day following the end of snowmelt and α_s^t is the proportion of summer water in the soil layer on day t . The approach is analogous to a series of serial dilutions of the initial winter precipitation pool by summer rain that are assessed daily on a volumetric basis.

After calculating α_s for each day in a layer within the soil profile, single layer proportions were then converted to winter precipitation proportions (α_w) such that:

$$\alpha_w = 1 - \alpha_s \tag{4}$$

and were aggregated into shallow and deep soil moisture pools by calculating the average of all layers in each pool weighted by Θ measurements in each respective layer:

$$\alpha_w^{pool} = \frac{\sum_{i=1}^n (\alpha_{w_i} \times \Theta_i)}{\sum_{i=1}^n \Theta_i} \tag{5}$$

where α_w^{pool} is the weighted average of the α_w values measured within either the deep or shallow pool, n is the number of layers measured in the pool, and α_{w_i} and Θ_i are the α_w and Θ measurements in the i^{th} soil layer. Thus, α_w^{pool} described the proportion of the total soil moisture in each pool (shallow or deep) derived from winter precipitation.

Using an isotopic mixing model to quantify landscape and species effects on soil moisture source

To assess the use of water by trees within a soil profile, we apportioned tree source water across a vertical soil profile from 0-50 cm (estimated to contain ~ 60-70% of total tree root biomass (Jackson *et al.*, 1996)). To simplify interpretation of the data, we utilized a two end-member mixing model by dividing this soil profile into shallow (0-25 cm) and deep (25-50 cm) pools. Because significant variation in isotope ratios was often systematically evident with depth, we quantified the soil water δ value of each pool by weighting soil water δ with soil moisture content (Θ) at each respective depth:

$$\delta^{18}\text{O}_{pool} = \frac{\sum_{i=1}^n (\delta^{18}\text{O}_i \times \Theta_i)}{\sum_{i=1}^n \Theta_i} \quad (6)$$

where $\delta^{18}\text{O}_{pool}$ is the weighted average of the $\delta^{18}\text{O}$ values measured within either the deep or shallow pool, n is the number of layers measured in the pool, and $\delta^{18}\text{O}_i$ and Θ_i are the $\delta^{18}\text{O}$ and Θ measurements, respectively, in the i^{th} soil layer. Because δ values typically decreased sharply with increasing depth to approximately 20 cm and were more stable as depth increased, we used soil water isotope samples from 0, 5, 10, and 20 cm to estimate the isotopic makeup of shallow soil water and samples from 30 and 40 cm for deep soil water.

A two end-member mixing model was used to apportion source water to deep and shallow pools (Williams & Ehleringer, 2000). The model assumes two different compartments within the soil profile: deep and shallow:

$$\delta^{18}\text{O}_{\text{xylem}} = \delta^{18}\text{O}_{\text{shallow}}f + \delta^{18}\text{O}_{\text{deep}}(1-f) \quad (7)$$

where $\delta^{18}\text{O}_{\text{xylem}}$, $\delta^{18}\text{O}_{\text{shallow}}$, and $\delta^{18}\text{O}_{\text{deep}}$ are the isotopic composition of the xylem water, shallow soil water, and deep soil water, respectively, and f is the fraction of shallow soil water in the xylem. Rearranging Eqn. (1), we can solve for the fraction of xylem water from shallow soils (f):

$$f = (\delta^{18}\text{O}_{\text{xylem}} - \delta^{18}\text{O}_{\text{deep}}) / (\delta^{18}\text{O}_{\text{shallow}} - \delta^{18}\text{O}_{\text{deep}}) \quad (8)$$

After comparing additive and non-additive models, we found little evidence for interactions between topographic factors in their effect on f (p-value = 0.326 from an ESS F-test with an F-stat = 1.071 on 1 and 174 df) and similarly found no support for an effect of diameter at breast height (dbh) on f (p-value = 0.605 from an ESS F-test with an F-stat = 0.2688 on 1 and 174 df). We quantified the effect of topography (elevation, aspect, landscape microtopography) on f across two years of data using the basic additive linear model for the study design, but excluding time as a predictor such that:

$$\mu\{f \mid \text{elevation, aspect, position}\} = \beta_0 + \beta_1 \times I.\text{low} + \beta_2 \times I.\text{south} + \beta_3 \times I.\text{slope}$$

and:

$$I.\text{low} = \begin{cases} 1 & \text{if elevation} = \text{low} \\ 0 & \text{if elevation} = \text{high} \end{cases}$$

$$I.\text{south} = \begin{cases} 1 & \text{if aspect} = \text{south} \\ 0 & \text{if aspect} = \text{north} \end{cases}$$

$$I.\text{slope} = \begin{cases} 1 & \text{if position} = \text{slope} \\ 0 & \text{if position} = \text{hollow} \end{cases}$$

In addition, we quantified the influence of prevailing soil moisture conditions on f by performing a simple linear regression of average f on average Θ for the entire study period such that: $\mu\{f | \Theta\} = \beta_0 + \beta_1 \Theta$.

Determining the relative contribution of winter precipitation to xylem water (α_w^{tree}) across the landscape

Determining the relative contribution of winter precipitation to xylem water proved to be more complicated than expected, due to two main reasons. First, because f (fraction of xylem water derived shallow soils) was calculated every two weeks from our field collections, but α_w^{pool} was calculated daily, in order to link f to α_w^{pool} , we evaluated if f should be treated as static over time, or if f should be interpolated between bi-weekly sampling periods. We found no statistical support for a change in f over time using both an ANOVA and regression analyses; only two of 24 trees exhibiting significant differences in f by month (ANOVA, $R^2=0.37$, $F(3,4)=13.28$, $p=0.000$ on average), and only two of 24 trees showed a trend in f , or change in rooting depth over time, when that variable was regressed against day of year ($R^2=0.16$, $F(1,5)=0.01$, $p=0.480$ on average). The second issue was that it was unclear if estimates of f represented spatial patterns in water use controlled by the tree or its morphology, or if f simply reflected the distribution of moisture in the soil profile at any given time. To address this issue, we regressed individual estimates of f against concurrently measured ratios of $\Theta_{shallow} / \Theta_{deep}$, reasoning that if f (itself a ratio of shallow vs deep water use) were a function of where in the soil profile moisture was available, $\Theta_{shallow} / \Theta_{deep}$ should be an excellent predictor of f . We found no evidence that this was the case, with $\Theta_{shallow} / \Theta_{deep}$ describing no variation in f .

($R^2 < 0.001$, $F(1,175) < 0.001$, $p = 0.939$). On the other hand, site specific estimates of Θ for the full soil profile averaged over both growing seasons described 93% of the variation in site specific estimates of f similarly averaged over both years $R^2 0.93$, $F(1,6) = 93.5$, $p < 0.001$. We interpreted these results as strong evidence that trees primarily sourced water from a consistent depth over time, likely determined by the spatial distribution of roots imposed by morphology, and that this depth was strongly controlled by the long term average soil moisture conditions at the site. Thus, we treated f as static through time, determined as the study period mean f for each tree.

After estimating f , as well as α_w^{pool} for deep and shallow soil moisture pools for each day at each study plot, daily deep and shallow values were averaged such that values of α_w were weighted by their respective f values. Then, the fraction of xylem water from shallow soils (f) was used to also quantify that from deep soils f_{deep} such that:

$$f_{deep} = 1 - f \quad (9)$$

and:

$$\alpha_w^{tree} = \frac{\sum_{i=1}^n (\alpha_w^{pool_i} \times f_i)}{\sum_{i=1}^n f_i} \quad (10)$$

where α_w^{tree} is the average of the α_w^{pool} values weighted by their respective f values.

α_w^{tree} is estimated for each plot on each day where n is the number of pools in the profile (2), and $\alpha_w^{pool_i}$ and f_i are the α_w^{pool} and f estimates for the i^{th} soil pool (either f or f_{deep}).

The resulting value (α_w^{tree}) described the estimated proportion of xylem water derived from winter precipitation on a given day. Using these daily estimates of α_w^{tree} , we then

leveraged the factorial design of the field study to explore the role of topographic variables including elevation, aspect, and convergence on growing season use of winter precipitation.

We investigated the roll of winter precipitation in tree water use under the general hypothesis that drier conditions would lead to a greater reliance on winter precipitation because trees living in dry conditions would preferentially source water from the more reliable moisture pool of deep soils, and that the deep pool was primarily recharged by spring snowmelt. The design of the field study allowed us to assess the combined effects of various topographic drivers on α_w^{tree} as well as how these effects evolved over the growing season. This design also dictated the development of the linear models used to assess differences in α_w^{tree} across the landscape and over time. We performed a square-root transformation of α_w^{tree} prior to regression to correct for positive skew and non-constant variance in α_w^{tree} over time, which produced excellent regression diagnostics for most candidate models. We also modeled α_w^{tree} (a proportion) using ordinary least squares (OLS) regression after confirming clear linearity in the response given the final model and checking that all predicted values from the model were reasonable values between 0 and 1. We expected topographic factors to effect α_w^{tree} , and expected interactions among the factors. We also expected that those effects should vary over the growing season. As such, we evaluated support for the full non-additive model for the study design fit to daily estimates of α_w^{tree} as a function of day or year, size of tree (dbh), elevation (high or low), aspect (south or north), and topographic convergence (slope or hollow).

We also explored the time dependent main effects of topographic variables on α_w^{tree} by fitting the additive model without interactions between topographic variables and found that day described the large majority of variation in α_w^{tree} . In terms of main effects, topographic factors contributed little to differences in α_w^{tree} after accounting for day ($t < 1.64$, $p > 0.1$, all cases). Considering this, we further developed the reduced model $\mu\{\sqrt{\alpha_w^{tree}} \mid day\} = \beta_0 + \beta_1 \times day$ using sequential F-tests to rule out the inclusion of other measured variables and to establish an importance of elevation in determining the relationship between α_w^{tree} and *day*, arriving at the final model $\mu\{\sqrt{\alpha_w^{tree}} \mid day\} = \beta_0 + \beta_1 \times day + \beta_3 \times I.low + \beta_4 \times day \times I.low$ where:

$$I.low = \begin{cases} 1 & \text{if elevation} = \text{low} \\ 0 & \text{if elevation} = \text{high} \end{cases}$$

Because we aimed to quantify the average seasonal characteristics of tree water use rather than inter-annual variability, we did not include study year in the models, effectively averaging the seasonal dynamics of 2014 and 2015. Because the variable ‘day’ in the model is a measure of days since snowmelt (measured independently each year), inter-annual differences in the timing of spring should not affect our interpretation of seasonal timing inferred from the model as seasons in this sense are relative to the end of snowmelt.

It should be noted that to characterize the seasonal evolution of α_w^{tree} , we assessed the effects of topography on α_w^{tree} on a daily basis using daily soil moisture data and assuming a constant value for f . However, to quantify our confidence in the estimation of α_w^{tree} we report all statistics for the above model based only on estimates of α_w^{tree} extracted from this daily dataset on days during which xylem water isotopes were

sampled. In this way, estimates of α_w^{tree} are not pseudo-replicated in time when matched to f values inferred from bi-weekly isotope sampling and represent our true confidence in estimates of α_w^{tree} based on our field sampling effort.

Quantifying the contribution of winter precipitation to radial growth

To link estimates of winter precipitation use to expressed growth, we use previously collected measurements of the daily radial growth of trees (stem radial increment, SRI) in each plot (Martin *et al.*, 2017). We first subtracted the last day of snowmelt from the day of year for SRI curves of trees in each plot within the high and low elevation sites for 2014 and 2015. This synchronized growth estimates with α_w^{tree} estimates relative to the end of snowmelt. We then average high and low elevation tree growth curves over both study years and linked them to daily high and low elevation estimates α_w^{tree} .

Because the actual magnitude of growth rates were nearly double at high elevation sites compared to low elevation sites, we scaled them to be comparable by quantifying SRI as a daily proportion of total annual growth ($\alpha\text{SRI}_{annual}$) calculated as the size increase from one day to the next divided by the total annual growth increment. We then multiplied $\alpha\text{SRI}_{annual}$ by α_w^{tree} on that day to yield the daily proportion of annual growth attributable to winter precipitation on that day. Daily proportions of annual growth then summed to 1 while daily proportions of annual growth attributable to winter precipitation summed to the proportion of the total annual radial growth increment attributable to winter precipitation (ARI_w) such that, expressed as a percentage:

$$\text{ARI}_w = \sum_{i=1}^n (\alpha\text{SRI}_{annual_i} * \alpha_w^{tree_i}) \times 100 \quad (10)$$

where $\alpha\text{SRI}_{\text{annual}_i}$ is the proportion of total annual growth that occurred on the i^{th} day of radial growth, n is the number days in the annual growth curve, and $\alpha_w^{\text{tree}_i}$ is the estimated proportion of winter precipitation in xylem water on the i^{th} day of growth.

RESULTS

Spatial variability in water isotope values

Spring snowpack and summer rain waters reflected the continental and mid elevation setting of the study site with δD of snow and rain water ranging from -157.48 to -69.00, and $\delta^{18}\text{O}$ of snow and rain ranging from -20.27 to -9.92. The local meteoric water line (LMWL) was $\delta\text{D} = 7.58 \delta^{18}\text{O} + 0.35$, $R^2=0.99$, $n=112$ (Fig. 2.1). Surface water sampled from streams at the high elevation sites plotted on the LMWL near a consistent value of $\delta\text{D} = -133.83$ and $\delta^{18}\text{O} = -17.65$ throughout the study. Soil water isotopes typically plotted to the right of the LMWL along the expected evaporation line describing the evolution of deuterium excess d , resulting from the evaporation of soil water. Tracking soil water isotope values back to the LMWL along this line, shallow samples tended to reflect the broad range of summer rains while deeper soils tended to reflect source waters closer to snow in isotopic composition. Water extracted from tree xylem consistently mapped within the range soil water in dual isotope space.

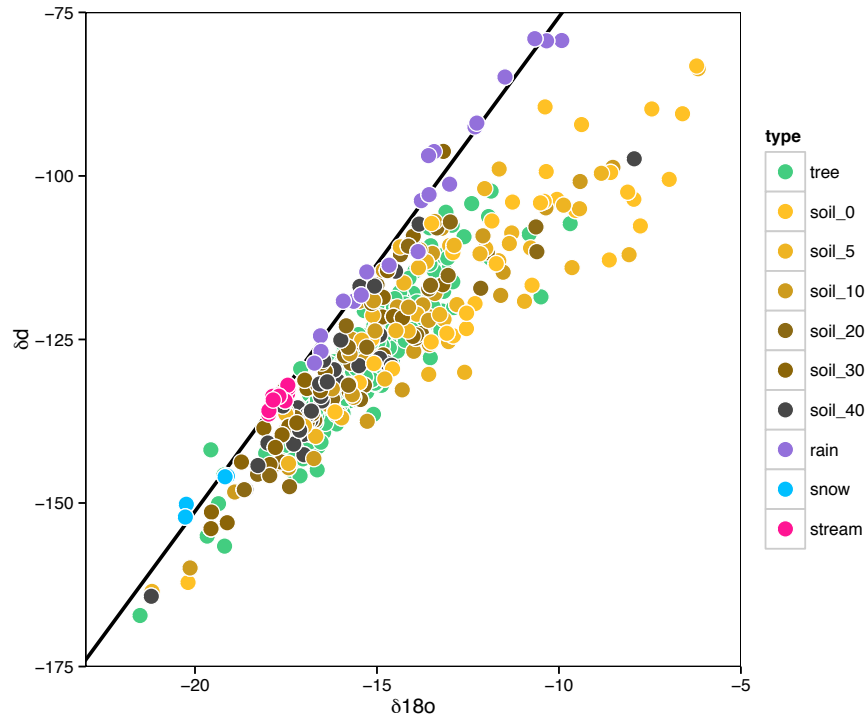


Fig. 2.1. δD vs. $\delta^{18}O$ of water sampled from trees, soils, rain, snow, and streams. To avoid over-plotting, only monthly average values for 2014 are shown. Color denotes sample type. The black line is the local meteoric water line (LMWL) determined as the best-fit line for all snow and rain samples.

Spatial patterns of precipitation and soil water evaporation

Deuterium excess (d) of soils indicated a consistent pattern of decreasing evaporation with depth. We observed that on average, d values at the soil surface were equal to -19.57 ‰ and -24.42 ‰ in high and low elevation soils respectively, and increased as a curvilinear function of depth such that $d = 1.06 \times \text{depth} - 0.02 \times \text{depth}^2$, and where depth is the absolute value of the depth of soil sampled in cm (Fig. 2.2). We found no significant differences in d of precipitation over time or between precipitation phases (snow/rain), which suggests that evaporation of soil water is well controlled by depth, with shallow soils experiencing exponentially more evaporative loss than deeper soils.

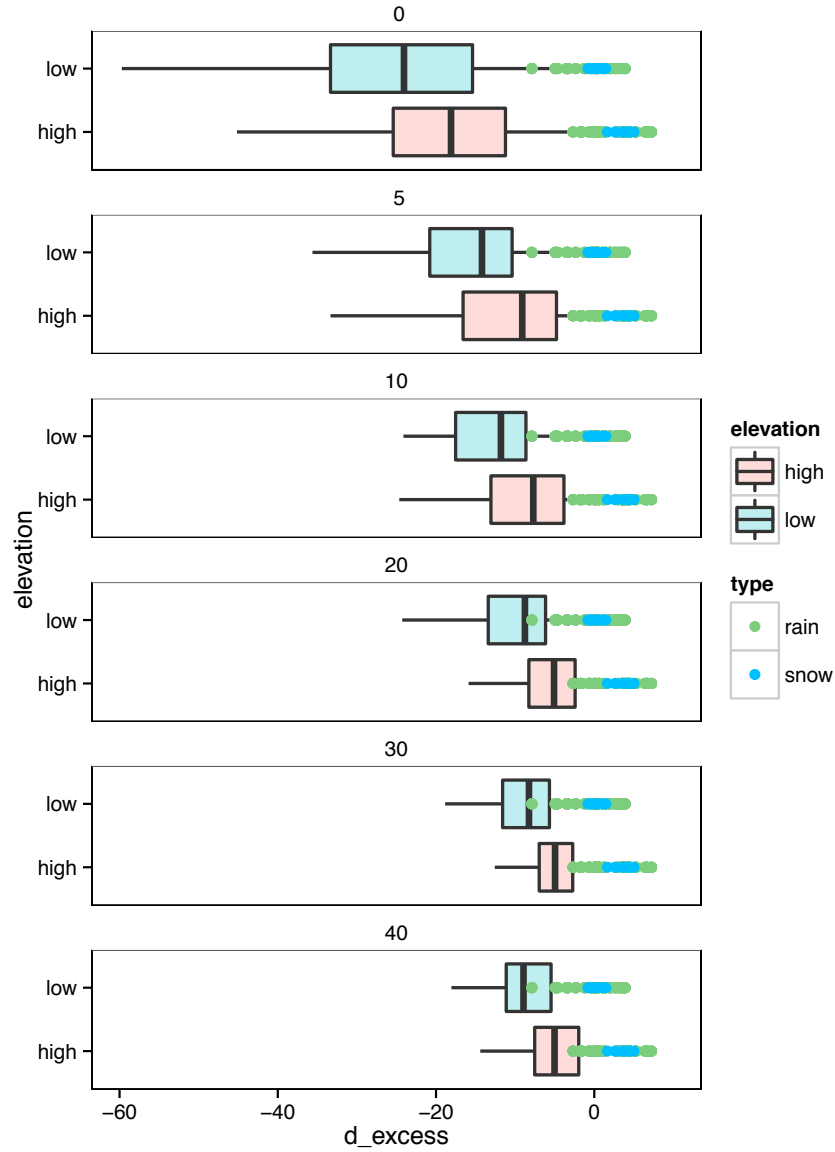


Fig. 2.2. Deuterium excess (d) of precipitation and soil water sampled at the surface and at 5, 10, 20, 30, and 40 cm depth. Boxplots show averages of soil water samples from high and low elevation plots from each sampling effort and points show similarly averaged values for rain and snow.

To examine whether the loss of soil moisture to evaporation was dependent on elevation, we quantified the difference in d between concurrent collections of

accumulated precipitation and soil water at each site and examined how this difference varied between high and low elevation sites. After accounting for soil depth, the decrease in soil d relative to precipitation inputs (soil water evaporation) was 1.93 % greater at low elevation sites compared to high elevation sites ($t=2.44$, $p=0.015$) and this difference was consistent across soil depths, suggesting that low elevation soils in general were subject to greater evaporative loss than high elevation soils on average. This pattern of evaporation was in contrast to that of precipitation inputs, as low elevation sights received less precipitation than high elevation sights during the 140-day study period following snowmelt. Low elevation sites received 97 mm of precipitation while high elevation sights received 118 mm of precipitation on average over the two study years. Thus, the lower elevation sites were drier both in terms of moisture delivery to, and loss from soils.

The evolution of winter precipitation in soil water (α_w^{pool}) over the growing season

In both high and low elevation sites, relatively consistent early summer rains (Fig. 2.3a) and loss of antecedent soil water to evaporation or drainage, led to modest reductions in α_w^{pool} in both deep and shallow soil moisture pools (Fig. 2.3b). This pattern was similar across elevations for approximately the first half of the growing season, with lower elevations retaining a slightly higher proportion of winter precipitation than upper elevations (Fig. 2.3b). However, these patterns between low and high elevations diverged during the hotter mid-summer period as upper elevations exhibited a consistent replacement of winter water with summer rain, while summer rain inputs to lower elevation soils largely ceased or even decreased (Fig. 2.3b). The fact that winter

precipitation could become more important as summer progresses is counterintuitive, but this occurred for much of the mid-summer period in the low elevation shallow soil moisture pool because rain inputs to the uppermost soil layers were apparently lost to evaporation faster than they were added, while antecedent water from winter precipitation present in deeper layers persisted (Fig. 2.3b). As a result, by day 100, the percentage of winter precipitation in low elevation soils was approximately 7% greater than high elevation soils for both deep and shallow soil layers. However, this difference was not statistically significant at any point during the growing season given our level of replication in the study (95% confidence interval for the difference between elevations included 0 on all days).

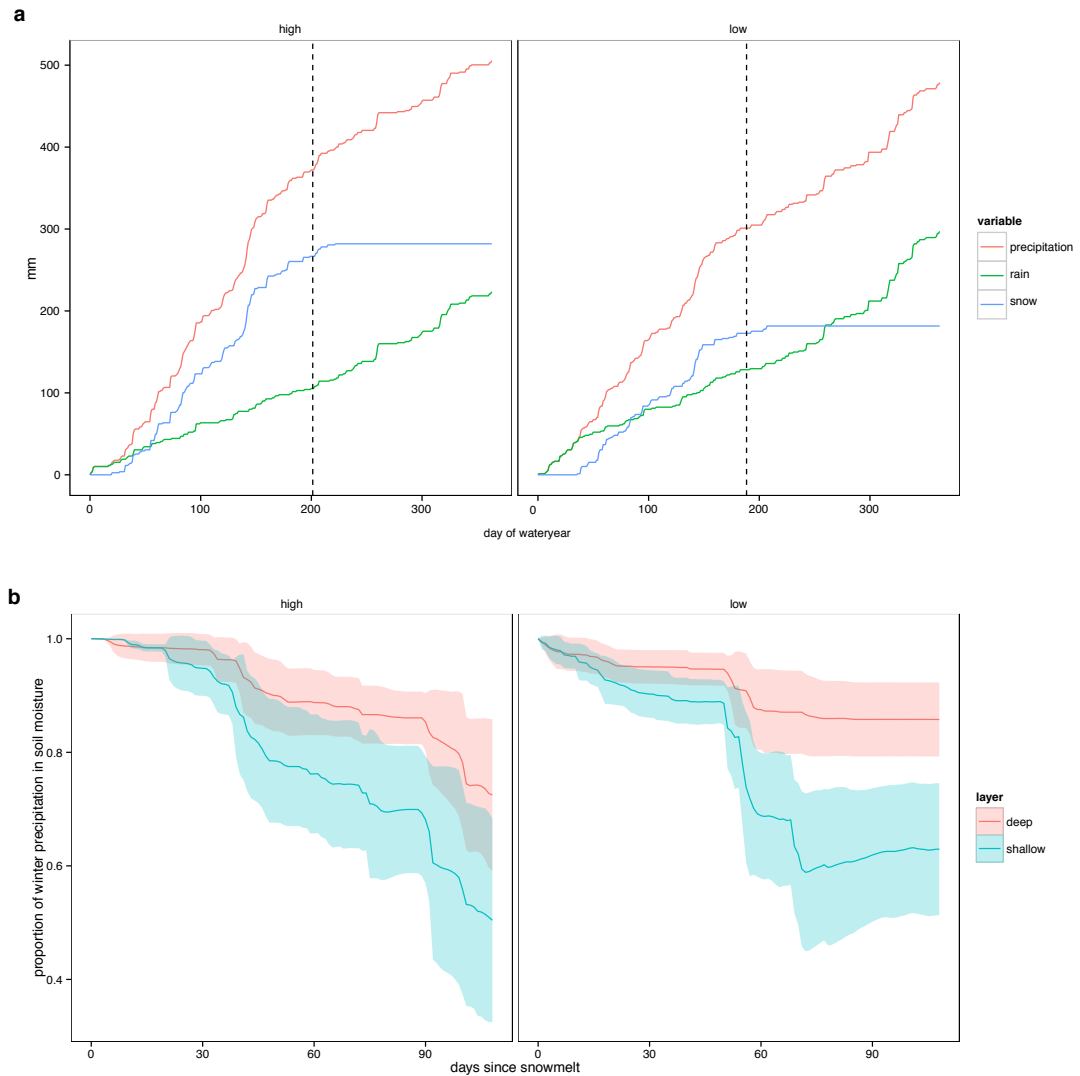


Fig. 2.3. **a**, Cumulative depth (mm) of snow, rain, and total precipitation vs. day of water year at high and low elevation SNOTEL sites, averaged over both study years. Color denotes precipitation type. Dashed lines indicate the timing of the end of snowmelt. **b**, The proportion of winter precipitation present in deep and shallow soil moisture pools at high and low elevations on each day following snowmelt. Values show the two-year mean proportions for each day since snowmelt, averaged across plots at high and low elevations. Shading denotes 1 standard error of the mean.

The relationships between tree rooting depth, topography, and soil moisture

Topographic factors (elevation, aspect, convergence) described only minimal variation in effective rooting depth inferred from f , the fraction of shallow soil moisture in the xylem ($t < 1.72$, $p > 0.09$ for all factors, $R^2=0.08$). However, of the topographic effects on rooting depth we did observe, differences across the elevation gradient was the strongest with high elevation trees sourcing an estimated $22.4\% \pm 13\%$ (mean $\pm$ SE) more water from the upper soil moisture pool

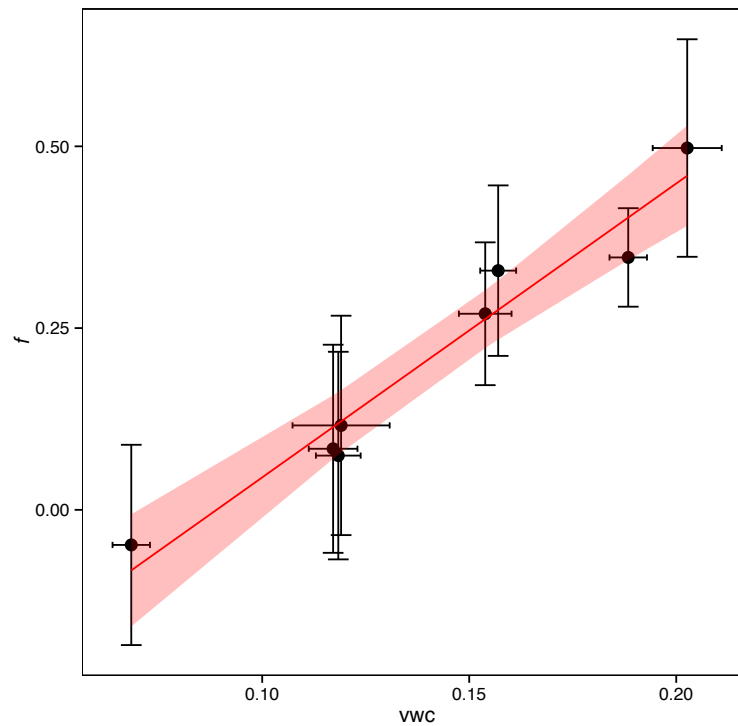


Fig. 2.4. The relationship between soil volumetric water content (Θ) and the fraction of tree xylem water sourced from shallow soils (f). Points show the two-year mean values for each study plot. Error bars show 1 standard error of the mean.

than low elevation trees $t(65)=1.71$, $p=0.092$. Daily point measurements of mean profile Θ were a weak predictor of concurrent estimates of f , describing only 5% of the

total variation in f for all trees over the course of the study ($R^2=0.05$, $F(1,175)$, $p=0.003$). However, when concurrent estimates of f and Θ were averaged over the two-year duration of the study, mean values of Θ were a powerful predictor of f , describing 48% of the variation in f on an individual tree basis and 93% of the variation in f on a plot aggregated basis ($R^2 = 0.48$, $F(1,22) = 19.94$, $p<0.001$ and $R^2 = 0.93$, $F(1,6) = 93.5$, $p<0.001$, respectively) (Fig. 2.4).

Temporal and spatial patterns in α_w^{tree}

Despite the variable and relatively minor role topography appeared to play in estimates of both f and α_w^{pool} , α_w^{tree} is a function of both of these variables and is difficult to predict without knowledge of both controlling factors. We found that while α_w^{tree} was primarily controlled by time, and the associated dilution and evaporative loss of winter derived soil moisture, temporal dynamics of winter water use was different for high and low elevation trees, with low elevation trees relying more on winter precipitation than high elevation trees as the growing season progressed (Fig. 2.5). The relationship between α_w^{tree} and days since snowmelt depended on elevation ($t(71) = 2.26$, $p=0.027$ for the interaction between days and elevation) with $\sqrt{\alpha_w^{tree}} = 1.017 - 0.002 \times \text{days since snowmelt}$, for high elevation trees, and $\sqrt{\alpha_w^{tree}} = 1.017 - 0.002 \times \text{days since snowmelt} - 0.030 + 0.001 \times \text{days since snowmelt}$ for low elevation trees. While these elevation-based estimates of α_w^{tree} were based only on estimates of α_w^{pool} that coincided in time with isotope measurements used to determine f , the model performed quite well in predicting the time series of daily α_w^{tree} as well. Figure 2.5 shows predicted values of α_w^{tree} (black

symbols) as well as those derived from daily estimates of α_w^{pool} (boxplots), aggregated and shown as a function of weeks since snowmelt.

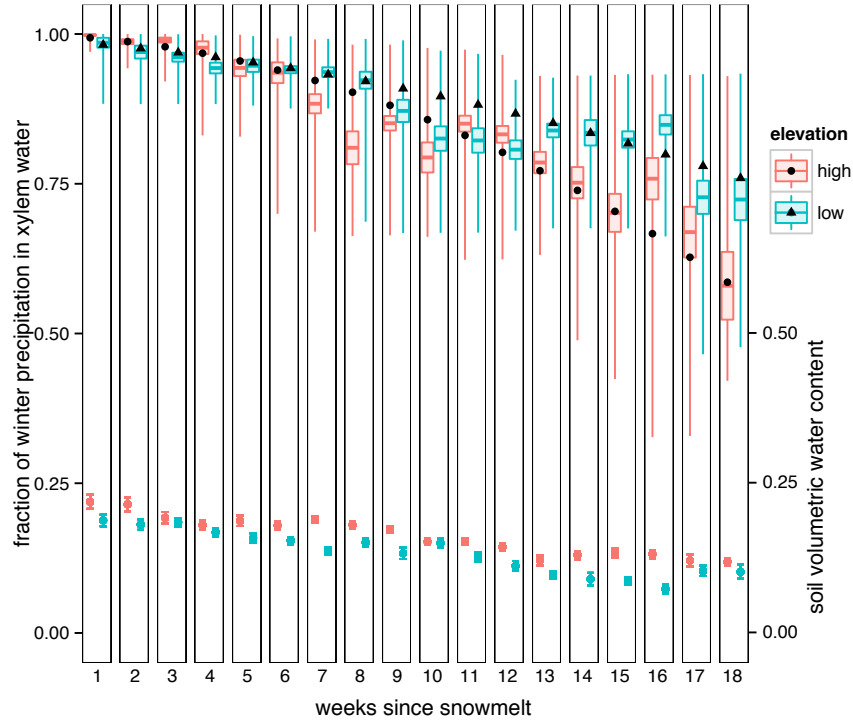


Fig. 2.5. The fraction of winter precipitation present in xylem water (α_w^{tree}) on each week following snowmelt (box-plots, left-axis) at high and low elevations. Black points show the predicted values of α_w^{tree} from the model $\mu\{\sqrt{\alpha_w^{tree}} \mid week\} = \beta_0 + \beta_1 \times week + \beta_3 \times I.high + \beta_4 \times week \times I.low$. Shape denotes elevation. The lower set of points (right-axis) shows the mean values of Θ at high and low elevations.

The contribution of winter precipitation to radial growth and estimates of biomass addition

The timing of radial growth relative to snowmelt varied by elevation, with high elevation trees beginning growth roughly 5 days after snowmelt at high elevation sites on average and low elevation trees beginning growth closer to 20 days after snowmelt at low elevation sites. Tree growth at high elevation peaked 65 days after snowmelt vs. 72 days

for low elevation sites, and growth ceased in trees at both elevations approximately 125 days after snowmelt, thus the growing season for low elevation trees was approximately 15 days shorter than for high elevation trees (Fig. 2.6, right axis).

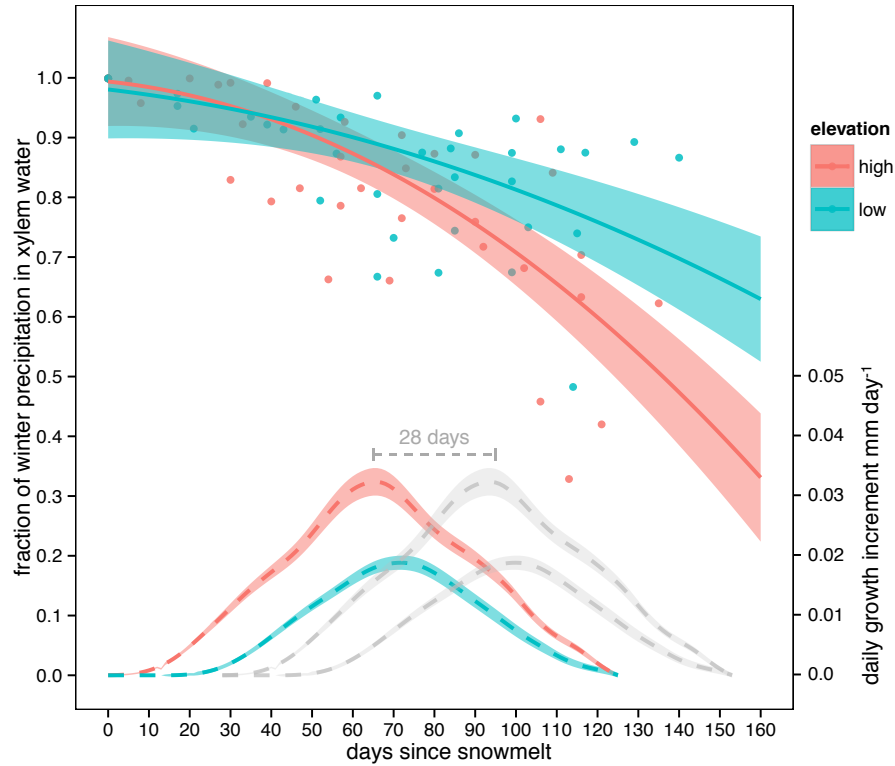


Fig. 2.6. The fraction of winter precipitation present in xylem water (α_w^{tree}) on each day following snowmelt (points, left-axis) at high and low elevations. Lines (left-axis) show the best-fit regression line for each elevation and shading shows the 95% confidence interval for the line. Dashed lines (right-axis) show daily stem radial growth rates (mm day^{-1}) at high and low elevations. Gray lines show the estimated rate of addition of biomass to the annual growth ring (unit-less – not measured).

When we assessed the contribution of α_w^{tree} to total annual radial growth (ARI_w), we found that α_w^{tree} increased in a sigmoidal fashion in response to time since snowmelt, with high and low elevation trees following slightly different trajectories. These trajectories led to an estimate of $\text{ARI}_{\text{winter}} = 87.5\%$ for low elevation trees and 84.0%

for high elevation trees, attributing 3.5 percent (95% CI = 0.1% to 6.8%) more growth to winter precipitation in low elevation trees compared to high (Fig. 2.7).

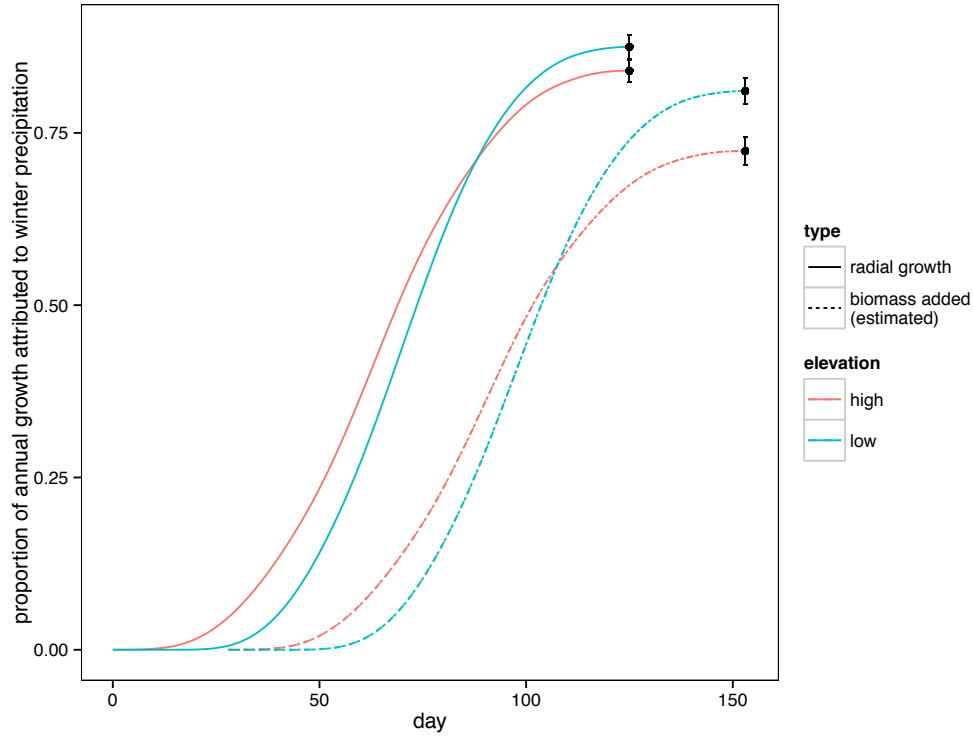


Fig. 2.7. The proportion of annual growth attributed to winter precipitation on each day following snowmelt (solid lines) at high and low elevations. Dashed lines show similarly estimated proportions of biomass production attributed to winter precipitation.

Because the majority of radial growth occurs quickly after snowmelt, when differences in α_w^{tree} across elevations diminish later in the season, elevation differences in ARI_{winter} are likely to be accordingly small. However, a broad survey of temperate forest xylem phenology conducted by Cuny *et al.*, (2015) clearly showed that the addition of biomass, and thus carbon, to an annual growth ring lags behind radial growth by approximately 28 days. The implications of this for the role α_w^{tree} in biomass production may be considerable, as this period is typically the driest time of year across much of the

west. Thus, in a post-hoc analysis we made the simple assumption (based on data from Cuny *et al.*, 2015) that the temporal distribution of biomass addition to xylem was reasonably similar to that of radial growth, and re-assessed the role of α_w^{tree} on biomass accumulation distribution with a 28 day lag (Fig 2.6, grey curves). In so doing we estimated that the percent contribution of α_w^{tree} to biomass added over the year was 81.1% for low elevation trees and 72.4% for high elevation trees, attributing 8.7% percent more biomass to α_w^{tree} at low elevations than at high (Fig. 2.7).

DISCUSSION

In light of recent studies that show a declining trend in snowpack in the western U.S. (Mote *et al.*, 2005; Pederson *et al.*, 2011), and the importance of winter snowpacks as moisture stores for dry western summers (Hamlet *et al.*, 2005), the first two goals of this study were to quantify the importance of snowmelt as a water source, and to estimate its role in tree productivity. The third goal was to assess if tree response would vary across the landscape; in other words, how important is topographic position (elevation, degree of divergence) in determining where trees access water and what is the seasonality of this water? Within the scope of our study, we found that lower elevation Douglas fir trees were more dependent on moisture delivered prior to snowmelt than their higher elevation counterparts. Although the effect of elevation on winter water use small in magnitude, the pattern was clear. However, this small difference may reflect the relatively minor elevation difference (c. 350m) between high and low elevation sites studied. If the elevation gradient in winter water use estimated here (c. -1% 100m⁻¹) holds over a larger range of elevations, the importance of winter water over large regions with

significant topographic relief (i.e the American West) may vary considerably. Perhaps the most obvious implication here is that the influence of winter weather (and in the long term climate) on forest water use during the summer is elevation dependent. Thus, while we cannot definitively say that decreases in snowfall, snowpack storage, and advances in melt timing hold greater consequences for low elevation forests than for higher elevation ones, our insights into how vital atmospheric water is ultimately delivered to growing trees serves as an important piece in the puzzle.

Understanding the processes underlying variation in summertime use of winter water

Stable isotopes of water have now long been used to explore where trees source water from within the belowground storage pool, however, in the years since Dawson & Ehleringer (1991) pioneered the approach to demonstrate that streamside trees may not necessarily utilize stream water, much of the subsequent research has been focused on source water apportionment between vadose zone and groundwater pools (Evaristo & McDonnell, 2017). This is despite observations that, globally, temperate forests are primarily rooted in shallow soils less than 1m deep where key nutrients are readily available (>80% of total root biomass) (Jackson *et al.*, 1996; Jobbagy & Jackson, 2001). While such forests may have access to water at much deeper depths in some cases (Canadell *et al.*, 1996), the sheer proportion of root biomass and resulting root surface area present in relatively shallow soils suggests that shallow soil layers should be the primary source of water for these trees (Evaristo & McDonnell, 2017).

We found only weak evidence to support our hypothesis that topography organizes patterns of rooting depth in a predictable way, probably because topographic

factors were a weak predictor of soil moisture within the sites at relatively short time scales. Soil moisture in our study was highly variable, and even within a small area, precipitation events lead to highly heterogeneous soil moisture values. However, we found that the average soil moisture condition (e.g. across an entire season) of a given location proved to be a very important variable controlling effective rooting depth (Fig. 2.4) (Flanagan *et al.*, 1992; Grossiord *et al.*, 2017). This suggests that long-term soil moisture conditions are a primary driver of effective rooting depth and that trees likely sourced water from a consistent depth somewhat irrespective of how much water was available in the soil profile (West *et al.*, 2007; Williams *et al.*, 2015). Furthermore, in cases where long-term soil moisture conditions are well predicted by topographic variables, we could expect topography to control spatial patterns in rooting depth as well. While our accounting of snow and rain inputs to soils did suggest that contributions of moisture from winter precipitation evolved differently over the season between high and low elevation soils (Fig. 2.3b), again, the large degree of spatial variability in soil moisture precluded a statistically robust assessment of the role of topography in this process.

The quantity of winter precipitation in water used by trees, however, is a function of both where trees get water from (assessed here as effective rooting depth) as well how much of that water was delivered to the landscape in winter. This study shows that across an elevation difference, the combined effects of rooting depth and winter soil moisture supply can be directional in such a way as to generate significant differences in α_w^{tree} over time (Figs 2.5 & 2.6). Despite considerable noise in the isotope data, we observed that

high elevation trees sourced $22.4\% \pm 13\%$ (mean $\pm$ SE) more water from the upper soil moisture pool than low elevation trees. At the same time, the majority of summer rain delivered to low elevation soils did not penetrate to the deep soil moisture pool and was thus, not likely available to the more deeply rooted trees at dryer, lower elevations (Fig. 2.4) (Reynolds & Knight, 1973; Hu *et al.*, 2010). The opposite was true at higher elevations with trees sourcing a higher proportion of water from shallow soil moisture pools which, by mid-summer, were c. 50% summer rainwater (Fig. 2.3b).

While our results suggest that seasonal water use differs between high and low elevation trees, this is not to say that trees at low elevation rarely use summer precipitation. Figure 2.5 illustrates that periodic increases in soil moisture due to summer rains tend to lead to brief decreases in the reliance on winter precipitation at both high and low elevations. Also, our sampling scheme precluded us from sampling soil and xylem samples after every precipitation event. There may have been instances when rain fell at the site and trees did take up that shallow rain water for several days post rain event; however, because we were sampling every two weeks, it was possible that we may have missed these uptake events in some cases, while capturing these uptake events in other cases. In reality, unknown time lags exist between when roots at varying distances from the bole take up water and when it appears in the bole xylem of the of the tree, and it is almost certainly impossible to perfectly sample the true soil water end members for a soil compartment mixing model, as this would require digging up the entire tree and all of the soil it has access to. For example, our results suggest that trees at the driest site actually source water from slightly deeper than our defined deep soil water pool (Fig. 2.4,

lowest f value < 0); however, dense regolith prevented practical sampling of deeper soils. We believe this is one of the main reasons why it is difficult to partition shallow and deep water use using isotopes at the bi-monthly time scales. However, over the long term, a strong trend average rooting depth dictated by soil moisture emerged and proved very robust (Fig. 2.4). We believe these results represent the overall water use-strategies of trees across this landscape and further supports our hypothesis that certain trees growing in drier landscape positions use deeper water (Grossiord *et al.*, 2017).

The temporal distribution of α_w^{tree} , soil moisture, radial growth, and biomass production

For trees in the northern Rockies and across much of the high elevation terrain of the western U.S., the summer growing season is somewhat of a race against time, with cold temperatures limiting the onset of growth (Oribe *et al.*, 2003; Rossi *et al.*, 2008) and water stress limiting the duration of growth (Martin *et al.*, 2017). Here we see that the rapid growth in size exhibited by trees in early summer is largely reliant on winter moisture, which accounted for 84% and 87.5% of annual radial growth in high and low elevation trees respectively (Fig 2.7). This was also a time of plentiful soil moisture with Θ values immediately following snowmelt nearly twice those of mid to late summer (Fig 2.5, right axis). Between 60 and 70 days post-snowmelt, we observed indications of radial growth limitation manifest in decreasing growth rates (Fig. 2.6, right axis) that were strongly associated with soil moisture limitation and atmospheric moisture demand (Martin *et al.*, 2017). As soil moisture declined, atmospheric demand increased, and water stress likely became more of a detriment to growth, the dependence on winter moisture also increasingly diverged for high and low elevation trees. This means that

lower elevation trees were not only under more water stress, but were also more dependent on stored winter water as the season progressed. While other studies in western U.S. conifer forests have found similar patterns of water limitation on productivity using NDVI data (Trujillo *et al.*, 2012), modeling efforts (Christensen *et al.*, 2008; Tague *et al.*, 2009), this is one of the first studies that directly links winter precipitation in xylem water to the seasonal patterns of stem growth.

Collectively, these results beg the questions: what does the combination of reduced snowpacks and warmer summers mean for lower elevation trees, and how much more vulnerable are they to increasing aridity than their higher elevation counterparts? Within our study area, the magnitude of radial growth at low elevation sites was nearly half of that of high elevation sites suggesting a strong disparity in the quality of growing conditions across a relatively small elevation difference (Martin *et al.*, 2017). Increased mortality of ponderosa pine populations growing in lower elevation forests has already been documented (Allen & Breshears, 1998; Paz-Kagan *et al.*, 2017) and studies show that these species have high variability in the sensitivity to climate (McCullough *et al.*, 2017). Our results support this growing body of literature suggesting that ponderosa pine growth may be greatly hindered under continuing decreases in snowpack.

Also intriguing, but only indirectly addressed in this study are the consequences of such a scenario for biomass production and subsequent long-term carbon sequestration in xylem tissues. While the role of immediate water availability in this process is difficult to quantify, the disparity in winter water use in high and low elevation trees is even greater during the time that xylem tissues are adding biomass via the process of cell wall

thickening (Cuny *et al.*, 2015). Dendrochronological surveys of the role of climate in determining maximum ring density suggest that this process is more sensitive to temperature than precipitation (Briffa *et al.*, 2002; Frank & Esper, 2005); however, only cells that are able to divide and expand are able to later fortify their cell walls with carbon. While earlywood forms under relatively mesic spring conditions, dense latewood cells are formed later, during drier soil conditions. However, although soils are typically dry during this period of latewood formation, stored winter water still makes up the majority of soil moisture, and in fact more likely to have an effect on the formation of latewood than earlywood. It follows then that lower elevation trees that receive little supplemental moisture from summer rains may be at a particular disadvantage relative to higher elevation trees in the formation of latewood.

Our results begin to untangle the highly complex relationship between spatiotemporal patterns of moisture delivery to forest ecosystems and the co-evolved strategies trees use to access water from their environment. Considering the rate of both observed (Portmann *et al.*, 2009) and projected (Seager *et al.*, 2007) changes to the hydroclimate of the western U.S., and its effects on prevailing patterns of both moisture supply and demand (Portmann *et al.*, 2009), a key question in understanding what our results mean for future forests arises; how plastic are trees in their physiological and morphological responses to these changes? Recent observations of widespread tree mortality associated primarily with rising temperature (Allen *et al.*, 2010; Williams *et al.*, 2013) suggest that in many cases, trees are not able to adapt to new climate conditions fast enough to survive the associated stresses. Considering our findings, already

document shifts in moisture delivery and storage (Mote *et al.*, 2005; Knowles *et al.*, 2006; Pederson *et al.*, 2011) can be expected to alter the timing and possibly the spatial distribution of soil moisture recharge as well as the loss of soil moisture to evapotranspiration (Hamlet *et al.*, 2007). To the degree that adaptation of tree rooting patterns can keep pace with such changes, the effects on tree function and growth may be minimal but this is not well understood. Our results support the notion that not all trees are likely to face the same challenges in a changing climate and landscape characteristics such as the elevation of a forest will likely dictate both the kind of challenges trees face as well as what type of adaptation is necessary to cope with changing conditions.

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CHAPTER FOUR

UNPRECEDENTED DROUGHT INTENSITY TRACKS RECENT
WARMING IN THE HEADWATERS OF THE UNITED
STATES' LARGEST RIVER BASIN

Contribution of Authors and Co-Authors

Manuscript in Chapter 4

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Contributions: Developed the streamflow data set and reconstructions, led the analysis, wrote, and edited the manuscript.

Co-Author: Gregory Pederson

Contributions: Designed the research, developed the tree ring data set, wrote, and edited the manuscript.

Co-Author: Connie Woodhouse

Contributions: Designed the research and edited the manuscript.

Co-Author: Edward Cook

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Contributions: Developed the temperature reconstruction and edited the paper

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UNPRECEDENTED DROUGHT INTENSITY TRACKS RECENT WARMING IN THE HEADWATERS OF THE UNITED STATES' LARGEST RIVER BASIN

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Abstract

Across the Upper Missouri River Basin, the recent drought of 2000-2010, known as the “Turn of the Century Drought”, was more intense than any in the instrumental record including the Dust Bowl drought, and was potentially the most intense accumulated water deficit in the last 1200 years. Since 1900, a consistent trend of increasing precipitation across the upper basin translated to modest declines in annual discharge, with recent unprecedented warming responsible for driving drought intensities greater than any observed over the last 12 centuries. We examine 1200 years of streamflow estimates from a network of 31 new tree-ring based reconstructions for stream gages across the Upper Missouri Basin in the context of reconstructed temperature. We find that

temperature has increasingly influenced the intensity of low-flow events in the basin, especially since the late 20th century, and may drive future acute water shortages in ways unseen over the last millennium.

Introduction

Few climatic phenomena transcend the focus of scientific study to command such societal attention as persistent drought. In terms of its impact on water resources, the stress of prolonged drought can disrupt agricultural systems and economies (National Climate Data Center, 2003; Howitt *et al.*, 2014; Wise *et al.*, 2018), challenge river system control and navigation (US Government Accountability Office, 1992; Mehta *et al.*, 2011), and complicate management of sensitive ecological resources (Garrick *et al.*, 2008; DeLonay *et al.*, 2009). Among the collective psyche of many North Americans, the historical benchmark for severe drought remains the “Dust Bowl” drought of the 1930’s. However, ample evidence has emerged to suggest that several, regionally specific drought events of the 21st century now rival the dustbowl in historical prominence including the 2012-2014 California drought (Griffin & Anchukaitis, 2014), and the 2000-2004 (Prairie *et al.*, 2008), or 2000-2015 (Udall & Overpeck, 2017) droughts in the Colorado River basin, all of which are unprecedented during the observed period.

Conspicuously absent from the discussion of remarkable drought has been the Missouri River, the full reach of which constitutes the longest river in the North America, and drains the largest main stem river basin in the United States (Seaber *et al.*, 1987). In terms of hydrologic drought, the Upper Missouri River Basin (UMRB) likely experienced

the most extreme conditions of the major river basins during the Dust Bowl considering the spatial coverage of that event (Diaz, 1983; Stahle *et al.*, 2007). However, like California and the Upper Colorado, the early 21st century has been remarkably dry across the UMRB (Cook *et al.*, 2010). In fact, our assessment of streamflow for the UMRB suggests that the west-wide drought period of 2000-2010, termed “The Turn of the Century Drought” by Cook and colleagues, 2010 (Cook *et al.*, 2010), establishes the beginning of this century as a period of observationally unprecedented and sustained drought across the UMRB, surpassing even the Dust Bowl years.

The early 21st century has also been characterized by unprecedented temperatures, with northern hemisphere summer temperatures potentially exceeding any in the last 1200 years including the warmest years of the medieval climate anomaly (MCA) (Anchukaitis *et al.*, 2017). The unprecedented nature of both recent temperatures (Anchukaitis *et al.*, 2017) and droughts in the west (Prairie *et al.*, 2008; Griffin & Anchukaitis, 2014; Udall & Overpeck, 2017) has led numerous authors to revisit the role of temperature in the water balance of the new millennium (Weiss *et al.*, 2009; Williams *et al.*, 2015; Woodhouse *et al.*, 2016; McCabe *et al.*, 2017; Udall & Overpeck, 2017). As a result, a growing body of evidence suggests that across much of the American West, the moisture demands of warming are reducing the effectiveness of precipitation and ultimately the resulting surface water supplies (Hamlet *et al.*, 2005; Andreadis & Lettenmaier, 2006; Williams *et al.*, 2015; Woodhouse *et al.*, 2016; McCabe *et al.*, 2017; Udall & Overpeck, 2017; Woodhouse & Pederson, 2017).

Here we turn our focus to the recent Turn of the Century Drought in the UMRB.

We adopt a management-focused, operational definition of drought developed by the U.S. Bureau of Reclamation (BOR) for the Upper Missouri River (USBOR, 2018) and couple this definition to a measure of drought *intensity*, that accounts for both the duration *and* severity of an event. We examine the recent role of increasing temperature on natural streamflow in the UMRB and contextualize this relationship and its role in basin-wide drought over the last 1200 years using the most comprehensive network of paleo- hydrologic and climatologic records yet developed for the region.

Streamflow and climate

The waters of the Missouri River originate primarily in the Rocky Mountains of Montana, Wyoming, and Colorado (Fig 3.1.) where high elevation catchments capture and store large volumes of water as winter snowpack to be released in late spring and early summer (Wise *et al.*, 2018). This mountain water is an important component of total annual flow on the Missouri, accounting for roughly a third of annual discharge to the Mississippi river (Norton *et al.*, 2014), most of which is delivered during the critical warm season months (May-September). Recent analyses have shown universal declines in water-year streamflow on every major tributary channeling water to the lower basin since 1960 (Norton *et al.*, 2014), and a consistent decrease in the proportional contribution of the upper basin to total streamflow on the Missouri (Wise *et al.*, 2018).

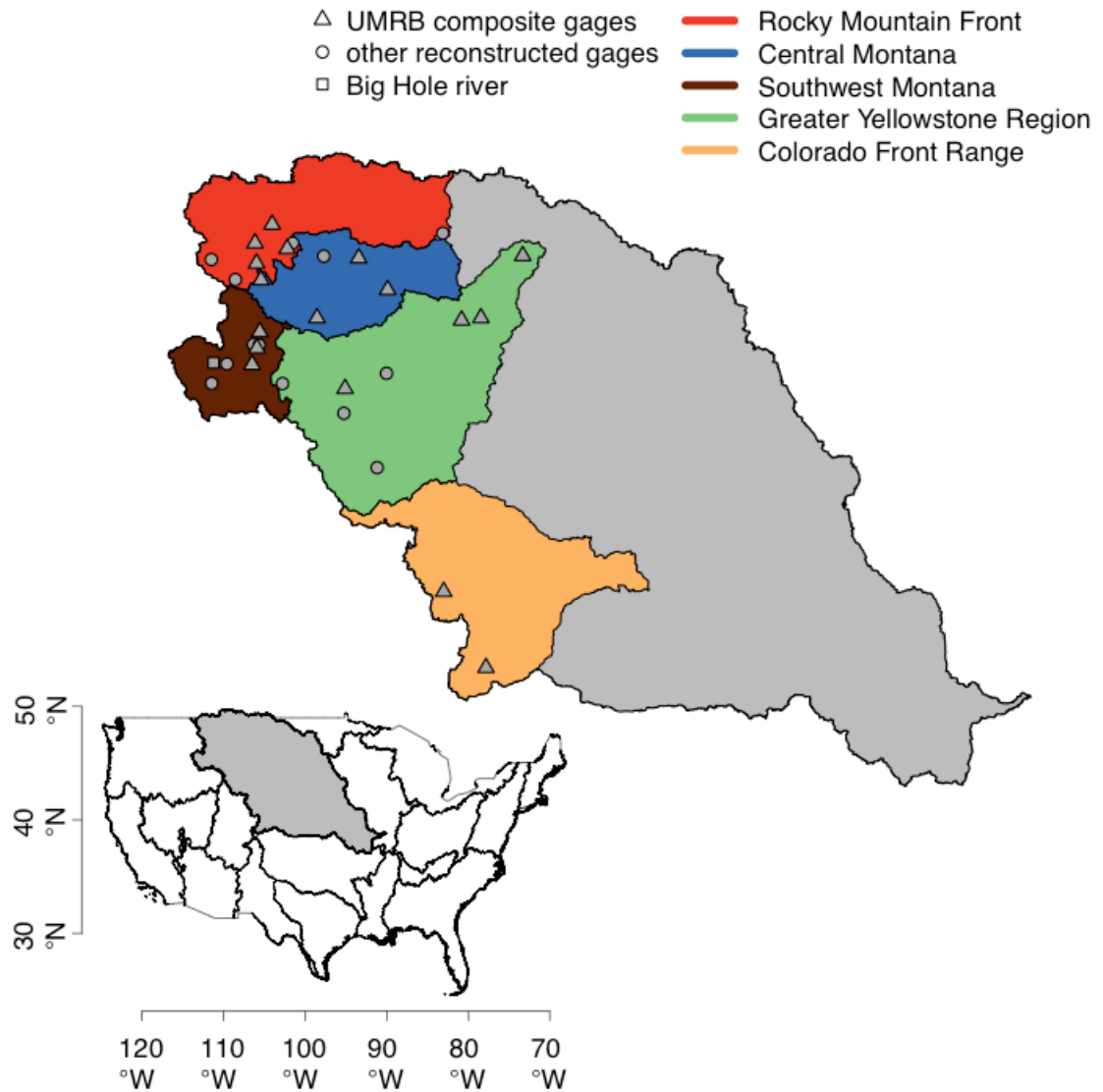


Figure 3.1. The Missouri river basin and its sub-regions. The location of the Missouri River Basin within the continental United States (grey watershed – lower left) and the location of the five hydrologically distinct sub-regions (colored watersheds) that define the Upper Missouri River Basin (UMRB). Reconstructed gages are shown as grey points and those gages used to develop the estimate of basin-wide mean annual streamflow are shown as triangles.

Across much of the UMRB, winter precipitation has historically been the primary driver

of streamflow, with April 1 snow water equivalent (SWE) and Oct-Jan precipitation accounting for at least half of the inter-annual variability in observed streamflow from the primary headwaters regions in Wyoming and Montana (Wise *et al.*, 2018). However, increasing spring temperatures have been implicated in significant snowpack declines in the region beginning as early as the 1950's and intensifying since 1980 (Pederson *et al.*, 2011, 2013). By 2006, these declines amounted to a 25-year average, negative snowpack anomaly that spanned nearly the entire North American Cordillera, the depth of which was likely unrivaled in the last 800 years (Pederson *et al.*, 2011). Meanwhile, both annual temperature and annual precipitation have generally increased across the basin since 1950 (Portmann *et al.*, 2009).

To assess how these climatic changes align with 20th and 21st century streamflow in the basin, we compiled 31 naturalized streamflow records from the region, covering nearly every major sub-basin in the UMRB (Supplementary Table S1, see Supplementary Information for full details on data and methods). We implemented a hierarchical clustering of streamflow to identify five hydrologically distinct regions across the UMRB, which are represented in a roughly north-south fashion by the Rocky Mountain Front, Central Montana, Southwest Montana, the Greater Yellowstone Region, and the Colorado Front Range (Fig 3.1). We then generated composite records of streamflow for each sub-region using *z*-scores of flow from constituent gage records and coupled these to regional records of temperature and precipitation to determine the relative forcing of these two key water balance components on observation-period estimates of natural streamflow in each sub-region. For each year of the common observational period, the

resulting estimates (Fig. 3.2, points) quantify the relative magnitude and direction of forcing (enhancing or reducing flow volumes) from the combined influence of temperature and precipitation on streamflow (Fig 3.2, line). These estimates also explain which variable (temperature or precipitation) was dominant in the total forcing for a given year (Fig. 3.2, color).

A striking, yet familiar feature emerged from our analysis of observed streamflow and climate for the UMRB, seen as an abrupt shift in the influence of temperature on

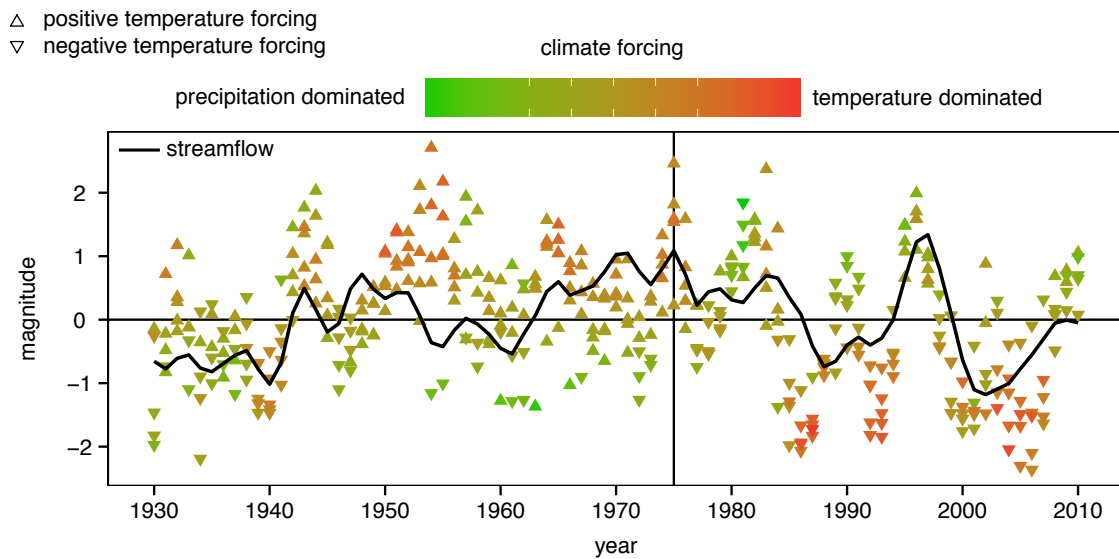


Figure 3.2. Climate forcing of streamflow. The relative forcing of precipitation and temperature on basin-wide mean annual streamflow (black line) in the Upper Missouri River Basin (UMRB). Colored points show the individual relative forcing estimates for each sub-region of the UMRB for each year. Colors denote which climate variable (precipitation or temperature) was dominant in the combined forcing of streamflow and the y – axis shows the relative magnitude and direction of that combined forcing. The direction of the arrows shows the direction of forcing of the temperature component of that combined forcing (enhancing or reducing streamflow). All data shown are derived from the 5-year cubic smoothing splines of streamflow and climate data.

streamflow c. 1975 (Fig. 3.2, vertical line). This point in time marks a near complete reversal in the climate forcing of streamflow across all sub-basins of the UMRB in that prior to 1975, temperatures generally exert a positive forcing effect on streamflow whereas, after 1975, temperature acts almost universally to suppress streamflow basin-wide, driving average UMRB flows in the late 80's to levels not seen since the 1930's, and surpassing those of the Dust Bowl by the early 2000's. Notably, reduced runoff efficiencies due to increased temperature have been implicated in very similar reductions in flow over the same timeframe in the Upper Colorado and the Rio Grande as well (Woodhouse *et al.*, 2016; McCabe *et al.*, 2017). Meanwhile, the temporal pattern of reduced streamflow and the shifting influence of temperature on water supplies in the UMRB mirrors, almost exactly, the severe declines of snowpack in the Northern Rockies from the mid 70's to late 80's, which has been attributed in large part to warming spring temperatures (Pederson *et al.*, 2013). A similar, temperature-forced snowpack decline in the Southern Rockies reached a peak in the early 2000's (Pederson *et al.*, 2013), coincident with the driest years of the Turn of the Century Drought.

We examined the seasonal correlations of temperature with annual streamflow and found that mean annual flow was most closely correlated with temperatures in early spring across the higher elevations of the Greater Yellowstone Region and Southwest Montana but was more closely related to summer temperatures on the Rocky Mountain Front and the Colorado Front Range. Seasonal correlations between temperature and annual flow were weakest in winter, but were clearly bi-modal (especially in Central Montana), also showing stronger correlations with temperatures in the fall months at the

beginning of the water year. This suggests not only the influence of temperature on antecedent moisture conditions prior to the buildup of winter snowpack (Woodhouse *et al.*, 2016), but also a greater impact of summer evaporation on the annual water balance (Wetherald & Manabe, 1995; McCabe *et al.*, 2017).

How unique was the Turn of the Century Drought in the UMRB?

An abundance of paleoclimatic and paleohydrologic data suggests the occurrence of very severe drought events in the American Southwest (Douglas, 1929, 1935, Woodhouse *et al.*, 2006, 2010), California (Stine, 1994), and the Southern Great Plains (Stahle *et al.*, 2000, 2007) during the last millennium. A handful of the drought events, often referred to as “megadroughts” are unrivaled in recent times in terms of either severity, duration, or both. Currently, no such analysis exist for the UMRB. In addition, a significant challenge in developing a cohesive picture of drought history in North America has been the definition of drought itself. With respect to paleohydrologic records, droughts have been defined and quantified by their duration (Stine, 1994), low-frequency magnitude (Woodhouse *et al.*, 2006, 2010; Stahle *et al.*, 2007; Prairie *et al.*, 2008; Cook *et al.*, 2010), peak year magnitude (Cook *et al.*, 2010, 2014), and spatial extent (Mitchell *et al.*, 1979; Cook *et al.*, 2004). As such, the relative significance of drought events over time can vary depending on how they are first defined, and subsequently quantified.

Severity and duration are characteristics of drought that can carry different consequences for water users and can work in tandem to either compound, or mitigate the negative impacts of a particular event. However, classifying droughts by these metrics

independently may fail to capture their combined impact. To address this shortcoming, we borrowed from the civil engineering approach to quantifying the impact of precipitation events where the *intensity* of an event is equal to the cumulative magnitude (severity) of the event divided by its duration (McCuen, 1998). In the case of streamflow, we quantified the relative *intensity* of drought events using a similar approach termed the drought intensity index (DII) such that;

$$DII_n = \frac{\sum_{i=1}^n \frac{x_i - \bar{x}}{s}}{n} \quad (\text{eqn. 1})$$

where x_i is the annual flow on the i^{th} year of the drought, $\bar{x}$ is the mean of the entire reconstructed flow record, s is the standard deviation of the entire reconstructed flow record, and n is the year of the drought being assessed. Thus DII is the cumulative streamflow deficit normalized to unit deviation, (i.e. z-scores) for a point in time during a drought, divided by the number of years the drought has been ongoing. DII has several appealing features. First, because it is calculated on z-scores of annual flow, droughts can be compared across rivers of different size. Also, DII is an annual assessment of drought status that combines information about not only the current severity of drought, but also the preceding severity and duration of the event. This is important because the true impact of drought is a matter of whether water is available when it is needed, but this is largely determined by the preceding characteristics of the drought itself.

To place Turn of the Century Drought into the context of long-term hydroclimatic variability in the UMRB, we developed a network 31 of tree-ring based reconstructions of streamflow at key, water manager-selected gages within the five sub-regions of the UMRB. The reconstructions span approximately 1200 years, skillfully

capture the observed variation of streamflow across the basin, and were specifically designed for the assessment of drought conditions over time (Supplementary Table S2, Supplementary Figs. S2-S4). Using this network of reconstructed streamflow records from across the UMRB, we developed a record of basin-wide mean streamflow beginning in year 800 and spanning the Turn of the Century Drought through 2010 (Fig 3.3b). From this record we identified drought years using the BOR's drought definition described in the Bureau's 2017 Climate Change Impacts Assessment for the UMRB (USBOR, 2018) (Supplementary Information, methods). We then quantified DII for each drought year in the record resulting in a 1200-year time series of drought intensity for the basin (Fig. 3.3c).

Contrary to our current view of historical extreme drought events in other major western river basins, over the past 1200 years, the Turn of the Century Drought was potentially unprecedented in its impact on the UMRB. Only a single event, evident in the early 11th century, rivals the intensity of the Turn of the Century Drought (Fig 3.3c). Yet this event was nearly half the duration of the Turn of the Century Drought (6 years vs. 10), and appears to have occurred during a period of below average temperature (Fig 3.3a), which likely would have limited terrestrial drought stress through enhanced evapotranspiration and reduced snow accumulation and persistence, which amplify the demands on hydrologic resources.

The Turn of the Century Drought lasted 10 years. In terms of duration, it was almost certainly surpassed by several drought events of the MCA, and particularly by very long droughts in the mid 15th and 17th centuries (Fig. 3.3c).

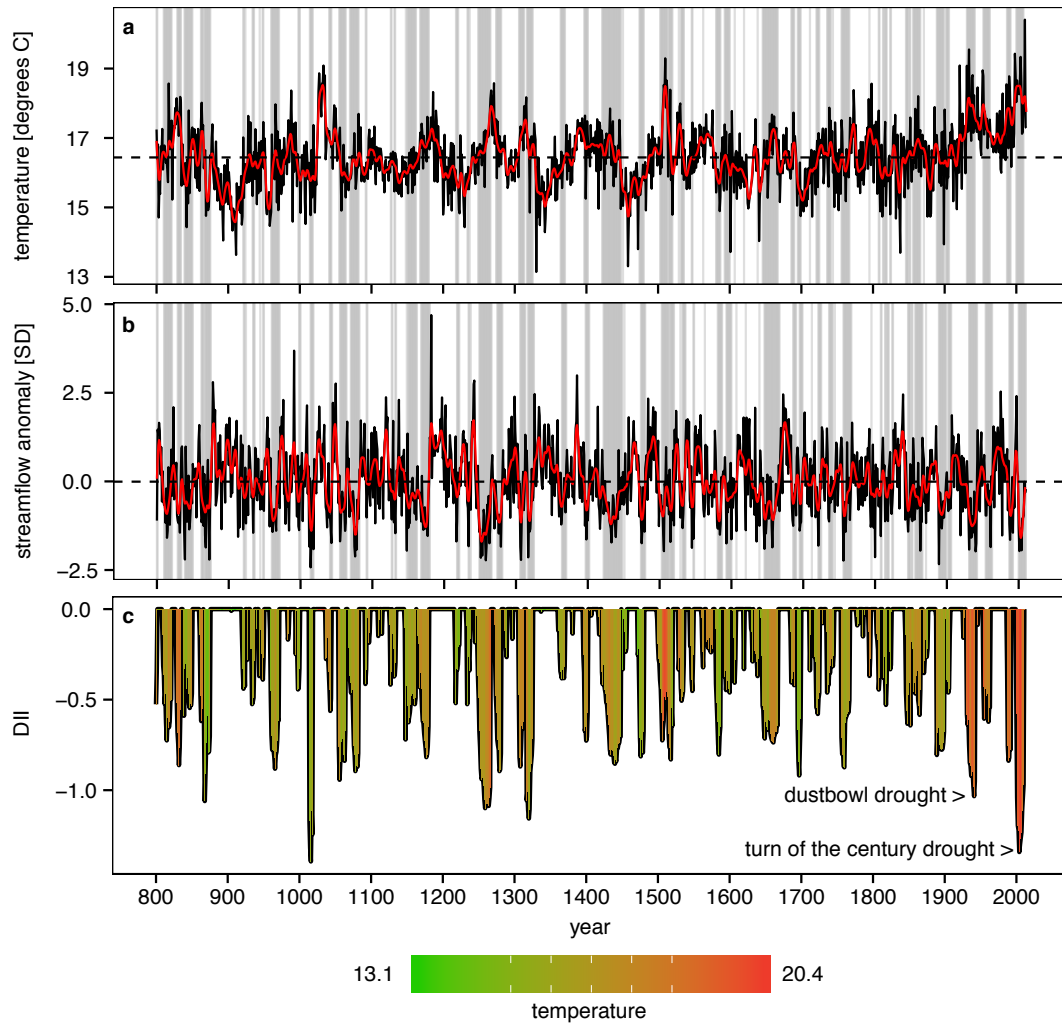


Figure 3.3. Temperature, streamflow, and drought reconstructions. The 1210-year time series of reconstructed temperature (a), streamflow (b), and the drought intensity index (DII) for the Upper Missouri River Basin (UMRB). Red lines in panels a and b are the 20-year cubic smoothing spline of temperature and streamflow respectively while dashed horizontal lines shown their respective mean levels. Color in panel c denotes temperature in the basin over the periods of various drought events.

On river systems with significant multi-year storage infrastructure such as the Upper Colorado, sustained drought may ultimately be most stressful to water resources through cumulative deficits to reservoir recharge. However, multi-year storage is limited in much

of the UMRB, where acute drought severity is immediately impactful and repeated drought years of high severity are likely more difficult to manage than in basins where large reservoirs allow managers to offset the deficits of the most severe low flow years with stored water.

The Turn of the Century Drought did not occur within the broader setting of a low-frequency trend in streamflow toward low flow that typifies the mega-droughts of the MCA and 1500's reported elsewhere in the West (Cook *et al.*, 2004, 2010). Rather, the early 21st century in the UMRB has been a period of increasing variance in high- to low-flow swings (Fig 3.2) which complicate management of water resources in the basin (USBOR, 2018). In the short eight years between the 1996 and 2004, the five-year spline of mean basin flow exceeds both the high and low extremes for the entire preceding observational period (Fig 3.2). Subsequently, the Turn of the Century Drought itself was abruptly ended by the UMRB's wettest year of the 21st century in 2011, a year which also saw the highest flows of the new century on the Upper Colorado (USGS, 2018).

Has the role of temperature in UMRB streamflow changed?

Relative to the last 1200 years, the 20th and 21st century temperature and DII records display conspicuous synchrony in the occurrence of extreme heat and drought intensity (Fig. 3.3 a&c). Comparing the relationship between streamflow and temperature over time using records of varying uncertainty is not straightforward (see discussion in Supplementary Information, methods). However, we explored the linkage between temperature and streamflow extremes over time by quantifying the likelihood of their co-occurrence (years where both temperature and streamflow values fall 1SD or

greater from their respective long-term means) over three distinct time periods. These were from 1750-2010, 1900-2010, and 1975-2010. Recall that 1975 marked a strong shift in temperature-streamflow relationship in the instrumental climate-streamflow analysis (Fig. 3.2). Figure 4a illustrates a striking increase in occurrence of hot-dry extremes in the UMRB since the beginning of the 20th century; with over 90% of extreme years falling into this category while less than 40% of extreme years would be classified as hot-dry years prior to 1900 (Fig. 3.4c). Restricting the definition of extreme years to that defined by temperature and streamflow variation since 1900, we find that approximately 70% of extreme years since 1900 were hot-dry years. However, since 1975, 5 of 6 extreme years have been hot-dry years (Fig. 3.4b), representing a roughly 10% increase in the likelihood of hot-dry extremes across the basin since 1975 (Fig. 3.4d).

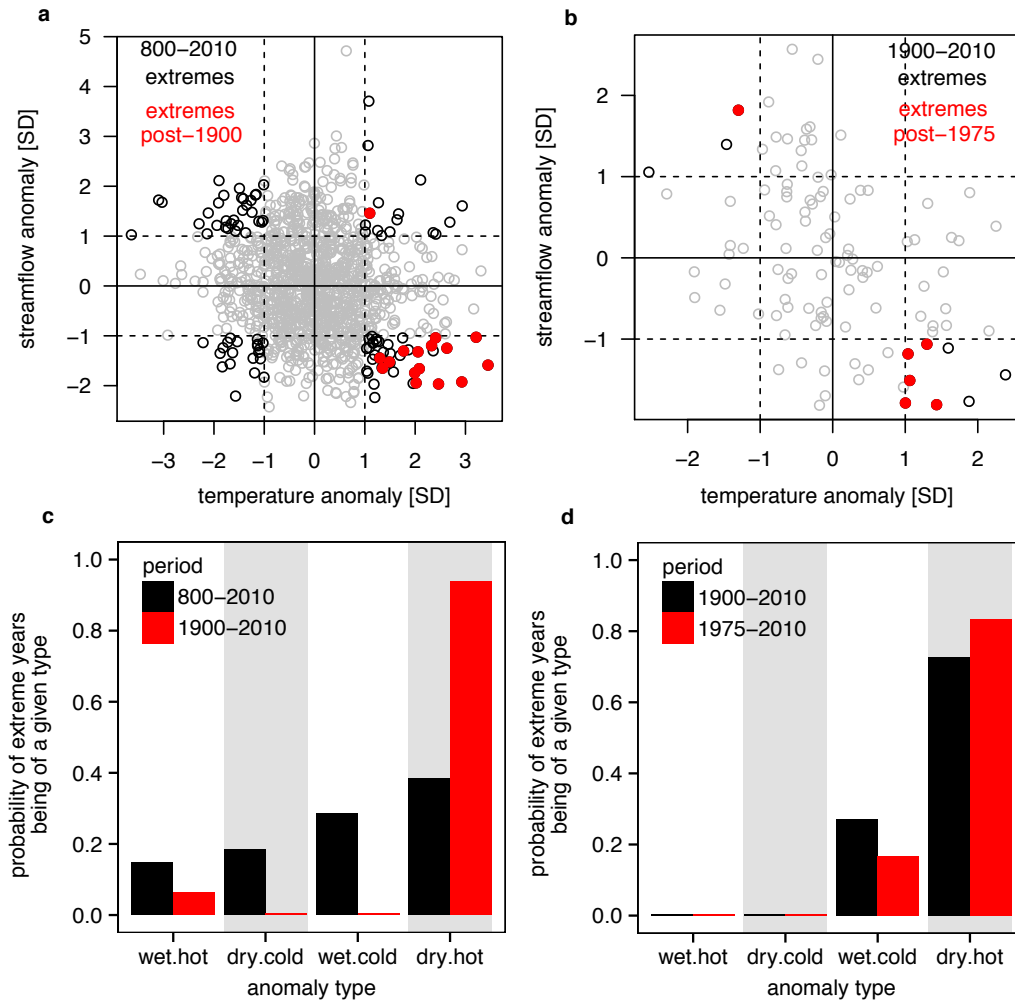


Fig 3.4. Extremes in the temperature-streamflow relationship. **a**, The relationship between temperature and streamflow anomalies for the period 800–2010 (grey points). Black points are show those years in which both temperature and streamflow values were greater than one standard deviation from their mean level (extremes). Red points show all of the extremes recorded from 1900 through 2010. **b**, The temperature streamflow anomaly relationship from 1900–2010 (grey points) and extremes (black points). Red points show the extremes recorded from 1975–2010. Here extremes are defined by the variability in the records from 800–2010. **c**, The probability of extreme years falling into a particular category (x-axis) for the period 800–2010 vs. 1900–2010. **d**, The probability of extreme years falling into a particular category (x-axis) for the period 1900–2010 vs. 1975–2010. Here extremes are defined by the variability in the records from 1900–2010.

In terms of the general correlation between streamflow and temperature, a similar pattern emerges (Fig. 3.5). Here we see a consistent increase in the strength of the negative relationship between temperature and streamflow over time with the period of 1975-2010 representing a roughly 35% increase in the correlation between the two since the end of the 19th century. This finding is in agreement with numerous assessments of the influence of temperature on streamflow and its drivers in recent years from across the west (Hamlet *et al.*, 2005; Andreadis & Lettenmaier, 2006; Williams *et al.*, 2015; Woodhouse *et al.*, 2016; McCabe *et al.*, 2017; Udall & Overpeck, 2017; Woodhouse & Pederson, 2017).

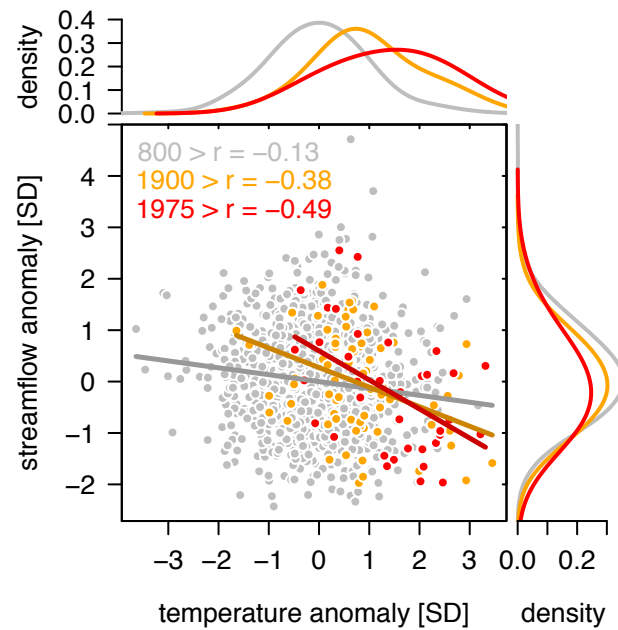


Figure 3.5. Correlations between streamflow and temperature over time. Color denotes the different time periods in the temperature vs. streamflow relationship over which correlation strength was assessed. The secondary axes show the smoothed distributions of streamflow and temperature over each time period assessed by kernel density estimation.

Spatial extent of severe droughts within the basin

In quantifying the average, basin-wide condition of major drought events across a region as large as the UMRB, an important question is whether severe droughts evident in the composite record reflect greater regional extremes, greater spatial extent, or both. We examined the spatial distribution of drought intensity during the six most intense droughts in the 1200-year drought record by comparing the mean level of DII within each sub-region over the duration of the drought event (Fig. 3.6).

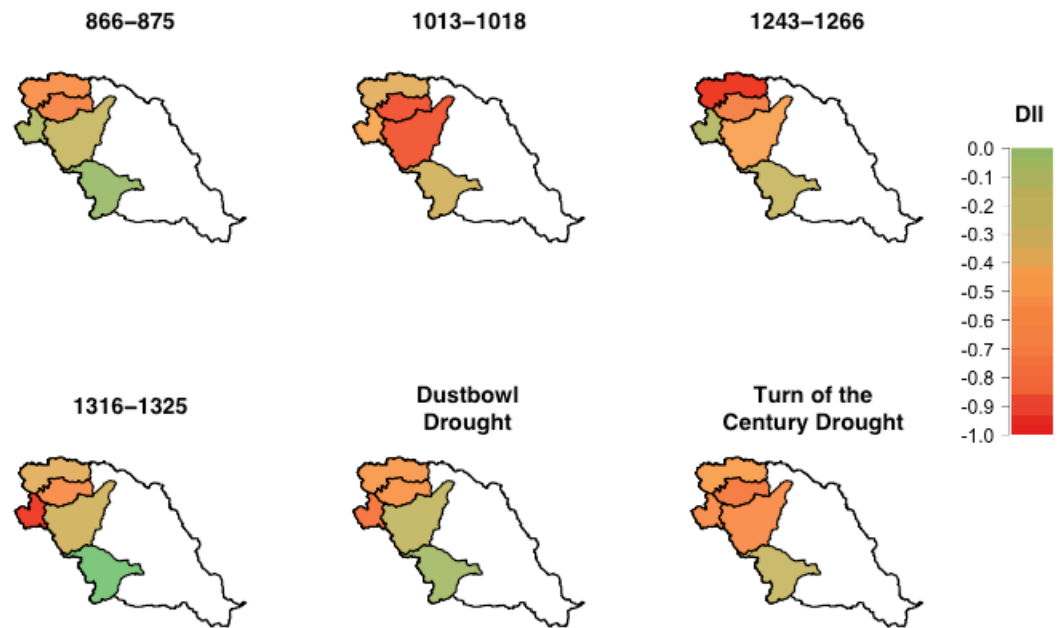


Figure 6. The spatial distribution of the six most intense droughts in the UMRB since 800 C.E. Color denotes the average level of DII in each sub-region of the basin over the period of the drought event.

The intense droughts of the 11th, 13th and early 14th centuries stand out for the localized occurrence of very intense drought conditions, however, in terms of the basin-wide-average drought intensity over the entire drought period, the Turn of the Century Drought

was slightly more intense than even the early 11th century drought, making it the most intense drought on record in this regard. In this sense, the Turn of the Century Drought was also the most widespread event with the entire northern tier of the basin under relatively intense drought conditions for much of the event (Fig. 3.6).

With the possible exception of the early 11th century event, drought intensity appears to follow the north-south dipole pattern also well reflected in paleo-reconstructions of snowpack accumulation across the Rocky Mountains (Pederson *et al.*, 2011) (Fig. 3.6). In all cases, basin-wide drought clearly reflects substantial drying across the northern tier of the basin, where the bulk of UMRB flows originate (Fig. 3.6). The northern tier is lower in terms of both mean and maximum elevation and is thus, more sensitive to temperature driven snowpack declines (Pederson *et al.*, 2013). Snowpack is historically the primary driver of streamflow in the UMRB (Wise *et al.*, 2018), and 20th as well as 21st century temperature-induced snowpack declines in the Northern Rockies essentially mirror drought intensity in the UMRB (Pederson *et al.*, 2011, 2013). Thus, it is likely that the remarkable intensity of the Turn of the Century Drought substantially reflects the vulnerability of this moderately elevated and snow-driven water supply to the effect of rising air temperature, primarily in spring, on mountain snowpack development.

Conclusions

In both instrumental and paleohydrologic records of streamflow in the UMRB, the Turn of the Century Drought appears nearly unrivaled in intensity and overall extent across the basin, a distinction that is mirrored by similarly unprecedented temperatures.

Most drought periods in the UMRB over the last 1200 years were synchronized with periods of above average temperature, however, analyses of recent temperature-drought dynamics presented here, as well as model projections of future drought conditions in the western United States (McCabe & Wolock, 2007; Dai, 2013) suggest that warming has increasingly amplified drought intensity in the UMRB, and that projected increases in temperature are likely to drive further increases in drought intensity in the future. Given this likelihood, and the stress that intense drought places on agricultural, economic, hydroelectric, and ecological resources throughout the basin, it is imperative to expand both the efficacy and flexibility of current water management strategies in the UMRB in order to cope with these new water resource challenges as they arise.

Supplementary Information

Naturalized streamflow data

For the purpose of this study, the Upper Missouri River Basin (UMRB) region ranges east to west from roughly 105° W longitude to the continental divide, and from north to south from the Milk River in Canada to the South Platte River in Colorado (Fig. 1). The region encompasses essentially 100% of the Rocky Mountain river basins that deliver water to the lower Missouri river via a network of 23 sub-drainages including the Milk, Marias, Teton, Sun, Dearborn, Big Hole, Beaverhead, Ruby, Jefferson, Madison, Gallatin, Judith, Smith, Musselshell, Yellowstone, Clark's Fork Yellowstone, Wind, Shoshone, Bighorn, Tounge, Powder, North Platte, and South Platte river basins (Supplementary Fig. S1).

An initial collection of 374 raw, estimated unregulated, and naturalized streamflow records were compiled from 252 gaging locations within Missouri River Hydrologic Region 10 (Seaber *et al.*, 1987). The streamflow records covered an average of 64yrs. The initial pool of streamflow records was first reduced to those located within the 23 sub-basins listed above, and then further reduced to only the naturalized flow records, or records deemed to reasonably represent natural flow with limited impacts from human activity (Slack *et al.*, 1994; Falcone, 2011). At least one naturalized, modeled-natural, or reasonably un-depleted streamflow record currently exists for each of these sub-drainages, and for several basins, natural flow estimates exist for multiple gaging locations. The final network of streamflow records used in generating the paleohydrologic reconstructions contains a total of 31 streamflow records (Supplementary table S.1 and Fig. S.1).

The majority of these records were estimated at existing USGS stream gaging locations with the exception of several records developed Cary and Parrett 1996 (Cary & Parrett, 1996) which were estimated at node locations in the Bureau of Reclamation's monthly streamflow accounting model. For these records, a drainage area correction factor was applied to the naturalized streamflow record to estimate naturalized flows at the actual gaging location from which the record was developed (see (Cary & Parrett, 1996) for correction factors and methodology). All original units of flow/discharge were converted to units of $\text{ft}^3 \text{sec}^{-1}$ as requested by basin water managers and stakeholders. .

Tree ring data

The Missouri River Basin and surrounding areas have an existing network of hydroclimatically sensitive tree-ring data that have previously been used to reconstruct snowpack, the summer Palmer Drought Severity Index, and streamflow in other basins (Cook *et al.*, 2004; Woodhouse *et al.*, 2006; Pederson *et al.*, 2011). The network contains a diversity of seasonal hydroclimatic sensitivities that are typically related to tree species, elevation, and topographic setting (Wettstein *et al.*, 2011; St. George, 2014). The diversity of climate-growth responses makes this network of tree-ring chronologies suitable for reconstructing streamflow for a network of gages located in a basin that exhibits complex climate and streamflow responses due to a range of factors related to geography, soils, and climate dynamics (Wise *et al.*, 2018).

In constructing the tree-ring database, we first acquired all publicly available ring-width chronologies located within 250 kilometers of the Missouri River Basin from the International Tree-Ring Database (‘(ITRDB) International Tree Ring Databank, (2014), National Centers for Environmental Information, NESDIS, NOAA, U.S. Department of Commerce.’) along with personally held records contributed by project collaborators. Next, the database was screened against naturalized flow records in the basin to identify chronologies with strong correlation to water year streamflow that were in need of recollection to bring the ring-width record as close to present as possible. As part of this project we updated five historical and produced four new ring-width chronologies along the Rocky Mountain front and the central Montana island ranges. For inclusion in the database all records were required to extend past the year 1800 Common Era (CE), which

resulted in a final dataset of 374 chronologies, 116 of which are new, updated, or were not previously publicly available (Supplementary Fig. S1). The database contains chronologies from 20 different species of tree spanning an elevation range of 89 to ~3700 m. The average chronology length is 576 years (1438 CE) with several records surpassing 2000 years in length. All newly acquired and updated ring-width records have been made available on the ITRDB at the time of this publication.

Chronologies were constructed by first removing the non-climatic biological growth curve from the individual ring-width records (i.e. a process known as “detrending”) following methods from (Melvin & Briffa, 2008). From this process, both the “standard” and “signal-free” versions of the chronologies were retained with the intention of assessing which type of ring-width chronology record replicates low-frequency streamflow variability reliably, and most similar to the observational record. Detrending and production of the standardized ring-width indices was performed in program “RCSsigFree47b_batch.app” (Cook *et al.*, 2016) using an age-dependent spline of unconstrained slope with initial spine stiffness set to 20-years (Melvin *et al.*, 2007). This individual-series detrending method should preserve low-frequency climate signals in a similar fashion to detrending with a negative exponential curve, but with some advantages over the juvenile growth years. However, the unconstrained slope of the detrending spline will remove positive monotonic growth trends if present. The final ring-width index chronologies were constructed by calculating a bi-weight robust mean from the power-transformed residuals of the individually detrended ring-width series. This method reduces the potential for trend distortion from end effects that can result

from the ratio method of chronology calculation. To correct for artificial increases in variance due to decreasing sample depth through time, variance stabilization was performed using the Rbar method with correction of trend in variance provided by an age-dependent spline. All chronologies were truncated before entering into the reconstruction framework when sample size fell below 5 series. The detrended chronologies used in the reconstruction framework described below are available online from the USGS (<https://doi.org/10.5066/XXXX>).

Climate data

The climate data used were the 4-kilometer (km) by 4-km gridded monthly temperature and precipitation data from the **P**recipitation-elevation **R**egression on **I**ndependent **S**lopes **M**odel (PRISM) dataset (Daly *et al.*, 2008) for water years (October-September) 1900 through 2014. The gridded monthly temperature and precipitation data were used as inputs to a monthly time-step water balance model (MWBM) from (McCabe & Wolock, 2011) to generate additional hydrologic variables related to streamflow. All hydroclimatic variables were then aggregated to several different basin scales based on U.S. Geological Survey Hydrologic Units (HU). The MWBM uses an accounting procedure to compute the allocation of water among various components of the hydrologic system, including climatic water supply and demand, seasonality in climatic water supply and demand, snow accumulation and melt, and soil-moisture storage (McCabe & Wolock, 2011). Estimated variables from the MWBM include monthly potential evapotranspiration, actual evapotranspiration, soil moisture storage, snow accumulation and melt, and runoff (i.e. flow per unit area). Water balance model

parameters used for this study were taken from parameter sets developed in previous studies (McCabe & Wolock, 2011; Wise *et al.*, 2018), and soil-moisture-storage capacity for each HU was computed using the available water-capacity values from the State Soil Geographic Data Base (STATSGO) dataset by assuming a one-meter rooting depth ('U.S. Department of Agriculture, 1994: State Soil Geographic (STATSGO) data base: Data use information. USDA Miscellaneous Publ. 1492, 113 pp.').

The MWBM has been assessed and verified in several previous studies (McCabe & Wolock, 2008, 2011; Gray & McCabe, 2010; Pederson *et al.*, 2013). Although there are some biases in water balance model runoff estimates (attributed to hydrologic processes not included in the water balance model, such as the effects of ground water contributions on runoff), strong temporal correlations between water balance model estimated and measured runoff suggest that the water balance model reliably simulates variability in runoff in response to temporal variability in temperature and precipitation (McCabe & Wolock, 2011). Additional details regarding the water balance model and evaluation of the model are described in (McCabe & Wolock, 2011). See (Wise *et al.*, 2018) for further information on the verification of input climate data, and additional details on model performance over the Missouri River Basin.

Addressing non-normality in the target streamflow data

Although the distributions of tree ring data used in the reconstruction of streamflow were typically normal, the distributions of annual mean naturalized streamflows in the upper Missouri basin were almost always positively skewed to some degree and often leptokurtic. To meet the assumptions of least squares regression (LSR),

we transformed the target streamflow data prior to regression to make the distribution of mean annual flows as normal as possible.

We tested numerous approaches to transforming these data including common transformations such as log and square root, as well as approaches such as an adaptive power transformation (Cook *et al.*, 1992), and traditional approaches for estimating Box-Cox transformations (Box & Cox, 1964; Guerrero, 1993). We found these tools to be unreliable at times in their ability to approximate normality in the streamflow distributions. As a result, some models performed poorly in predicting the observed distribution of streamflow, especially in small streams with heavily skewed annual flow distributions. To correct for this problem, we iteratively assessed the success of many possible box-cox transformations against a hypothetical normal distribution with variance and number of observations equal to that of the target streamflow record as follows:

We first generated a vector of 500 potential λ values from 0.01 to 5 and iteratively transformed the streamflow time series using each λ such that:

$$f_{\lambda}(\text{streamflow}) = \frac{\text{streamflow}^{\lambda}-1}{\lambda} \quad (\text{eqn. S1}),$$

We then generated kernel density estimates for each iteratively transformed streamflow time series as well as the hypothetical normal distribution using default bandwidth parameters and a Gaussian kernel (Venables & Ripley, 2002; Team, 2013). We regressed the density curve for each transformed streamflow time series on that of the normal distribution and selected the λ value that resulted in the highest squared

correlation between density estimates of transformed streamflow and the normal distribution as the λ to use for the box-cox transformation (eqn. S1). This approach was very effective in transforming skewed streamflow distributions to an acceptable degree of normality and generated excellent results in regression diagnostics of multiple linear regression (MLR) models used to predict streamflow from RWI.

Climate screening of tree ring chronologies

A central aim of the streamflow reconstruction process was to generate models capable of predicting streamflow from tree rings that incorporated a diverse set of climate information that tends to be seasonally specific. Streamflow itself is controlled by a diversity of season specific climate factors (Lettenmaier & Gan, 1990; Hamlet & Lettenmaier, 1999; Dettinger *et al.*, 2004). Thus, a network of tree-ring records that each contain some portion of the hydroclimatic information required to estimate water year average flows is ideal in a regression modeling framework if the records are integrated optimally into the reconstruction framework. To foster the hydroclimatic diversity of information available to inform the models, we first screened all tree-ring chronologies for their sensitivity to 9 climate variables that seasonally influence streamflow. These 9 variables were monthly precipitation, temperature, actual evapotranspiration, potential evapotranspiration, soil moisture, precipitation minus potential evapotranspiration, and potential evapotranspiration minus actual evapotranspiration, observed April 1 snow water equivalent (SWE), and modeled April 1 SWE. This allowed us to create subsets of chronologies particularly sensitive to each climate variable and provided an

understanding of how closely the ring-width index (RWI) for each chronology was related to each climate variable.

The screening was performed in the following manner. First, the three-month period of each water-year over which each climate variable was most closely correlated with mean annual streamflow was determined. This was implemented using the “*seascorr*” function in R package “*treeclim*” (Meko *et al.*, 2011; Zang & Biondi, 2015), which provided an evaluation of the correlation between streamflow and climate for a range of seasonal windows all within the HUC8 watershed region containing the target gage. The three-month period that best correlated with annual streamflow over the length of the streamflow record was extracted for each climate variable over the period of 1900-2014. A seasonal average, or total in the case of precipitation, was calculated for the length of record and used to screen for potential predictor chronologies. April 1 SWE was used as the annual value for both modeled and observed SWE.

For each tree ring chronology in the database, the RWI for 1900-2014 (or whatever portion of that period was available), was regressed against these 114 years of ‘annual’ climate values for each climate variable. Any chronology that was not significantly correlated ($p \leq 0.05$) to a particular climate variable was removed from the potential predictor pool associated with that specific climate variable. The chronologies that passed this initial climate screening were then ordered in a descending fashion by their correlation with each climate variable and the climate screened chronology lists were saved for use in the model building process. The result was 9 lists (one for each climate variable) of chronologies significantly correlated to the three month season that

most influenced streamflow for each climate variable, at each target gage, over the length of the gage record, and ordered by correlation strength.

Streamflow reconstruction model development

In developing regression models for reconstructing streamflow, we used a best subsets approach to model selection made possible by the “*regsubsets*” function in R package “leaps” (Lumley & Miller, 2004). The function performed an exhaustive search of a pool of potential predictor chronologies, and provided the best model of each possible number of predictors up to a specified maximum number ($n = 12$). The nine lists of climate screened chronologies served as the potential regression predictor pool by the best subsets algorithm for each of the 31 target streamflow records. As mentioned above, this was done to encourage the integration of climate information most strongly related to streamflow at the target gage from a ‘climate signal diverse’ set of potential predictor chronologies. To guide in the selection of the best and most parsimonious model, the Mallows C_p (Mallows, 1973) statistic was used to identify the model with the lowest difference between the statistic and parameter number. Then, selection between models with similar number of predictors was informed by identifying the model with the highest the adjusted R^2 (coefficient of variation adjusted for degree of freedom) statistic. In selecting the final “best” model, both metrics were weighed evenly, which balanced the potential for over fitting the model with the increased predictive power of multiple predictors.

Once the best model was selected, we fit the generic model: $\mu\{streamflow | RWI\} = \beta_0 + \beta_1 chronology_1 + \beta_2 chronology_2 + \dots + \beta_n chronology_n + \varepsilon$, to the transformed streamflow data, and back-transformed the predicted values such that:

$$streamflow = (\lambda \times fitted\ values + 1)^{\frac{1}{\lambda}} \quad (\text{eqn. S2})$$

Ninety percent confidence bounds were estimated using the delta method (Dorfman, 1938) and back transformed in the same way. To extend the length of the streamflow reconstructions we then nested successive “best” fit models forward and backward in time. This was done by successively dropping, any chronologies from the predictor pool that did not extend as far back in time as the predicted values of the previous fitted model. These chronologies were then replaced by the next best-correlated chronology in each of the climate screened chronology lists that had sufficient length to extend the next model either forward or backwards in time. This procedure of nesting successively longer reconstructions by fitting the best model and then removing any reconstruction length limiting chronologies was repeated until no chronologies remained in the potential predictor pool. More details related to this nesting method are provided in the section below.

Bias correction and nesting of reconstructions through time

Over a sufficient period of time and space, many climate variables tend to be relatively normally distributed. In reconstructing a network of streamflow records across the UMRB, we faced an uncommon problem in working with numerous non-normal reconstruction targets. Because a least squares regression procedure used to generate a proxy climate record will always underestimate the variance of the target (Esper *et al.*,

2005), it is common practice to scale the variance of the proxy to match that of the target following the regression procedure (Mann *et al.*, 1999; Cook *et al.*, 2007; Briffa *et al.*, 2013). However, as McCarroll and colleagues (McCarroll *et al.*, 2015) point out, scaling the variance of the proxy inevitably inflates the variance of the error in that proxy as well. When the reconstruction target is normally distributed, that error is relatively unbiased, being normally distributed about the mean. However, a more difficult problem arises when the target distribution is skewed and the predictors are more normal - such as is the case with tree-ring RWI. The distribution of a reconstruction will always fail to match that of the target perfectly, however, when the target is skewed, rescaling the proxy after regression creates directional bias in the entire reconstruction as follows.

Making the purely theoretical assumption that the target can be transformed to a perfectly normal distribution to meet regression assumptions, the back-transformed reconstruction will inevitably have a less-skewed distribution than the target because the reconstruction will contain a certain proportion of normally distributed noise, which, in the case of LSR, is assumed to exist entirely within the predictors. This can be seen in Supplementary Fig. S2a which shows distributions of hypothetical reconstructions (colors) of a skewed target (black), carried out using a set of three predictors which are simply the fourth root of a normally distributed target raised to the 4th power (initially perfect predictors), but to which progressively more noise is added. The red distributions represent the reconstructions with the most noise in the predictors, and thus the most normally distributed reconstructions. When such a reconstruction is scaled to its target, it's mean is also set equal to the mean of the target. Now, because the time series is

distributed differently about the same mean as the target, a directional bias is introduced into the entire reconstruction. In the case of positive skew in the target, this bias will be negative, or towards the short tail of the target distribution. Fig. S3a shows similar reconstructions displayed in Fig. S2a but in a more realistic scenario in which the full reconstruction is modeled on only a small portion of the target data (calibration period), and the complete reconstruction time series is built by sequentially nesting weaker models with means and variances scaled to the target. In this case the full reconstruction target is known and is shown in red. Note the increasing bias towards low values as model skill declines (further back in time). Figure S2a demonstrates that this bias is fundamentally a function of model skill, and even an excellent model will suffer some loss of distributional information.

Because we compared the depth of low flows over time, we attempted to reduce this bias (which created known, artificially low flows in positively skewed streamflow reconstructions in simulation, Supplementary Fig. S3a) by scaling not only the first and second moments of the distribution of the reconstructions (mean and variance), but also the third and fourth as well (kurtosis and skew). This was accomplished by iteratively performing candidate sinh-arcsinh transformations (Jones & Pewsey, 2009) of the regression output until the closest match between target and reconstruction was identified using equally weighted comparisons of kurtosis, skew, and the correlation between target and reconstruction. Because the accurate estimation of a probability distribution requires a large number of observations, we used the reconstruction resulting from the best LSR model for each gage as the target for bias correction of weaker models, reasoning that the

least squares approach provided the most robust estimate of the distribution we could make in cases where only relatively short observed streamflow records were available for calibration. The resulting reconstructions were then traditionally mean and variance scaled to the target (Lutz *et al.*, 2012). Supplementary Fig. S2b demonstrates the ability of the approach to reduce distributional bias, and Supplementary Fig. S3b shows the associated reduction in low flow bias as models becomes weaker back in time. The necessary cost of bias correction is a loss of model skill but this loss is quite minimal. This is shown in Fig S4a, while target levels of kurtosis Fig S4b and skew Fig S4c are better maintained as overall model quality declines further back in time.

Simulation reconstruction exercises using randomly generated target and predictor time series provided an important understanding of the distributional bias discussed above because the full target could be known in relation to a reconstruction developed on only a subset of target data. This added confidence to the interpretation of these records, especially with respect to drought intensity. Because accurate models require little variance scaling, but still fail to capture the full variation of the target, these models (forming the more recent years of a reconstruction) tended to underestimate the true drought calculated from the known timeseries. In contrast, poorer models required more variance scaling, pushing low flows further from the mean level used to define drought and generating larger flow deficits than those calculated from the known target. This means that reconstructions of skewed targets likely underestimated recent drought while overestimating droughts further back in time calculated from less accurate reconstruction models.

The model development process yielded sequentially longer reconstructions of progressively less skill as the available pool of predictor chronologies declined. After all models had been bias corrected to the best model for the gage, the reconstructed flow value for each year was selected from the available suite of models by choosing the model with the highest validation R^2 value from a leave one out cross-validation procedure. The process was repeated until only a single reconstruction model existed for the year to be estimated, and the length of this model determined the potential length of the reconstruction. However, as explained by McCarroll et al. (McCarroll *et al.*, 2015), we should understand that when model R^2 approaches 0.25 as one can expect limited skill in the variance scaled reconstruction to remain.

Cross validation of modeled streamflow

For each subsequently nested model used to reconstruct each gage record, we performed cross validation of model performance using a leave-one-out approach. We first stored full estimates of calibration period streamflow from the model fitting process such that each annual value of observed streamflow was not included in the training data used to predict streamflow for that year. These records were then run through the same bias correction and variance scaling procedure as the actual reconstruction output. Then, from the best model for each gage, we calculated the R^2 for the observed record explained by the model parameterized only on training data (VRSQ). We calculated the prediction error (PE) in units of $\text{ft}^3 \text{sec}^{-1}$ as follows:

$$PE = \frac{\sum_{i=1}^n \sqrt{(\text{observed}_i - \text{modeled}_i)^2}}{n}$$

where *observed* is the i^{th} year of the calibration period of the naturalized streamflow record, *modeled* is the i^{th} year of the predicted, bias corrected, and variance scaled reconstruction of the calibration streamflow value for that year from the model parameterized only on training data, and n is the number of years in the calibration period for the model. Thus, cross validation statistics for each nested portion of each gage reconstruction reflect the cross-validated performance of the regression model as well as the effects of bias correction and variance scaling.

Spatial clustering of observed flows

To assess patterns of the spatial variability of streamflow in the upper basin we performed a hierarchical cluster analysis (clustering based on Ward's method (Murtagh, 1985)) of the naturalized streamflow records over the 40 years common to all gages (1950-1989). All stream gages clustered neatly into groups reflecting their geographic proximity or location above/below other gages on the same river (Fig. 1) with one exception. The Big Hole River in southwest Montana clustered with gages further north on the Rocky Mountain front. The Big Hole is unique among the gages of southwest Montana in that it is primarily fed directly by runoff from a major, north-south oriented portion of the continental divide, as are the rivers of the Rocky Mountain front. As such, it is likely that the Big Hole is more sensitive to precipitation associated with zonal flow over the continental divide (like the Rocky Mountain front) than it is to the more meridional flow patterns that tend to favor the rest of southwest Montana. Given this observation, the Big Hole river was removed from further spatial analyses based on the clusters. After using the remaining suite of 30 streamflow records to identify cluster

membership for each gage, we reduced the total number of gages used for further analysis to only those gages whose records covered the period of 1930-2010 ($n = 18$, Fig. 1). We did so in order to compare the period of the dustbowl drought to the drought of 2000-2010 using the naturalized streamflow data, and because we wanted to exclude from the drought analysis, those reconstructions for which calibration data did not exist over the dustbowl period. Composite streamflow records for each cluster were generated by first converting the annual streamflow record at each gage into z scores, then taking the average of all gage z scores for the cluster for each year.

Composite climate data for each naturalized flow defined cluster

In order to investigate the relationship between climate and streamflow for each cluster, we identified the major HU 8 level watersheds that make up the primary drainage area for each cluster and averaged the climate conditions for each month of each year for each variable across the HU 8 level climate data sets for each cluster. The identification of the HU 8 watersheds used to estimate climate in each cluster are displayed in Supplementary table S3.

Estimating the relative forcing of precipitation and temperature on streamflow over the instrumental period

To understand how precipitation and temperature have simultaneously influenced streamflow reflected in the instrumental record, we followed the approach of Pederson et al. 2013 (Pederson *et al.*, 2013). We regressed the time series of annual streamflow z scores for each cluster against the time series of annual precipitation and temperature z scores where annual temperature and precipitation values are the average of the 8 month

season over which each variable is most correlated with mean annual streamflow values for each cluster. We then multiplied the regression coefficients by time series of precipitation and temperature z scores to estimate the relative forcing of each variable on streamflow. We quantified the magnitude and sign of the combined forcing of both variables as the sum of the relative forcings (Fig. 2, y-axis) and display the dominant variable as well as the degree of dominance (absolute value of the dominant forcing – absolute value of the subordinate forcing) using color in Fig. (2) where redder colors represent stronger temperature dominance, greener colors represent stronger precipitation dominance, and intermediate colors represent relatively balanced forcing between both variables.

Splicing observed streamflow and temperature records to the reconstructions and assessing potential bias between record types.

Tree ring based reconstructions of streamflow and temperature used in this study end in 1988 and approximately 1998 for temperature and streamflow respectively. Because a primary aim of the study was to contextualize the Turn of the Century drought with paleoclimatic and paleohydrologic records, it was necessary to splice the reconstructions to the observed temperature and streamflow records which run through 2010. Because both the streamflow and temperature reconstructions are mean and variance scaled to their respective observational records over their common period, splicing the two record types is a straightforward process of joining the records end to end. However, doing so inevitably introduces bias at the transition of record types in that the reconstruction itself will fail to perfectly capture the variation in the observed climate

or hydrology. An important prerequisite for drawing conservative inference from comparisons made across the splice is in understanding the biases that exist in the reconstruction relative to the observational record.

Because our primary analyses centered on comparison of drought intensity over time, we attempted to explicitly quantify the low-flow bias in the streamflow reconstructions vs. the observed records. Over the common period for both reconstruction and observational record for each gage, we compared reconstructed and observed flows from years where flow values were less 1 SD below the mean flow level. We examined the slope and intercept for the relationship between the two and compared the means of these low observed flow levels vs. those of the reconstruction. As was expected from our simulation exercises, which showed a slight wet bias in the most accurate models, low flows in the reconstructions were biased slightly wet over the calibration period such that the mean low-flow level for the reconstructions was 0.156 SD higher than the observed flow. Reconstructions predicted a flow of 0.145 SD when for an observed flow of 0, and the slope of reconstructed flow/observed flow was 0.990.

Given the nearly perfect slope parameter describing the low-flow relationship between modeled and observed records, we reasoned a robust test of the impact of this estimated low-flow bias on the comparison of droughts over time was to explicitly align the low flow means of the observed and reconstructed flows, essentially biasing the entire reconstructed streamflow record dry, while matching the lowest flows which contribute most to the intensity of drought. Supplementary figure S5 shows the time series of DII for the UMRB calculated on this low-flow “bias corrected” flow record. We see that

even under this extreme scenario in which the entire reconstruction is biased dry, the intensity of Turn of the Century Drought still appears nearly unprecedented over the last 1200 years.

Basin-wide drought history analysis

To assess the basin wide record of drought evident in the reconstruction network, we averaged the time series of z-scores for all reconstructions for which the naturalized streamflow record used to calibrate the reconstruction covered the period of 1930-2010.

We then classified particular years in the composite streamflow record as drought years using the operationally defined drought criteria used in the recently published Bureau of Reclamation Water Supply Assessment for the Upper Missouri River Basin (USBOR 2018). As such drought is defined as; *Two or more years of below average flows, ended only by two or more years of average to above average flows, or an individual event greater than three standard deviations above the mean.* Once drought years were identified, the annual drought intensity index (DII) for a given drought year was determined using eqn. 1 found in the main text.

A particular concern in comparing droughts over time was that the operationally defined droughts might be overly sensitive to the criteria of the definition. As such, we also examined droughts defined using a more statistical approach by fitting a cubic smoothing spline (Cook & Kairiukstis, 1990) to the composite streamflow record and classifying drought years as those in which the spline fell below the mean streamflow level. The number of years chosen to calculate the spline over was that which yielded the closest match in the classification of drought years to that arrived at using the

operational definition of drought (5 yrs). We then assessed DII for each drought year defined using the spline approach and found that DII derived from the operationally defined drought matched very well with the that defined based on low frequency variation expressed by the spline. This finding adds confidence to the identification of drought periods and the DII metric derived from their duration and accumulated streamflow deficits.

Estimating the strength and probability of extremes in the temperature streamflow relationship over time

A conspicuous feature of the recent composite streamflow record is the occurrence of very low flows associated with hot periods (Fig. 2). We investigated the probability distribution of extremes in the relationship between temperature and streamflow by first identifying years in which both temperature and streamflow values were further than 1 SD from their respective means (hereafter “extreme” years). This established four possible conditions in which extreme years could occur; hot-low, cold-low, hot-high, and cold-high in terms of temperature and streamflow respectively. We then calculated the probability of any of the extreme years falling into each category, carrying out the calculation for the full 1200 year period, the period since 1900, and the period since 1975 when temperature shows and increased influence on the instrumental streamflow record. The probabilities for the period since 1900 are in reference to extreme years defined over the full 1200 years, while the probabilities for the period since 1975 are in reference to extreme years defined over the period since 1900.

Spatial distributions of the most severe droughts

Six events in the UMRB composite DII time series stand out as particularly intense, however, the spatial extents of these events are not evident from the basin-wide record. In order to characterize the geographic distribution of drought during these basin-wide dry periods, we first calculated DII separately for each cluster region. This provided a record of drought intensity for each region relative to the long-term variation in streamflow for the region itself. We then assessed the minimum value of DII for each region over the period of each of the six major droughts evident in the basin-wide DII record. The minimum values describe the peak of drought intensity for each cluster within the individual drought timeframe indicated in the basin-wide DII record. These minimum values for each major drought are displayed for each cluster region using color in Fig. 6.

USGS num	River	Gage	Latitude	Longitude
6016000	Beaverhead	Barretts	45.12	-112.75
6018500	Beaverhead	TwinBridges	45.38	-112.45
6025500	Big Hole	Melrose	45.53	-112.70
6287000	Bighorn	St.Xavier	45.32	-107.92
6207500	Clarks Fork Yellowstone	Belfry	45.01	-109.07
6073500	Dearborn	Craig	47.20	-112.10
6052500	Gallatin	Logan	45.89	-111.44
6036650	Jefferson	ThreeForks	45.90	-111.60
6114700	Judith	Winifred	47.67	-109.65
6041000	Madison	McAllister	45.49	-111.63
6042500	Madison	ThreeForks	45.82	-111.50
6101500	Marias	Chester	48.31	-111.08
6174500	Milk	Nashua	48.13	-106.36
6090800	Missouri	FtBenton	47.82	-110.67
6115200	Missouri	Landusky	47.63	-108.69
6054500	Missouri	Toston	46.15	-111.42
6120500	Musselshell	Harlowton	46.43	-109.84
6130500	Musselshell	Mosby	46.99	-107.89
6620000	North Platte	NorthGate	40.94	-106.34
6326500	Powder	Locate	46.43	-105.31
6023000	Ruby	TwinBridges	45.51	-112.33
6282000	SHOSHONE	BuffaloBill	44.52	-109.10
6077500	Smith	Eden	47.19	-111.39
6707500	South Platte	SouthPlatte	39.41	-105.17
6079500	Sun	GibsonRes	47.60	-112.76
6089000	Sun	Vaughn	47.53	-111.51
6108000	Teton	Dutton	47.93	-111.55
6108800	Teton	Loma	47.93	-110.51
6308500	Tongue	MilesCity	46.38	-105.85
6259000	WIND	Boysen	43.42	-108.18
6191500	Yellowstone	CorwinSprings	45.11	-110.79
6329500	Yellowstone	Sidney	47.68	-104.16

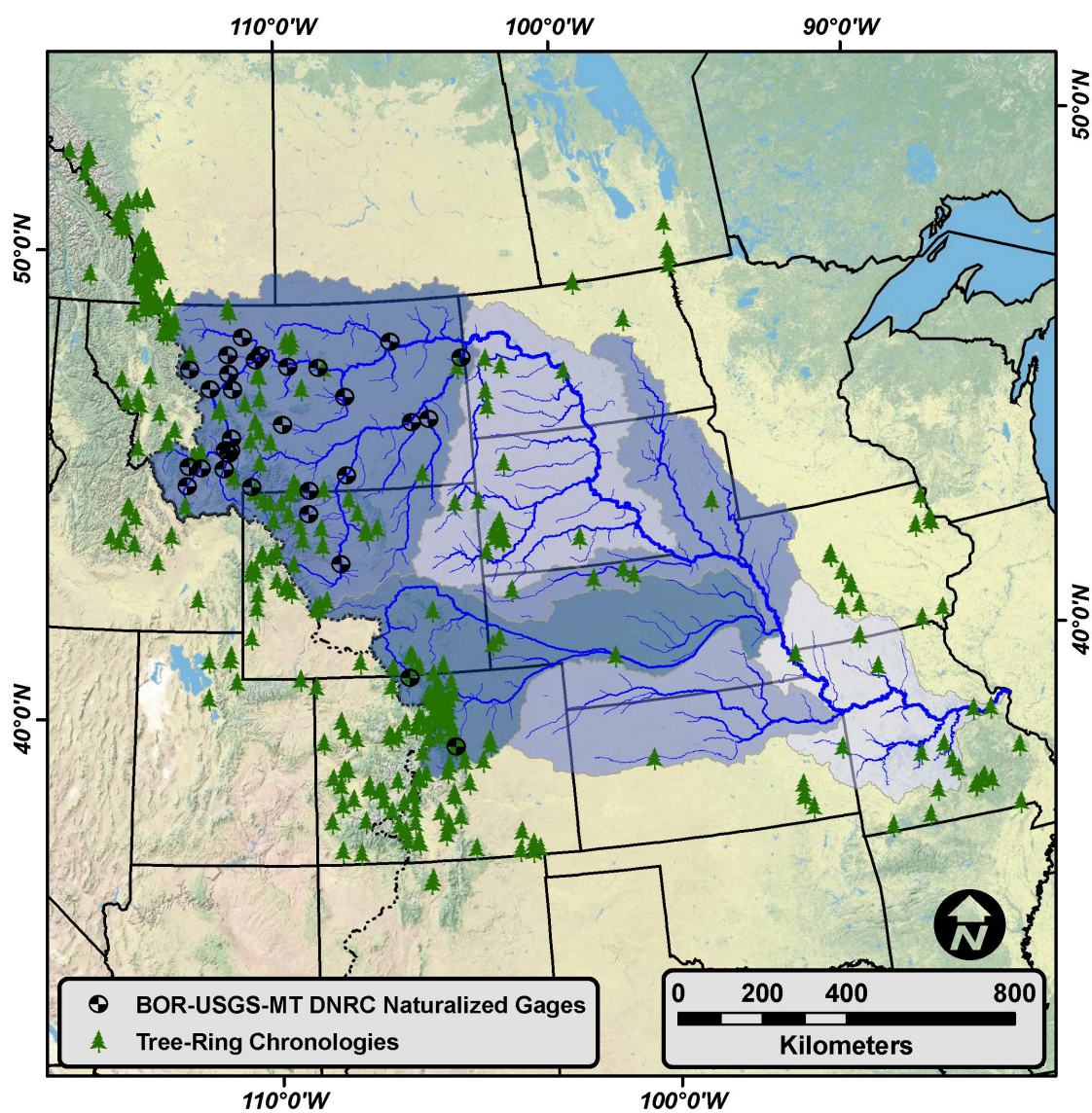
Supplementary table S1 Streamflow gaging locations.

Gage	VRSQ	PE	Start Year
BIGHORN RIVER NEAR ST. XAVIER, MT	0.85	270.52	722
WIND RIVER BELOW BOYSEN RESERVOIR, WY	0.82	171.82	722
NORTH PLATTE RIVER NEAR NORTHGATE CO	0.79	69.93	380
SHOSHONE RIVER BELOW BUFFALO BILL RESERVOIR, WY	0.78	103.48	680
MISSOURI RIVER NEAR LANDUSKY MT	0.78	929.93	769
MADISON RIVER BELOW ENNIS LAKE NEAR MCALLISTER MT	0.76	116.03	680
SMITH RIVER NEAR EDEN MT	0.76	60.83	986
MILK RIVER AT NASHUA MT	0.73	154.66	1104
MUSSELSHELL RIVER AT MOSBY MT	0.73	106.14	1027
JUDITH RIVER NEAR MOUTH, NEAR WINIFRED MT	0.73	33.07	769
MADISON RIVER NEAR THREE FORKS MT	0.73	138.57	818
GALLATIN RIVER AT LOGAN MT	0.72	117.88	680
MUSSELSHELL RIVER AT HARLOWTON MT	0.71	42.64	986
SOUTH PLATTE RIVER AT SOUTH PLATTE CO	0.7	65.84	379
MISSOURI RIVER AT TOSTON MT	0.7	538.92	680
MARIAS RIVER NEAR CHESTER MT	0.68	127.21	1154
YELLOWSTONE RIVER NEAR SIDNEY MT	0.68	1355.96	882
MISSOURI RIVER AT FORT BENTON MT	0.67	907.9	769
SUN RIVER NEAR VAUGHN MT	0.66	130.67	882
TETON RIVER AT LOMA MT	0.65	39.8	987
RUBY RIVER NEAR TWIN BRIDGES MT	0.64	41.36	769
JEFFERSON RIVER NEAR THREE FORKS MT	0.64	311.75	769
YELLOWSTONE RIVER AT CORWIN SPRINGS MT	0.63	325.5	769
TETON RIVER NEAR DUTTON MT	0.62	34.46	1027
CLARKS FORK YELLOWSTONE RIVER NEAR BELFRY MT	0.59	106.47	722
DEARBORN RIVER NEAR CRAIG MT	0.59	44.07	882
TONGUE RIVER AT MILES CITY MT	0.58	89.87	875
BEAVERHEAD RIVER AT BARRETTS MT	0.58	64.75	1062
BIG HOLE RIVER NEAR MELROSE MT	0.56	178.81	882
SUN AT GIBSON RESERVOIR NEAR AUGUSTA, MT	0.55	138.35	882
POWDER RIVER NEAR LOCATE MT	0.41	166.99	1269
Average	0.68	225.3	838

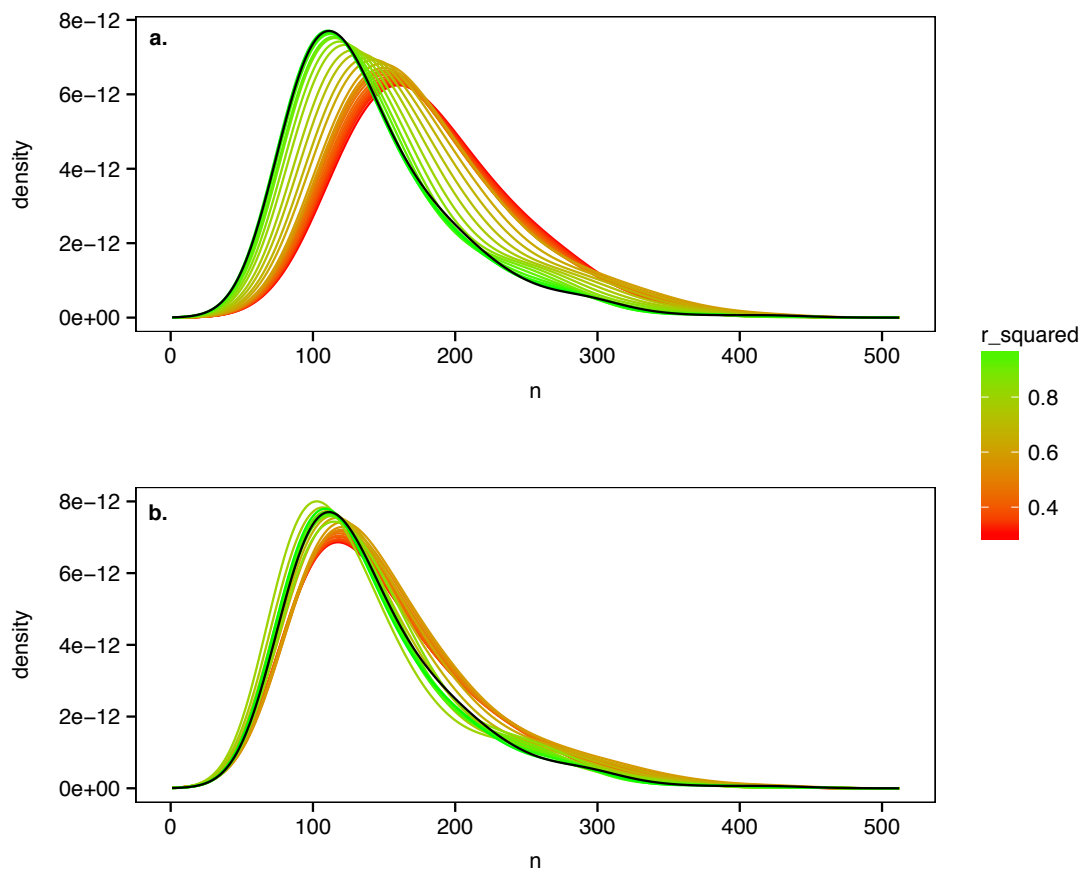
Supplementary figure S2. Streamflow reconstruction cross-validation statistics.

cluster	huc
Southwest Montana	10020001
Southwest Montana	10020007
Southwest Montana	10020008
Southwest Montana	10020003
Southwest Montana	10020002
Southwest Montana	10020005
Central Montana	10030101
Central Montana	10030103
Central Montana	10030105
Central Montana	10040103
Central Montana	10040201
Greater Yellowstone	10070001
Greater Yellowstone	10080012
Greater Yellowstone	10080013
Greater Yellowstone	10080009
Greater Yellowstone	10070006
Greater Yellowstone	10070005
Greater Yellowstone	10070002
Greater Yellowstone	10080010
Greater Yellowstone	10080001
Greater Yellowstone	10080002
Greater Yellowstone	10080003
Greater Yellowstone	10080008
Rocky Mountain Front	10030104
Rocky Mountain Front	10030201
Rocky Mountain Front	09040001
Rocky Mountain Front	17010207
Colorado Front Range	10190001
Colorado Front Range	10190002
Colorado Front Range	14010002
Colorado Front Range	14010001
Colorado Front Range	10180001
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Colorado Front Range	10190005
Colorado Front Range	10190004
Colorado Front Range	10180002

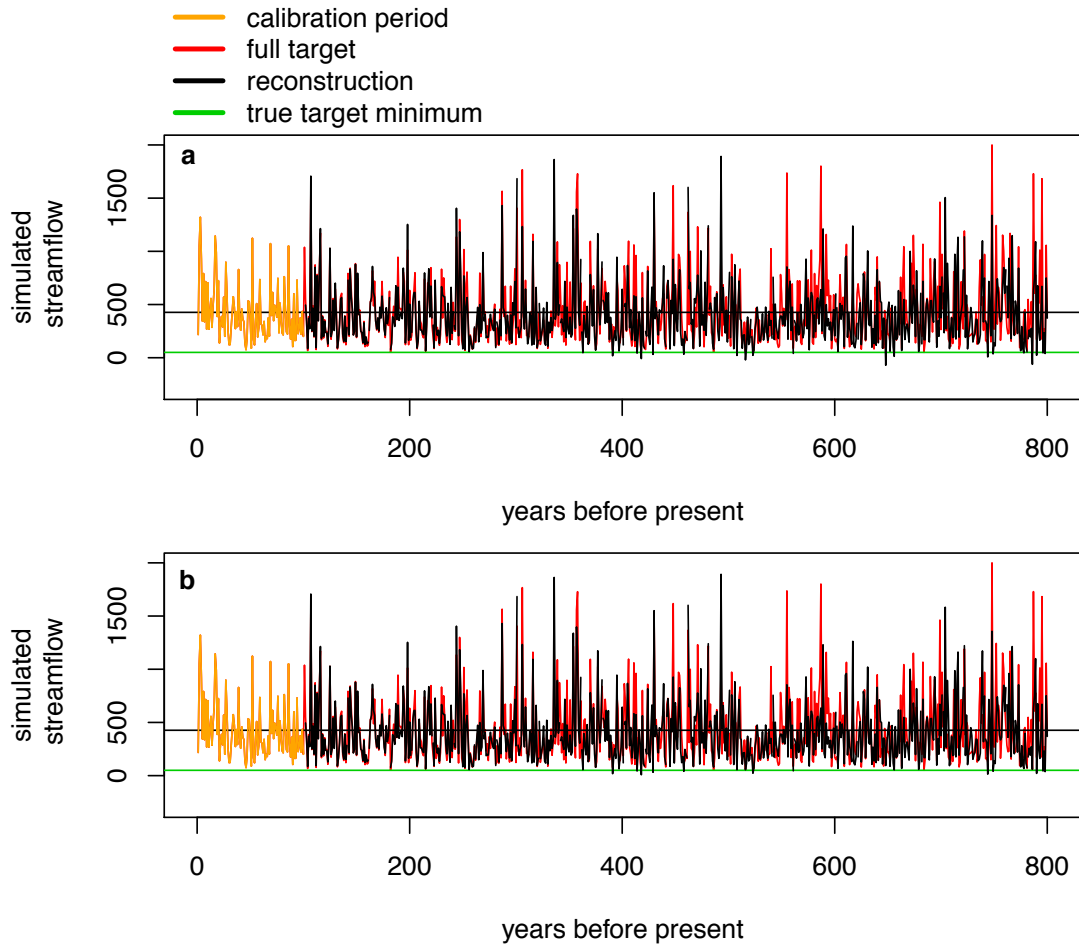
Supplementary table S3 HUC 8 regions aggregated for cluster climate data.



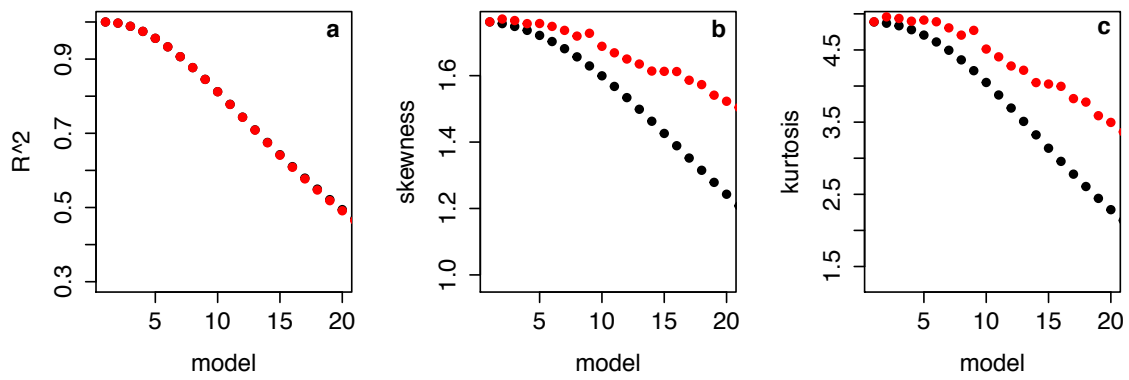
Supplementary Figure S1. Stream gage network and tree ring chronology network.



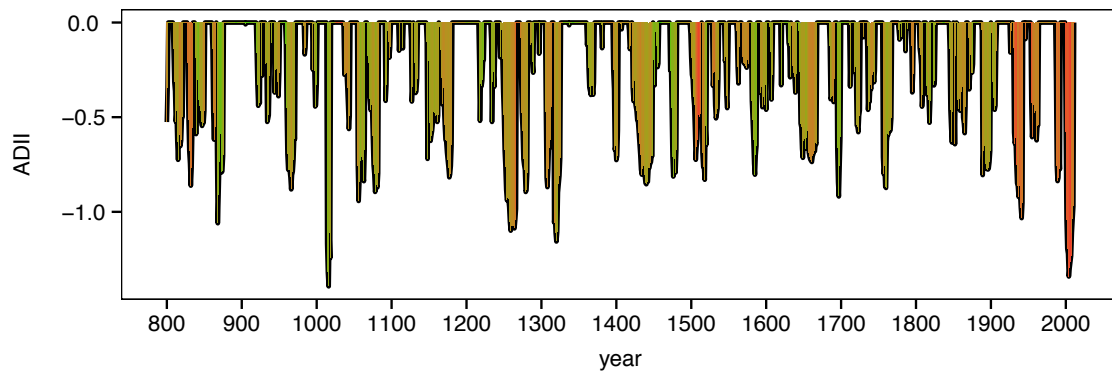
Supplementary Figure S2 Loss of skew in simulated reconstructions due to increased noise for a reconstruction without bias correction (a) and with bias correction (b).



Supplementary Figure S3 Low flow bias in reconstructions from progressively weaker models for a reconstruction without bias correction (a) and with bias correction (b).



Supplementary Figure S4 Reconstruction skill (a), skewness (b) and kurtosis (c) for progressively weaker models without bias correction (black) and with bias correction (red).



| **Supplementary Figure S5** Basin-wide DDI reconstruction generated from maximally dry-biased reconstructions spliced to observed flows.

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