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## Drought responses of conifers in ecotone forests of northern Arizona: tree ring growth and leaf $\delta^{13}\text{C}$

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**Abstract** We sought to understand differences in tree response to meteorological drought among species and soil types at two ecotone forests in northern Arizona, the pinyon-juniper woodland/ponderosa pine ecotone, and the higher elevation, wetter, ponderosa pine/mixed conifer ecotone. We used two approaches that provide different information about drought response: the ratio of standardized radial growth in wet years to dry years (W:D) for the period between years 1950 and 2000 as a measure of growth response to drought, and  $\delta^{13}\text{C}$  in leaves formed in non-drought (2001) and drought (2002) years as a measure of change in water use efficiency (WUE) in response to drought. W:D and leaf  $\delta^{13}\text{C}$  response to drought for *Pinus edulis* and *P. ponderosa* did not differ for trees growing on coarse-texture soils derived from cinders compared with finer textured soils derived from flow basalts or sedimentary rocks. *P. ponderosa* growing near its low elevation range limit at the pinyon-juniper woodland/ponderosa pine ecotone had a greater growth response to drought (higher W:D) and a larger increase in WUE in response to drought than co-occurring *P. edulis* growing near its high elevation range limit. *P. flexilis* and *Pseudotsuga menziesii* growing near their low elevation range limit at the ponderosa pine/mixed conifer ecotone had a larger growth response to drought than co-occurring *P. ponderosa* growing near its high elevation range limit. Increases in WUE in response to drought were similar for all species at the ponderosa pine/mixed conifer ecotone. Low elevation populations of *P. ponderosa* had greater growth response to drought than high-elevation populations, whereas populations had a similar increase in WUE in response to drought. Our findings of different responses to drought among co-occurring tree species and between low- and high-

elevation populations are interpreted in the context of drought impacts on montane coniferous forests of the southwestern USA.

**Keywords** Climate change · Elevation · *Pinus edulis* · *Pinus flexilis* · *Pinus ponderosa*

### Introduction

Drought is the most limiting factor to tree growth in southwestern USA (Fritts 1976; Meko et al. 1995; Swetnam and Betancourt 1998; Hidalgo et al. 2001). Climate change models predict higher temperatures and increased variability in precipitation in the future for the Southwest (Gregory et al. 1997; Rosenberg et al. 2003). These changes may increase the frequency and intensity of drought (Lawford 1993; Hanson and Weltzin 2000) and change the distribution of tree species and forest types (Allen and Breshears 1998).

Tree rings have been widely used to understand relationships between tree growth and climate factors such as drought (e.g., LeBlanc and Foster 1992; Graumlich 1993; Loehle and LeBlanc 1996; Villalba et al. 1994; Ettl and Peterson 1995; Barber et al. 2000; Cook et al. 2001; Cullen et al. 2001; Peterson and Peterson 2001). The carbon stable isotope composition ( $\delta^{13}\text{C}$ ) of leaves is a time-integrated index of the ratio of leaf internal to ambient  $\text{CO}_2$  concentration that can be used to infer photosynthetic WUE (Ehleringer 1991; Pate 2001; Dawson et al. 2002) and has been used to compare response to drought among species and environments (e.g., Lajtha and Getz 1993; Marshall and Zhang 1994; Williams and Ehleringer 1996; Panek and Waring 1997; Sparks and Ehleringer 1997; Leffler and Evans 1999; Warren et al. 2001). The use of  $\delta^{13}\text{C}$  and tree ring data can provide a rich perspective on differences and underlying mechanisms of drought response in trees (Mazany et al. 1980; Livingston and Spittlehouse 1993; McNulty and Swank 1995; Panek and Waring 1997; Saurer et al. 1997; Brooks et al. 1998; Ferrio et al. 2003).  $\delta^{13}\text{C}$  can provide

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information on WUE, whereas tree rings provide information on carbon allocation to stem growth and characteristics correlated with tree size, such as competitive ability. Tree species that are sensitive to drought have been reported to respond to drought with larger reductions in growth and greater increases in WUE inferred from  $\delta^{13}\text{C}$  than more drought tolerant species (e.g., Ferrio et al. 2003).

In this study, we used tree ring growth and leaf  $\delta^{13}\text{C}$  to better understand differences in tree response to meteorological drought among species at two ecotone forests in northern Arizona, the pinyon-juniper woodland/ponderosa pine forest ecotone, and the higher elevation, wetter, ponderosa pine/mixed conifer forest ecotone. Trees in ecotones are at the limits of their distributions growing under stress (Shelford 1931; Allen and Breshears 1998). Tree stress and mortality due to climate change and drought are likely to occur first and be most severe at ecotones (Allen and Breshears 1998; Loehle 2000). Differences in mortality among tree species at the pinyon-juniper woodland/ponderosa pine forest ecotone in response to drought can cause dramatic shifts in the spatial occurrence of forest communities (Allen and Breshears 1998). Large inter-annual variation in tree ring growth of *P. edulis* at this ecotone has been linked to high mortality after drought (Ogle et al. 2000). In contrast, effects of drought on higher elevation forests of southwestern USA are largely unknown.

We compared response to drought using leaf  $\delta^{13}\text{C}$  and tree-ring growth: (1) among soils and species at the pinyon-juniper/ponderosa pine forest ecotone, (2) among species at the ponderosa pine/mixed conifer ecotone, and (3) between high- and low-elevation populations of *P. ponderosa*. We expected the greatest response to drought in growth and WUE inferred from leaf  $\delta^{13}\text{C}$  for tree species, or populations within a species, that occurred on unusually dry sites, such as excessively drained soils, or at low elevations within the range of a species, such as at ecotones. At the pinyon-juniper/ponderosa pine ecotone we hypothesized that response to drought would be highest for trees growing on the coarsest soils which were derived from volcanic cinders, intermediate for trees growing on soils derived from flow basalts (moderate texture), and lowest for trees growing on the finest texture soils derived from sedimentary parent materials (H1). At both ecotones, we hypothesized that a species growing near its low elevation range limit would be more responsive to drought than a species growing near its high elevation range limit (H2). Thus, we predicted *P. ponderosa* to be more responsive to drought than *P. edulis* at the pinyon-juniper/ponderosa pine forest ecotone, and *P. menziesii* and *P. flexilis* to be more responsive to drought than *P. ponderosa* at the ponderosa pine/mixed conifer forest ecotone. We hypothesized that low-elevation populations of *P. ponderosa* would be more responsive to drought than high-elevation populations because of less available soil water at low elevations (H3). Last, we hypothesized that species with a large response of growth to drought would have a large increase in WUE in

response to drought because of a large reduction in stomatal conductance that decreases water loss and photosynthate available for growth (H4).

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## Materials and methods

### Study areas

We selected 12 sites near roads and hiking trails within the Coconino National Forest in the vicinity of Flagstaff, Arizona. Nine sites at the pinyon-juniper/ponderosa ecotone were located near the low elevation range limit (2,000 m) of *P. ponderosa*. Accurate characterization of the pinyon-juniper/ponderosa pine ecotone required sampling over three soils. Three sites each were selected on soils derived from sedimentary bedrock (limestone and sandstone), flow basalt, and basalt cinders. These soils differ in texture; the sedimentary soils were classified as fine sandy loams, the flow basalt soils as clay loams or coarse sandy loams, and the cinder soils as loamy coarse sands or coarse sands. Previous studies have shown lower levels of soil nitrogen mineralization, soil water content, and tree predawn water potential in soils derived from basalt cinders compared with sedimentary rocks near our study sites (Mopper et al. 1991; Gehring and Whitham 1995). We selected three additional sites at the ponderosa pine/mixed conifer forest ecotone on the western side of the San Francisco Peaks near the low elevation range limits of *P. menziesii* and *P. flexilis* and the high elevation limit of *P. ponderosa* (2,600 m). All soils at the ponderosa pine/mixed conifer forest ecotone are derived from andesite or basalt. Geographical location, soil data, and other site characteristics are summarized in Adams (2003).

### Dendrochronological methods

At each site, we selected ten trees of each species in dominant or co-dominant canopy positions and avoided trees with heavy insect or other damage. Between July 2001 and February 2003, two increment cores were sampled from each tree at 1.4 m above the ground from the south and west sides of the tree, mounted, sanded using successively finer sandpaper, and then polished. We measured ring widths to the nearest 0.01 mm using a Microcode II measuring banister system (Boeckler Instruments, Tucson, Ariz.) and the Measure J2X computer software (Project J2X), and crossdated cores visually using narrow marker years from a *P. ponderosa* chronology at the Gus Pearson natural area (2,237 m in elevation) in the Coconino national forest (Graybill and Rose 1989; P.Z. Fulé, unpublished data) available from the International Tree-Ring Data Bank (World Data Center for Paleoclimatology, NOAA). Cross-dating was validated using skeleton plots (Stokes and Smiley 1968; Schweingruber 1988) and COFECHA computer software (Holmes et al. 1986; Grissino-Mayer 2001, International tree ring data bank program library). Cores that would not crossdate well were excluded from further analysis.

We averaged pairs of ring-width series for each tree, and then standardized series using linear regression and by dividing residuals by predicted values to create a ring-width index (RWI) for each annual ring (Schweingruber 1988; Fritts and Swetnam 1989). This de-trending method results in a unitless RWI with a constant variance. Only rings formed between 1950 and 2000 were standardized because this period contained much variability in precipitation and Palmer drought severity index (PDSI), instrumental climate data are not available locally before 1909, and because crossdating and measuring only these years on each core made it possible to include more trees in the study.

## Tree-ring data analysis

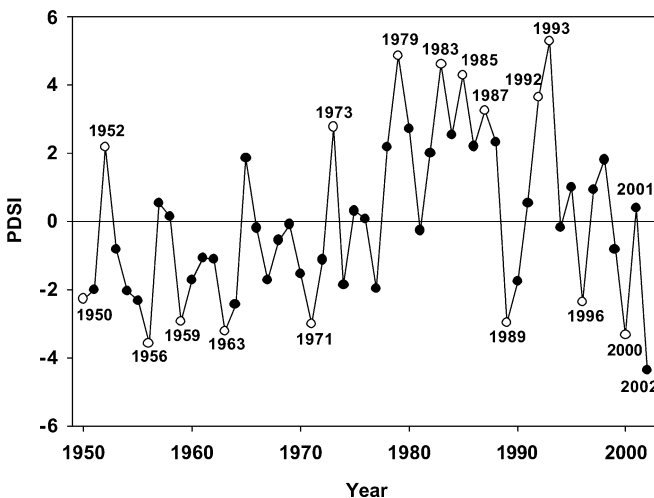
We used PDSI, a region-specific index of meteorological drought calculated from precipitation, temperature, and potential evapotranspiration (Palmer 1965; Alley 1984), as a measure of drought. We obtained instrumentally calculated PDSI data for Arizona region 2 from the National Climate Data Center at NOAA. Eight dry and eight wet years were selected between 1950 and 2000 for comparisons of tree radial growth (Fig. 1). Selected dry years had an annual average PDSI less than  $-2.0$  and selected wet years had an annual average PDSI greater than  $2.0$ . Between 1950 and 2000, PDSI in Arizona region 2 was strongly related to winter precipitation ( $r=0.76$ ,  $P<0.01$ ); dry winters were associated with low PDSI.

We calculated an average RWI for each tree for the eight dry years and for the eight wet years, and then calculated the ratio of RWI in wet years to dry years (W:D) (Fekedulegn et al. 2003). We compared W:D among elevations, species, and soil parent materials using ANOVA with SPSS 11.0 for Windows statistical software (SPSS, Chicago). At the pinyon-juniper/ponderosa pine ecotone, we used species, soil, site nested within soil, and the species  $\times$  soil interaction as sources of variation. At the ponderosa pine/mixed conifer ecotone we used species, site, and the species  $\times$  site interaction in the ANOVA model. For the elevation comparison of *P. ponderosa*, elevation and site nested within elevation were the sources of variation in the ANOVA. Because differences in W:D can be caused by a growth reduction during dry years, a growth increase in wet years, or both, we also analyzed RWI separately for dry and wet years using ANOVA.

Autocorrelation coefficients were calculated for each species at each ecotone to understand how much radial growth in the previous year influenced current year radial growth (Fritts 1976; Orwig and Abrams 1997). Lag one autocorrelation was generally low, averaged 0.23 over all species and communities, ranged between 0.01 and 0.41, and 77% of all values were  $\leq 0.3$ . Therefore, growth in the previous year had a small effect on growth in the current year.

## Leaf $\delta^{13}\text{C}$ and N

Between November 2002 and February 2003, we sampled leaves of eight trees per species that were previously cored at each site. Nearby similar dominant trees were sampled to replace a few dead



**Fig. 1** Annual average instrumental Palmer drought severity index (PDSI) for Region 2, Arizona from 1950 to 2002. Positive values of PDSI indicate wetter than average conditions and negative values indicate drier than average conditions. Open circles are selected wet (1952, 1973, 1979, 1983, 1985, 1987, 1992, 1993) and dry (1950, 1956, 1959, 1963, 1971, 1989, 1996, 2000) years used in tree growth comparisons. Leaf  $\delta^{13}\text{C}$  was measured in 2001 (non-drought) and 2002 (extreme drought)

trees. We sampled from mid-canopy branches exposed to full sun on the south and west sides of each tree, and removed green leaves formed during each of the 2001 and 2002 growing seasons. Annual PDSI values indicated that 2001 (0.4) was much wetter than 2002 ( $-4.4$ ) (Fig. 1). We sampled leaves formed during the entire length of the growing season of each year to avoid intra-seasonal bias (Pate 2001).

We oven-dried leaves at  $70^\circ\text{C}$ , pooled samples from the south and west sides of each tree, and ground samples to 40 mesh. Ground samples were analyzed for  $\delta^{13}\text{C}$  and nitrogen concentration (N) at the Colorado Plateau Stable Isotope Laboratory at Northern Arizona University, Flagstaff Ariz. using elemental analyzer-continuous flow isotope ratio mass spectrometry with an Erba NC 2100 EA (Carlo) interfaced to a Finnigan Delta Plus XL IRMS (Thermoquest, San Jose, Calif.).

We analyzed  $\delta^{13}\text{C}$  data with repeated measures MANOVA with year as the repeated factor and species, soil, site nested within soil, and all interactions with year as sources of variation, using SPSS for Windows 11.0. Differences in carboxylation capacity can be a source of variation in  $\delta^{13}\text{C}$  data (Dawson et al. 2002), and leaf nitrogen concentration (N) is a good indicator of maximum carboxylation capacity (Field and Mooney 1986). Thus, we tested the assumption that carboxylation capacity was similar among species, soils, sites, and elevations by comparing leaf N with the same model.

We measured  $\delta^{13}\text{C}$  on whole leaf tissue rather than extracted cellulose because  $\delta^{13}\text{C}$  of whole tissue and cellulose are often positively and strongly correlated (Ehleringer and Osmond 1989; Schleser 1990; McNulty and Swank 1995; MacFarlane and Adams 1998; West et al. 2001; Jaggi et al. 2002). Structural non-labile carbon is a much larger proportion of whole leaf tissue than non-structural, labile carbon and thus variation in whole tissue  $\delta^{13}\text{C}$  reflects variation in isotopes of carbon used for leaf synthesis more than variation in amounts of labile constituents (Pate 2001). The effect of shading on leaf  $\delta^{13}\text{C}$  of older needles was not a confounding factor because only current year (2002) and 1-year-old (2001) needles were sampled on branches exposed to full sun. Branch and leaf growth in 2002 were suppressed due to drought which resulted in little shading of 2001 foliage.

## Results

### Tree ring W:D

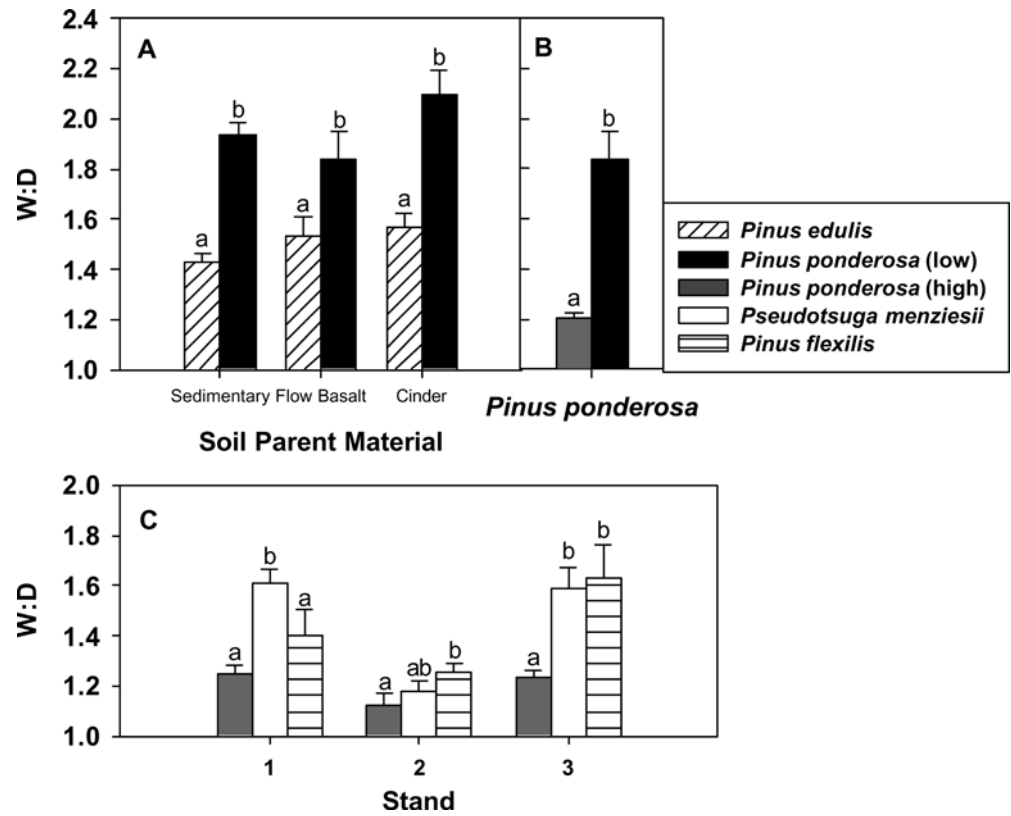
At the pinyon-juniper/ponderosa pine ecotone, W:D did not differ among soils ( $P>0.1$ ). *P. ponderosa* had a higher W:D than *P. edulis* at all soils ( $P<0.01$ , Fig. 2a). The low-elevation population of *P. ponderosa* had a greater W:D than the high-elevation-population ( $P<0.01$ , Fig. 2b).

At the ponderosa pine/mixed conifer ecotone a significant species  $\times$  site interaction ( $P<0.05$ ) complicated interpretation of main effects, so ANOVA was performed on data from each site separately (Fig. 2c). At site one, *P. menziesii* had higher W:D than *P. ponderosa* and *P. flexilis* ( $P<0.05$ ). At site 2, *P. flexilis* had higher W:D than *P. ponderosa* ( $P<0.05$ ), and W:D for *P. menziesii* did not differ from the other species ( $P>0.05$ ). At site three, *P. menziesii* and *P. flexilis* had higher W:D than *P. ponderosa* ( $P<0.05$ ).

### Wet and dry year RWI

Average RWI in wet and dry years did not differ among soils at the pinyon-juniper/ponderosa pine ecotone

**Fig. 2a-c** Mean ratio of RWI in wet years to dry years (W:D) for species (*P. edulis*, *P. ponderosa*) and soil parent materials (sedimentary, flow basalt, cinder) at the pinyon-juniper/ponderosa pine ecotone (a), for low- and high-elevation populations of *P. ponderosa* (b), and for species (*P. flexilis*, *P. ponderosa*, *P. menziesii*) and stands at the ponderosa pine/mixed conifer ecotone (c). For the ponderosa pine/mixed conifer ecotone a significant species  $\times$  site interaction prevented interpretation of the main effects, so an ANOVA was performed separately for each stand. Different letters indicate significant differences ( $P < 0.05$ ) between species at each soil type in panel A, between populations in panel B, and among species at each site in panel C. Error bars are standard errors



( $P > 0.1$ ). *P. ponderosa* had a greater RWI in wet years than *P. edulis* ( $P < 0.001$ , Table 1). In contrast, *P. edulis* had a greater RWI in dry years than *P. ponderosa* ( $P < 0.001$ , Table 2).

At the ponderosa pine/mixed conifer ecotone, *P. menziesii* and *P. flexilis* had higher RWI in wet years than *P. ponderosa* ( $P < 0.001$ , Table 1). A significant species  $\times$  site interaction complicated interpretation of main effects in an ANOVA on dry year RWI at the ponderosa pine/mixed conifer ecotone, so separate analyses were performed at each site. Mean RWI in dry years was greater for *P. ponderosa* than *P. menziesii* and *P.*

*flexilis* at site three ( $P < 0.01$ ), but there were no differences among species at the other two sites ( $P > 0.05$ , Table 2).

Low-elevation populations of *P. ponderosa* had higher RWI in wet years than high-elevation populations ( $P < 0.001$ , Table 1). In contrast, low-elevation populations had lower RWI in dry years than high-elevation populations ( $P < 0.001$ , Table 2).

#### Leaf $\delta^{13}\text{C}$ and N

For each species at each ecotone, leaf  $\delta^{13}\text{C}$  was less negative in 2002 than 2001 ( $P < 0.001$ , Fig. 3a–e). At the pinyon-juniper/ponderosa pine ecotone, the year  $\times$  species interaction was significant ( $P < 0.01$ ), but the year  $\times$  soil interaction was not ( $P > 0.1$ ). *P. ponderosa* had a greater response in leaf  $\delta^{13}\text{C}$  to the 2002 drought than *P. edulis* (Fig. 3a–c). Average leaf  $\delta^{13}\text{C}$  was more negative for *P. ponderosa* than *P. edulis* (Fig. 3a–c). Leaf N did not differ among soils or between species at the pinyon-juniper/ponderosa pine ecotone ( $P > 0.05$ ).

At the ponderosa pine/mixed conifer ecotone the year  $\times$  species interaction in leaf  $\delta^{13}\text{C}$  was not significant ( $P > 0.1$ , Fig. 3e), indicating a similar change in leaf  $\delta^{13}\text{C}$  from 2001 to 2002 for all species. However, *P. ponderosa* had more negative  $\delta^{13}\text{C}$  than *P. flexilis* and *P. menziesii* ( $P < 0.05$ ). *P. ponderosa* had greater N for leaves formed in 2001 and 2002 ( $13.7 \text{ mg g}^{-1}$ ,  $12.8 \text{ mg g}^{-1}$ , respectively) than *P. flexilis* ( $12.1 \text{ mg g}^{-1}$ ,  $12.2 \text{ mg g}^{-1}$ , respectively) and *P. menziesii* ( $12.1 \text{ mg g}^{-1}$ ,  $10.5 \text{ mg g}^{-1}$ , respectively) ( $P < 0.05$ ).

**Table 1** Mean RWI in wet years for tree species at the pinyon-juniper/ponderosa pine and ponderosa pine/mixed conifer ecotones, and for low- and high-elevation populations of *P. ponderosa*. Higher values of RWI indicate that a species or population had greater growth during wet years relative to the overall growth trend between years 1950 and 2000. Values in parentheses are standard errors. Different letters indicate significant differences ( $P < 0.05$ ) among species at each ecotone, and between populations of *P. ponderosa*

	Species/population	Mean RWI
Pinyon-juniper/ ponderosa ecotone	<i>P. edulis</i>	1.16 ( $\pm 0.013$ )a
	<i>P. ponderosa</i>	1.28 ( $\pm 0.015$ )b
<i>P. ponderosa</i> (between elevations)	High elevation	1.04 ( $\pm 0.012$ )a
	Low elevation	1.32 ( $\pm 0.023$ )b
Ponderosa/mixed conifer ecotone	<i>P. ponderosa</i>	1.04 ( $\pm 0.012$ )a
	<i>P. menziesii</i>	1.16 ( $\pm 0.017$ )b
	<i>P. flexilis</i>	1.14 ( $\pm 0.019$ )b

**Table 2** Mean RWI in dry years for tree species at the pinyon-juniper/ponderosa pine and ponderosa pine/mixed conifer ecotones, and for low- and high-elevation populations of *P. ponderosa*. Lower values of RWI indicate that a species or population had lower growth during dry years relative to the overall growth trend between years 1950 and 2000. At the ponderosa pine/mixed conifer ecotone a

significant species  $\times$  site interaction ( $P < 0.05$ ) prevented interpretation of the main effects, so ANOVA was performed on each site. Values in parentheses are standard errors. Different letters indicate significant differences ( $P < 0.05$ ) among species at each ecotone or site, and between populations of *P. ponderosa*

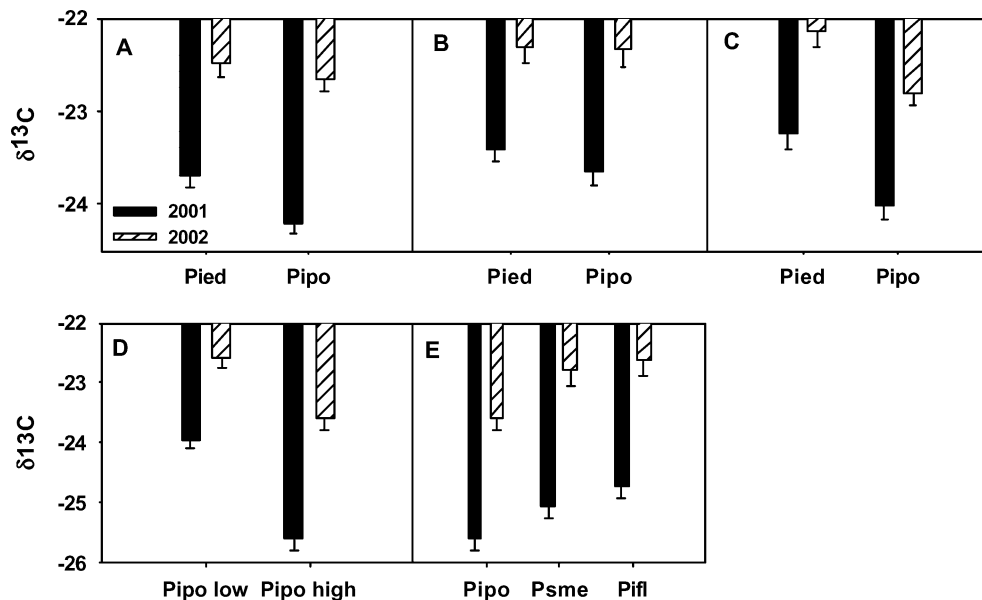
		Species/population		Mean RWI		
Pinyon-juniper/ponderosa ecotone		<i>P. edulis</i>		0.79 ( $\pm 0.013$ )a		
		<i>P. ponderosa</i>		0.67 ( $\pm 0.013$ )b		
<i>P. ponderosa</i> (between elevations)		High elevation		0.87 ( $\pm 0.013$ )a		
		Low elevation		0.75 ( $\pm 0.027$ )b		
		Site				
		1	2	3	Overall	
Ponderosa/mixed conifer ecotone	<i>P. ponderosa</i>	0.82 ( $\pm 0.015$ ) a	0.92 ( $\pm 0.019$ )a	0.88 ( $\pm 0.021$ )a	0.87 ( $\pm 0.013$ )	
	<i>P. menziesii</i>	0.75 ( $\pm 0.016$ )a	0.92 ( $\pm 0.022$ )a	0.73 ( $\pm 0.019$ )b	0.80 ( $\pm 0.019$ )	
	<i>P. flexilis</i>	0.82 ( $\pm 0.047$ )a	0.88 ( $\pm 0.017$ )a	0.76 ( $\pm 0.045$ )b	0.82 ( $\pm 0.024$ )	

For *P. ponderosa*, the year  $\times$  elevation interaction was a significant ( $P < 0.001$ ) source of variation in leaf  $\delta^{13}\text{C}$ , and high-elevation populations had a greater increase in leaf  $\delta^{13}\text{C}$  in response to the 2002 drought than low-elevation populations (Fig. 3d). There was no difference in leaf N between populations for *P. ponderosa* ( $P > 0.1$ ).

## Discussion

Our leaf N results suggest that variation in leaf  $\delta^{13}\text{C}$  among species and between populations of *P. ponderosa*

was due to factors other than carboxylation capacity as leaf N is a good indicator of maximum carboxylation capacity (Field and Mooney 1986). Average N of current- and 1-year-old *P. ponderosa* leaves sampled between November and February in our study was similar to N of leaves sampled in August in other studies in the vicinity of our study sites (Feeney et al. 1998; Kolb et al. 1998; Kolb and Stone 2000), suggesting little change in leaf N between summer when most carbon assimilation occurs and winter when we sampled for this species. Leaf N was similar between species and among soils at the pinyon-juniper/ponderosa pine ecotone, and between high- and low-



**Fig. 3a-e** Mean leaf  $\delta^{13}\text{C}$  in non-drought (2001) and extreme drought (2002) years for *P. edulis* (Pied) and *P. ponderosa* (Pipo) at the pinyon-juniper/ponderosa pine ecotone on sedimentary soils (a), flow basalt soils (b), and cinder soils (c), for high- and low-elevation populations of *P. ponderosa* (d), and for *P. flexilis* (Pifl), *P. ponderosa*, and *P. menziesii* (Psme) at the ponderosa pine/mixed conifer ecotone (e). Error bars are standard errors. Differences in

leaf  $\delta^{13}\text{C}$  between years were significant ( $P < 0.001$ ) for all species in all panels. For panels A, B, and C, the year  $\times$  species interaction was significant ( $P < 0.01$ ) and the year  $\times$  soil interaction was not ( $P > 0.1$ ). For panel D, the year  $\times$  elevation interaction was significant ( $P < 0.001$ ). For panel E, the year  $\times$  species interaction was not significant ( $P > 0.1$ )

elevation populations of *P. ponderosa*, which suggest similar carboxylation capacity. However, differences in leaf N occurred at the ponderosa pine/mixed conifer ecotone where *P. ponderosa* had higher leaf N than *P. flexilis* and *P. menziesii*. Higher leaf N and carboxylation capacity for *P. ponderosa* compared with *P. flexilis* and *P. menziesii* should have caused lower leaf internal CO<sub>2</sub> concentration and less negative leaf  $\delta^{13}\text{C}$  for *P. ponderosa* if all other influences on leaf  $\delta^{13}\text{C}$  were similar among species. However, we found the opposite pattern; leaf  $\delta^{13}\text{C}$  was more negative in *P. ponderosa* than *P. flexilis* and *P. menziesii* in drought and non-drought years. This finding suggests higher leaf internal CO<sub>2</sub> concentration in *P. ponderosa* than the other species because of higher stomatal conductance, higher stomatal density (Hultine and Marshall 2000), or because of differences in foliar concentration of carbon compounds that differ in  $\delta^{13}\text{C}$ , such as resins, lignin, and cellulose (Benner et al. 1987; Ehleringer and Osmond 1989; Pate 2001).

Differences in photosynthetic WUE among plants can be inferred from leaf  $\delta^{13}\text{C}$  because both are inversely related to the ratio of leaf internal to ambient CO<sub>2</sub> concentration if ambient CO<sub>2</sub> concentration and leaf-to-air vapor pressure deficit are similar (Farquhar et al. 1989; Ehleringer 1991). Ambient CO<sub>2</sub> concentration should have been similar among the co-occurring species and between sample years in our study because comparisons were made with leaves from upper canopy, sunlit branches of trees in the same stand. Leaf-to-air vapor pressure deficit also should have been similar among co-occurring species because leaf temperature of the needle-leaved species used in our study is closely coupled with air temperature (Campbell and Norman 1998).

Water use efficiency inferred from leaf  $\delta^{13}\text{C}$  was not consistently associated with differences in elevation range among species in the two ecotone forests we studied. At the pinyon-juniper/ponderosa pine ecotone, WUE was higher for *P. edulis*, which can grow on lower elevation, drier sites than *P. ponderosa*. However, the pattern of difference in WUE at the pinyon-juniper/ponderosa pine ecotone—higher WUE for the species with a lower elevation range—did not occur at the ponderosa pine/mixed conifer ecotone, where *P. flexilis* and *P. menziesii* had higher WUE than *P. ponderosa*, which has a lower elevation range. Our results for photosynthetic WUE inferred from leaf  $\delta^{13}\text{C}$  are the opposite of reports of lower WUE for *P. menziesii* compared with *P. ponderosa* in the northern Rocky Mountains (Pinol and Sala 2000).

Contrary to H1, response to drought measured by tree ring W:D and leaf  $\delta^{13}\text{C}$  did not differ among soils derived from volcanic cinders (coarse texture), flow basalts (moderate texture), and sedimentary rocks (fine texture) at the pinyon-juniper/ponderosa pine ecotone. Similar to our results, other studies have shown little variation in leaf  $\delta^{13}\text{C}$  of *P. edulis* across environmental gradients (Lajtha and Getz 1993; Williams and Ehleringer 1996). However, soil type can affect leaf-level gas exchange of *P. ponderosa* in greenhouse experiments (Heidmann and King 1992) and field plantations (Reynolds et al. 2000).

Other studies (Gehring and Whitham 1995; Ogle et al. 2000) have shown higher absolute radial growth rates of *P. edulis* grown in soils derived from sedimentary compared with cinder parent materials at the pinyon-juniper/ponderosa pine ecotone near our study sites. However, drought had similar negative effects on tree radial growth and WUE at all soils at the pinyon-juniper/ponderosa pine ecotone in our study.

Our second hypothesis (H2) was that a species growing near its low elevation range limit would be more responsive to drought than a co-occurring species growing near its high elevation range limit. Consistent with H2, both leaf  $\delta^{13}\text{C}$  and W:D showed that *P. ponderosa* was more responsive to drought than *P. edulis* at the pinyon-juniper/ponderosa pine ecotone. *P. ponderosa* had a larger increase in leaf  $\delta^{13}\text{C}$  in response to the 2002 drought than *P. edulis*, suggesting more stomatal closure and a larger increase in WUE in response to drought for *P. ponderosa*. Higher W:D of *P. ponderosa* compared with *P. edulis* was due to a larger positive response of growth to wet years and a larger negative response of growth to dry years for *P. ponderosa*.

Support for H2 at the ponderosa pine/mixed conifer ecotone varied between leaf  $\delta^{13}\text{C}$  and W:D. *P. flexilis* and *P. menziesii* had a larger W:D than co-occurring *P. ponderosa*. This difference in W:D was due to a larger positive response of growth to wet years and a larger negative response of growth to dry years for *P. flexilis* and *P. menziesii*. However, all species had similar increases in leaf  $\delta^{13}\text{C}$  between non-drought (2001) and drought (2002) years which suggests similar increases in WUE in response to drought.

Other research supports H2 and our interpretation from tree ring W:D of a greater response to drought for *P. flexilis* and *P. menziesii* compared with *P. ponderosa*. For example, growth of *P. menziesii* was more responsive to watering than *P. ponderosa* in a seedling study (Zhang et al. 1996). *P. flexilis* had greater stomatal sensitivity to vapor pressure deficit than *P. ponderosa* in a high-elevation meadow in northern Arizona (Fischer et al. 2002). This finding suggests that drought, which is often accompanied by high vapor pressure deficit, has a greater negative effect on stomatal aperture and photosynthesis of *P. flexilis* than *P. ponderosa*. Despite their high elevation ranges on relatively mesic sites in southwestern USA, our results and others (Biondi 2000; Hidalgo et al. 2001) indicate that growth of *P. menziesii* and *P. flexilis* is clearly sensitive to drought.

Our third hypothesis (H3) was that low-elevation populations of *P. ponderosa* would be more responsive to regional drought than high-elevation populations because of less soil water availability at low elevations. This hypothesis was supported by the tree ring growth results where low-elevation (2,000 m) populations had higher W:D than high-elevation (2,600 m) populations indicating greater growth response to drought at low elevations. However, low-elevation populations had a smaller increase of leaf  $\delta^{13}\text{C}$  between non-drought and drought years than high-elevation populations, suggesting

less stomatal closure and a smaller increase in WUE in response to drought at low elevations. In both drought and non-drought years, leaf  $\delta^{13}\text{C}$  of low-elevation populations was less negative than high-elevation populations, and we speculate that this pattern resulted from lower stomatal conductance and higher overall WUE at low elevations. Lack of variation in leaf  $\delta^{13}\text{C}$  among populations of *P. ponderosa* from different elevations in common garden tests (Zhang and Marshall 1995; Zhang et al. 1997) suggests that the differences between elevations in our study were due to differences in environmental factors, not genetic differences among populations.

In contrast to our results for low- and high-elevation populations of *P. ponderosa* in northern Arizona, leaf  $\delta^{13}\text{C}$  has been reported to increase with elevation in other studies of forest trees in western USA (Marshall and Zhang 1993, 1994; Sparks and Ehleringer 1997; Hultine and Marshall 2000). Such an increase may occur because of factors that lower the ratio of leaf intercellular to ambient concentration of  $\text{CO}_2$ , such as higher photosynthetic capacity (Marshall and Zhang 1993; Sparks and Ehleringer 1997) and greater resistance to  $\text{CO}_2$  diffusion into the leaf at high elevations because of a decrease in stomatal density and increase in leaf mass per area (Hultine and Marshall 2000). We speculate that the decrease in leaf  $\delta^{13}\text{C}$  with elevation in our study was caused by greater water availability at high elevations that increased stomatal conductance and leaf internal  $\text{CO}_2$  concentration. Differences in water availability between low and high elevations, and the influence of water availability on elevation changes in leaf  $\delta^{13}\text{C}$ , may be more pronounced in upland forests of southwestern USA than in more northern forests of western USA (Marshall and Zhang 1993, 1994; Hultine and Marshall 2000) or wetter, riparian forests (Sparks and Ehleringer 1997) where an increase in leaf  $\delta^{13}\text{C}$  with elevation has been reported.

Our fourth hypothesis (H4) was that species with a large growth response to drought (high W:D) would have a large increase in WUE in response to drought because of a large reduction in stomatal conductance that decreases water loss and photosynthate available for growth. This hypothesis was not consistently supported by all comparisons. Support for H4 was strongest at the pinyon-juniper/ponderosa pine ecotone, where *P. ponderosa* had a greater response to drought in W:D and WUE than *P. edulis*. In contrast, at the ponderosa pine/mixed conifer ecotone, *P. flexilis* and *P. menziesii* had a greater response to drought in W:D than *P. ponderosa*, but the increase in WUE in response to drought was similar for all species. Leaf  $\delta^{13}\text{C}$  is an index of only one (i.e., WUE) of the many factors that may influence tree growth response to drought. Our results suggest that a large increase in WUE in response to drought is associated with a large negative response of tree growth to drought on dry sites, such as the pinyon-juniper/ponderosa pine ecotone, but not on higher elevation, wetter sites, such as the ponderosa pine/mixed conifer forest ecotone.

Different effects of drought on growth and WUE of co-occurring tree species demonstrated in our study suggest that frequent intense droughts predicted in some climate change scenarios may shift ranges of tree species in montane ecotone forests of southwestern USA (e.g., Allen and Breshears 1998). Specifically, we speculate that intense drought will have greater negative impacts on species and populations in our study with high sensitivity of radial growth to drought than species or populations with low sensitivity. This speculation is based on the key role of tree growth in resource competition, and evidence that radial growth rate of conifers is positively associated with carbon allocation to resin defenses against bark beetles that often kill trees during drought (Larsson et al. 1983; Mitchell et al. 1983). Our speculation is supported by observations of droughts in the 1950s and 1996 in southwestern USA. For example, several years of drought in the 1950s changed the dominant tree species at the pinyon-juniper/ponderosa pine forest ecotone in northern New Mexico from *P. ponderosa* to *P. edulis* and *Juniperus* species because of high mortality of *P. ponderosa* (Allen and Breshears 1998). This report is consistent with our finding of higher negative response of growth to drought in *P. ponderosa* than *P. edulis*. Moreover, *P. edulis* trees that died after the 1996 drought in northern Arizona had greater inter-annual variation in tree radial growth than trees that lived (Ogle et al. 2000); this result implies greater response of growth to drought for the trees that died because most inter-annual variation in tree ring growth in upland forests of the southwestern US is caused by variation in water availability (Fritts 1976). Consequently, we predict that frequent severe drought will cause the following changes: (1) decreased growth and dominance of *P. ponderosa* at the pinyon-juniper/ponderosa pine ecotone on a wide range of soil types, (2) decreased growth and dominance of *P. menziesii* and *P. flexilis* at the ponderosa pine/mixed conifer ecotone, and (3) a decline of low-elevation populations of *P. ponderosa*. Evaluation of these predictions is beyond the scope of our study, and should be addressed in future studies of climate change and drought on montane forests of southwestern USA.

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