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# Photosynthetic sensitivity to historic meteorological variability for conifers in the eastern Sierra Nevada

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## Abstract

Increased climatic variability can impact tree physiological processes beyond what is predicted from changes in mean conditions. We assessed the sensitivity of conifer saplings to spatial and temporal variability in meteorological conditions, taking advantage of the end of California's historic drought and the exceedingly wet winter of 2017. We sought to understand how very dry and very wet conditions constrain photosynthesis and growth in four regionally dominant conifers and whether sensitivity in these processes changes across a 500 m gradient in elevation. All species demonstrated phenotypic plasticity in response to temporal differences in precipitation on both inter-annual and seasonal timescales. Net photosynthesis in *Pinus contorta* decreased from an early season 2016 average of 12.4 to 6.89  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  later in the summer, but increased 14.1% between seasons in the wet year. By contrast, elevation had almost no effect on instantaneous photosynthetic gas exchange,  $\text{CO}_2$  response curve parameters, or stem water potential in any of the years for any of the species. Effects of the heavy snow year (2017) on needle growth differed between elevations. *Pinus contorta* showed a 38.9% increase in average needle length at the lower two elevations but a 31.6% decrease at the highest site compared to the height of the drought. Despite these differences, biological variation was dampened compared to the physical variation between years, suggesting these trees can effectively withstand substantial meteorological variability. Our results show that these species demonstrated considerable ability to tolerate and recover from an extreme drought event.

**Keywords** *Abies magnifica* · Meteorological variation · *Pinus contorta* · *P. jeffreyi* · Stomatal conductance · Water potential

## Introduction

Warming under climate change will be felt throughout California, with greater increases in temperature expected in inland locations and during the summer months (Pierce et al. 2013), but more frequent occurrences of anomalously warm winter temperatures also likely (Swain et al. 2016). Projections of future precipitation trends in California suggest greater inter-annual variability and that the incidence of extreme years will likely increase by the end of the century (Berg and Hall 2015; Swain et al. 2018). At the same time, higher temperatures make extremely warm and dry conditions more likely to co-occur, increasing risk of drought (Diffenbaugh et al. 2015). As the majority of precipitation falls during the

winter months as snow, soil moisture in the Sierra Nevada is lowest in late summer and early fall when the snowpack disappears (Bales et al. 2011), making this season especially susceptible to extremes in annual precipitation. Both rising temperatures and reduced precipitation enhance climatic water deficit (CWD), or the extent to which evaporative demand exceeds available soil moisture (Stephenson and Das 2011). Moreover, warming reduces winter snowpack, exacerbating the effect of low precipitation on the state's water resources for both human and natural systems (Berg and Hall 2017).

Phenotypic plasticity across both time and space can increase plant fitness and provide a mechanism through which species can respond to climate change. Especially for long-lived species, the ability of individuals to adjust physiological processes in response to environmental conditions over time may be sufficient to allow populations to persist even under rapid, human-induced environmental changes (Chevin et al. 2013). Fotelli et al. (2019) found Aleppo pine exhibited considerable plasticity in needle water potential, net photosynthesis, and stable carbon isotope ratio (a measure of water use

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efficiency) in response to both seasonal and inter-annual variation in temperature and precipitation, as well as clear recovery from drought effects as soil water availability increased. Inter-annual variation in the timing of leaf unfolding, flowering, and fruit maturation increased modeled fitness across the ranges of three European tree species, primarily by improving fitness in the margins of the niche (Duputié et al. 2015). However, effects were not consistent across species; phenological plasticity improved fitness in the warmer areas of their distributions of two species, but negatively affected fitness of the third, which the authors attributed to unmet chilling requirements for breaking bud dormancy under warmer conditions (Duputié et al. 2015). These results indicate that plasticity is not uniformly adaptive for all species in coping with the impacts of climate change.

Physiological processes can vary considerably along environmental gradients within a species' range, which may provide insight into the effects of climatic changes on ecophysiological patterns and processes. Reed and Loik (2016) found that stem water potential and photosynthesis increased with elevation for sagebrush (*Artemisia tridentata*) in the eastern Sierra Nevada during the extreme drought year of 2014, consistent with increased precipitation and soil moisture at higher elevation sites. Experimental watering significantly increased photosynthetic rates and stomatal conductance, but only at the lowest, driest site (Reed and Loik 2016). Zhang and Cregg (2005) found that the morphological and physiological traits of Ponderosa pines grown in a common garden experiment changed significantly along a mesic-to-xeric gradient of three sites. Height, DBH, and needle length, which were greater at more mesic sites, also showed significant differentiation based on source population. In contrast, water potential and carbon isotope discrimination differed between sites, but did not vary by source population, suggesting physiological plasticity is important in allowing these trees to grow in differing environments (Zhang and Cregg 2005). Likewise, Wertin et al. (2012) observed that loblolly pine seedlings grown at two locations near the warm and cool extremes of the species current range had similar responses to experimentally elevated water stress, temperature, and CO<sub>2</sub> concentration.

Spatial and temporal physiological plasticity can interact to influence tree sensitivity to future climate warming. In a common garden experiment in the Colorado Rockies across three sites spanning a range of ~6 °C, Carroll et al. (2017) found that both Lodgepole and Ponderosa pine showed considerable phenological plasticity. Growing season length, as determined by the onset of bud break, increased by an average of 40.5 days between the coldest and the middle sites, but only ~5 days between the middle and warmest site (Carroll et al. 2017). Potts et al. (2017) found strong seasonal responses in photosynthetic traits, but these responses were not uniform across their three study species in southern Arizona; compared to Douglas fir and southwestern white pine, Ponderosa pine

had higher rates of photosynthesis during the cooler seasons. Changes in relative stomatal limitation for the three species followed similar patterns over time but differed between species consistent with the study site's position within their respective elevational distributions. Ponderosa pine, which was near its upper range limit, experienced lower relative stomatal limitation than Douglas fir, which was near the lower edge of its elevational range (Potts et al. 2017). Together these results suggest greater physiological sensitivity in Douglas fir at this site, with potential consequences for community composition under future warming (Potts et al. 2017).

Although predictions of future precipitation in the Sierra Nevada suggest considerable spatial and temporal variability, rising temperatures will increase CWD throughout the region (Rapacciuolo et al. 2014). This may lead to increased drought stress, especially for conifer species that are water limited at their lower elevation margins (Das et al. 2013). In California, there have recently been years of precipitation exceeding one standard deviation of the long-term mean, including 2011 and 2017, that have "bookended" the historic drought of 2012–2016. The degree to which the water relations, photosynthesis, and growth of conifer saplings are sensitive to such meteorological variability is not clear. Notably, the historic drought, followed by the exceptionally wet winter of 2016–2017, provides an opportunity to capture historically minimal and maximal water relations, photosynthesis, and growth of trees. In order to better understand historic variation in the physiology of young trees in response to spatial and temporal changes in precipitation, we compared the physiological sensitivity of four conifer species over 3 years and at four different elevations, spanning the lower distributional edge of conifers at the Sierra Nevada–Great Basin Desert ecotone in eastern California. We hypothesized that:

- (1) Across the four species sampled, photosynthesis, stomatal conductance, and stem water potential would (a) generally increase with elevation and (b) decrease over the course of the growing season, corresponding to trends in precipitation and soil moisture. This prediction assumes that temperatures are lower and soil moisture is greater at higher compared to lower elevations, and that sapling physiology tracks the seasonal pulse of snowmelt-derived soil water.
- (2) Photosynthesis, stem water potential, and growth would reflect the tremendous inter-annual variation in precipitation between the last year of the drought in 2016 and summer following the very snowy winter of 2017, but that trees at lower elevations, which are more likely to be water limited, would be more sensitive to this variation.
- (3) Stomatal, as compared to biochemical, limitations on photosynthesis would be lower at higher elevations and in wetter years, reflecting patterns of precipitation and soil water availability.

## Materials and methods

### Study site and species

This study was conducted along an elevation gradient of approximately 500 m covering the lower portion of a desert-to-forest ecotone connecting the Great Basin Desert sagebrush steppe to the subalpine forest of eastern CA, USA. We selected four study sites in the area around Mammoth Lakes, CA, based on their elevation and accessibility (Online Resource 1). The elevation of these sites are approximately 2290 m, 2510 m, 2700 m, and 2800 m; the linear distance between the farthest two sites is approximately 12 km. The soils at all four sites are derived from geologically recent volcanic deposits, primarily well-drained rhyolitic pumice (Rinehart and Ross 1964; Huber and Rinehart 1965). To maximize sun exposure, we chose areas that were as flat as possible. The lower three sites had slope ranging from 0 to 10%. At the highest site, the slope ranged from 0 to 25%, with an eastern aspect. History of harvest and fire is widespread but have not occurred on these sites for at least 50 years. All four sites are located on federal land managed by the US National Forest Service. The lowest site represents the lower distributional edge of conifers in this area. The highest site is below the tree line, which is highly irregular and discontinuous but can extend up to ~ 3300 m. Four conifer species from the family Pinaceae occur at these sites. *Pinus contorta* subsp. *murrayana* (Balsf.) Critchf. is present at all four sites. *P. jeffreyi* Balf. occurs at the lowest two. *Abies magnifica* A. Murray is at the highest three, while *P. albicaulis* Engelm. occurs at the highest site only. Six individuals of each species were arbitrarily selected at their respective sites in June of 2016 (Online Resource 2). At the 2510 m site, only four individuals of *P. jeffreyi* could be located that were small enough to access needle-bearing branches. For this species and site, measurements were made only on these four individuals. Individuals were < 5 m in height to ensure accessibility of needle-bearing branches. All individuals received direct sunlight during the morning, ensuring that photosynthetic measurements were conducted on fully induced needles. Physiological measurements were conducted for the next three summers. In addition, water potential for the same species had been previously collected in 2014 and 2015 at the lowest site. Needle growth based on retained fascicles was determined from 2014 to 2018, and meteorological data reflect this 5-year time period.

### Climate

The eastern Sierra Nevada receives the majority of its precipitation over the winter between the months of October and March and much of it falls as snow. The growing season begins when the snow has melted, usually in March to May, though this occurs later at higher elevations and the timing

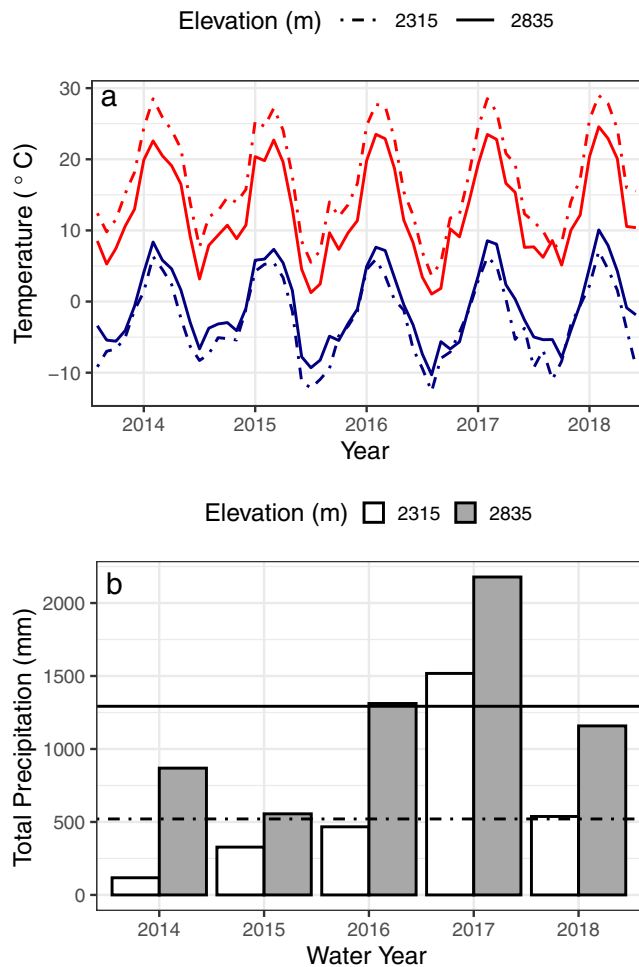
varies considerably between years. Climate and meteorological information for Mammoth Pass, near the highest site, was obtained from the California Data Exchange Center of the California Department of Water Resources ([cdec.water.ca.gov](http://cdec.water.ca.gov)). Data for Crestview CA, near the lowest site, were obtained from the Western Regional Climate Center ([wrcc.dri.edu](http://wrcc.dri.edu)). Data included daily and/or monthly minimum, maximum, and average air temperature, and incremental and accumulated precipitation. Daily temperature and precipitation were also compiled for the growing seasons of 2016, 2017, and 2018 for both stations. Records from Crestview started in November 1993. At Mammoth Pass, starting dates differed, but all variables were recorded after 2005. April 1 snow water content was available starting in 1929. This variable primarily serves as a proxy for total water year precipitation, as it is measured when most of the annual snowfall for the season has accumulated, but before warmer temperatures have started the spring melt.

From 2006 to 2018, average summer air temperature (between June and September) is 14.9 °C ( $\pm 2.28$ ) at 2315 m and 11.9 °C ( $\pm 2.29$ ) at 2835 m, a difference consistent with the wet adiabatic lapse rate (Fig. 1a). By contrast, average winter air temperatures (December–February) were  $-2.54$  °C ( $\pm 1.94$ ) and  $-2.60$  °C ( $\pm 1.99$ ) for the lower and higher stations, respectively. Based on a Welch two sample *t* test, average temperature in the study years did not differ from the previous decade at either station.

Precipitation was greater at the higher elevation. Mean total annual precipitation (by water year 1 October–30 September) was 521 mm at the lower site and 1293 mm at the higher site. Both sites experience considerable between-year variation (Fig. 1b), but total annual precipitation varies more at the lower site, which had a coefficient of variation of 82.9% compared to 33.8% at the higher site. The second year of data collection (2017) corresponded with an unusually wet winter, with April 1 snow water content at Mammoth Pass greater than two standard deviations above the mean snow water content since 1929 (Online Resource 3). Summer rainstorms also contributed precipitation, although this was a relatively small fraction of the annual total. June–September precipitation was about 3.3% of total precipitation in water year 2016 and just over 2% in water year 2017.

### Photosynthesis and water potential

Stem water potential and instantaneous needle-level gas exchange were measured twice for each individual tree during the 2016, 2017, and 2018 growing seasons in June (hereafter referred to as “early summer”) and again in late August or early September (“late summer”). Due to the heavy snowpack in 2017, June measurements were not possible at the highest site, where trees were still covered with snow on June 25.



**Fig. 1** **a** Monthly maximum (red) and minimum (blue) air temperature at 2835 m (solid lines) and 2315 m (dashed lines) from January 2014 through November 2018. Broken lines indicate missing data. **b** Total annual precipitation (by water year, October 1 to September 30) at 2835 m (gray) and 2315 m (white). Horizontal lines indicate long-term averages at 2835 m (solid lines) and 2315 m (dashed lines)

Measurement dates for stem water potential and instantaneous gas exchange are listed in Online Resource 4.

Stem water potential was measured for branches taken from heights of 0.5–1.25 m above the ground between 07:30 and 09:30 h local time. Water potential was measured on distal branch samples averaging 12 cm long using a Scholander-type pressure chamber (Model 600, PMS Instrument Company, Santa Barbara, CA).

Net photosynthesis and stomatal conductance to water vapor were measured using an open-mode portable photosynthesis system (Model LI-6400, LI-COR, Lincoln, NE) with a 6400-02 LED source. Needles from the most recent mature flush were used for all gas exchange measurements. Five to six fascicles, for *P. contorta*, and one to two fascicles, for *P. jeffreyi* and *P. albicaulis*, were arranged in a single layer inside the chamber. Fascicle length and width were measured for determination of leaf area. For *A. magnifica*, a terminal node was placed inside the chamber in its natural orientation.

Leaf area was estimated relative to the 2 by 3 cm area of the chamber and confirmed using plastic calibration standards and calipers. Conditions inside the leaf cuvette included a light saturating PAR of  $1500 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ , a  $\text{CO}_2$  concentration of  $400 \mu\text{mol mol}^{-1}$ , and a flow rate of  $500 \mu\text{mol s}^{-1}$ . Measurements were recorded when all three stability criteria were met, usually requiring 3 to 4 min. Instantaneous net photosynthesis was measured between approximately 09:00 and 10:30 h to limit the impact of daily fluctuations in temperature and vapor pressure deficit on comparisons between sites. In addition,  $\text{CO}_2$  response curves (Farquhar et al. 1980) were conducted for each individual once per year, in June of 2016 and 2018 and in August of 2017 (Online Resource 4). Data for creating response curves were also collected in June 2017 for the lowest site only. For  $\text{CO}_2$  response curves, net photosynthesis was measured at 14–16  $\text{CO}_2$  concentrations ranging from 50 to  $1800 \mu\text{mol mol}^{-1}$ . Photosynthesis ( $A_{\text{net}}$ ,  $g_s$ , and  $C_i$ ) and microclimatic conditions ( $T^{\text{air}}$ ,  $T^{\text{leaf}}$ , and  $VPD^L$ ) were recorded at reference  $\text{CO}_2$  concentrations of 400, 300, 200, 100, 50, 400, 400, 500, 600, 700, 800, 900, 1000, 1200, 1500, and  $1800 \mu\text{mol mol}^{-1}$ . Needles were exposed to chamber conditions for approximately 4 min and until all three stability variables indicated the measurements were stable. Response curves were conducted between approximately 07:00 and 14:00 h, when needles were photosynthetically active and before afternoon stomatal closure.

In August 2018, one branch was removed from each individual tree to determine needle and node length for the 2014–2018 cohorts. For the pine species, the longest needles in five fascicles from each cohort were measured from each branch, starting with the most proximal part of the branch and moving distally along a randomly selected side. Their average was used as estimate of needle length for that individual and year. For *A. magnifica*, which has much greater variation in needle length within cohorts, the node length for each year was measured along the central part of the branch. Needle length was estimated as half the node width where the nodes were widest. Needles were dried at  $65 \text{ }^\circ\text{C}$  for 48 h and weighed to determine needle biomass.

## Analysis

For each individual at each site visit, instantaneous, needle-level net photosynthesis ( $A$ ) and stomatal conductance ( $g_s$ ) were calculated as the mean of three successive subsamples over 30 s. Intrinsic water use efficiency ( $i\text{WUE}$ ) was calculated as the ratio of  $A$  to  $g_s$ . The  $\text{CO}_2$  response curve parameters maximum carboxylation efficiency ( $V_{\text{cmax}}$ ) and maximum rate of electron transport ( $J_{\text{max}}$ ) were estimated using the “fitaci” function in R’s plantecophys package, which fits the Farquhar-Berry-von Caemmerer model (Duursma 2015). Stomatal limitation was determined analytically using the methods of Long and Bernacchi (2003).

Water potential, stomatal conductance, net photosynthesis,  $V_{cmax}$ ,  $J_{max}$ , and needle growth were determined for six individuals of each species at each site. Linear mixed effect models, with individual tree as a random effect, and elevation, year, and/or season as fixed effects were made for each species using the “nlme” package in R (Pinheiro et al. 2018). Leaf vapor pressure deficit ( $VPD^L$ ) was included as a fixed effect in models for all gas exchange response variables, and stomatal conductance was included as a fixed effect in models for photosynthesis. Differences between elevations, years, and seasons for the response variables were tested with an ANOVA of each model. Pairs of elevations and years were compared with a post-hoc Tukey test. All analyses were done in R version 3.5.1 (R core Team 2018). All figures were produced using “ggplot2” (Wickham 2016).

## Results

### Water potential

The effects of year, season, and their interaction on stem water potential ( $\Psi$ ) were significant for all four species (Table 1). In the wetter year of 2017,  $\Psi$  was higher (less negative) overall and increased later in the season. By contrast, it tended to decrease later in the season in the drier years, though for some species and years, it did not change at all (Fig. 2). Contrary to the first hypothesis, elevation had no effect on  $\Psi$  for any of the species.

**Table 1** Summary of ANOVA of a linear mixed effects model for mid-morning stem water potential of the four study species

Species	Source of Variation	df	F	<i>p</i> value
<i>Pinus contorta</i>	Elevation	3	1.2195	0.3273
	Year	2	<b>14.1346</b>	<b>&lt;0.0001</b>
	Season	1	<b>11.2945</b>	<b>0.0011</b>
	Year*Season	2	<b>27.3967</b>	<b>&lt;0.0001</b>
<i>Pinus jeffreyi</i>	Elevation	1	0.7754	0.4042
	Year	2	<b>9.7573</b>	<b>0.0003</b>
	Season	1	<b>10.2073</b>	<b>0.0026</b>
	Year*Season	2	<b>4.5190</b>	<b>0.0163</b>
<i>Pinus albicaulis</i>	Year and Season	4	<b>20.1702</b>	<b>&lt;0.0001</b>
<i>Abies magnifica</i>	Elevation	2	0.0850	0.9189
	Year	2	<b>14.7706</b>	<b>&lt;0.0001</b>
	Season	1	<b>12.1320</b>	<b>0.0008</b>
	Year*Season	2	<b>25.0932</b>	<b>&lt;0.0001</b>

Elevation, year, and season are included as fixed effects, with individual tree as a random factor. Table shows F and *p* values for each species. Significant effects ( $p < 0.05$ ) are in bold

At the lowest elevation,  $\Psi$  recorded in 2014 and 2015 for individuals of both *P. contorta* and *P. jeffreyi* (the only species measured in these years) was significantly lower than in 2017 and 2018 ( $p < 0.001$  for all four comparisons). Moreover,  $\Psi$  of *P. jeffreyi* was significantly lower than *P. contorta* ( $p < 0.001$ ).

### Needle photosynthesis

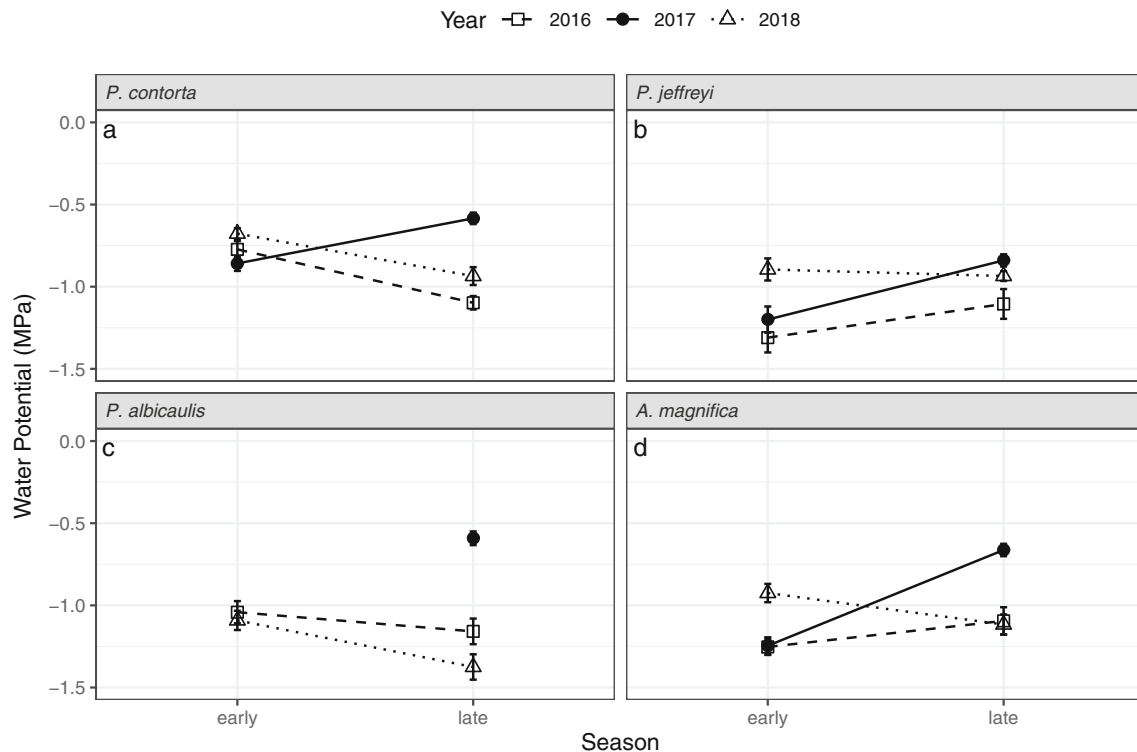
Almost all photosynthetic gas exchange parameters were significantly affected by year, season, and their interaction for all four species (Table 2). Like stem water potential, stomatal conductance decreases for all species over the season during the drier years but increases during the wet year of 2017 and is higher in the wet year overall (Fig. 3). The effect of elevation was not significant for *P. contorta* or *A. magnifica*, but stomatal conductance was slightly greater at the lower site for *P. jeffreyi*.

Net photosynthesis was strongly related to stomatal conductance across all species. For the three pine species, it follows the same general pattern as stomatal conductance, dropping later in the season in the drier years, but not in 2017 (Fig. 3). Net photosynthesis for *A. magnifica* was lower in 2017 and 2018 than in 2016 and decreased later in the season all 3 years, though the within-season difference was greatest in 2016. Net photosynthesis for *A. magnifica* was also significantly higher at the highest site, the only significant effect of elevation observed in this response variable.

For all four species, year and season had a significant effect on *i*WUE (Table 2), which tended to be highest in the late season of drier years (Online Resource 5). Elevation was also significant for *i*WUE of *P. jeffreyi* and marginally significant for *P. contorta*, though this was likely driven by unusually low values measured at the lowest site in the late season of 2018. A post-hoc test examining pairwise comparisons (Tukey Contrasts) showed no significant difference for *i*WUE for any pair of elevations.

### Farquhar-von Caemmerer photosynthetic model

Compared to stem water potential, net photosynthesis, and stomatal conductance, the patterns of the  $A-C_i$  response curve parameters were less consistent across species. For *P. contorta*, both maximum carboxylation efficiency ( $V_{cmax}$ ) and maximum rate of electron transport ( $J_{max}$ ) differ significantly between years but not elevations, while the year  $\times$  elevation was significant for  $J_{max}$  only (Table 3).  $V_{cmax}$  was higher in 2016 compared to the other 2 years, though this was only significant compared to 2018 (Fig. 4a), while  $J_{max}$  was slightly, but significantly, lower in 2018 than 2017. Both variables differed significantly between years and elevations for *A. magnifica*. A post-hoc test examining pairwise comparisons (Tukey Contrasts) showed that  $V_{cmax}$  was significantly



**Fig. 2** Stem water potential for (a) *P. contorta*, (b) *P. jeffreyi*, (c) *P. albicaulis*, and (d) *A. magnifica* in early and late summer 2016–2018. Data are means aggregated across sites ( $n = 24$ ,  $n = 10$ ,  $n = 6$ , and

$n = 18$  for *P. contorta*, *P. jeffreyi*, *P. albicaulis*, and *A. magnifica*, respectively). Error bars are one standard error

higher at the 2800 m site than the 2510 m site, but no pair of elevations differed significantly for  $J_{\max}$ , and no pair of years differed for either parameter. Similar to *P. contorta*,  $V_{\max}$  was higher in 2016 (Fig. 4g), while  $J_{\max}$  was similar across elevations in 2016, and increases over the 3 years but only at the highest site. For *P. jeffreyi*,  $J_{\max}$  differed significantly between years but was highest in 2016 and lowest in 2018. Leaf vapor pressure deficit was the only factor that had a significant effect on  $V_{\max}$  for this species. For *P. albicaulis*, there were no differences between years for either parameter (Table 3).

Stomatal limitation of photosynthesis was strongly associated with leaf vapor pressure deficit for all four species (Table 3). For *P. contorta*, year and its interaction with elevation were significant. Post-hoc pairwise comparisons found no significant differences in stomatal limitation between any 2 years or elevations, though it was greatest in 2017 and at the highest elevation (Fig. 4b). Both year and the interaction of year and elevation had a significant effect on stomatal limitation in *A. magnifica* (Table 4). At the lower two elevations, it increased across all 3 years, while at the highest elevation, it was the highest in 2017, the wetter year (Fig. 4h).

### Needle length and biomass

For *P. contorta*, needle length was shorter at the lowest two sites in 2014 and 2015, during the height of the drought.

Similarly, *P. jeffreyi*, which occurs only at the lowest two sites, also had significantly shorter needle length in 2014 and 2015. In contrast, *P. albicaulis*, which occurs only at the highest site, had significantly shorter needle length in 2017, the wettest year (Fig. 5). For some individuals in both pine species, needles never emerged, and the 2017 needle cohort was completely missing the following summer. Node length and width for *A. magnifica* follow a similar pattern, with significant effects of elevation, year, and their interactions (Table 4). At the lowest site, nodes were shorter in 2014 and 2015, the driest years, while at the highest site, they were shorter in 2016 and 2017. Needle biomass generally follows the same pattern as needle length for all four species, with biomass increasing in the wetter years at the lower elevations but decreasing at the highest ones (Table 4). Needle length and biomass are largely uncorrelated with rates of net instantaneous photosynthesis (Online Resource 6).

### Discussion

Total annual precipitation in the study region, as measured by April 1 snow water content, has had considerable inter-annual variability over the past century. The recent 2012–2014 drought represents an extreme event in its combination of high temperatures and low precipitation (Griffin and Anchukaitis

**Table 2** Summary of an ANOVA of a linear mixed effects models of stomatal conductance ( $g_s$ ), photosynthesis ( $A$ ), and intrinsic water use efficiency ( $iWUE$ ) of the four study species

Species	Dependent variable	Source of variation	df	<i>F</i>	<i>p</i> value
<i>Pinus contorta</i>	Stomatal conductance	Vapor pressure deficit (leaf)	1	2.5335	0.1145
		Elevation	3	1.1570	0.3436
		Year	2	<b>23.8548</b>	<b>&lt;0.0001</b>
		Season	1	<b>33.8306</b>	<b>&lt;0.0001</b>
		Year*season	2	<b>7.1074</b>	<b>0.0013</b>
	Net photosynthesis	Conductance	1	<b>871.582</b>	<b>&lt;0.0001</b>
		Vapor pressure deficit (leaf)	1	2.030	0.1572
		Elevation	3	0.352	0.7884
		Year	2	1.688	0.1901
		Season	1	0.480	0.4899
	Intrinsic water use efficiency	Year*season	2	<b>10.675</b>	<b>0.0001</b>
		Vapor pressure deficit (leaf)	1	<b>17.726</b>	<b>0.0001</b>
		Elevation	3	2.758	0.0609
		Year	2	<b>22.613</b>	<b>&lt;0.0001</b>
		Season	1	<b>53.008</b>	<b>&lt;0.0001</b>
<i>Pinus jeffreyi</i>	Stomatal conductance	Year*season	2	<b>5.869</b>	<b>0.0039</b>
		Vapor pressure deficit (leaf)	1	<b>12.4035</b>	<b>0.0010</b>
		Elevation	1	<b>24.6045</b>	<b>0.0008</b>
		Year	2	<b>22.7164</b>	<b>&lt;0.0001</b>
		Season	1	<b>35.6737</b>	<b>&lt;0.0001</b>
	Net photosynthesis	Year*season	2	<b>7.9284</b>	<b>0.0011</b>
		Conductance	1	<b>335.332</b>	<b>&lt;0.0001</b>
		Vapor pressure deficit (leaf)	1	<b>5.626</b>	<b>0.0222</b>
		Elevation	1	0.704	0.4230
		Year	2	<b>4.880</b>	<b>0.0123</b>
	Intrinsic water use efficiency	Season	1	<b>5.814</b>	<b>0.0202</b>
		Year*season	2	<b>3.559</b>	<b>0.0371</b>
		Vapor pressure deficit (leaf)	1	0.8295	0.3674
		Elevation	1	<b>15.7068</b>	<b>0.0033</b>
		Year	2	<b>25.4465</b>	<b>&lt;0.0001</b>
<i>Pinus albicaulis</i>	Stomatal conductance	Season	1	<b>27.4089</b>	<b>&lt;0.0001</b>
		Year*season	2	<b>5.7417</b>	<b>0.0061</b>
		Vapor pressure deficit (leaf)	1	2.53108	0.1356
	Net photosynthesis	Year and season	4	<b>5.8599</b>	<b>0.0064</b>
		Conductance	1	<b>192.7006</b>	<b>&lt;0.0001</b>
Intrinsic water use efficiency	Vapor pressure deficit (leaf)	1	0.7090	0.4162	
	Year and season	4	<b>8.2557</b>	<b>0.0019</b>	
	Vapor pressure deficit (leaf)	1	4.0912	0.0642	
<i>Abies magnifica</i>	Stomatal conductance	Year and season	4	<b>7.7959</b>	<b>0.0020</b>
		Vapor pressure deficit (leaf)	1	<b>8.8097</b>	<b>0.0041</b>
		Elevation	2	0.0471	0.9541
		Year	2	<b>29.9995</b>	<b>&lt;0.0001</b>
		Season	1	<b>67.8692</b>	<b>&lt;0.0001</b>
	Net photosynthesis	Year*season	2	<b>18.2696</b>	<b>&lt;0.0001</b>
		Conductance	1	<b>403.285</b>	<b>&lt;0.0001</b>
		Vapor pressure deficit (leaf)	1	0.050	0.8230
		Elevation	2	<b>4.943</b>	<b>0.0164</b>
		Year	2	<b>7.541</b>	<b>0.0011</b>
	Intrinsic water use efficiency	Season	1	<b>6.882</b>	<b>0.0107</b>
		Year*season	2	<b>18.987</b>	<b>&lt;0.0001</b>
		Vapor pressure deficit (leaf)	1	<b>8.6439</b>	<b>0.0044</b>
		Elevation	2	1.5361	0.2365
		Year	2	<b>6.2385</b>	<b>0.0032</b>
Intrinsic water use efficiency	Season	1	<b>5.4627</b>	<b>0.0222</b>	
	Year*season	2	<b>4.3278</b>	<b>0.0168</b>	

Elevation, year, and season are fixed effects and individual tree is included as a random factor. Table shows *F* and *p* values. Significant effects ( $p < 0.05$ ) are in bold

2014). The winter of 2015 was particularly notable for its low snow levels—there was essentially no snow at the highest site on April 1—a consequence of an unusually warm winter and a

persistent blocking high-pressure system over the Pacific Ocean (Williams et al. 2015). Though the wet 2017 water year was not unprecedented in terms of total precipitation, it does

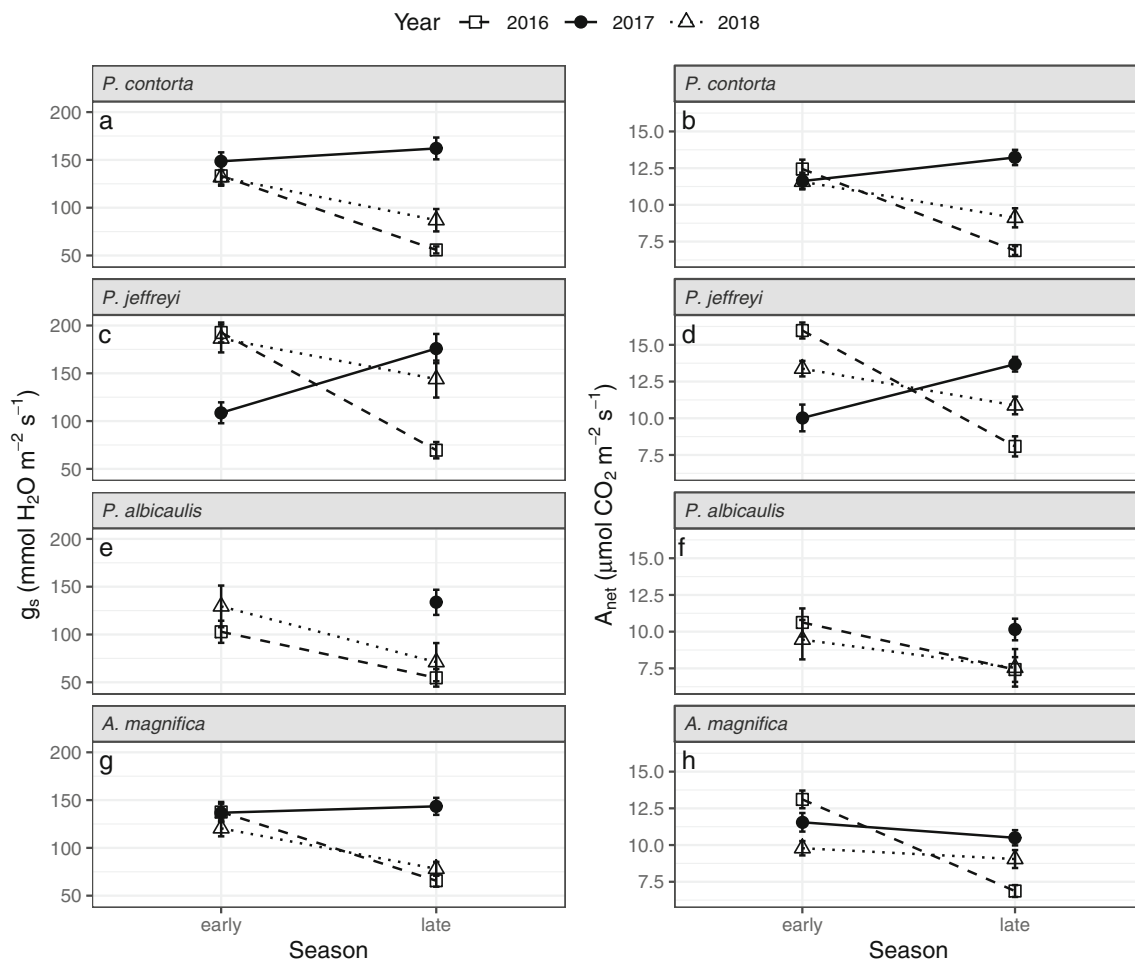


represent a dramatic increase in comparison to the prior drought years, and it markedly delayed the melt date and the onset of the growing season, especially at the higher elevations. Contrasting the two high and low elevations produced the expected patterns of lower temperatures—at least during the growing season—and increased precipitation at the higher elevation, but also less inter-annual variability. Trees at higher elevations not only received more moisture, it was more reliable between years than at lower elevations.

All four conifer species demonstrated plasticity in water status, stomatal conductance, and photosynthetic rates in response to temporal differences in precipitation on both seasonal and inter-annual timescales. Late season gas exchange and water potential were most sensitive to differences in water year, and the seasonal effects in the wetter year (2017) were reversed from the other 2 years for stomatal conductance, net photosynthesis, and water potential. Grulke (2010) found seasonal differences in *i*WUE of both white fir and Jeffrey pine, with greater efficiency later in the summer when conditions

were drier, suggesting these species can adjust growth rates under both high and low water availability. In the present study, *i*WUE was similarly higher later in the season in 2016 and 2018, but not in the wetter year of 2017. On the whole, inter-annual differences in these physiological traits manifested primarily in late summer measurements, suggesting favorable early season conditions across all 3 years. Contrary to the hypotheses and despite observed elevational differences in temperature, precipitation, and soil moisture (Online Resource 7), elevation had almost no effect on instantaneous photosynthetic gas exchange,  $\text{CO}_2$  response curve parameters, or water potential in any of the years for any of the species. The species were relatively insensitive to elevational differences in the physical environment at the scale captured by this gradient. Therefore, we conclude that conifer sapling physiology in this area is sensitive to variability in inter-annual precipitation, but not to this elevation gradient.

Needle growth did show elevational differences for *P. contorta* and *A. magnifica*, suggesting the integrated



**Fig. 3** Stomatal conductance and net photosynthesis in early and late summer season of 2016–2018 for (a) and (b) *P. contorta*, (c) and (d) *P. jeffreyi*, (e) and (f) *P. albicaulis*, and (g) and (h) *A. magnifica*. Data are means aggregated across four sites ( $n = 24$ ), two sites ( $n = 10$ ), one

site ( $n = 6$ ), and three sites ( $n = 18$ ) for *P. contorta*, *P. jeffreyi*, *P. albicaulis*, and *A. magnifica*, respectively. Error bars are one standard error

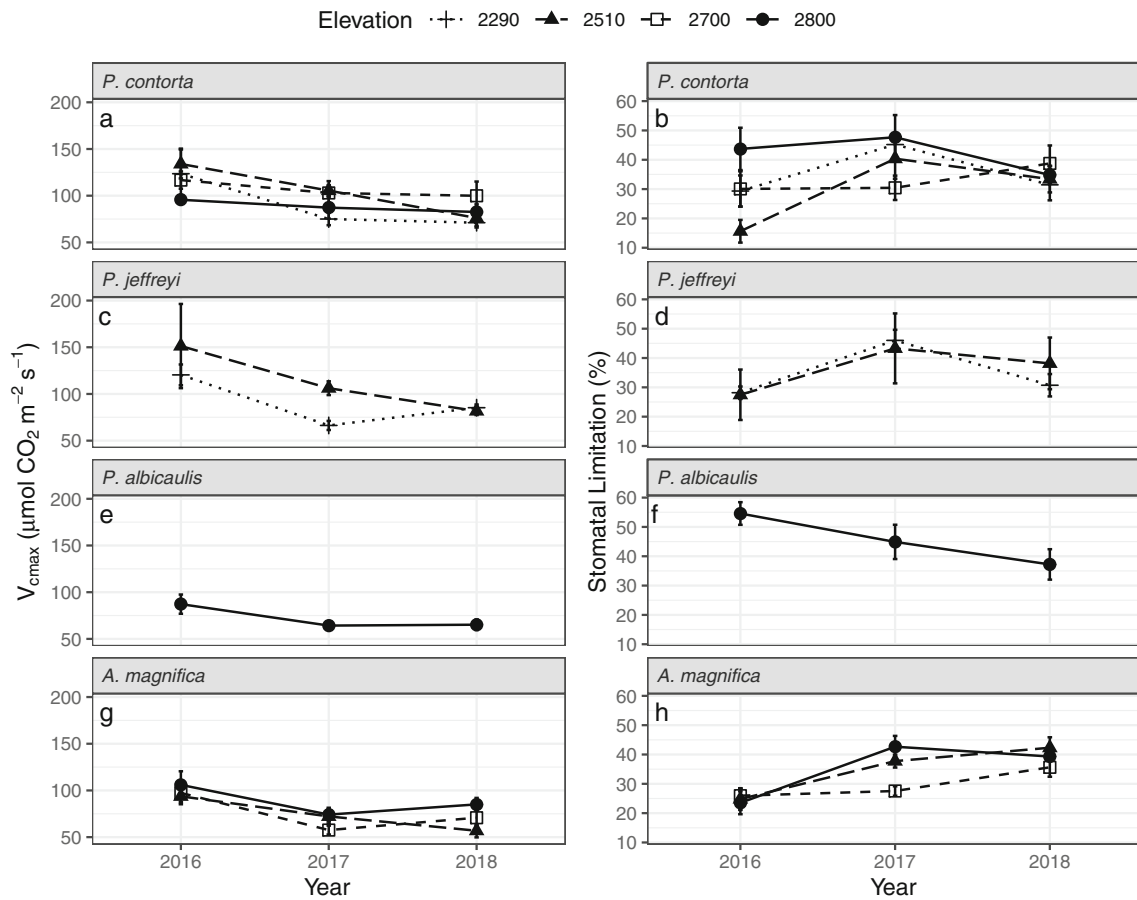
**Table 3** Summary of an ANOVA of a linear mixed effects model for each CO<sub>2</sub> response curve parameter of the four study species

Species	Response variable	Source of variation	df	<i>F</i>	<i>p</i> value
<i>Pinus contorta</i>	CO <sub>2</sub> -Vcmax	Vapor pressure deficit (leaf)	1	<b>83.7776</b>	<b>&lt;0.0001</b>
		Elevation	3	0.3978	0.7557
		Year	2	<b>7.5948</b>	<b>0.0016</b>
		Year*elevation	6	0.7394	0.6211
	CO <sub>2</sub> -Jmax	Vapor pressure deficit (leaf)	1	<b>9.9310</b>	<b>0.0031</b>
		Elevation	3	0.1018	0.9583
		Year	2	<b>10.6380</b>	<b>0.0002</b>
		Year*elevation	6	<b>2.5177</b>	<b>0.0372</b>
	CO <sub>2</sub> -stomatal limitation	Vapor pressure deficit (leaf)	1	<b>152.3752</b>	<b>&lt;0.0001</b>
		Elevation	3	0.9972	0.4097
		Year	2	<b>4.6272</b>	<b>0.0157</b>
		Year*elevation	6	<b>2.7872</b>	<b>0.0236</b>
<i>Pinus jeffreyi</i>	CO <sub>2</sub> -Vcmax	Vapor pressure deficit (leaf)	1	<b>27.3384</b>	<b>&lt;0.0001</b>
		Elevation	1	2.3134	0.1668
		Year	2	3.4066	0.0544
		Year*elevation	2	0.7071	0.5056
	CO <sub>2</sub> -Jmax	Vapor pressure deficit (leaf)	1	<b>7.2495</b>	<b>0.0144</b>
		Elevation	1	0.0105	0.9209
		Year	2	<b>4.8964</b>	<b>0.0193</b>
		Year*elevation	2	1.8991	0.1771
	CO <sub>2</sub> -stomatal limitation	Vapor pressure deficit (leaf)	1	<b>77.3200</b>	<b>&lt;0.0001</b>
		Elevation	1	2.0281	0.1591
		Year	2	2.0281	0.1765
		Year*elevation	2	2.1819	0.1403
<i>Pinus albicaulis</i>	CO <sub>2</sub> -Vcmax	Vapor pressure deficit (leaf)	1	2.3752	0.2632
		Year	2	9.4107	0.0961
	CO <sub>2</sub> -Jmax	Vapor pressure deficit (leaf)	1	0.2199	0.6853
		Year	2	4.2708	0.1897
	CO <sub>2</sub> -stomatal limitation	Vapor pressure deficit (leaf)	1	<b>20.4204</b>	<b>0.0456</b>
		Year	2	0.6551	0.6042
<i>Abies magnifica</i>	CO <sub>2</sub> -Vcmax	Vapor pressure deficit (leaf)	1	<b>37.0431</b>	<b>&lt;0.0001</b>
		Elevation	2	<b>5.6827</b>	<b>0.0107</b>
		Year	2	<b>12.8169</b>	<b>0.0002</b>
		Year*elevation	4	2.1981	0.1010
	CO <sub>2</sub> -Jmax	Vapor pressure deficit (leaf)	1	0.3624	0.5531
		Elevation	2	<b>4.4199</b>	<b>0.0250</b>
		Year	2	<b>5.3174</b>	<b>0.0126</b>
		Year*elevation	4	2.2199	0.1096
	CO <sub>2</sub> -stomatal limitation	Vapor pressure deficit (leaf)	1	<b>51.3593</b>	<b>&lt;0.0001</b>
		Elevation	2	1.6555	0.2150
		Year	2	<b>19.6228</b>	<b>&lt;0.0001</b>
		Year*elevation	4	<b>5.1967</b>	<b>0.0039</b>

Elevation and year are fixed effects and individual tree is included as a random factor. Table shows *F* and *p* values from for each parameter and species. Significant effects (*p* < 0.05) are in bold

measure was more reflective of differences in water availability than instantaneous photosynthetic gas exchange or water potential. Similarly, Carroll et al. (2017) found needle size

was significantly greater at their warmest site for Ponderosa, though not for Lodgepole pine, while net photosynthesis did not vary for either species. However, in the present study, it

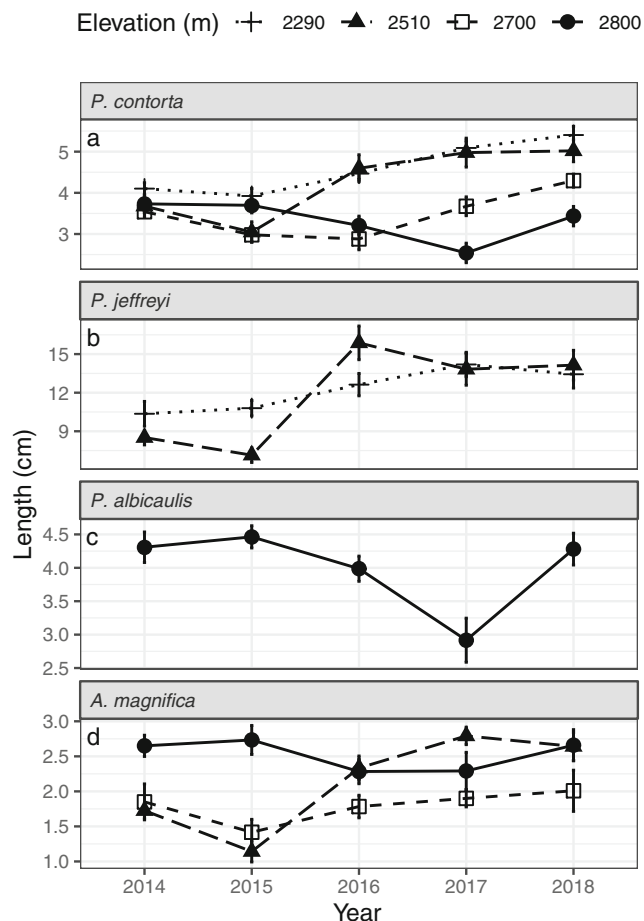


**Fig. 4** Maximum carboxylation efficiency and relative stomatal limitation for (a) and (b) *P. contorta*, (c) and (d) *P. jeffreyi*, (e) and (f) *P. albicaulis*, and (g) and (h) *A. magnifica* by year and elevation. Data are means from each measuring time and site ( $n = 6$ ). Error bars are one standard error

**Table 4** Summary of an ANOVA of a linear mixed effects model of needle length and biomass of the four study species

Species	Response variable	Source of variation	df	<i>F</i>	<i>p</i> value
<i>Pinus contorta</i>	Needle length	Elevation	3	<b>22.4669</b>	<b>&lt;0.0001</b>
		Year	4	<b>16.1952</b>	<b>&lt;0.0001</b>
		Year*Elevation	12	<b>10.8107</b>	<b>&lt;0.0001</b>
	Needle biomass	Elevation	3	<b>8.0212</b>	<b>0.0011</b>
		Year	4	2.3009	0.0663
		Year*Elevation	12	<b>10.8252</b>	<b>&lt;0.0001</b>
<i>Pinus jeffreyi</i>	Needle length	Elevation	1	0.0621	0.8096
		Year	4	<b>27.5735</b>	<b>&lt;0.0001</b>
		Year*Elevation	4	<b>7.0490</b>	<b>0.0004</b>
	Needle biomass	Elevation	1	0.01606	0.9023
		Year	4	<b>12.96265</b>	<b>&lt;0.0001</b>
		Year*Elevation	4	<b>5.96657</b>	<b>0.0012</b>
<i>Pinus albicaulis</i>	Needle length	Year	4	<b>15.4519</b>	<b>&lt;0.0001</b>
	Needle biomass	Year	4	<b>12.78932</b>	<b>&lt;0.0001</b>
<i>Abies magnifica</i>	Node width	Elevation	2	<b>7.4383</b>	<b>0.0057</b>
		Year	4	<b>8.3184</b>	<b>&lt;0.0001</b>
		Year*Elevation	8	<b>7.5872</b>	<b>&lt;0.0001</b>
	Needle biomass	Elevation	2	<b>4.4635</b>	<b>0.0301</b>
		Year	4	<b>7.2764</b>	<b>0.0001</b>
		Year*Elevation	8	<b>7.2134</b>	<b>&lt;0.0001</b>

Elevation and year are included as fixed effects, with individual tree as a random factor. Table shows *F* and *p* values for each response variable and species. Significant effects ( $p < 0.05$ ) are in bold



**Fig. 5** Needle length for (a) *P. contorta*, (b) *P. jeffreyi*, (c) *P. albicaulis*, and (d) *A. magnifica* by cohort year and elevation. Data are means from each cohort year and site ( $n = 6$ ). Error bars are one standard error

was the interaction of year and elevation that was consistently significant for needle growth, with the effect of the heavy snow year contrasting at the low and high elevations. At the lowest two elevations, growth increased in the wettest year (2017), probably as a consequence of greater soil moisture in spring and summer. Meanwhile at the highest elevation, growth was depressed, probably because the deep, long-lasting snowpack delayed the emergence of the needles or prevented their development entirely. Duputié et al. (2015) found phenological plasticity decreased fitness in the cold margins of the range for all three of their European study species, while in the warmer areas, it improved fitness for two of the species, as warmer temperatures increased growth rates. For *P. contorta* in this study, needle growth did not differ across all elevations in 2016 at the end of the drought but was much greater at the lowest elevation in higher water years (Fig. 5). This suggests at lower elevations, warmer air temperatures and an earlier melt date meant the pines could take advantage of the wetter year. At the highest elevation, likely due to snowpack persistence and the shortened growing season, individuals could not exploit the increase in available

water. In contrast to the pines, within-year differences in node width between elevations for *A. magnifica* were more evident in the drier years (especially 2015) but converged in wet years, suggesting the growth of *A. magnifica* was more sensitive to drought conditions than the pine species. This species was also primarily able to take advantage of the increase in available water in 2017 at the lower elevations.

At the lowest elevation, where stem water potential was measured for both *P. contorta* and *P. jeffreyi* over 5 years, it increased with total annual precipitation up to approximately 500–550 mm (as in 2018). This appears to be the threshold above which increased precipitation exceeds the water needs of these species in this area. Indeed,  $\Psi$  was not significantly higher in 2017, despite total precipitation being nearly three times as much. Similarly, Buechling et al. (2017) found ring growth in four conifer species in the Rocky Mountains increased with annual precipitation to a point, but above this moisture level, the relationship reversed and growth declined. Even at the lowest elevation, precipitation close to the long-term average is apparently adequate for these species. Interestingly, total annual precipitation at the highest elevation did not drop below 500 mm even at the height of the drought (Fig. 1b), supporting the supposition that sufficient water was available to the trees at this site.

Maximum carboxylation efficiency ( $V_{cmax}$ ) was highest in 2016 for all four species, though year was significant for only *P. contorta* and *A. magnifica*, likely in part because of the small sample sizes for the other two species. This suggests the amount of active ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) decreased during and after the wet winter across all species and elevations, perhaps as a result of reduced nitrogen availability if the high-water year flushed nitrogen from the system or made it otherwise unavailable. No consistent patterns emerged across species or elevations in linear electron transport ( $J_{max}$ ). Unlike Potts et al. (2017), we found patterns in species' relative stomatal limitation differed over time in ways that were not predictable from their elevational distributions. For *P. albicaulis*, occurring only at the highest site, relative stomatal limitation is greatest in 2016 and decreased the next 2 years (Fig. 4f). For *P. contorta*, *A. magnifica*, and *P. jeffreyi*, it is greatest in the wet year of 2017 across sites (Fig. 4), in contrast to hypothesis three. This was somewhat surprising because stomatal opening should not be limited by soil water availability in wet years. Elevation was significant only in its interaction with year and only for *P. contorta* and *A. magnifica*. For these two species, stomatal limitation was greater at the highest site, contradicting our expectations. It was strongly tied to leaf vapor pressure deficit for all four species, with higher VPD<sup>L</sup> associated with greater stomatal limitation. It is possible that our measurements of stomatal limitation were too

greatly influenced by short-term (hourly or shorter) conditions to reflect responses to yearly or elevational differences in water availability.

Over the 3 years of the study, total precipitation had coefficients of variation of 76.0% and 38.5% at the lowest and highest elevation, respectively, while mean net photosynthesis ranged from 6.89 to 16.0  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  (Online Resource 8). In general, the biological variation over time was dampened compared to the physical variation between years, suggesting these trees can effectively withstand temporal changes in climatic factors. Moreover, across all species and years (2016–2018), the lowest recorded stem water potential was a relatively wet  $-1.85 \text{ MPa}$ . However, in 2014 and 2015,  $\Psi$  was  $-2.35 \text{ MPa}$  for *P. jeffreyi* at the lowest site. Thus, we conclude that both species were already rehydrating in 2016, when April 1 snow water content was 96.0% of the long-term average. Even at the lowest elevation, the trees in this study were doing well in 2016 after experiencing the historic drought of 2012–2016. This recent California drought represents the most severe event over the past 1200 years, driven by unusually low, though not unprecedented, amounts of precipitation combined with temperatures that reached record highs (Griffin and Anchukaitis 2014). Thus far, these species have shown the ability to readily tolerate and recover from such dramatic meteorological variation.

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**Availability of data and material** The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

**Authors' contributions** KR and ML conceived the ideas and the designed methodology; KR collected and analyzed the data and led the writing of the manuscript. Both authors contributed critically to the drafts.

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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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