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ORIGINAL ARTICLE

Anisohydric water use behavior links growing season evaporative demand to ring-width increment in conifers from summer-dry environments

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Abstract

Key message **Compared to isohydric Pinaceae, anisohydric Cupressaceae exhibited: (1) a threefold larger hydroscape area; (2) growth at lower pre-dawn water potentials that extended longer into the growing season; and (3) stronger coupling of growth to growing season atmospheric moisture demand in summer-dry environments.**

Abstract Conifers in the Pinaceae and Cupressaceae from dry environments have been shown to broadly differ in their stomatal sensitivity to soil drying that result in isohydric versus anisohydric water use behavior, respectively. Here, we first employ a series of drought experiments and field observations to confirm the degree of isohydric versus anisohydric water use behavior in species of these two families that are representative of the Interior West of the United States. We then use experimental soil drying to demonstrate how growth of anisohydric *Juniperus osteosperma* was more closely tied to pre-dawn water potentials than isohydric *Pinus monophylla*. Finally, we confirm that measured leaf gas-exchange and growth responses to drying hold real-world consequences for conifers from the Interior West. More specifically, across the past ~ 100 years of climate variation, pairwise comparisons of annual ring-width increment responses indicate that growth of Cupressaceae species (*J. osteosperma* and *J. scopulorum*) was more strongly coupled to growing season evaporative demand than co-occurring Pinaceae species (*Pinus monophylla, P. edulis, P. flexilis, P. longaeva, P. ponderosa*, and *Pseudotsuga menziesii*). Overall, these experimental and observational results suggest that an a priori distinction based on family and associated hydric water use behavior should lead to more accurate and mechanistically correct dendrochronological reconstructions of growing season evaporative demand (i.e., Cupressaceae) versus antecedent precipitation (i.e., Pinaceae) in summer-dry environments. Moreover, these differences in growth sensitivity to evaporative demand among these groups suggest that incorporating hydric water use behavior into models of forest responses to global warming can provide more accurate projections of future forest composition and functioning.

Keywords Dendrochronology · Drought tolerance · Stomatal conductance · Tree growth · Water potential · Water use behavior

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Introduction

Severe drought events often cause widespread mortality and varying rates of survival among woody species (Breshears et al. 2009, 2013; Williams et al. 2013). Survival through protracted droughts depends on interactions of diverse but coordinated traits that confer hydraulic safety and efficiency and so help protect plant photosystems and xylem functionality by contributing to overall strategies of drought avoidance or tolerance (Meinzer et al. 2010; Bartlett et al. 2016; Matheny et al. 2017). Among these traits is sensitivity of stomatal conductance (g_s) to plant xylem water potential (Ψ) that determines different water use behaviors (i.e., hydric water use behavior: isohydry to anisohydry—or greater to lesser stomatal sensitivity to dry air and dry soil that moderates xylem water tension—*sensu* Tardieu and Simonneau 1998). The contribution of water use behavior to drought survival has been of growing interest (Franks et al. 2007; McDowell et al. 2008, 2013; Klein 2014; Martinez-Vilalta et al. 2014; Meinzer et al. 2014, 2016; Garcia-Forner et al. 2016). In angiosperms, hydric water use behavior correlates with leaf osmotic potential at full and zero turgor as well as photosynthetic gas-exchange traits (Meinzer et al. 2016, 2017) and differs with stem xylem anatomical traits and rooting depth (Meinzer et al. 2013; Klein 2014; Matheny et al. 2017). Among conifers from dry environments, water use behavior of the Pinaceae diverges greatly from the Cupressaceae due to stomatal opening being regulated by differing patterns of abscisic acid in leaves (Brodribb et al. 2014). Therefore, in many parts of the Interior West where species of both conifer families coexist, there is the potential for comparing climate responses of mature trees that have water use behaviors near the endpoints of the isohydric versus anisohydric continuum. If hydric water use behavior does indeed have important consequences for carbon assimilation and plant productivity, we hypothesize that co-occurring species from the Pinaceae and Cupressaceae should display differing growth responses to climate variability. Documentation of such differing responses in the absence of recent insect outbreaks should add clarity to the many studies recently carried out in the southwestern United States, where bark beetles have interacted with drought stress to cause widespread mortality in isohydric *Pinus edulis* Engelm., whereas co-occurring and anisohydric *Juniperus monosperma* (Engelm.) Sarg. have not been subject to increased bark beetle or insect pest damage and has suffered much less mortality (Breshears et al. 2009; Gaylord et al. 2013).

Isohydry, by definition, decouples leaf gas-exchange and hydraulic architecture from moderate to severe drought via strong stomatal sensitivity to dry air and dry soil that moderates xylem water potential and associated risk of xylem embolism. In isohydric species such as *Pinus edulis*, stomatal closure initiates this decoupling at relatively high Ψ, often starting at $\Psi < -1$ MPa and continuing toward near-complete stomatal closure at Ψ nearing -2.0 MPa (Plaut et al. 2012), and accelerated by dry air as vapor pressure deficit (VPD) approaches 3 MPa (Oren et al. 1999; Ruehr et al. 2014). Therefore, a drought of only moderate evaporative demand may suppress growth rates of isohydric trees nearly as much as a drought of the same length with high evaporative demand, and thereby result in growth that is unresponsive to progressively more severe seasonal droughts. By contrast, under moderate to severe soil drying, anisohydric Cupressaceae (McDowell et al. 2008; Brodribb et al. 2014) are characterized by stomatal conductance and transpiration that is still responsive to xylem Ψ from -2.0 to -4.0 MPa (Plaut et al. 2012). Therefore, in a summer-dry location like Utah, where protracted droughts often cause upper soil horizons at most sites to dry past the wilting point for most plants (i.e., below -1.5 MPa), the growth of Cupressaceae should more closely reflect variation in cumulative growing season evaporative demand compared to co-occurring species of Pinaceae. The anisohydric water use behavior of *Juniperus monosperma* has been linked to dynamic regulation of turgor loss point as drought stress varies, and the ability to withstand more severe drought stress compared to a more rigid turgor loss point and greater vulnerability to such severe drought stress in isohydric *Pinus edulis* (Meinzer et al. 2014). Compared to isohydric species in the Pinaceae, anisohydric behavior, regulation of turgor loss point and other hydraulic characteristics (Willson et al. 2008) should allow the leaves of anisohydric *Juniperus* spp. to continue to maintain positive net carbon gain during hot and dry growing seasons where both mid-day and pre-dawn leaf water potentials (Ψ_{PD} and Ψ_{MD}, respectively) are gradually drawn down (Lajtha and Barnes 1991). However, to what extent anisohydric water use behavior and other associated functional traits may influence annual tree growth responses to climate variability has not been well-established.

Across the western United States, traits that confer drought tolerance in the Cupressaceae are typically described for low elevation, dry habitats that have greater peak and cumulative growing season evaporative demand when compared to the higher elevation-distributions of many species in the Pinaceae (Willson et al. 2008; Bowker et al. 2012; Limousin et al. 2013). However, across much of the Interior West, putatively anisohydric *Juniperus osteosperma* Torr. and *J. scopulorum* Sarg. can co-occur on mid- to low-elevation sites with any number of isohydric Pinaceae (*Pinus monophylla* Torr and Frém., *P. edulis*., *P. flexilis* James, *P. longaeva* D.K. Bailey, *P. ponderosa* Lawson and C. Lawson,

and *Pseudotsuga menziesii* (Mirb.) Franco). While both behaviors likely help maintain species coexistence under some conditions, we speculate that compared to isohydric Pinaceae, the inter-annual growth of Cupressaceae will be more sensitive to progressive growing season soil water depletion, as driven by evaporative demand.

The use of Cupressaceae tree rings, specifically *Juniperus* spp., in dendroclimatology has been rare until recently (Maxwell et al. 2012; Allen et al. 2013; Spond et al. 2014; DeRose et al. 2014, 2015, 2016; Riddle et al. 2014). The development of *Juniperus* tree-ring chronologies, as well as those in co-occurring Pinaceae now allows us to determine if one or the other families, representing broadly conserved hydric water use behaviors (Brodribb et al. 2014), has been characterized by a tighter coupling of year-to-year growth variability and cumulative summer evaporative demand. In turn, this should lead to insights on: (1) whether future climate warming may alter the balance of species coexistence across many areas where anisohydric and isohydric conifers coexist, and (2) whether a priori knowledge of water use behavior can lead to physiologically tractable and more accurate reconstructions of cool season precipitation versus warm season evaporative demand. To help address this question, we first build upon previous physiological studies by experimentally demonstrating isohydric versus anisohydric behavior in *J. osteosperma, J. scopulorum, P. monophylla* and *P. menziesii*. We then explore species-level differences in intra-annual growth responses to variation in soil drying for paired *J. osteosperma* and *P. monophylla* in a field experiment. Finally, using observational tree-ring data, we compare inter-annual growth responses to growing season evaporative demand between co-occurring species from the Cupressaceae versus Pinaceae families.

Materials and methods

Study region and climate

The experimental data and tree-ring sites collected for this study were located in a region best characterized as northern Utah, but that includes sites from central Utah to southern Idaho (Fig. 1). The climatic regime of the study area is dominated by Pacific westerly storm tracks that deliver the majority of annual precipitation as snow during the cool season (Mock 1996), whereas by late June regional climate

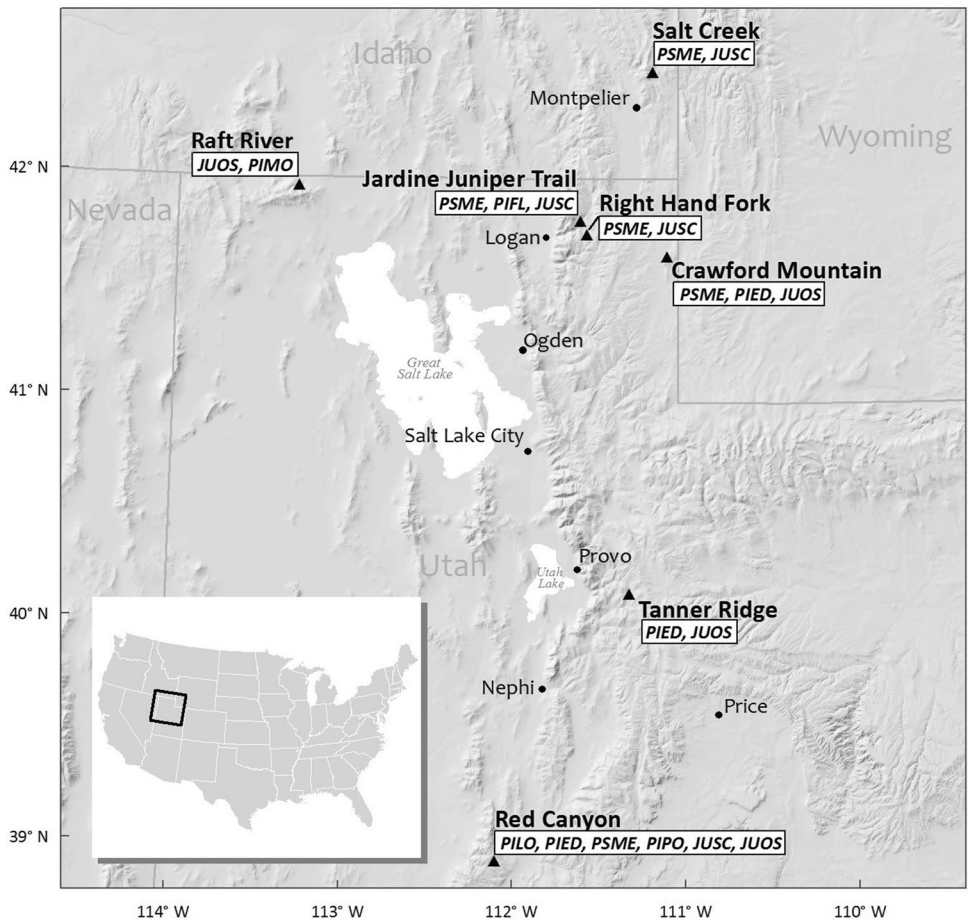

Fig. 1 Study area, study sites, and associated species that comprised the tree-ring chronologies

shifts dramatically to a high-pressure pattern driven by Pacific Ocean conditions (Wise 2012). Plant available water is highly variable across the growing season and includes snowmelt and spring rain. A well-developed seasonal drought during the late-growing season (July, August, September), with little to no monsoonal flow (Wang et al. 2009), is a predominant feature of the region (Fig. 2, daily precipitation (1911–2010) Utah State University GHCN weather station #USC00425186, http://climate.usurf.usu.edu). While on any given day between December and March, the probability of precipitation is ~40%, the day-to-day likelihood and amount becomes increasingly variable in April through June (Fig. 2a, b). Annually, rainfall probability plummets in June just as reference evapotranspiration (ET_o, after Hargreaves and Samani 1985) begins to peak (Fig. 2c), which accentuates the seasonal drought in the region.

Quantification of plant hydric water use behavior

To explore hydric water use behavior, we measured or obtained data on xylem water potential at pre-dawn (Ψ_{PD}) and during the mid-day (Ψ_{MD}) from selected study species for which we had also developed tree-ring chronologies. Data were collected during the growing seasons of 2012, 2014 and 2016. The experiments were conducted at the Utah State University Research Farm (41.7°N, 111.8°W, 1382 m elevation). In 2012, we used ten trees of *J. scopulorum* that had been previously grown in 20 L containers and then transferred to 45 L containers in spring. A well-drained organic substrate (90% peat moss 10% perlite) was used at both stages. Transplanted trees were allowed to establish for two weeks to accommodate the larger root zone. Visual inspection verified the roots that reached the container walls, confirming establishment. Similar growth conditions were used in 2014 for *J. osteosperma*, and in 2016 for both *J. osteosperma* and *P. monophylla*. In all trees and years, the heights ranged from 50 to 120 cm. The greatest tree sizes occurred in 2016, with the mean (± SE) diameters measured just above the root collar in September 2016 having been 31.1 (1.0) and 27.1 (1.4) mm for *J. osteosperma* and *P. monophylla*, respectively.

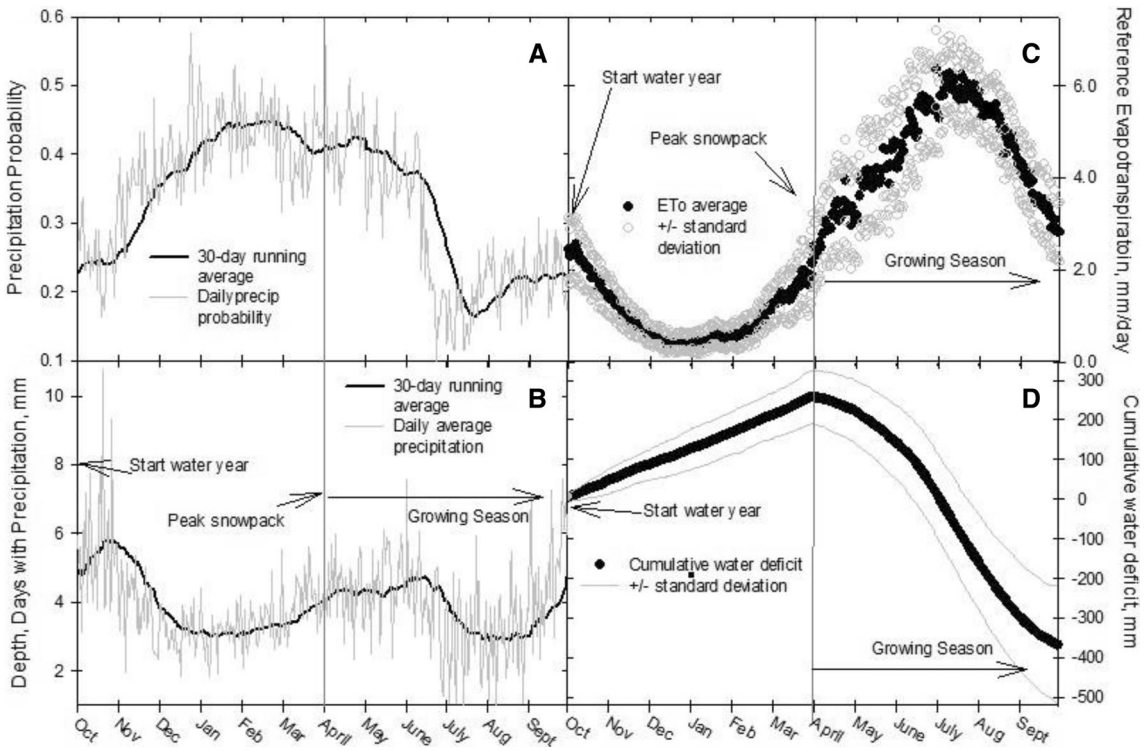

Fig. 2 Climate data from the USU, Logan, Utah climate station from 1911 to 2010: **a** probability of precipitation (# days with precipitation divided by 100) on every day of the year (gray lines) and 30 day (running average); **b** average depth of precipitation on days with precipitation every day of the year (gray lines) and 30 day (previous running average); **c** average reference evapotranspiration ± standard deviation based on the Hargreaves equation; **d** cumulative climatic water deficit/surplus: October–March accumulated precipitation surplus (assuming no evapotranspiration losses), and April–September water deficit (accumulated precipitation minus evapotranspiration), ± standard deviation. For this region, April 1st denotes the approximate timing of peak snowpack as per water management convention, at high elevation sites (> 2500 m) and the start of the growing season at low elevation sites (< 2000 m). Our experimental and tree-ring collection sites are at low- to mid-elevations (Table 1)

Following establishment, water application to the studied trees was managed with a hanging load cell lysimeter system described by Beeson (2011) that measured daily water use of trees grown in containers suspended in in-ground sleeves from a load-cell transducer connected to a data logger system (CR-1000, Campbell Scientific, Logan UT). The pre-dawn to midnight mass difference measured from each tree by a load cell yielded the volume of water used each day. Depending on the drought treatment assigned to each tree, a certain proportion of this water (i.e., either 0 replacement, 50% for slow dry down, or 110% to ensure the root zone was refilled) was replaced at midnight, to allow time for drainage before sunrise, with a drip irrigation system consisting of three, 4-L per hour drip emitters spaced evenly across the surface of the container. Irrigation timing and amount was controlled by solenoid valves connected to the data logger via relay switches. Trees were irrigated at midnight to ensure leaching was completed prior to sunrise. As the trees grew larger and were placed in larger pots the treatments were applied over longer periods: three weeks in 2012 (July 12–August 3), six weeks in 2014 (August 6–September 16), and nine weeks in 2016 (June 9–August 18).

During the treatment periods described above, stomatal conductance (g_s) and Ψ_L were measured weekly or bi-weekly. Measurements of g_s were conducted mid-morning and again mid- to late-afternoon to obtain g_s maxima and the extent of mid-day depression. The similar timing of g_s morning maxima in both species and mid-day depression minima in *P. edulis* were determined by extensive previous dawn to dusk measurements of both species (R. Kjelgren and S. Voelker, *unpublished data*). Measurements of g_s were conducted with a Decagon SC-1 porometer (Decagon Devices, Inc., Pullman WA) on two shoots per tree on each of the ten trees per species. Water potential at pre-dawn ($\Psi_{PD,}$ i.e., measured between 4:30 and 6:30) and mid-day (Ψ_{MD}, i.e., measured between 12:30 and 14:30) were measured on the same days as stomatal conductance using a Scholander-type pressure chamber (model 600, PMS Instrument Company, Corvallis, OR). At each time, two small shoot samples per tree on each of ten trees per species were excised with a razor, wrapped in cellophane and then in aluminum foil and placed in a cooler on top of a towel-wrapped ice block. Shoots were transported to an adjacent facility where xylem balance pressure (i.e., the measured value, assumed to be equal to but opposite of xylem Ψ) was measured on these equilibrated shoots within an hour of being excised. Pre-dawn and mid-day water potential data for *P. menziesii* were obtained by digitizing data from figures reporting these measurements (Running 1976; Eissenstate and; Mitchell 1983; Newton and Preest 1988; Davis 2005). Only data from seedlings and saplings were used, so tree size and the associated hydrostatic gradient in Ψ_L would be comparable to the experimental data we collected. Ψ_L data from the *Juniperus* spp. were combined for further analyses due to the relatively short dry-down period used for *J. scopulorum* in 2012 that resulted in this species having a relatively narrow range in measured Ψ_L. To quantify hydric water use behavior, Ψ_{MD} was plotted versus Ψ_{PD} to quantify the "hydroscape area" (*sensu* Meinzer et al. 2016). A hydroscape area estimates the potential range of water potentials in which a tree or species operates. In turn, this metric is closely associated with hydric water use behavior, because it connotes how strictly stomata constrain leaf water potentials in relation to soil water potentials. To obtain the lower boundary of the hydroscape area, we summed the ranks of Ψ_{PD} and the difference between Ψ_{PD} and Ψ_{MD} and used the lower 50% of the observations for each species. A linear regression was fitted to the resulting data and extrapolated to the 1:1 line and the point in which Ψ_{PD} was equal to zero to establish the lower boundary of the hydroscape area. The area between this linear regression line and the 1:1 line was used to determine the hydroscape area for each species.

Quantification of growth responses in experimental trees

Stem growth of *J. osteosperma* and *P. monophylla* was measured approximately weekly for all but 1 week during the growing season of 2016. These measurements were obtained using a digital caliper to record stem diameter at the same height and radial orientations (North–South and East–West directions; for repeatability, the measurement locations were marked on the bark with a felt pen) near the stem base of each tree. These two measurements were averaged for each tree and converted to periodic change in stem diameter as compared to the total stem diameter measured during the previous measurement period and multiplied by 100 to yield a percentage change in stem diameter. These data were converted to daily percentage growth rates by dividing the obtained values by the number of days between measurement periods. Periods in which the measured stem diameter was greater during a previous week, due to measurement error and/or stem shrinkage, yielded negative percentage growth values. Negative values do not connote a shrinkage of the functional xylem area, as that would require severe dehydration to a level in which water bound to cell walls is removed and parenchyma cells would have previously died. Nonetheless, negative values were kept within the data set as a means of tracking phloem and inner bark responses to prolonged drought stress.

Tree-ring data collection and preparation

We collected tree core samples that comprise 20 chronologies from within the region, consisting of 23–114 trees at each of six separate sites (Fig. 1). These included

Table 1 Descriptive statistics for the twenty northern Utah region tree-ring chronologies from the Cupressaceae and Pinaceae

Chronology identification	Species	Elev. (m)	Series inter-correlation	Mean sensitivity	Percent missing rings	Expressed population signal	Mean auto-correlation model (years)	Mean series length
Cupressaceae								
CMU	*J. osteo*	2345	0.82	0.64	3.70	0.97	1.48	304
JTR	*J. scop*	2100	0.61	0.23	0.08	0.93	1.63	368
RCU	*J. osteo*	2280	0.77	0.48	2.01	0.88	1.70	486
RCR	*J. scop*	2280	0.67	0.41	0.96	0.79	1.75	409
RFR	*J. scop*	2000	0.61	0.30	0.29	0.90	1.30	323
RRU	*J. osteo*	1828	0.79	0.67	3.11	0.96	1.79	207
SCR	*J. scop*	2000	0.66	0.38	0.64	0.90	1.66	305
TRU	*J. osteo*	1960	0.71	0.37	0.82	0.90	1.39	365
Pinaceae								
CMD	*P. menziesii*	2345	0.77	0.40	0.40	0.95	2.07	314
CMP	*P. edulis*	2345	0.80	0.47	2.52	0.96	1.96	338
JTD	*P. menziesii*	2100	0.67	0.19	0.02	0.96	1.16	286
JTL	*P. flexilis*	2100	0.59	0.18	0.05	0.93	1.09	274
RCB	*P. longaeva*	2280	0.74	0.39	1.44	0.96	1.97	582
RCC	*P. edulis*	2280	0.73	0.35	1.55	0.92	1.24	348
RCD	*P. menziesii*	2280	0.81	0.37	0.97	0.97	1.78	343
RCP	*P. ponderosa*	2280	0.75	0.35	1.25	0.90	1.38	405
RFD	*P. menziesii*	2000	0.71	0.21	0.00	0.92	1.50	266
RRS	*P. monophylla*	1828	0.77	0.50	2.05	0.98	1.33	234
SCD	*P. menziesii*	2000	0.72	0.26	0.04	0.95	1.17	281
TRC	*P. edulis*	1960	0.73	0.31	0.57	0.96	1.69	381

eight chronologies from family Cupressaceae (four *J. osteosperma*, four *J. scopulorum*), and twelve from family Pinaceae (five *P. menziesii*, three *P. edulis*, one *P. flexilis*, one *P. ponderosa*, one *P. longaeva*, and one *P. monophylla*) (Table 1). All sites were on south- and west-facing, rocky, steep slopes or low-elevation ridges with little soil development where water was likely to be the factor most limiting to growth (*sensu* Fritts 1976). We removed at least two cores per tree where possible with an increment borer, or obtained cross-sections from the lower boles of dead and down stems.

Increment cores were prepared with progressively finer sandpaper to 600 grit and 9 micron finishing film, until individual cells were clearly visible under a binocular microscope. Tree-ring series were visually crossdated using the list and memorization methods (Speer 2010), measured to 0.001 mm, and dating accuracy confirmed using the computer program COFECHA (Holmes 1983). To remove non-climatic growth trends and produce a dimensionless ring-width index from the tree-ring series, we used a 100-year cubic smoothing spline with a 50% frequency cutoff (Cook et al. 2007). Autoregressive modeling was applied to each series before they were averaged for each site to a composite chronology (Cook 1985) to reduce the biological legacy-effects of climate events in years previous to that under consideration for comparison to current year climate data.

Climate data

To explore the evaporative demand-related ecophysiological mechanisms that might drive ring-width variability, we first determined whether and how each species responded to monthly climatic moisture deficit by relating the ring-width index from each chronology to monthly climatic moisture deficit generated using ClimateNA software (Wang et al. 2016). Monthly ClimateNA data were available back to the year 1900, so for dendroclimatic analyses the common period to each site that was investigated was 1900–2010. For the historical data used to assess tree growth sensitivity to climate, Wang et al. (2016) employed a Parameter Regression of Independent Slopes Model (PRISM, *sensu* Daly et al. 2008) to interpolate primary and derived climate fields across North America from the CRU-TS 3.22 data set gridded at 0.5° (Mitchell and Jones 2005). Climatic moisture deficit is calculated in ClimateNA by subtracting monthly reference evapotranspiration (after Hargreaves and Samani 1985) from monthly precipitation.

Statistical analyses

For the tree physiological data, regression analyses were conducted with Sigmaplot software (Systat Software, San Jose California, USA). We also used two-tailed *T* tests to determine whether mean correlations between stomatal conductance and water potential data among trees and among dates were significantly different among species.

For the tree-ring data, we assessed the climate response of each chronology using bootstrapped correlation (alpha level of 0.05) for climate data summed across the March through October growing season for the period 1901–2010 using the bootRes package in the R computing environment (Biondi and Waikul 2004; R. Development Core Team 2012; Zang and Biondi 2013). To test for family-level differences in response to climatic moisture deficit, we compared the month of maximum response between Cupressaceae and Pinaceae for all chronologies within a given site. Results were pooled for all sites and evaluated using a contingency table under the assumption that the observed/expected ratio between families should be 50/50.

Results

Hydric behavior and controls on growth during experimental drought treatments

The relationship of Ψ_{MD} to Ψ_{PD}, after filtering to identify the lower boundary conditions, were significant for *J. osteosperma* and *J. scopulorum* ($\Psi_{MD} = 0.8037 \times \Psi_{PD} - 1.5622$, $r^2 = 0.98$, $P < 0.0001$), *P. monophylla* ($\Psi_{MD} = 0.5100 \times \Psi_{PD} - 1.2455$, $r^2 = 0.90$, $P < 0.0001$) and for *P. menziesii* ($\Psi_{MD} = 0.3556 \times \Psi_{PD} - 1.5934$, $r^2 = 0.70$, $P = 0.0001$) (Fig. 3a–c). These relationships defined the lower boundaries of the hydroscape area, whereas the other two boundaries were defined by the 1:1 line and a line defined by Ψ_{PD} equal to zero (see gray triangles in Fig. 3a–c). The hydroscape areas for *Juniperus* spp., *P. monophylla*, and *P. menziesii* were equal to 6.26, 1.59 and 1.93 MPa^2, respectively (see inset in Fig. 3b). In our experimental setting, g_s was measured just after Ψ_{PD} and Ψ_{MD}. These two sets of measurements were generally more strongly coupled (i.e., average correlations across measurement dates or across trees) in the afternoon than in the morning, but differences among periods were not significant ($P > 0.05$, Table 2). Among species, g_s measured in the morning was more strongly coupled to Ψ_{PD} in *J. osteosperma* compared to *P. monophylla* across measurement dates and trees ($P = 0.041$ and 0.034, respectively). Differences in these correlations as well as the hydroscape areas also reflected a relatively greater dependence of morning g_s on Ψ_{PD} in *J. osteosperma* compared to *P. monophylla* (Fig. 4). Coupling of afternoon g_s to Ψ_{MD} was

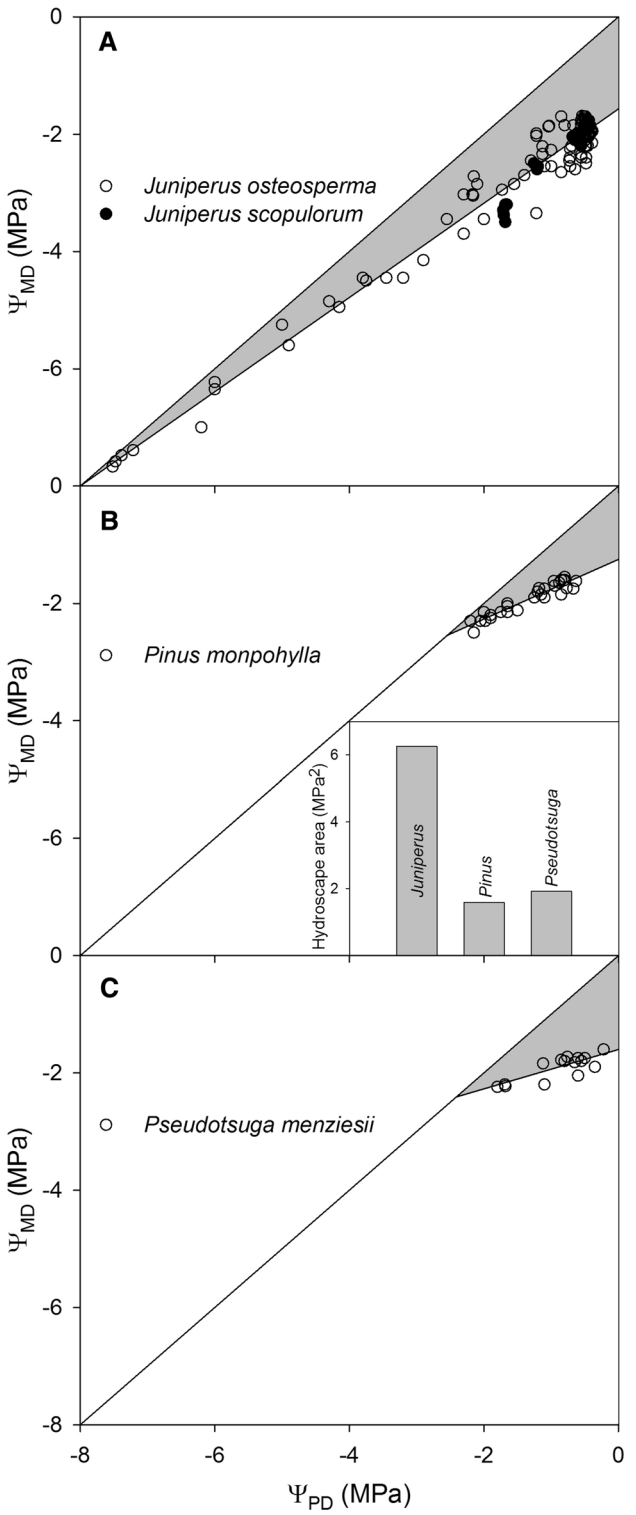

Fig. 3 Hydroscape areas (gray-filled triangles, *sensu* Meinzer et al. 2016), as determined by mid-day versus pre-dawn xylem water potentials (Ψ_{MD} and Ψ_{PD}, respectively): **a** hydroscape area for two *Juniperus* spp.; **b** hydroscape area for *P. monophyla*; **c** hydroscape area for *P. menziesii*. Larger versus smaller hydroscape areas indicate more versus less strict stomatal control over leaf water potential (i.e., anisohydric or isohydric water use behavior), respectively. The inset histogram in panel B shows that *Juniperus* spp. had a hydroscape area about threefold larger than that of *P. monophylla* and *P. menziesii*

Table 2 Pearson correlations (±SE) for morning or afternoon stomatal conductance (g_s) versus pre-dawn or mid-day xylem water potential (Ψ_{PD} or Ψ_{MD}, respectively) for *Juniperus osteosperma* and *Pinus monophylla*

Species	Mean correlation comparison type	Morning		Afternoon	
J. osteosperma	g_s versus Ψ_{PD} or Ψ_{MD} across measurement dates, averaged across trees	**0.59**	**±0.07**	0.66	±0.15
P. monophylla	g_s versus Ψ_{PD} or Ψ_{MD} across measurement dates, averaged across trees	**0.20**	**±0.15**	0.36	±0.17
J. osteosperma	g_s versus Ψ_{PD} or Ψ_{MD} across trees, averaged across measurement dates	**0.63**	**±0.07**	**0.70**	**±0.08**
P. monophylla	g_s versus Ψ_{PD} or Ψ_{MD} across trees, averaged across measurement dates	**0.23**	**±0.18**	**0.35**	**±0.18**

Measurements of morning and afternoon stomatal conductance were measured nine and five times, respectively, during the 2016 growing season. Values in bold were significantly different ($P < 0.05$) among species for a given comparison type and period

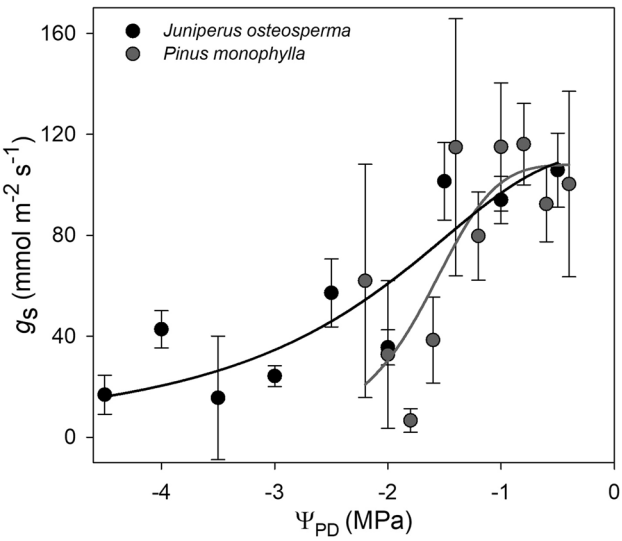

Fig. 4 Stomatal conductance (g_s ±SE) measured in the morning for *J. osteosperma* and *P. monophylla* as compared to pre-dawn xylem water potential (Ψ_{PD}) measured previously on the same morning. Ψ_{PD} data were binned into a similar number of groups representing the range of commonly measured Ψ_{PD} values. Sigmoid linear regressions were significant for *J. osteosperma* ($R^2 = 0.81$, $P = 0.007$) and *P. monophylla* ($R^2 = 0.59$, $P = 0.045$)

not significantly different across measurement dates but was different across trees ($P = 0.186$ and 0.047, respectively). These among-species differences in the coupling of g_s to Ψ (Table 2; Fig. 4) were consistent with the large range in hydric water use behavior quantified by the hydroscape areas (Fig. 3).

Percentage growth rates (% growth), when assessed between the start of the growing season at Julian day of year (DOY) 138 and the inflection point where both species recorded negative % growth values (DOY 229), indicated that *J. osteosperma* grew longer into the growing season by approximately 23 days compared to *P. monophylla* (Fig. 5a). Negative % growth values represent reversible shrinkage of the bark and inner bark and phloem that occurs in trees undergoing moderate to severe drought conditions. Because % growth is based on the size of the tree in the previous measurement period, the positive values of % growth occurring after the negative values at DOY 229 at least partially reflect rehydration of these tissues. Among trees, both species showed positive correlations between % growth and Ψ_{PD}, but Julian date did not have a significant effect on these relationships (Fig. 5b). By contrast, % growth was increasingly controlled at more negative average water potentials, particularly in *J. osteosperma* (Fig. 5c, d). Direct comparisons of % growth to Ψ_{PD} data using sigmoidal relationships showed that the regression-predicted Ψ_{PD}, where % growth was equal to zero, was only 1.25 MPa for *P. monophylla*, whereas *J. osteosperma* maintained positive % growth to 2.5 MPa. In turn, this suggested that *J. osteosperma* makes greater use of carbon gained by stomata being less sensitive to moderate soil drying. Taken together, these results indicated that stomatal closure in isohydric *P. monophylla* limited water uptake and soil drying in the rooting zone and resulted in growth being less coupled to summer evaporative conditions compared to anisohydric *J. osteosperma*. Transpiration and growth maintained further into the seasonal drought resulted in growth rates that were increasingly controlled by summer evaporative demand as these conditions drove Ψ_{PD} of *J. osteosperma* to be more negative.

Tree-ring response to climate

All studied species exhibited strong interseries correlations and moderate to high mean sensitivity (Table 2), the latter of which primarily expresses the standard deviation in year-to-year growth variability. For species in both families, these two metrics, common to conventional dendrochronological studies, indicated accurate crossdating, and excellent potential as climatic proxies. However, the Cupressaceae chronologies, and specifically three of the four *J. osteosperma* chronologies had stronger ($r > -0.5$) responses to climatic moisture deficit than the Pinaceae. June in particular, the month when most tree growth occurs at low- to middle elevations in this region (Fig. 5a), showed the strongest contrasts in controls on growth by climatic moisture deficit, whereby six of eight *Juniperus* chronologies exceeded $r =$

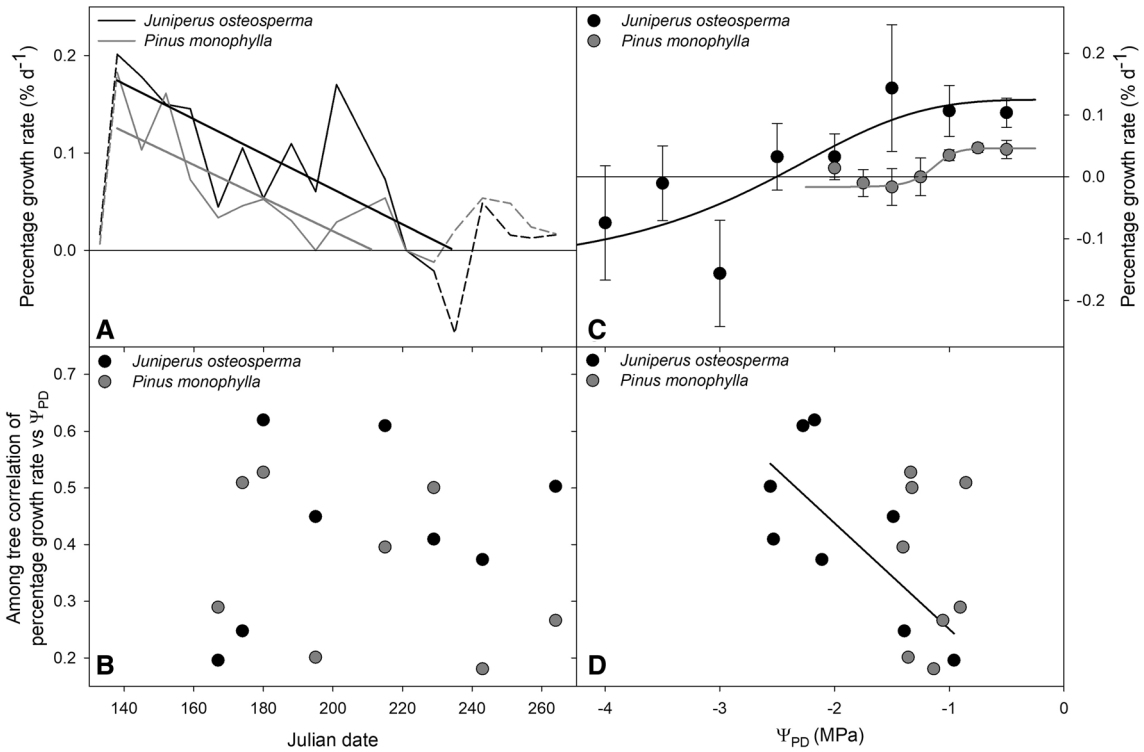

Fig. 5 Growth patterns in relation to Julian date and with respect to pre-dawn xylem water potentials (Ψ_{PD}) for ten *J. osteosperma* and *P. monophylla* that experienced a range of drought stress during the 2016 growing season. **a** Percentage growth rates (% growth) for each species are indicated by thin black and gray lines. Linear regressions (bold lines) were fitted to data measured between the start (DOY 138) and end of the growing season (DOY 229). These growing season boundary dates were identified by the initiation and near-complete cessation of positive net stem growth. **b** Correlations between % growth and Ψ_{PD} across 10 trees of each species by Julian Date. Only the two most positive correlations for *J. osteosperma* at DOY 180 and 215 reached significance ($P<0.05$). **c** the same % growth data as in panel A summarized in 0.50 or 0.25 MPa bins (±SE). Logistic regressions were fitted to data for *J. osteosperma* and *P. monophylla*, were $R^2=0.69$, $P=0.056$ and $R^2=0.76$, $P=0.058$, respectively, to identify the point after which progressively more negative Ψ_{PD} will cause % growth to be negative and then equilibrate near zero, explaining why the lowest % growth values are not the lowest Ψ_{PD} (D). The same correlation data in **b**, but plotted by the average Ψ_{PD} across the ten trees for each species to show how controls on growth are similar under less negative pre-dawn water potentials and diverge as water potentials decrease and moisture stress increases (the linear regression for *J. osteosperma,* $R^2=0.51$, $P=0.047$; regression line for both species combined not shown, $R^2=0.27$, $P=0.038$)

−0.4, but only a single Pinaceae chronology reached this correlation level (Fig. 6).

Collectively, pairwise comparisons indicated that across sites, Cupressaceae ring-width indices consistently responded more negatively to climatic moisture deficit than co-occurring Pinaceae ($X_2=7.57$, $P<0.005$). Because monthly responses were stronger in general for *J. osteosperma* compared to *J. scopulorum*, we repeated the analysis using only *J. osteosperma* comparisons to Pinaceae species and obtained similar results ($X_2=6.66$, $P<0.009$).

Discussion

Hydric water use behavior, defined by the strictness in which stomata regulate leaf water potential in response to plant hydration status, falls along a continuum when viewed across diverse assemblages of species (Klein 2014; Meinzer et al. 2016). However, in conifers from dry regions, the two families Cupressaceae and Pinaceae have been shown to occupy evolutionarily divergent pathways in hydric water use behavior and a number of other functional traits, including xylem resistance to embolism, turgor loss point, photosynthesis and non-structural carbohydrates (Linton et al. 1998; Biondi and Waikul 2004; West et al. 2007; Meinzer et al. 2014; Brodribb et al. 2014; Woodruff et al. 2015). Indeed, most species in the Cupressaceae have low levels of abscisic acid (ABA) and generally lack ABA-induced stomatal closure responses to prolonged drought, whereas species in the Pinaceae show strong ABA-induced stomatal closure responses to drought stress (Brodribb et al. 2014). Therefore, the species we studied can be considered as close to the anisohydric versus isohydric endpoints on this spectrum of hydric water use behaviors as can be found among commonly co-occurring conifers in these two families. Building on

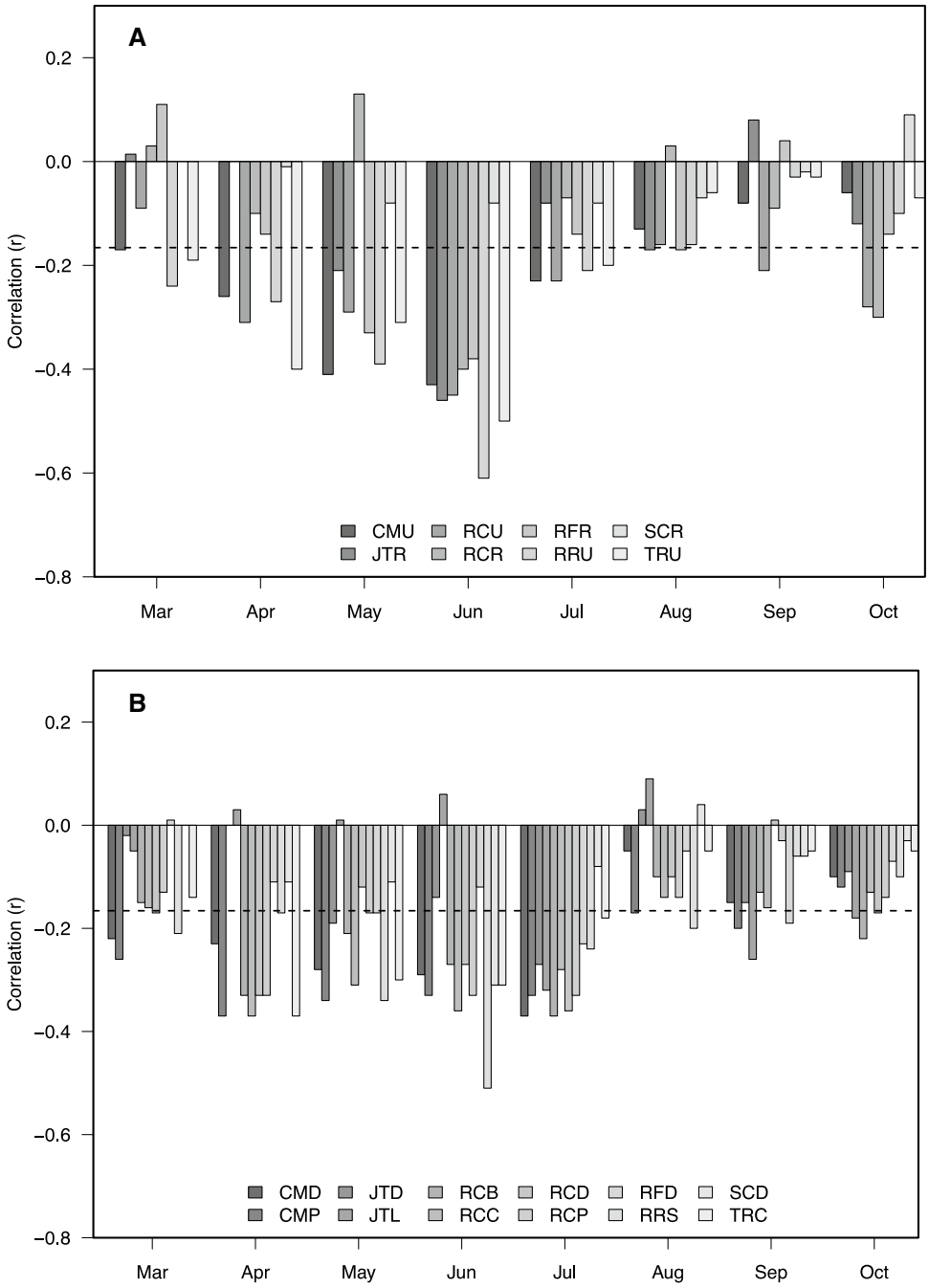

Fig. 6 Response of tree-ring-width to monthly climatic moisture deficit over the March through October season. **a** Cupressaceae and **b** Pinaceae. Dotted line indicates significance at the 0.05 level

this knowledge, we demonstrated that two *Juniperus* spp. had a hydroscape area (*sensu* Meinzer et al. 2016) that was approximately threefold larger than *P. monophylla* and *P. menziesii* (Fig. 3), providing a clear example of how strictly stomata constrain leaf water potentials in isohydric Pinaceae compared to anisohydric Cupressaceae. Moreover, *Juniperus* spp. also withstood greater drought stress (i.e., lower Ψ_L, Fig. 3) compared to the co-occurring *P. monophyla* and *P. menziesii*. In comparison to isohydric Pinaceae, anisohydric stomatal regulation of Cupressaceae ostensibly resulted in maintenance of g_s that yielded greater net photosynthesis and carbon gain under protracted drought conditions (*sensu* Woodruff et al. 2015).

We also demonstrated that g_s was more closely coupled to Ψ_{PD} and Ψ_{MD} in *J. osteosperma* compared to *P. monophylla* (Table 2) during a slowly imposed summer dry-down, thus confirming the types of differences in stomatal control of leaf gas-exchange that can be expected between species in these two families that commonly grow together in summer-dry environments of the Interior West. These data, along with another recent study (Garcia-Forner et al. 2016), both strongly support the notion that anisohydric species do

closely regulate their stomata, but at different boundaries of Ψ compared to isohydric species. Indeed, the impacts of hydric water use behavior, among many other aspects of tree physiological responses to soil drying, have been discussed at length over the past decade (McDowell et al. 2008; Plaut et al. 2012; Eamus et al. 2013; Limousin et al. 2013; Klein 2014; Sevanto et al. 2014; Garcia-Forner et al. 2016). However, apart from a study by Matheny et al. (2017) of two angiosperm species differing in hydric water use behavior, wood anatomy (i.e., diffuse-porous versus ring-porous), and rooting depth, we are aware of no other studies formally comparing whether differences in hydric water use behavior may be associated with variable responses of tree radial growth to past climate.

Fick's law predicts that photosynthetic carbon assimilation should be directly modulated by stomatal aperture and the resulting rate of diffusion of CO_2 into leaves (Farquhar et al. 1989), which decreases in response to increasing evaporative demand (Oren et al. 1999) to limit cavitation, embolism and increased risk of hydraulic system failure (Taneda and Sperry 2008). Therefore, species differing in hydric water use behavior have very different photosynthetic responses to soil drying (Lajtha and Barnes 1991). It is possible that during such conditions, the additional photosynthate fixed by an anisohydric species compared to an isohydric species may be negligible or used in part for osmotic adjustment and distal respiratory sinks before it can be utilized for stem radial growth. Furthermore, under dry soil conditions that limit growth due to low turgor pressure, but where positive net photosynthetic rates persist, excess carbon may be shunted towards other sinks such as storage, defense, and/or root exudation. Besides, g_s having been more closely coupled to Ψ_{PD} in *J. osteosperma* when compared to *P. monophylla* (Table 2), our data also indicated that g_s was equivalent during relatively wet soil conditions of $\Psi_{PD} > -1.0$, but declined to near zero at Ψ_{PD} of approximately −5.0 versus −3.0 MPa, respectively (Fig. 4). Indeed, control of transpiration by Ψ_{PD} in closely related and co-occurring Cupressaceae and Pinaceae species show similar patterns (Plaut et al. 2012). By comparing threshold % growth values for zero or negative growth in *J. osteoperma* versus *P. monophylla* (−1.25 and −2.5 MPa, respectively, Fig. 5c), % growth approaches zero at 1.75–2.5 MPa before g_s. Therefore, the maintenance of g_s and growth during substantially drier Ψ_{PD} in *J. osteoperma* compared to isohydric *P. monophylla* demonstrates how coordinated suites of traits associated with hydric water use behavior can contribute to a significant divergence in carbon gain and growth during increasingly drier conditions.

A caveat to the broader applicability of these findings is that the effects of hydric water use behavior should differ depending on climate regime. In regions of the southwestern U.S. where a hyper-arid early growing season is interrupted by intense summer monsoon storms, the roots and stomata of isohydric species may respond more sensitively to summer precipitation and attendant evaporative conditions compared to anisohydric species (West et al. 2007). These climate patterns are more likely to synchronize water use behavior and the times that are conducive to positive net photosynthesis and growth among isohydric and anisohydric species (Garcia-Forner et al. 2016). Likewise, in the eastern deciduous forest, growth of isohydric and relatively shallowly-rooted *Acer rubrum* L. was more strongly correlated with soil moisture in the upper 30 cm compared to anisohydric and more deeply-rooted *Quercus rubra* L. (Matheny et al. 2017). In contrast, for the protracted seasonal droughts of the Interior West, we expect patterns of g_s and tree growth of dry-site conifers to be reasonably represented by our experimental drought treatment, which showed that radial growth of *J. osteosperma* was maintained longer and during progressively drier soil conditions than that of *P. monophylla* (Fig. 5).

If, as we expect, these experimental results apply to more complex, natural systems of the Interior West, anisohydric species such as *Juniperus* would be characterized by g_s responses that more accurately reflect a wide range of growing season drought compared to co-occurring species in the Pinaceae that are characterized by g_s being decoupled from moderate to severe droughts (Fig. 4). In combination with photosynthesis and growth being actively maintained at $\Psi < -2$ MPa, stem growth variability in anisohydric species should thereby be more sensitive to cumulative evaporative demand compared to isohydric species characterized by growth that is essentially unresponsive to $\Psi < -2$ MPa (Fig. 5). Our dendroclimate analyses demonstrated that all dry-site conifers were characterized by negative responses to growing season climatic moisture deficit, which given the lack of substantive summer precipitation in the Interior West, is largely driven by how variation in summer air temperatures drive evapotranspiration. In support of our contention that growth of anisohydric species should more closely reflect evaporative conditions, ring-width increment responses to climatic moisture deficit were stronger in *J. osteosperma* and *J. scopulorum* as collectively compared to seven Pinaceae species sampled across seven different sites (Fig. 6; Table 1). The continuum along which hydric water use behavior and other important hydraulic traits are expressed (Klein 2014; Meinzer et al. 2016) should underscore the potential for important differences in hydric water use behavior to exist even among closely related species that are otherwise characterized within the same broad category of hydric water use behavior. Indeed, the greater strength of ring-width responses in *J. osteosperma* compared to *J. scopulorum* agrees with the approximately 3.0 MPa lower value of 50% loss in xylem conductivity values between these *Juniperus* species (Willson et al. 2008) as well as the

difference in the typical environments where these species co-occur (DeRose et al. 2016). These lines of evidence collectively suggest that *J. scopulorum* is less drought tolerant, has shallower roots, and/or falls on a less anisohydric part of the hydric water use behavior continuum than *J. osteosperma*.

Across the southwestern United States, the two primary co-limitations to ring-width growth of Pinaceae are antecedent fall/winter precipitation and current growing season evaporative demand (Williams et al. 2013). Dendrochronological studies of Pinaceae species have recently provided a better understanding of how antecedent cool season precipitation versus warm season monsoonal precipitation differentially affected tree growth rates in the southwestern U.S. by isolating earlywood versus latewood components of annual growth (Griffin et al. 2011, 2013). Similarly, given the evidence we provide here, it stands to reason that *a priori* separation of species based on hydric water use behavior could more accurately specify dendroclimate reconstruction targets such as cool season precipitation versus growing season evaporative demand across the Interior West. Moreover, this distinction can lend confidence to such climate reconstructions by being based on our mechanistic knowledge of the biology of these species rather than purely statistical decisions for why one site and species combination may be better than another.

Although differences in hydric water use behavior apparently explained much of the difference in growth responses to climatic moisture deficit between Cupressaceae and Pinaceae, other factors may have also been important. *Juniperus* spp. exhibit indeterminate shoot growth, in contrast to Pinaceae, which are primarily determinate (i.e., leaf primordia formed in the bud in the season prior to growth, Kozlowski 1964). Shoot elongation in determinate species depends more on previous year conditions. Indeed, Adams et al. (2015) found that greater drought stress in the previous season leads to a delay in the phenology of shoot growth and foliar expansion in determinate Pinaceae, whereas there were no detectable effects on the phenology of Cupressaceae. This could provide a second mechanism, outside of hydric water use behavior, to differentiate seasonal signals recorded in tree rings of these two groups. In the field of dendrochronology autocorrelation in ring-width data, or the dependence of tree-ring growth in the current year on the previous growing season conditions, has long been recognized (Fritts 1976). If differences in determinate versus indeterminate growth and the associated phenology of shoot expansion had a strong influence on radial growth, and not just shoot expansion, then we would expect to see species in the Pinaceae expressing greater autocorrelation among ring-width index values compared to Cupressaceae growing on the same sites. Our tree-ring data sets of co-occurring species showed that the autocorrelation models chosen (i.e., the number of years previously where radial growth influenced the current year, after detrending to remove potential differences due to ontogenetic growth patterns) revealed no detectable difference among Pinaceae versus Cupressaceae (Table 1).

It is also possible that an unquantified trait or set of traits could have contributed to differences in growth patterns between Pinaceae and Cupressaceae. In summer-dry regions such as the Interior West, perhaps the most important of these traits is rooting depth. The maximum rooting depth and/or rooting depth distributions are not known for the species we investigated. Therefore, we cannot rule out the possibility that these traits could have affected patterns in water use and growth. However, in *J. osteosperma* and *P. edulis* co-occurring at sites in Utah and Arizona, the proportion of soil water taken up from shallow layers (i.e., monsoon rainfall) versus deep uptake did not strongly differ despite clear differences in depth of water uptake across the growing season and among years investigated (Williams and Ehleringer 2000). Interestingly, Williams and Ehleringer (2000) also showed that anisohydric *Quercus gambelii* clearly took up most water from deep soil horizons in all seasons, years and locations, indicating a robust ability to detect differences in the relative depth of soil–water uptake, and that lessons from hydric water use behavior in conifers cannot be simply extrapolated to other tree species without considering other aspects of physiology including rooting depth. Because of the lack of evidence supporting significant differences in growth autocorrelation or water uptake depth between these two families, we conclude that hydric water use behavior was the primary reason for the stronger response to growing season evaporative demand in Cupressaceae compared to Pinaceae.

Conclusions

Isohydric behavior, including stomatal closure at $\Psi_L < -2$ MPa, helps species in the Pinaceae to more often avoid extreme xylem tensions and resulting risk of xylem embolism. However, compared to Pinaceae, the anisohydric Cupressaceae (i.e., *Juniperus* spp.) boasts a threefold larger hydroscape area (Fig. 3), which has been shown to be associated with greater maintenance of stomatal conductance, photosynthesis and growth under drier soil conditions (Lajtha and Barnes 1991; Fig. 5c). Greater mortality rates in Pinaceae species compared to Cupressaceae have been previously noted and related to hydraulic failure versus carbon starvation (McDowell et al. 2008, 2013; Breshears et al. 2009). However, insects and pathogens are complicating factors to tree drought responses that need careful consideration (Anderegg et al. 2015). Our evidence for differences in growth response to growing season evaporative conditions

among our extensive dendrochronological collections of co-occurring Pinaceae and Cupressaceae lends another line of support for hydric water use behavior having important real-world effects on species fitness and resulting patterns of conifer coexistence across regions with well-developed seasonal droughts. Our findings have two key implications for further research. The first is that *a priori* separation of species based on hydric water use behavior should be able to improve the targeting of tree-ring-based climate proxies for either antecedent moisture conditions or growing season evaporative conditions. Second, our findings suggest that process-based and/or landscape-level models of tree and forest function could more accurately capture baseline water and carbon fluxes and species competitive interactions under future climate change scenarios by including hydric water use behavior of conifers.

Author contribution statement All authors contributed to field data collection, laboratory work, analyses and writing of the paper.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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