



Short- and long-term responses of riparian cottonwoods (*Populus* spp.) to flow diversion: Analysis of tree-ring radial growth and stable carbon isotopes

Derek M. School^{a,b,*}, Jonathan M. Friedman^c, Craig A. Stricker^d, Adam Z. Csank^e, David J. Cooper^a

^a Colorado State University, Department of Forest and Rangeland Stewardship, Campus Delivery 1472, Fort Collins, CO 80523, USA

^b National Park Service, Water Resources Division, 1201 Oakridge Drive #250, Fort Collins, CO 80525, USA

^c U.S. Geological Survey, 2150 Centre Avenue, Building C, Fort Collins, CO 80526, USA

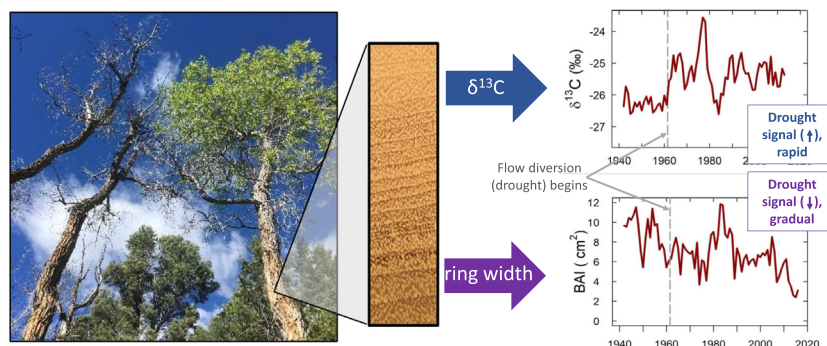
^d U.S. Geological Survey, Denver Federal Center, Building 95, MS963, Denver, CO 80225, USA

^e University of Nevada, Department of Geography, 1664 N. Virginia St., Reno, NV 89557, USA

HIGHLIGHTS

- Streamflow diversion created hydrological drought in a riparian cottonwood forest.
- Tree rings provided biological perspectives on altered hydrological processes.
- Tree-ring width, $\delta^{13}\text{C}$, tree mortality, and canopy were used to investigate drought.
- $\delta^{13}\text{C}$ immediately reflected drought while ring width and mortality lagged by decades.
- Elevated $\delta^{13}\text{C}$ served as an early warning of branch and tree mortality.

GRAPHICAL ABSTRACT



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ABSTRACT

Long duration tree-ring records with annual precision allow for the reconstruction of past growing conditions. Investigations limited to the most common tree-ring proxy of ring width can be difficult to interpret, however, because radial growth is affected by multiple environmental processes. Furthermore, studies of living trees may miss important effects of drought on tree survival and forest changes. Stable carbon isotopes can help distinguish drought from other environmental factors that influence tree-ring width and forest stand condition. We quantified tree-ring radial expansion and stable carbon isotope ratios ($\delta^{13}\text{C}$) in riparian cottonwoods (*Populus angustifolia* and *P. angustifolia* x *P. trichocarpa*) along Snake Creek in Nevada, USA. We investigated how hydrological drought affected tree growth and death at annual to half-century scales in a partially dewatered reach (DW) compared to reference reaches immediately upstream and downstream. A gradual decline in tree-ring basal area increment (BAI) began at DW concurrent to streamflow diversion in 1961. BAI at DW diverged from one reference reach immediately but not from the other until nearly 50 years later. In contrast, tree-ring $\delta^{13}\text{C}$ had a rapid and sustained increase following diversion at DW only, providing the stronger and clearer drought signal. BAI and $\delta^{13}\text{C}$ were not significantly correlated prior to diversion; after diversion they both reflected drought and were correlated for DW trees only. Cluster analyses distinguished all trees in DW from those in reference reaches based on $\delta^{13}\text{C}$, but BAI patterns left trees intermixed across reaches. Branch and tree mortality were also highest and canopy vigor was lowest in DW. Results indicate that water scarcity strongly limited cottonwood

* Corresponding author at: National Park Service, Water Resources Division, 1201 Oakridge Drive #250, Fort Collins, CO 80525, USA.

E-mail address: derek_school@nps.gov (D.M. School).

photosynthesis following flow diversion, thus reducing carbon assimilation, basal growth and survival. The die-back was not sudden, but occurred over decades as carbon deficits mounted and depleted streamflow left trees increasingly vulnerable to local meteorological drought.

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1. Introduction

Rivers in the northern hemisphere often support riparian forests that are dominated by cottonwood trees (*Populus spp.*) (Friedman et al., 2005; Stettler, 1996). Riparian cottonwoods frequently depend on alluvial groundwater that is replenished by rivers (Cooper et al., 2003; Tai et al., 2018), and their forests have experienced widespread changes as humans modify streamflows (Andersen et al., 2007; Lytle and Merritt, 2004). Decreases in flood peaks and channel migration have led to reduced cottonwood regeneration (Merigliano et al., 2013; Schook et al., 2017; Wilding et al., 2014), reductions in basal growth rates (Schook et al., 2016a), shifts to shade tolerant and invasive species (DeWine and Cooper, 2007; Stromberg et al., 2007), and reduced branch and tree survival (Busch and Smith, 1995; Cooper et al., 1999; Rood et al., 2003; Scott et al., 1999). If cottonwoods receive ample moisture from local precipitation, the effect of flow reduction may be largely undetected (Friedman et al., 2018; Reily and Johnson, 1982) or delayed until transpiration demands increase. At that time the ecological resistance of individual trees may be exceeded, and widespread forest loss and habitat transitions can ensue (Martínez-Vilalta and Lloret, 2016). Cottonwood tree-ring width can be strongly correlated with flow in regions where growth is limited by water availability (Edmondson et al., 2014; Schook et al., 2016b).

Drought can affect trees when precipitation decreases, evapotranspiration increases, or altered runoff patterns reduce tree water access. Resulting physiological stresses may be capable of decreasing tree growth and survival endogenously via hydraulic failure and carbon starvation, or exogenously from increased susceptibility to insects and pathogens (Allen et al., 2015; McDowell and Sevanto, 2010; Sevanto et al., 2013). When evaporative demand exceeds water supply, xylem water potential decreases, leading to xylem cavitation and mortality of branches or whole trees (Rood et al., 2003; Tai et al., 2018; Tyree et al., 1994). Trees often respond to hydraulic stress by closing their stomata, which limits transpiration but also the diffusion of CO₂ into the leaf (Allen et al., 2015; Farquhar et al., 1982). Decreased leaf CO₂ reduces photosynthetic rate and the production of structural carbohydrates. This mechanism causes drought to limit annual tree growth, often making tree-ring width a useful proxy for understanding the ecological consequences of past precipitation and runoff (Fritts, 1966).

Reduced water access does not always decrease tree-ring growth, however (Ferrio et al., 2003; St. George, 2014). Growth may also be limited by variables such as low or high temperatures (St. George, 2014), pathogen outbreaks (Cailleret et al., 2017), masting events (Hackett-Pain et al., 2015), and flooding (Astrade and Bégin, 1997). Even when photosynthetic rate is affected by drought, if the drought is moderate a tree might respond by reallocating resources away from flowers and fruits (Ogaya and Peñuelas, 2007) or carbohydrate stores (McCarroll et al., 2017) rather than reducing radial growth. Additionally, tree mortality may release survivors from competition, reducing or reversing the expected decrease in growth of surviving trees during environmental stress events (Aakala et al., 2011; Berg et al., 2006). For example, gravel mining along a stream in eastern Colorado lowered the water table and led to mortality of 88% of affected riparian *Populus deltoides*, but ring width did not decrease in surviving trees (Scott et al., 1999). In other cases branch dieback or strip-bark formation can result in growth releases within a tree, again masking the impact of environmental stress on ring width (Leland et al., 2018). A more complete reconstruction of past droughts can be developed by incorporating information from

dead trees and from additional tree-ring proxies that are related to water availability, including early- and late-wood widths, wood density, wood anatomy, and stable isotope ratios of carbon, oxygen, and hydrogen (Farquhar et al., 1982; Schollaen et al., 2013; Mischel et al., 2015; Pacheco et al., 2020). Proxies that are clearly and immediately related to drought stress, such as stable carbon isotopes, may be particularly informative (Klusek et al., 2019).

In arid and semi-arid regions the ratio of ¹³C to ¹²C in tree-ring cellulose can reveal past drought stress (McCarroll and Loader, 2004). Plants discriminate against ¹³C during carbon fixation, lowering the ¹³C/¹²C ratio ($\delta^{13}\text{C}$) in plant cells compared to atmospheric CO₂. In wetter regions, higher $\delta^{13}\text{C}$ often reflects increased photosynthetic rate (Israeli et al., 1996; McCarroll and Pawellek, 2001). In contrast, in drier regions increased $\delta^{13}\text{C}$ is usually caused by stomatal closure from drought stress, and the $\delta^{13}\text{C}$ in tree rings tends to be negatively correlated with water available at the time of ring formation (Leavitt, 2002; Saurer et al., 1995; Warren et al., 2001). If $\delta^{13}\text{C}$ and ring width are not strongly correlated they can be investigated together to improve reconstruction of past droughts (Au and Tardif, 2012; Csank et al., 2016; Ferrio et al., 2003; Gagen et al., 2004; Schollaen et al., 2013). Additionally, the seasonality of climate reflected in $\delta^{13}\text{C}$ and ring width may differ, making investigation of both proxies complementary (Au and Tardif, 2012; Friedman et al., 2019).

We investigated a riparian cottonwood forest along a mountain stream in Nevada, USA, where a diversion pipeline has partially dewatered a portion of Snake Creek since 1961 (Schook et al., 2020). This study can be considered a semi-natural drought experiment investigating effects of long-term (55-year) flow reduction and the resulting hydrological drought. The known timing of dewatering provides an excellent setting to investigate drought effects on tree-ring proxies, effects that could also manifest during precipitation reductions and climate change. The aim of this study was to answer the question: How do different tree-ring proxies reflect short- and long-term drought in a forest where water supply has declined? We analyzed histories of tree-ring radial growth, $\delta^{13}\text{C}$, canopy vigor, and mortality of branches and whole trees to understand how flow diversion affected riparian cottonwoods over a 55-year period.

2. Methods

2.1. Study site

The study site is in the southern Snake Range in Great Basin National Park, Nevada, USA (Fig. 1). Annual precipitation averages 16 cm/yr in the nearby Snake Valley basin and 81 cm/yr at high elevations (Prudic et al., 2015) where mountain peaks reach 3982 m.a.s.l. The local National Weather Service station at 2080 m elevation (GHCND: USC00263340, USC00264514) is at a similar elevation to the study reaches and had mean annual precipitation of 35 cm/yr for 1981–2010, which was well-distributed throughout the year with slightly higher amounts in winter that generate mountain snowpack. Mean daily temperature ranged from -7°C in December and January to 29°C in July. We characterized temperature, precipitation, and vapor pressure deficit for the period 1940–2017 for a location in the study watershed using PRISM (Daly et al., 2008). Climate data were graphed as 5-year-averaged percentiles of the total record, where the median year was the 50th percentile and the highest year was the 99th percentile (Fig. 2A).

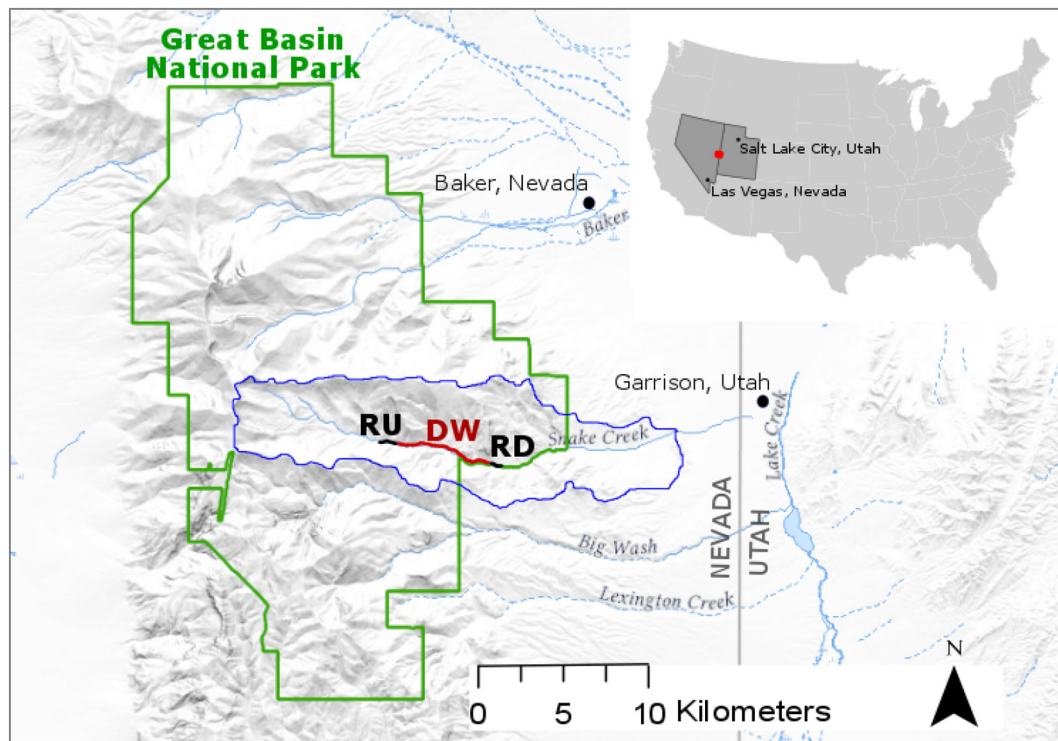


Fig. 1. Snake Creek and the study reaches in Great Basin National Park, Nevada. DW = Dewatered reach, RU = Reference Upstream, RD = Reference Downstream. The Snake Creek watershed is outlined in blue, the diversion pipeline and DW reach are red, and reference reaches are black. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Snake Creek flows east from Nevada into the Snake Valley in Utah and occupies the largest watershed in Great Basin National Park (59 km²). Bedrock is influenced by normal-faulting from crustal expansion, and many streams in the Great Basin region flow over diverse rock units with variable permeabilities. Snake Creek flows for 2 km over Pole Canyon limestone, a porous carbonate, where some surface water naturally enters the groundwater system. Past water users aiming to limit water infiltration into the limestone built a 5-km water diversion pipeline in 1961 to bypass this reach and deliver water downstream. The pipeline diverts up to 0.28 m³s⁻¹ and transports it through this reach before returning it to the channel, although the pipeline inlet occasionally clogs with debris that reduces its capacity. Any discharge exceeding the pipeline's intake capacity remains in the channel. Historical land uses in the study area included hardrock mining (1913–1916), placer mining (1940s), logging (1860s–1960s), and livestock grazing (1860s–1999).

We analyzed 3 reaches of Snake Creek: the pipeline-dewatered reach (DW) and reference reaches immediately upstream (RU) and downstream (RD) (Fig. 1). The DW reach extends 5 km from the pipeline inlet to outlet. It contains areas where groundwater discharges to the stream, and areas where the pipeline leaks. Flow in the DW reach is generally intermittent or ephemeral. The riparian corridor has both wetland and upland trees and shrubs. Deciduous species include cottonwood (*Populus angustifolia* and *P. angustifolia* × *P. trichocarpa*), aspen (*P. tremuloides*), water birch (*Betula occidentalis*), sandbar willow (*Salix exigua*), Wood's rose (*Rosa woodsii*), and chokecherry (*Prunus virginiana*). Evergreen species include singleleaf pinyon pine (*Pinus monophylla*), Utah juniper (*Juniperus osteosperma*), and white fir (*Abies concolor*). The pure and hybrid cottonwoods spatially overlapped, had no apparent difference in vigor or survival, and were analyzed as one. All analyses address the cottonwoods that dominate much of the riparian forest.

The RU reach extends for 780 m upstream from the DW reach. It has perennial flow with baseflows of <0.03 m³s⁻¹. The riparian forest is composed of tall white firs and cottonwoods. The RD reach extends

for 340 m below the pipeline outlet and has an extensive cottonwood forest with understory vegetation including Wood's rose. It has perennial flow (baseflow <0.03 m³s⁻¹) from groundwater emergence and pipeline discharge. It is unknown to what extent pipeline operation augments flow through the reach, but the change in water table depth is thought to be small.

2.2. Streamflow

Snake Creek has a snowmelt-dominated flow regime, with annual peak flows in May or June and baseflows that are punctuated by occasional rainstorm runoff. The Snake Creek flow record at NPS gauging station SNK3, located in the RU reach, began in 2011 so was insufficient for long-term analysis. Mean annual flow was 0.12 m³s⁻¹. We used the 1960–2017 flow record from Cleve Creek, USGS station #10343700, as a proxy for Snake Creek flow (Prudic et al., 2015). Cleve Creek drains the Schell Creek Range 45 km northwest of and in a similar landscape position as Snake Creek. We compared the two streams using daily and monthly discharges for the overlapping period, 2011–2017. The Pearson correlation for monthly flows was $r = 0.89$. 22% of the Cleve Creek record was missing so we used monthly regression equations developed from 40 years of overlap with the adjacent and highly correlated Steptoe Creek to impute missing data (monthly $0.87 < r < 0.97$). We estimated undiverted monthly flows in Snake Creek using a linear best-fit equation constructed from the shared months of measured discharge in Snake and Cleve Creeks (Fig. 2B). We subtracted 0.28 m³s⁻¹ from each month to estimate flow bypassing the pipeline inlet and entering the DW reach, which resulted in no flow for 87.5% of months.

2.3. Tree-ring growth chronologies

Tree-ring growth chronologies were developed using trees randomly selected from all live cottonwoods >20 cm diameter in the

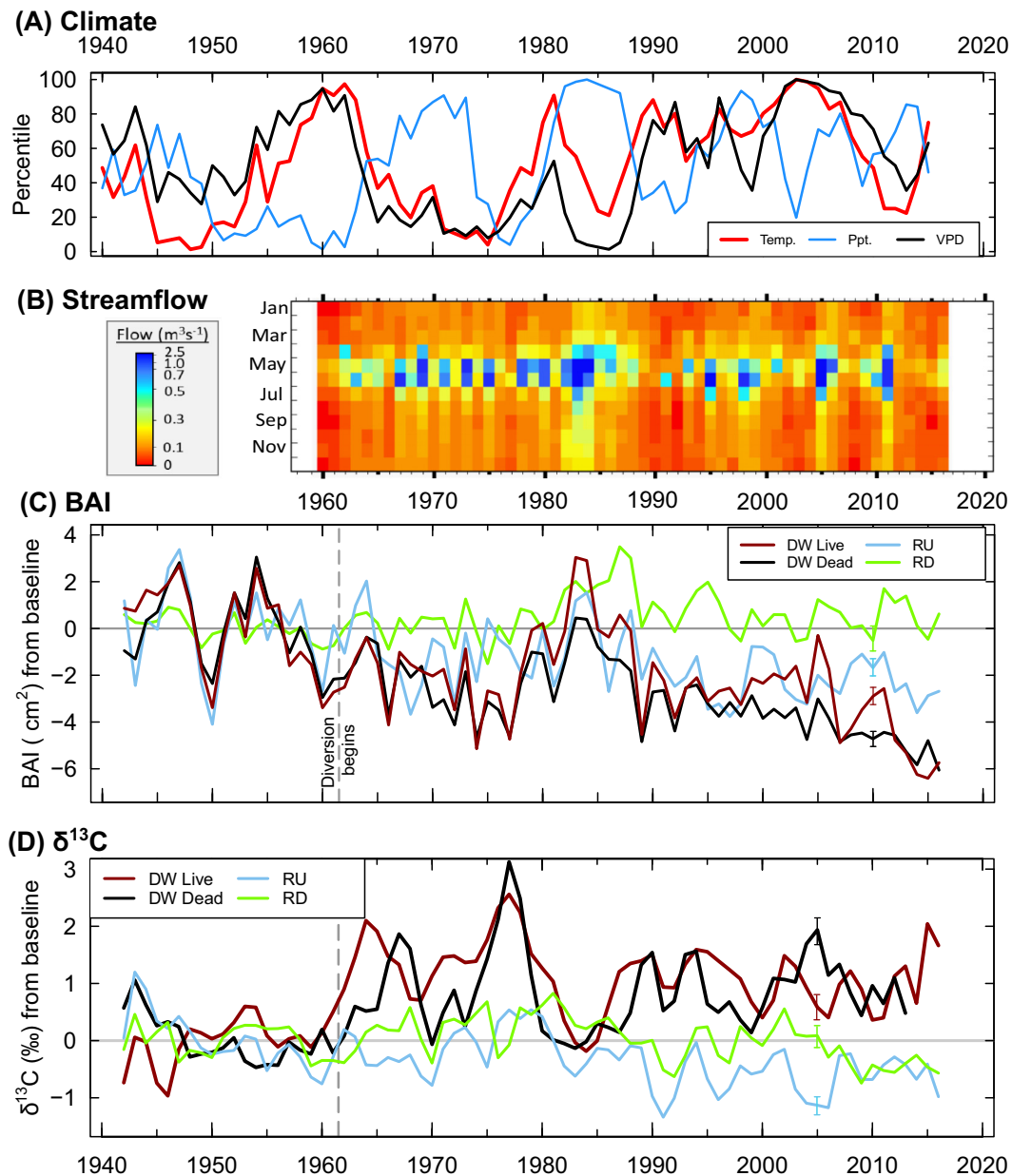


Fig. 2. Climate, streamflow, and tree ring proxy chronologies. (A) 5-year running averages of mean annual temperature, total precipitation, and vapor pressure deficit (VPD) displayed as percentiles of the record. (B) Snake Creek undiverted mean monthly flow estimated for 1960–2016. Note that flow entering the dewatered (DW) reach can be estimated by subtracting the diversion intake capacity of $0.28 \text{ m}^3 \text{ s}^{-1}$, which reduces flow to zero in all cells currently red or orange. Tree-ring (C) basal area increment and (D) $\delta^{13}\text{C}$, with values scaled to reflect deviation from the pre-diversion period. The average annual standard error for each series is shown only once for simplicity, in (C) 2010 or (D) 2005. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

study reaches. In 2017 and 2018, two cores were collected from each tree at 1.3 m above ground using a 5.15-mm diameter increment borer. Cores were mounted and sanded using progressively finer sandpaper from 120 to 1200 grit, cross-dated under a dissecting microscope using skeleton plots (Stokes and Smiley, 1968), measured to 0.01 mm precision using a Velmex Manual UniSlide micrometer and MeasureJ2X software, and quality controlled using COFECHA (Holmes, 1983).

Basal area increment (BAI), the cross-sectional area of each growth ring, reflects ring width and also accounts for increasing stem diameter. We calculated BAI using measured ring widths and tree diameter at the time of ring formation (Biondi, 1999). If a sample did not contain pith, we estimated the missing inner diameter using methods from Meko et al. (2015), then we summed all prior ring widths to find the tree

radius in each year. BAI was selected because it did not require detrending, which could have removed low-frequency growth trends of interest. Although ring width usually decreases as trees age and radius expands, BAI generally increases asymptotically if trees are in good condition (Biondi and Qeadan, 2008). Conversely, decreasing BAI is indicative of declining tree condition (Bigler and Bugmann, 2004, 2003; Wyckoff and Clark, 2000).

We created BAI chronologies using 213 cores from 131 live trees in the three study reaches and 110 wedges from 110 dead trees in the DW reach only (Table 1). Tree death date was assigned as that of the last growth ring as determined from cross-dating. Because BAI increased during the first 25 years of growth and was relatively stable afterwards, we only analyzed rings produced when trees were at least

Table 1

The cottonwood samples for each group tested. BAI = Basal area increment, DW = dewatered reach, RU = reference upstream, RD = reference downstream.

Reach	Status	Tree ring proxy	Sample size	Tree establishment year (mean $\pm$ SD)
DW	Live	BAI	114 cores from 78 trees	1904 $\pm$ 34
		$\delta^{13}\text{C}$	8 cores from 4 trees	1870 $\pm$ 25
DW	Dead	BAI	110 wedges from 110 trees	1883 $\pm$ 39
		$\delta^{13}\text{C}$	4 wedges from 4 trees	1888 $\pm$ 27
RU	Live	BAI	46 cores from 25 trees	1882 $\pm$ 17
		$\delta^{13}\text{C}$	8 cores from 4 trees	1882 $\pm$ 4
RD	Live	BAI	53 cores from 28 trees	1913 $\pm$ 25
		$\delta^{13}\text{C}$	8 cores from 4 trees	1907 $\pm$ 10

26 years old to eliminate age effects. BAI chronologies were created using the dplR library in R (Bunn et al., 2019).

2.4. Carbon isotope ($\delta^{13}\text{C}$) chronologies

We analyzed the stable carbon isotope ratios ($\delta^{13}\text{C}$) of individual growth rings from 1942 to 2016 for 16 cottonwoods ($n = 783$ rings). A sample of four to six trees usually yields a reliable sample (Leavitt, 2010). We sampled four trees in each of the four groups from BAI analysis: live trees from the DW, RU, and RD reaches and dead trees from DW. The selected trees had clearly delineated annual rings, had BAI well correlated with the reach chronology, and for DW Dead had survived to at least 2013. The trees all had pith dates of 1852 to 1913, so the analysis avoids the juvenile tree effect (McCarroll and Loader, 2004) that has been shown in the first 26 years in *Populus deltoides* (Friedman et al., 2019).

Wood samples were collected with a 12 mm diameter increment borer for live trees or cut from cross sectional slabs from dead trees. We excised each ring with a razor blade and discarded the glued bottom and sanded top surfaces to avoid contamination. We combined equal weights from two cores from each tree to produce a 4.5–5.5 mg sample. Slabs were cut into a narrow strip and the sanded top surface was removed. Years were processed individually for every DW reach tree. RU and RD samples were pooled in four out of five years by combining equal mass from eight cores from the reach's four trees (Treydte et al., 2007). For every 5th year, from 1945 to 2015, the four trees were processed individually to enable tree-level assessment.

Wood samples were pulverized using a Mini-beadbeater-16 (Bio Spec Products Inc., USA) in 2 ml tubes containing a steel bead. We performed isotopic analysis on purified cellulose because $\delta^{13}\text{C}$ ratios in cellulose, but not in whole wood, were found to be independent of age in *Populus* (Friedman et al., 2019). Cellulose was isolated following methods of Brendel et al. (2000). Samples were rinsed with sodium hydroxide to eliminate hemicellulose (Gaudinski et al., 2005), and we added two extra rinses with deionized water to prevent contamination by acetyl groups (Anchukaitis et al., 2008). A sample containing 0.75–0.85 mg of cellulose was placed in a 4 $\times$ 6 mm tin cup. $\delta^{13}\text{C}$ was analyzed using continuous flow isotope ratio mass spectrometry using a Carlo Erba NC1500 interfaced to a Micromass Optima mass spectrometer. Stable carbon isotope data are reported as $\delta^{13}\text{C}$ in parts per thousand (‰) as in Eq. (1):

$$\delta^{13}\text{C} = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) * 1000 \quad (1)$$

where R_{sample} and R_{standard} are the $^{13}\text{C}/^{12}\text{C}$ ratios in our tree-ring samples and the standard, Vienna Pee Dee belemnite (VPDB). We normalized stable carbon isotope data to VPDB using internal lab standards ($\delta^{13}\text{C} = -24.60\text{‰}$ for Holly sugar; -10.82‰ for C&H sugar). We corrected for changing $\delta^{13}\text{C}$ of atmospheric carbon dioxide caused by global fossil fuel emissions using annual corrections developed by McCarroll and Loader (2004) for 1942–2003 that we updated for 2004–2016 using a linear regression of annual averages from the same South Pole dataset (<https://www.esrl.noaa.gov/gmd/ccgg/flask.php>).

Sample reproducibility was evaluated by processing duplicate samples from 61 tree rings (7.8% of samples). 67% of replicates were within 0.20‰ of each other, and 93% were within 0.40‰. Individual trees varied in their mean $\delta^{13}\text{C}$ value by up to 2.6‰, so we analyzed relative $\delta^{13}\text{C}$ changes through time by defining 1942–1961 as the pre-diversion baseline period (Rood et al., 2013).

2.5. Data analysis

We separated the analysis into two study periods: 1942 to 1961 was the pre-diversion baseline period, and 1962 to 2016 was the diversion period. Tree ring proxies were characterized as relative changes between periods within a reach to account for non-diversion related differences, such as those from differences in genetics, soils, and microhabitats. Changes in mean BAI or $\delta^{13}\text{C}$ between periods were identified using *t*-tests.

Regime shift detection was used to identify when transitions in tree-ring series occurred (Rodionov, 2004), a method previously used to investigate changes in *Populus nigra* BAI in France (Stella et al., 2013). To isolate reach-scale factors while minimizing the influence of climatic and watershed-scale factors, we created four differenced time series per tree ring proxy by subtracting BAI or $\delta^{13}\text{C}$ values for the treatment groups (DW Live, DW Dead) from that of the reference groups (RU, RD). We tested for shifts from initial conditions using the Microsoft Excel regime shift detection add-in with a significance level of 0.01, cut-off length of 20 years, Huber's weight parameter of 2, and autocorrelation estimated by the inverse proportionality method on 12 year subsamples (Rodionov, 2006). We hypothesized that shifts in average values would manifest as breakpoints around 1962, the first year after flow diversion.

We investigated streamflow, precipitation, and temperature as possible hydroclimatic drivers of $\delta^{13}\text{C}$ and BAI using the seasorr function in the treeclim library in R (Bunn et al., 2019; Meko et al., 2011). Precipitation and temperature were from the Coop Station while flow was the reconstructed undiverted Snake Creek record. The shorter flow record restricted this analysis to the diversion period. We report correlations between the tree-ring proxies and physical variables averaged from the previous July through current June because that was the most strongly correlated 12-month period. This analysis used detrended tree-ring width series created from splines with 75% frequency response cutoff at 67% of the series length, selected over BAI because splining removed low-frequency trends undesired in comparisons to high-frequency weather variation.

We grouped growing conditions in the DW and reference reaches using a k-means cluster analysis for each tree-ring proxy. We used data for every fifth year from 1945 to 2015 because they were the subset of years when isotopes were processed for each tree individually. Each series was standardized using a z-scores transformation to isolate trends through time. The $\delta^{13}\text{C}$ cluster analysis was performed using all 16 sampled trees. For BAI clustering we first identified the cores with measurements in all 15 analysis years, which was 40 cores from RU and 29 from RD. We then randomly subsampled to get 69 DW cores to match the combined reference reach sample size. We conducted k-

Table 2

Timing and magnitude of regime shifts that identify when the tree ring proxies transitioned from a period of one average value to another. Note that all ten shifts indicated drying at DW relative to reference reaches. BAI = basal area increment, DW = dewatered reach, RU = reference upstream, RD = reference downstream.

Tree ring proxy	Groups compared	Shift year ^a	Shift magnitude
BAI	DW Live - RU	2007	−2.20 cm ²
	DW Live - RD	1960, 2007	−2.61 cm ² , −2.78 cm ²
	DW Dead - RU	2008	−1.96 cm ²
	DW Dead - RD	1960, 1987	−2.66 cm ² , −1.70 cm ²
$\delta^{13}\text{C}$	DW Live - RU	1960	+1.56‰
	DW Live - RD	1961	+1.09‰
	DW Dead - RU	1964	+1.23‰
	DW Dead - RD	2004	+0.93‰

^a Excluding the final 3 years of a series because the end is less reliable in regime shift analyses (Rodionov, 2004).

means cluster analyses of principle components to reduce dimensionality and simplify visualization (Kassambara, 2017) using the prcomp and kmeans functions in the R stats package, and the Calinski-Harabasz index identified that two groups was optimal for each proxy.

2.6. Tree canopy and dieback

We classified canopy vigor for all 2153 standing cottonwoods >20 cm diameter in the study reaches using methods adapted from the US Forest Service Crown Condition Classification assessment (Schomaker et al., 2007). Trees were binned into groups with 0%, 1–20%, 21–40%, 41–60%, 61–80%, and 81–100% live canopy.

We also analyzed 13 cottonwoods in the DW reach to reconstruct within-tree patterns of branch dieback preceding tree mortality. Study trees were chosen to include the variety of morphological variation of dead standing trees. Branch structure was evaluated then 9–18 locations on the tree were selected for dating. We felled trees then collected a disc from each branch for cross-dating ($n = 158$). Trunks were cross-dated to the DW chronology to identify the tree death year. Each branch was cross-dated to its trunk, with the last growth ring assigned as the death date.

3. Results

3.1. Tree-ring growth (BAI) and $\delta^{13}\text{C}$ through time

Tree-ring BAI and $\delta^{13}\text{C}$ both shifted in directions indicating more water stress through time for DW trees relative to reference trees in all eight regime shift detection tests. Over the 1942–2016 study period, all four of the $\delta^{13}\text{C}$ comparisons (DW Live or DW Dead trees vs. RU or RD trees) had a single breakpoint where DW $\delta^{13}\text{C}$ increased by an average of 1.20‰ relative to reference reaches (Table 2). Three of the four $\delta^{13}\text{C}$ breakpoints occurred in 1960, 1961 and 1964, within 3 years of the 1961 pipeline construction, while the fourth occurred in 2004. Breakpoints in the BAI series less frequently occurred when flow diversion started. Both DW groups declined relative to RD trees twice, once in 1960 and again in either 1987 or 2007 (Table 2). Multiple breakpoints suggested that BAI separation between DW and RD was the most

Table 4

Pearson correlations (r) between basal area increment (BAI) and $\delta^{13}\text{C}$ for the pre-diversion (1942–1961) and diversion (1962–2016) periods across study reaches. Significant relationships are expressed with * if $p < 0.05$ and ** if $p < 0.01$.

	Correlation (r) for periods:	
	Pre-diversion	Diversion
Dewatered live	−0.24	−0.41**
Dewatered dead	−0.05	−0.29*
Ref. upstream	+0.25	+0.19
Ref. downstream	+0.41	+0.02

gradual of the regime shift comparisons. BAI for both DW groups also declined relative to RU, but the breakpoints did not occur until 2007 and 2008. This illustrated that BAI mutually declined for DW and RU trees over most of the study period, and the groups only separated following the period of highest temperature and vapor pressure deficit in the early 2000s (Fig. 2A, C). The six documented BAI breakpoints averaged 2.33 cm² declines, or 29.8% of the average pre-diversion growth of DW trees (Table 3).

Trees in the DW Dead, DW Live, and RU groups averaged significantly lower annual BAI (56–74%) during the diversion period compared to the pre-diversion period ($p < 0.01$; Table 3). In contrast, RD trees averaged higher BAI (116%) in the diversion period ($p < 0.05$). BAI declines for DW and RU trees began in the late 1950s during the lowest precipitation period of the study (Fig. 2A). Low post-diversion values persisted except during the high-flow years from 1978 to 1984, when BAI temporarily rebounded (Fig. 2C). The DW Dead trees grew at 85% the rate of DW Live trees in the pre-diversion period but only at 58% in the diversion period before they died.

Compared to pre-diversion averages, $\delta^{13}\text{C}$ in the diversion period increased by an average of 1.16‰ for DW Live trees and 0.86‰ for DW Dead trees (Table 3; $p < 0.01$), indicating increased water-stress. DW reach $\delta^{13}\text{C}$ values exceeded their pre-diversion average in every year of the diversion period except during the high flow period of the early 1980s (Fig. 2B, D). In contrast, $\delta^{13}\text{C}$ values remained similar to pre-diversion values at RD (+0.03‰) and decreased slightly at RU (−0.39‰) in the diversion period (Table 3), indicating that water stress did not increase at either reference reach.

3.2. Relationships between $\delta^{13}\text{C}$ and BAI

Prior to flow diversion, tree-ring BAI and $\delta^{13}\text{C}$ were not significantly correlated to each other in any study reach (Table 4). However, under diversion BAI and $\delta^{13}\text{C}$ were significantly negatively correlated for trees in the DW reach ($r = -0.41$ DW Live, $r = -0.29$ DW Dead), consistent with water stress reducing ring growth by inducing stomatal closure. In contrast, in the two reference reaches BAI and $\delta^{13}\text{C}$ were not significantly negatively correlated during either period, suggesting that growth was not strongly limited by water in areas where flow was not diverted.

Table 3

Mean values for BAI and $\delta^{13}\text{C}$ in the pre-diversion (1942–1961) and diversion (1962–2016) periods. Significant changes are expressed with * if $p < 0.05$ and ** if $p < 0.01$.

Group	BAI (cm ²)			$\delta^{13}\text{C}$ (‰)		
	Pre-diversion	Diversion	Change	Pre-diversion	Diversion	Change
Dewatered live	8.81	6.54	−2.28**	−26.25	−25.09	+1.16**
Dewatered dead	6.85	3.81	−3.04**	−26.31	−25.45	+0.86**
Ref. upstream	5.74	4.16	−1.58**	−25.83	−26.21	−0.39**
Ref. downstream	3.84	4.45	+0.60*	−25.43	−25.39	+0.03

Table 5

Pearson correlations (r) for tree ring basal area increment (BAI) or $\delta^{13}\text{C}$ with undiverted Snake Creek flow, precipitation, and temperature for the diversion period for all study reaches. Significant relationships are expressed with * if $p < 0.05$ and ** if $p < 0.01$.

Reach	Tree-ring proxy	Flow	Precipitation	Temperature
Dewatered live	BAI	0.65**	0.48**	-0.27*
	$\delta^{13}\text{C}$	-0.56**	-0.34*	0.20
Dewatered dead	BAI	0.64**	0.54**	-0.25
	$\delta^{13}\text{C}$	-0.25	-0.20	0.09
Ref. upstream	BAI	0.31*	0.13	-0.32*
	$\delta^{13}\text{C}$	-0.03	-0.36**	-0.10
Ref. downstream	BAI	0.41**	0.37**	-0.09
	$\delta^{13}\text{C}$	0.27*	0.02	-0.05

3.3. Hydroclimatic drivers of tree-ring proxies

During the diversion period, cottonwood tree-ring BAI and $\delta^{13}\text{C}$ both were most correlated to flow, then precipitation, and finally temperature. For the DW Live trees, flow and precipitation were significantly positively correlated with BAI and negatively correlated with $\delta^{13}\text{C}$ (Table 5), consistent with water stress hypotheses. BAI had slightly stronger within-period correlations with flow and precipitation than did $\delta^{13}\text{C}$, which could have been due to a larger sample size stabilizing the pooled means across trees for a given year (Table 1). Similar patterns indicative of water-limited growth were observed for the DW Dead trees except that the correlations with $\delta^{13}\text{C}$ were not significant. At reference reaches the correlations relating precipitation and flow to BAI were smaller and the correlation between $\delta^{13}\text{C}$ and flow was non-significant (RU) or positive (RD), indicating less water stress (Table 5). Precipitation relationships to $\delta^{13}\text{C}$ in the reference reaches were inconsistent with each other, with $r = -0.36$ at RU and non-significant at RD. Temperature was not significantly correlated with $\delta^{13}\text{C}$ in any reach, but had a negative correlation with BAI for DW Live and RU trees, indicating a tendency for high temperatures to decrease growth.

3.4. Statistical separation of dewatered and reference reach trees

Trees within a given reach had consistent trends through time in $\delta^{13}\text{C}$ but not BAI. Both cluster analyses best separated trees into two groups. For BAI, the first three principle components explained 25%, 15%, and 10% (50% total) of the variation. The BAI cluster analysis created groups that only weakly differentiated between the DW and

reference reaches. 65% of DW trees were in Group 1 and 35% were in Group 2, while 46% of reference reach trees were in Group 1 and 54% in Group 2 (Fig. 3A). RU and RD trees tended to separate along principle component 2. The lack of clear separation in cores from the DW and reference reaches reflected BAI patterns varying substantially at the tree-scale, not the reach-scale.

For $\delta^{13}\text{C}$, a similar amount of variation was explained by the top three principal components as for BAI, with PC's 1, 2, and 3 explaining 26%, 17%, and 11% (54% total) of the variation. In contrast to BAI, the cluster analysis performed using $\delta^{13}\text{C}$ values divided the 16 sampled trees into two groups that were perfectly separated into DW and reference reaches. 100% of DW Live and DW Dead trees were in Group 1, and 100% of RU and RD trees were in Group 2 (Fig. 3B). The interspersed DW Live and DW Dead trees suggests that their responses to drought were similar. Trees from RU and RD formed sub-clusters within the reference group, but their $\delta^{13}\text{C}$ signatures still grouped as more similar to each other than to the geographically intermediate DW trees.

3.5. Tree canopy and dieback

The DW reach had more dead trees and less live canopy compared to trees in reference reaches. 28% of standing trees in DW were dead, compared to 11% and 12% of trees in RU and RD. Living trees averaged 43% live canopy in DW, significantly lower than the 64% in RU and 76% in RD. Of the five canopy classes for living trees, the most common in the DW reach was 1–20% live canopy, while in both reference reaches it was 81–100% live canopy (Fig. 4).

We documented a long history of branch dieback from 1903 to 2016, which preceded tree mortality in all 13 DW trees investigated (Fig. 5). Branch death peaked in the 1960s and 1970s, the first two decades after flow diversion. High streamflow in the early 1980s coincided with reduced branch mortality, high BAI, and $\delta^{13}\text{C}$ values that temporarily returned to pre-diversion values. The average branch died a mean of 20 years before the whole tree died (median = 14 years, range = 10 to 44 years, $n = 145$ branches). The number of branches dying in a year was inversely correlated to BAI (F-stat = 4.3, $p = 0.04$), indicating that branch death tended to occur in years of low growth.

4. Discussion

Tree-ring BAI and $\delta^{13}\text{C}$ provided different signals of cottonwood response to stream dewatering. $\delta^{13}\text{C}$ indicated a rapid shift to sustained water stress in DW beginning at the onset of flow diversion, a pattern

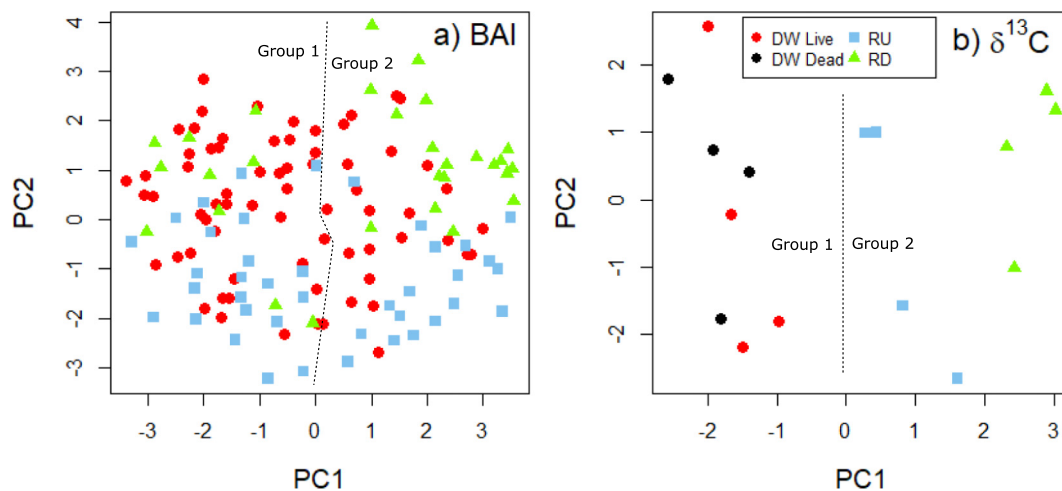


Fig. 3. Cluster analysis ordination plots graphed on the first two principle components for (a) basal area increment (BAI), and (b) $\delta^{13}\text{C}$. Clustered groups are separated by dashed lines. Red circles = Dewatered (DW) Live, black circles = DW Dead, blue squares = Reference upstream (RU), and green triangles = Reference downstream (RD). Note that DW trees are distinct from reference trees for $\delta^{13}\text{C}$ but not for BAI. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

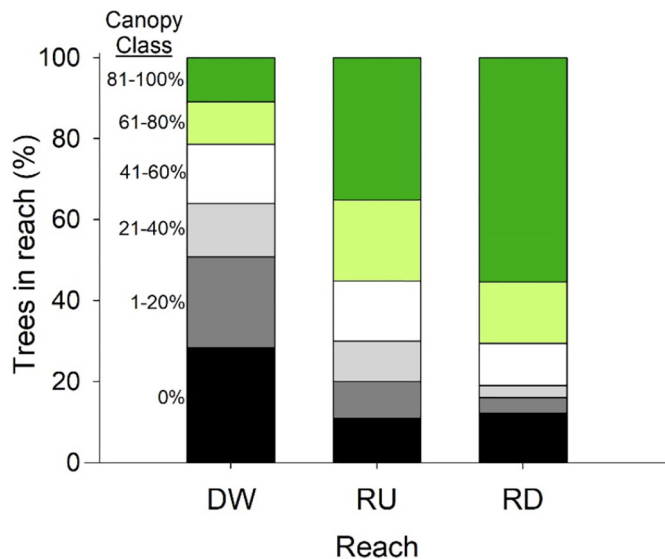


Fig. 4. Stacked bar graph showing the percent of standing trees in each canopy class for the study reaches (DW = Dewatered, RU = Reference Upstream, RD = Reference Downstream). The color scheme shows canopy classes ranging from 0% live canopy (i.e., dead) to 81–100% live canopy.

not found in either reference reach. This suggests that trees in DW closed stomata to limit water loss because flow had been diverted. In contrast, tree-ring BAI in the DW reach declined more gradually throughout the 55-year diversion period, which could be interpreted as either increasing drought stress through time or an accumulating carbon deficit. The DW reach BAI decline distinguished it from the RD reach as soon as diversion began. DW reach BAI did not immediately separate from RU reach trees, however, where its landscape position meant that the decline in BAI at RU was caused by factors other than flow diversion. Forty years after diversion began, a meteorological drought and high temperatures increased vapor pressure deficit and appear to have compounded diversion-induced hydrological drought at DW. This further narrowed tree rings in DW compared to RU and RD, finally distinguishing DW reach BAI from that of both reference reaches.

Evidence beyond BAI was needed to identify that cottonwood decline was initiated by flow diversion in 1961. Diversion led to a sharp rise in tree-ring $\delta^{13}\text{C}$ followed by a pulse of branch dieback in the 1960s and 1970s. Therefore, although the increased water stress from flow diversion was initially insufficient to kill the trees, carbon starvation or xylem cavitation beginning at the onset of flow diversion

apparently led to canopy dieback. The rapid $\delta^{13}\text{C}$ increase and gradual reduction in BAI during diversion is consistent with carbon starvation from decreased stomatal conductance and reduced photosynthetic assimilation rates (Gessler et al., 2018). After a half-century of flow diversion we observed higher tree mortality and lower canopy vigor in the DW reach than in reference reaches. The accumulated carbon deficits and reduced streamflow left its trees more vulnerable to local atmospheric drought, leading to the observed low tree vigor, growth, and survival. Although extreme changes to flow regimes can immediately and irreversibly impact river corridors (Nilsson and Berggren, 2000), the effects of moderate perturbations such as partial diversion of Snake Creek are harder to identify (Poff and Zimmerman, 2010; Schook et al., 2016a; Stella et al., 2013) and may resemble the changes of drought from shifting climates. Factors such as ecological resistance and time lags can also obscure cause-effect relationships and our understanding of ecosystem changes (Chin et al., 2014; Frank et al., 2015; Poepl et al., 2017), as evidenced in BAI analysis.

Hydrogeomorphic heterogeneity can influence how *Populus* stands respond to increased drought stress within a river corridor (Stella et al., 2013). Our two reference reaches differed, and their integration strengthened interpretations of conditions in the DW reach. The RU reach had natural flows but its BAI declined similarly to DW reach trees from about 1957 to 2007. The RU BAI decline could reflect that it contained the oldest trees that were more susceptible to factors such as rot. This was supported within DW, where dead trees were both older and slower growing than surviving trees, as found by Stromberg and Patten (1992). Additionally, shading from white firs in the RU reach could have reduced BAI in the shade-intolerant cottonwoods, and our findings may foreshadow a successional transition. The absence of a BAI decline in RD could reflect slightly augmented flow from the diversion. However, the flow increase in this perennial reach would have only slightly raised the alluvial water table, so the augmentation likely affected the studied tree-ring proxies little.

Our observations of hydrological drought and riparian cottonwood response are consistent with other studies of trees in the family *Salicaceae*. A negative correlation of $\delta^{13}\text{C}$ with water availability has been found in *Populus fremontii* from New Mexico (Leffler and Evans, 2001), *Salix* spp. in New York (Schifman et al., 2012), and *P. nigra* in France (Chamaillard et al., 2011). In *P. fremontii* from Arizona, tree rings from intermittent reaches had higher $\delta^{13}\text{C}$ and stronger correlations of $\delta^{13}\text{C}$ with flow and vapor pressure deficit than tree rings from a perennial reach (Potts and Williams, 2004). Their findings and ours both identified photosynthesis to be more water limited in intermittent reaches. In Alberta, Canada, low flow was correlated with decreased *P. angustifolia* growth, $\delta^{13}\text{C}$ increased especially in trees higher or further from the river, and the authors concluded that the trees were

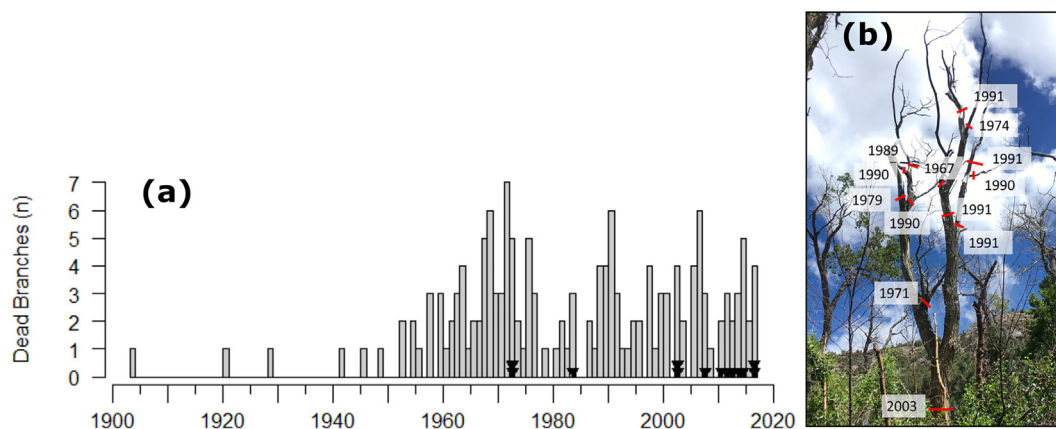


Fig. 5. (a) Histogram showing death dates of the sampled branches, with triangles showing the last year of trunk growth for the 13 trees. (b) Branch death dates from an example tree that died in 2003 (Photo by DMS).

vulnerable to declining river flows from withdrawals and climate change (Rood et al., 2013). There have already been widespread declines in cottonwood regeneration and loss of native riparian communities in the western USA (Andersen et al., 2007; Friedman et al., 2005), and natural flows are most suitable for sustaining these ecosystems (Lytle and Merritt, 2004; Lytle and Poff, 2004). Given projected increases in drought severity in some regions and the ubiquity of human intervention in river flows for hydropower, flood protection, irrigated agriculture, and recreation, riparian ecosystems are increasingly vulnerable to future drought.

Investigating and contrasting tree basal growth and $\delta^{13}\text{C}$ together improved interpretations of riparian forest response to human-caused hydrological drought. Although the tree-ring proxies were uncorrelated pre-diversion, after diversion both proxies reflected hydrological drought by becoming significantly negatively correlated for DW Live and DW Dead trees but not RU and RD trees. This could partly reflect increased interannual flow variability after the diversion removed base flows and small floods. The higher correlations and subsequent increased mortality we found at DW following diversion are consistent with the observation that tree-ring growth variability can demonstrate increased sensitivity by increasing in the decades prior to tree death (Caillieret et al., 2019). Even though $\delta^{13}\text{C}$ was the proxy that sharply changed between periods, our hydroclimatic driver analysis found that it was BAI that had stronger correlations to both flow and precipitation within the diversion period. This may reflect the larger sample size for BAI than for $\delta^{13}\text{C}$, although combining DW trees into one group and reference trees into another ($n = 8$ per group) would not have changed our conclusions. Other studies have found differences in seasonal relations of $\delta^{13}\text{C}$ and ring width to climate. For example, in North Dakota *P. deltoides* ring widths reflected precipitation from spring and early summer, and $\delta^{13}\text{C}$ better reflected precipitation from June and July (Friedman et al., 2019). Similar findings were reported for latewood chronologies of conifers in the southwestern US (Leavitt et al., 2011) and for *Tectona grandis* in Indonesia (Scholten et al., 2013). Given projected changes in the intensity, seasonality, and form of precipitation under climate change, these seasonal influences on $\delta^{13}\text{C}$ and ring width are an important area for future work.

The future of forest ecosystems hinges on interacting relationships among the five spheres of the total environment. Understanding if a forest will persist through drought, or if species composition is likely to transition into a new community or habitat (Martínez-Vilalta and Lloret, 2016) depends on factors such as local geomorphology and climate (Stella et al., 2013). Predicting future shifts is a key challenge for scientists and managers. Tree-ring proxy investigations will be particularly valuable if they help people predict when shifts in environmental conditions will change ecosystems. For example, tree-ring lumen area declines have been shown to precede whole-tree declines by several decades (Pellizzari et al., 2016). Similarly, our results identify $\delta^{13}\text{C}$ as a tree-ring proxy capable of providing an early warning of tree death decades in advance. While droughts in most of the 20th century were largely caused by reduced precipitation, those in the 21st century have been exacerbated by high temperatures that increase evapotranspiration (Berg et al., 2006; Udall and Overpeck, 2017). Future meteorological droughts with hotter temperatures are likely to compound the effects of reduced precipitation and result in widespread forest decline. Early warnings in tree rings, like the stable carbon isotopes explored in this study, will therefore be increasingly important predictive tools for forest managers.

CRedit authorship contribution statement

Derek M. Schook: Conceptualization, Methodology, Writing - original draft, Investigation, Formal analysis, Funding acquisition, Visualization. **Jonathan M. Friedman:** Conceptualization, Writing - review & editing, Funding acquisition, Resources. **Craig A. Stricker:** Investigation, Data curation, Resources, Writing - review & editing. **Adam Z. Csank:**

Investigation, Resources, Writing - review & editing. **David J. Cooper:** Conceptualization, Writing - review & editing, Funding acquisition, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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