



Tree growth response to drought and temperature in a mountain landscape in northern Arizona, USA

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ABSTRACT

Aim To understand how tree growth response to regional drought and temperature varies between tree species, elevations and forest types in a mountain landscape.

Location Twenty-one sites on an elevation gradient of 1500 m on the San Francisco Peaks, northern Arizona, USA.

Methods Tree-ring data for the years 1950–2000 for eight tree species (*Abies lasiocarpa* var. *arizonica* (Merriam) Lemm., *Picea engelmannii* Parry ex Engelm., *Pinus aristata* Engelm., *Pinus edulis* Engelm., *Pinus flexilis* James, *Pinus ponderosa* Dougl. ex Laws., *Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco and *Quercus gambelii* Nutt.) were used to compare sensitivity of radial growth to regional drought and temperature among co-occurring species at the same site, and between sites that differed in elevation and species composition.

Results For *Picea engelmannii*, *Pinus flexilis*, *Pinus ponderosa* and *Pseudotsuga menziesii*, trees in drier, low-elevation stands generally had greater sensitivity of radial growth to regional drought than trees of the same species in wetter, high-elevation stands. Species low in their elevational range had greater drought sensitivity than co-occurring species high in their elevational range at the pinyon-juniper/ponderosa pine forest ecotone, ponderosa pine/mixed conifer forest ecotone and high-elevation invaded meadows, but not at the mixed conifer/subalpine forest ecotone. Sensitivity of radial growth to regional drought was greater at drier, low-elevation compared with wetter, high-elevation forests. Yearly growth was positively correlated with measures of regional water availability at all sites, except high-elevation invaded meadows where growth was weakly correlated with all climatic factors. Yearly growth in high-elevation forests up to 3300 m a.s.l. was more strongly correlated with water availability than temperature.

Main conclusions Severe regional drought reduced growth of all dominant tree species over a gradient of precipitation and temperature represented by a 1500-m change in elevation, but response to drought varied between species and stands. Growth was reduced the most in drier, low-elevation forests and in species growing low in their elevational range in ecotones, and the least for trees that had recently invaded high-elevation meadows. Constraints on tree growth from drought and high temperature are important for high-elevation subalpine forests located near the southern-most range of the dominant species.

Keywords

Abies lasiocarpa, climate change, dendrochronology, *Picea engelmannii*, *Pinus aristata*, *Pinus edulis*, *Pinus flexilis*, *Pinus ponderosa*, *Pseudotsuga menziesii*, *Quercus gambelii*.

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INTRODUCTION

Drought is the most limiting factor to tree growth in most forests in the Southwest USA (Fritts, 1976; Meko *et al.*, 1995; Swetnam & Betancourt, 1998; Hidalgo *et al.*, 2001; Meko & Baisan, 2001). Climate change models predict higher temperatures and increased variability in precipitation in the Southwest USA for the future (Gregory *et al.*, 1997; Gleick, 2000; Rosenberg *et al.*, 2003). These changes may lead to increases in the frequency and intensity of drought (Lawford, 1993; Hanson & Weltzin, 2000). Studies of tree rings can provide insight into the effects of climate factors on tree growth (LeBlanc & Foster, 1992; Graumlich, 1993; Szeicz & MacDonald, 1994; Ettl & Peterson, 1995; Buckley *et al.*, 1997; Cook *et al.*, 2001; Cullen *et al.*, 2001; Peterson & Peterson, 2001; Beniston, 2002; Dittmar *et al.*, 2003). Such studies have shown differences in tree growth response to precipitation and temperature among sites and species (Villalba *et al.*, 1994; Orwig & Abrams, 1997; Cook *et al.*, 2001; Galuszka & Kolb, 2002; Fekedulegn *et al.*, 2003) that need to be better understood in order to evaluate the effects of climate change on forested landscapes.

Variable climate and topography make northern Arizona an ideal location for biogeographical investigation of tree growth response to climatic variation. The El Niño Southern Oscillation and Pacific Decadal Oscillation contribute to high interannual variability of precipitation in northern Arizona (Swetnam & Betancourt, 1998; Sheppard *et al.*, 2002). Precipitation in northern Arizona is bimodal, with *c.* 50% of precipitation in winter and 40% in summer, and summer monsoon rains are preceded by an arid pre-monsoon period and followed by a dry autumn (Swetnam & Betancourt, 1998; Sheppard *et al.*, 2002). The topography of northern Arizona includes a 2300-m elevation gradient from the upper Sonoran and Great Basin Deserts through several forest types to alpine communities. Higher elevations in this region have a wetter, cooler climate compared with lower elevations (Pearson, 1920; Sheppard *et al.*, 2002). For example, on the San Francisco Peaks in northern Arizona, average air temperature for May 2003 through April 2004 decreased by 5 °C (11.7–6.7 °C) and precipitation increased by 499 mm (274–773 mm) from an elevation of 2020 to 2615 m a.s.l. (P. Dijkstra, M. Montes-Helu and B. Hungate, unpubl. data).

In this study we examine sensitivity of tree radial growth to regional drought, precipitation and temperature for eight species at 21 sites consisting of different forest types located along a moisture and temperature gradient across a 1500-m change in elevation on the San Francisco Peaks in northern Arizona. Specifically, we compare sensitivity of tree radial growth to regional drought and temperature (1) among stands growing at different elevations for *Picea engelmannii* Parry ex Engelm., *Pinus flexilis* James, *Pinus ponderosa* Dougl. ex Laws. and *Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco, and (2) among all dominant co-occurring species in six forest types along the elevational moisture and temperature gradient ranging from the ecotone between the pinyon-juniper and ponderosa pine forest types at an elevation of *c.* 2000 m to the

subalpine forest at an elevation of *c.* 3300 m. For within-community, among-species comparisons, we expected that species growing in drier, low-elevation stands would be more sensitive to regional drought than species growing in wetter, high-elevation stands. At low elevations we expected measures of regional water availability to correlate best and positively with yearly variation in growth. At high elevations we expected temperature to correlate best and positively with yearly variation in growth.

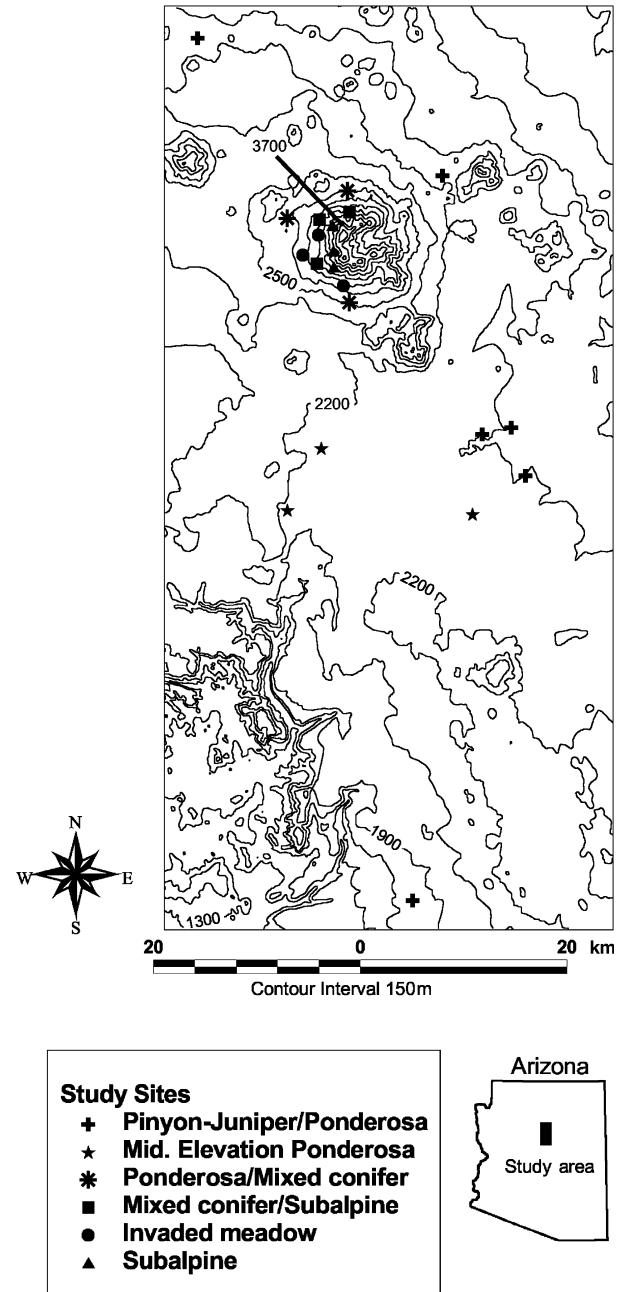


Figure 1 A map of the 21 sites sampled in the study in northern Arizona at the pinyon-juniper/ponderosa pine ecotone, the mid-elevation ponderosa pine forest, the ponderosa pine/mixed conifer forest ecotone, the mixed conifer/subalpine ecotone, the invaded meadow and the subalpine forest.

METHODS

Study areas

Our study was situated in upland forests on the Coconino National Forest in northern Arizona (Fig. 1). Forests dominated by *Pinus edulis* Engelm. and various *Juniperus* species occur at the lowest elevations, *Pinus ponderosa* dominates at intermediate elevations, and mixed conifers dominate at the highest elevations (Brown, 1994). These forests have been grazed by sheep and cattle and logged since the late 1880s (Cline, 1994; Dahms & Geils, 1997). Most forests of *Pinus ponderosa* and mixed conifers on flat terrain are secondary growth after logging, whereas old-growth stands are more common on steep terrain. Grazing still occurs in some stands, but grazing intensity is much lower than in the early 1900s (Cline, 1994; Dahms & Geils, 1997). Suppression of fire and heavy grazing in the last 100 years has been associated with large increases in tree density in both low- and high-elevation forests in northern Arizona (Covington & Moore, 1994; Fulé *et al.*, 2002, 2004; Moore *et al.*, 2004; Moore & Huffman, 2004; Gascho Landis & Bailey, 2005).

We selected 21 sites within the Coconino National Forest in the vicinity of Flagstaff, Arizona (Fig. 1). Sites representative of several forest types and ecotones were selected near roads and hiking trails for ease of access. Six sites were selected at the pinyon-juniper/ponderosa pine forest ecotone near the low-elevation range limit of *Pinus ponderosa*. Accurate characterization of the pinyon-juniper/ponderosa pine forest ecotone required sampling over two types of soil. Three sites in this ecotone, ranging between 1834 and 2103 m a.s.l., were selected on soils with flow basalt parent material; one of the sites also

contained *Quercus gambelii* Nutt. Three sites, ranging between 2032 and 2050 m a.s.l., were selected on soils with sedimentary parent material where *Q. gambelii* was present. All other forest types included in the study occurred on soils derived from volcanic rocks, usually basalt. Three sites, ranging between 2120 and 2185 m a.s.l., were selected in the ponderosa pine forest where *Q. gambelii* was present. Three sites were selected in each of the following two ecotones: between the ponderosa pine and mixed conifer forest types (2547–2603 m a.s.l.), and between the mixed conifer and subalpine forest types (2871–2946 m a.s.l.). Three sites were selected in each of the invaded meadow (2749–2871 m a.s.l.) and subalpine (3286–3412 m a.s.l.) forest communities. Trees have invaded many high elevation meadows on the San Francisco Peaks in the last 100 years, as a likely consequence of fire exclusion, heavy sheep grazing and periods of favourable climate for tree recruitment (Covington & Moore, 1994; Moore & Huffman, 2004). We selected invaded meadow sites where crown closure has not occurred near the lower range limit of *Pinus aristata* Engelm. Subalpine forest sites were selected just below the treeline where sufficient numbers of *Picea engelmannii* and *Pinus aristata* occurred for sampling. Elevation, slope, aspect and tree basal area are summarized for all sites in Table 1.

Tree-ring sampling and measurement

Our goal was to sample representative mature trees of each dominant tree species at each of the 21 study sites. At each site we selected 10–12 trees of approximately similar size of each species growing in same vicinity. Tree age and diameter at breast height (d.b.h.) were not used as strict criteria for

Table 1 Characteristics of the 21 study sites. Latitude and longitude for aspect were measured in decimal degrees. Basal area was estimated by point sampling with an angle gauge (Avery & Burkhart, 2002)

Study site ecotone or community	Site	Elevation (m a.s.l.)	Slope (%)	Aspect	Basal area (m ² ha ⁻¹)
Pinyon-juniper/ponderosa (basalt soils)	1	1834	4	268° (W)	1.1
	2	2092	2	342° (N)	13.8
	3	2103	3	342° (N)	13.9
Pinyon-juniper/ponderosa (sedimentary soils)	1	2063	15	195° (S)	2.5
	2	2032	1	35° (NE)	19.2
	3	2050	6	212° (SW)	16.1
Mid-elevation ponderosa	1	2144	9	208° (SW)	36.7
	2	2120	5	45° (NE)	39.5
	3	2185	16	269° (W)	27.6
Ponderosa/mixed conifer	1	2598	13	5° (N)	34.0
	2	2603	15	325° (NW)	43.2
	3	2547	36	168° (S)	29.4
Mixed conifer/subalpine	1	2946	36	306° (NW)	78.1
	2	2871	25	276° (W)	28.5
	3	2941	38	263° (W)	50.5
Invaded meadow	1	2749	15	252° (W)	3.8
	2	2871	28	244° (SW)	3.7
	3	2783	31	197° (S)	3.1
Subalpine	1	3358	41	218° (SW)	46.8
	2	3286	55	266° (W)	65.2
	3	3412	52	232° (SW)	76.2

Ecotone or community	No. of sites	Species	d.b.h. (cm)	Range of d.b.h. (cm)	Age	Age range
Pinyon-juniper/ponderosa (basalt soils)	2	<i>Pinus edulis</i>	24.0	14.2–42.4	110	47–281
		<i>Pinus ponderosa</i>	33.7	19.5–49.3	73	45–165
Pinyon-juniper/ponderosa (basalt soils)	1	<i>Pinus edulis</i>	25.4	15.4–42.4	147	55–281
		<i>Pinus ponderosa</i>	31.7	19.5–43.3	68	45–94
		<i>Quercus gambelii</i>	16.9	11.9–22.0	52	30–82
Pinyon-juniper/ponderosa (sedimentary soils)	3	<i>Pinus edulis</i>	25.2	12.2–40.0	89	52–140
		<i>Pinus ponderosa</i>	33.9	16.3–48.5	85	35–218
		<i>Quercus gambelii</i>	20.1	11.2–40.7	85	25–145
Mid-elevation ponderosa	3	<i>Pinus ponderosa</i>	37.2	28.7–46.4	75	56–97
		<i>Quercus gambelii</i>	24.4	13.3–38.7	106	65–153
Ponderosa/mixed conifer	3	<i>Pinus flexilis</i>	35.1	20.7–48.0	77	51–117
		<i>Pinus ponderosa</i>	32.9	22.0–44.9	66	45–89
		<i>Pseudotsuga menziesii</i>	35.3	21.5–57.7	68	56–161
Mixed conifer/subalpine	3	<i>Abies lasiocarpa</i>	33.4	21.9–48.3	88	47–177
		<i>Picea engelmannii</i>	32.5	22.3–52.5	74	31–138
		<i>Pinus flexilis</i>	38.6	26.0–52.4	147	68–279
		<i>Pseudotsuga menziesii</i>	40.3	23.5–63.2	117	61–259
Invaded meadow	3	<i>Pinus aristata</i>	42.7	27.8–54.6	56	29–80
		<i>Pinus flexilis</i>	45.7	24.7–75.0	47	24–74
		<i>Pinus ponderosa</i>	44.8	29.3–58.0	50	23–64
Subalpine	3	<i>Picea engelmannii</i>	39.1	26.0–51.4	136	70–226
		<i>Pinus aristata</i>	41.0	25.8–60.1	229	78–402

Table 2 Number of sites sampled ($n = 10$ to 12 trees per species per site), average and range of diameter at breast height (d.b.h.), and average and range of age in years at breast height in 2003 for tree species sampled at each ecotone or community

sampling, but all sampled trees were in dominant or co-dominant canopy positions and were representative of mature trees at all sites. Sites at the mixed conifer/subalpine forest ecotone and in the subalpine forest tended to have closed canopies, thus we avoided sampling trees in or at the edge of clearings. Also, we avoided trees that appeared to be unhealthy or with insect or other damage. Between July 2001 and February 2003, d.b.h. was measured (Table 2) and two increment cores were taken from each tree at breast height from the south and west sides of the tree using a 5-mm diameter increment borer (Suunto, Espoo, Finland). Cores were mounted (Stokes & Smiley, 1968) and sanded with a belt sander (Makita Corp., La Mirada, CA, USA) using FEPA (Federation of European Producers of Abrasives) 100-, 220-, 320- and 400-grit belts (162, 68, 44.7–47.7 and 33.5–36.5 μm , respectively; Orvis & Grissino-Mayer, 2002). Next, cores were polished by hand with sandpaper of 40-, 30- and 15- μm grits and with 30- μm polishing paper.

We measured the width of each annual ring to the nearest 0.01 mm using a Microcode II measuring banister system (Boeckler Instruments, Tucson, AZ, USA) and the Measure J2X computer software (VoorTech Consulting, Holderness, NH, USA). Cores were cross-dated visually using narrow marker years from *Pinus ponderosa* chronologies at the Gus Pearson Natural Area (2237 m a.s.l.) in the Coconino National Forest (Graybill & Rose, 1989; International Tree-Ring Data Bank; World Data Center for Paleoclimatology; NOAA; P. Fulé, pers. comm.). Cross-dating was validated using skeleton plots (Stokes & Smiley, 1968) and COFECHA computer

software (Holmes *et al.*, 1986; Grissino-Mayer, 2001; International Tree Ring Data Bank program library). Cores that would not cross-date well were excluded from further analysis. Age at breast height was recorded for each tree (Table 2). When the pith was absent from increment cores, a pith locator was used to estimate age at breast height (Applequist, 1958).

Because tree-ring width and ring-width variation often decrease as tree diameter increases, ring width measurements should be standardized in order to meet the assumptions of most statistical analyses, and to decouple ring-width variation from changes in tree age and diameter (Fritts & Swetnam, 1989). Before standardizing, pairs of ring-width series were averaged per tree. We used the simplest form of standardization that retains high-frequency variation. Ring widths were standardized using linear regression of annual width on year of ring formation, and by dividing residuals by predicted values to create a ring-width index (RWI) for each annual ring. This standardization method results in a unitless RWI with a mean of 1 and a constant variance over time (Fritts & Swetnam, 1989). Only rings formed between 1950 and 2000 were standardized as this period contained ample variability in precipitation and climate factors for our analyses. Instrumental climate data are available locally since 1909. However, the period of 1909–1949 was relatively wet with only two years in this period having a Palmer Drought Severity Index (PDSI) < -2 . PDSI is a region-specific index of drought calculated from precipitation, temperature and potential evapotranspiration (Palmer, 1965; Alley, 1984). Cross-dating and measuring a 51-year period (1950–2000)

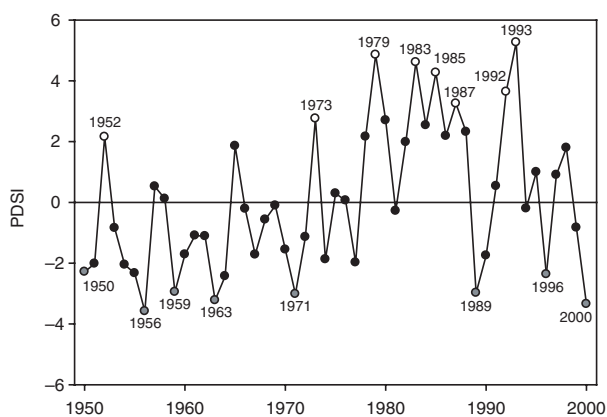


Figure 2 Annual average Palmer Drought Severity Index (PDSI) for Region 2, Arizona, from 1950 to 2000. Positive values of PDSI indicate wetter than average conditions and negative values indicate drier than average conditions. Open circles are selected wet years (1952, 1973, 1979, 1983, 1985, 1987, 1992 and 1993) and shaded circles are selected dry years (1950, 1956, 1959, 1963, 1971, 1989, 1996 and 2000) used in tree growth comparisons.

on each core also made it possible to include more trees in the study.

Data analysis

We obtained PDSI data calculated from instrument environmental data for Arizona region 2 from the National Climate Data Center, USA. We selected eight dry and eight wet years between 1950 and 2000 for comparisons of tree radial growth (Fig. 2). Selected dry years had an average PDSI < -2.0 and selected wet years had an average PDSI > 2.0 . A secondary criterion for the selection of these years was temporal dispersion of wet and dry years throughout the 51-year measurement period. An average RWI for each tree was calculated for the eight dry years and for the eight wet years. The ratio of RWI in wet years to dry years (W : D) was calculated by dividing the average RWI for the eight wet years by the average RWI for the eight dry years for each tree (Fekedulegn *et al.*, 2003). As we were interested primarily in response to severe drought, we used the W : D approach instead of a variable based on growth response in all years of the measurement period, such as mean sensitivity (Fritts, 1976; Fritts & Swetnam, 1989).

To examine differences in sensitivity of tree growth to regional drought, we compared W : D among elevations and species using ANOVA with SPSS 11.0 for Windows statistical software (SPSS, Inc., Chicago, IL, USA). Our ANOVA model for within-species comparisons among elevations included elevation class (low, middle and high) and site nested within elevation as sources of variation. Our model for between-species comparisons had species, site and species-by-site interaction as sources of variation. As differences in W : D can be caused by differences in growth during dry years, wet years, or both, we also analysed

mean RWI separately for the eight dry and eight wet selected years using ANOVA with the same models used for W : D.

We created 51-year chronologies (1950–2000) by averaging RWI for trees of each species at each community. We correlated RWI chronologies with monthly, seasonal and hydrological year (October–September) values of total precipitation, average, minimum temperature, maximum temperature and average PDSI (Fritts, 1976; Villalba *et al.*, 1994, 1997; Peterson & Peterson, 2001). Climate data from a weather station at the US Forest Service Fort Valley Experimental Station, located 10 km north-west of Flagstaff at an elevation of 2237 m on the footslope of the San Francisco Peaks in the vicinity of our study sites, were used in correlations and were obtained from the Western Regional Climate Center. Auto-correlation coefficients were calculated for each chronology to understand how much radial growth in previous years influenced growth in the current year (Fritts, 1976; Orwig & Abrams, 1997).

RESULTS

Autocorrelation

Lag 1 autocorrelation was generally low: average 0.27 over all species and communities, range between -0.09 and 0.59 , and 77% of all values were < 0.4 (Table 3). Therefore, for a given year, radial growth in the previous year generally had a small effect on radial growth in the current year.

Wet : dry ratio

For *Picea engelmannii*, *Pinus flexilis*, *Pinus ponderosa* and *Pseudotsuga menziesii*, W : D was greater in high-elevation stands than low-elevation stands, and the difference was significant ($P < 0.05$) for *Picea engelmannii* ($n = 60$) and *Pinus ponderosa* ($n = 90$; Fig. 3). For *Pinus flexilis* ($n = 56$) and *Pseudotsuga menziesii* ($n = 60$), W : D differed significantly ($P < 0.01$) among sites within elevations (data not shown).

At the pinyon-juniper/ponderosa pine forest ecotone, *Pinus ponderosa* had higher W : D than *Pinus edulis* ($P < 0.001$, $n = 128$; Fig. 4a). W : D also differed significantly ($P < 0.05$) among sites at this ecotone (data not shown).

At the ponderosa pine/mixed conifer ecotone, a significant species-by-site interaction complicated interpretation of main effects, so an ANOVA was performed at each site to compare species (Fig. 4b). At site 1, *Pseudotsuga menziesii* had higher W : D than *Pinus ponderosa* ($P < 0.05$, $n = 30$), but not higher than *Pinus flexilis*. At site 2, *Pinus flexilis* had higher W : D than *Pinus ponderosa* ($P < 0.05$, $n = 28$), and W : D of *Pseudotsuga menziesii* did not differ from either species. At site 3, *Pseudotsuga menziesii* and *Pinus flexilis* had higher W : D than *Pinus ponderosa* ($P < 0.01$, $n = 30$).

There were no differences in W : D among species at the mixed conifer/subalpine forest ecotone ($P > 0.1$, $n = 112$, Fig. 4c). At invaded meadow sites, *Pinus aristata* and *Pinus*

Ecotone or community	Species	Autocorrelation		
		Lag 1	Lag 2	Lag 3
Pinyon-juniper/ponderosa (basalt soils)	<i>Pinus edulis</i>	0.01	-0.11	-0.02
	<i>Pinus ponderosa</i>	0.41	0.22	0.11
Pinyon-juniper/ponderosa (basalt soils)	<i>Pinus edulis</i>	0.30	0.18	0.14
	<i>Pinus ponderosa</i>	0.49	0.41	0.22
	<i>Quercus gambelii</i>	0.38	0.35	0.35
Pinyon-juniper/ponderosa (sedimentary soils)	<i>Pinus edulis</i>	0.16	0.03	0.25
	<i>Pinus ponderosa</i>	0.20	0.06	0.13
	<i>Quercus gambelii</i>	0.17	-0.05	0.26
Mid-elevation ponderosa	<i>Pinus ponderosa</i>	0.12	-0.13	-0.18
	<i>Quercus gambelii</i>	-0.09	-0.22	0.10
Ponderosa/mixed conifer	<i>Pinus flexilis</i>	0.29	0.15	0.14
	<i>Pinus ponderosa</i>	0.23	0.09	0.22
	<i>Pseudotsuga menziesii</i>	0.17	0.02	0.24
Mixed conifer/subalpine	<i>Abies lasiocarpa</i>	0.59	-0.17	-0.03
	<i>Picea engelmannii</i>	0.21	0.02	0.08
	<i>Pinus flexilis</i>	0.14	0.04	0.07
	<i>Pseudotsuga menziesii</i>	0.20	0.07	0.16
Invaded meadow	<i>Pinus aristata</i>	0.28	0.02	0.02
	<i>Pinus flexilis</i>	0.58	0.42	0.21
	<i>Pinus ponderosa</i>	0.43	0.27	0.10
Subalpine	<i>Picea engelmannii</i>	0.29	0.10	0.15
	<i>Pinus aristata</i>	0.20	0.06	0.09

Table 3 Autocorrelation at 1-, 2- and 3-year lags for RWI chronologies of each species at each ecotone or community

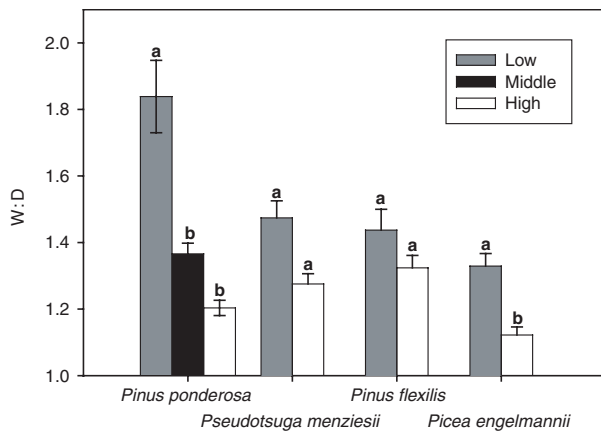


Figure 3 Ratio of ring-width index in wet years to dry years (W : D) for *Pinus ponderosa* Dougl. ex Laws., *Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco, *Pinus flexilis* James and *Picea engelmannii* Parry ex Engelm., growing at different elevations (low, middle and high) on the San Francisco Peaks, Arizona. Letters indicate significant differences ($P < 0.05$) among elevations in an ANOVA for each species. Error bars are 1 SE.

flexilis had higher W : D than *Pinus ponderosa* ($P < 0.01$, $n = 91$; Fig. 4d).

In the subalpine forest community, W : D for *Pinus aristata* was higher than W : D of *Picea engelmannii* ($P < 0.05$, $n = 64$), but the difference was small (Fig. 4e). Site differences in W : D in the subalpine forest were also significant ($P < 0.001$, data not shown).

At the pinyon-juniper/ponderosa pine forest ecotone on the site with basalt-derived soil, W : D did not differ between *Pinus ponderosa* and *Q. gambelii* ($P > 0.05$, $n = 32$), but both had higher W : D than *Pinus edulis* ($P < 0.001$; Fig. 5a). However, at the pinyon-juniper/ponderosa pine forest ecotone sites on soils derived from sedimentary rocks, *Pinus ponderosa* had higher W : D than *Q. gambelii* ($P < 0.001$, $n = 96$), which had higher W : D than *Pinus edulis* ($P < 0.001$; Fig. 5b). In the mid-elevation ponderosa pine forest, *Pinus ponderosa* again had higher W : D than *Q. gambelii* ($P < 0.05$, $n = 55$; Fig. 5c).

Analysis of average RWI in wet years and dry years separately revealed that species with high W : D in most communities resulted from both wide rings in wet years and narrow rings in dry years. One exception was the pinyon-juniper/ponderosa pine forest ecotone on basalt-derived soil, where dry-year RWI was similar among species (Table 4), indicating that species differences in W : D (Figs 4 & 5) were caused primarily by differences in RWI in wet years. The second exception was the subalpine forest, where RWI in dry years was the dominant influence on differences in W : D among species (Table 4).

RWI-climate correlations

Several overall patterns emerged from correlation analysis of RWI and climate variables (Fig. 6). RWI of most species was significantly ($P < 0.05$, $n = 51$) and positively correlated with annual and winter precipitation, and with PDSI in the winter, growing, pre-monsoon, and monsoon seasons. Moreover, RWI for most species was negatively correlated with annual, winter

Figure 4 Ratio of ring-width index in wet years to dry years (W : D) for tree species growing in five different forest community types: (a) pinyon-juniper/ponderosa pine ecotone, (b) ponderosa pine/mixed conifer ecotone, (c) mixed conifer/subalpine ecotone, (d) invaded meadow and (e) subalpine. For the ponderosa pine/mixed conifer ecotone, a species-by-site interaction prevented interpretation of the main effects so an ANOVA was performed separately for each site. Different letters indicate significant differences ($P < 0.05$) among species in an ANOVA for panels (a), (c), (d) and (e), and among species within sites in panel (b). Error bars are 1 SE.

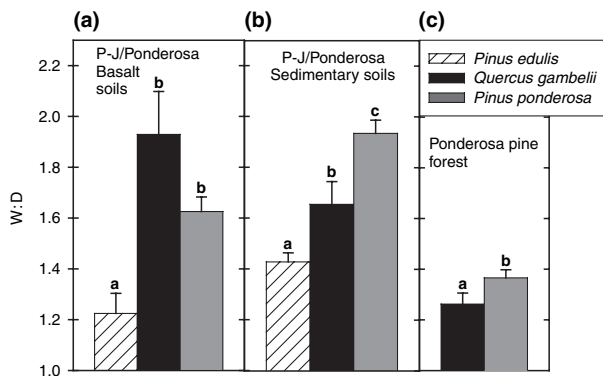
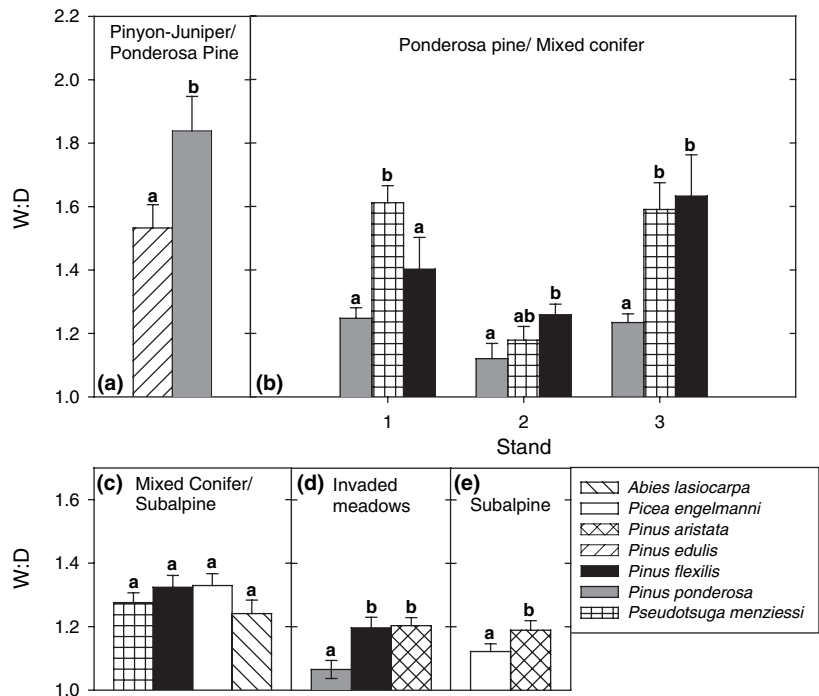


Figure 5 Ratio of ring-width index in wet years to dry years (W : D) at three forest communities where *Quercus gambelii* Nutt. was present: (a) on soils derived from basalt at the pinyon-juniper/ponderosa pine ecotone, (b) on soils derived from sedimentary rocks at the pinyon-juniper/ponderosa pine ecotone, and (c) mid-elevation ponderosa pine forest on soils derived from volcanic rocks. Different letters indicate significant differences ($P < 0.05$) among tree species for each panel. Error bars are 1 SE.

and growing season maximum temperatures. Correlations of RWI with growing season, pre-monsoon and monsoon precipitation, and annual PDSI were low or not significant ($P > 0.05$) for most species (Fig. 6). Across all communities and species, only RWI of *Pinus ponderosa* was significantly and positively correlated with temperatures; RWI of *Pinus ponderosa* was positively correlated with growing season average temperature at the mid-elevation ponderosa pine forest ($r = 0.31, P < 0.05$), and the ponderosa pine/mixed conifer forest ecotone ($r = 0.34, P < 0.05$).

At the pinyon-juniper/ponderosa pine forest ecotone (Fig. 6a), correlations between RWI and climate variables were similar for *Pinus edulis* and *Pinus ponderosa*, except for pre-monsoon precipitation where *Pinus edulis* was positively correlated and *Pinus ponderosa* was not. At this community, the highest absolute r -values of any community occurred for correlations of RWI with annual and winter precipitation, and winter, growing season, pre-monsoon, and monsoon PDSI. *Quercus gambelii* had a pattern of correlations similar to *Pinus ponderosa* and *Pinus edulis* at the pinyon-juniper/ponderosa pine forest ecotone (data not shown).

At the mid-elevation ponderosa pine forest (Fig. 6b), *Q. gambelii* had a similar pattern of RWI-climate correlations as *Pinus ponderosa*, but *Q. gambelii* typically had higher r -values than *Pinus ponderosa*. *Quercus gambelii* had the highest absolute r -values of all species for RWI correlations with annual and winter maximum temperatures.

At the ponderosa pine/mixed conifer forest ecotone (Fig. 6c), *Pinus flexilis* and *Pseudotsuga menziesii* had higher r -values for winter, growing season, pre-monsoon and monsoon PDSI than *Pinus ponderosa*. *Pinus ponderosa* had significant positive correlations ($P < 0.05$) with growing season and pre-monsoon precipitation, whereas *Pinus flexilis* and *Pseudotsuga menziesii* did not.

At the mixed conifer/subalpine forest ecotone (Fig. 6d), *Picea engelmannii*, *Pinus flexilis* and *Pseudotsuga menziesii* had correlations of similar strength, whereas *Abies lasiocarpa* [(Merriam) Lemm.] had weaker correlations for annual and winter precipitation, winter, growing season, pre-monsoon and monsoon PDSI. *Abies lasiocarpa*, *Pinus flexilis* and *Pseudotsuga menziesii* had similar positive significant correla-

Table 4 Mean ring-width index (RWI) in dry years for tree species for all sites and communities. Letters next to values indicate significant ($P < 0.05$) differences among species within sites or communities from ANOVA. Overall means marked with * indicate a significant ($P < 0.05$) species-by-site interaction. Lower values of RWI indicate that a species had narrower rings during dry years relative to the overall growth trend from 1950 to 2000

Community	Species	Site 1	Site 2	Site 3	Overall
Pinyon-juniper/ponderosa (basalt soils) (species, $P = 0.25$; site, $P = 0.03$; species \times site, $P = 0.38$; $n = 62$)	<i>Pinus edulis</i>	0.88	0.74	0.74	0.78a
	<i>Pinus ponderosa</i>	0.78	0.71	0.74	0.74a
Pinyon-juniper/ponderosa (basalt soils) (species, $P = 0.16$; $n = 32$)	<i>Pinus edulis</i>	0.88a			
	<i>Pinus ponderosa</i>	0.78a			
	<i>Quercus gambelii</i>	0.75a			
Pinyon-juniper/ponderosa (sedimentary soils) (species, $P < 0.001$; site, $P < 0.001$; species \times site, $P = 0.63$; $n = 92$)	<i>Pinus edulis</i>	0.81	0.77	0.79	0.79b
	<i>Pinus ponderosa</i>	0.65	0.59	0.64	0.63a
	<i>Quercus gambelii</i>	0.71	0.81	0.83	0.78b
Mid-elevation ponderosa (species, $P < 0.001$; site, $P = 0.001$; species \times site, $P = 0.03$, $n = 55$)	<i>Pinus ponderosa</i>	0.85a	0.78a	0.74a	0.79*
	<i>Quercus gambelii</i>	0.93b	0.79a	0.89b	0.87*
Ponderosa/mixed conifer (species, $P = 0.007$; species \times site, $P = 0.03$; $n = 88$)	<i>Pinus flexilis</i>	0.82a	0.88a	0.76b	0.82*
	<i>Pinus ponderosa</i>	0.82a	0.92a	0.88a	0.87*
	<i>Pseudotsuga menziesii</i>	0.75a	0.92a	0.73b	0.80*
Mixed conifer/subalpine (species, $P = 0.38$; site, $P = 0.03$; species \times site, $P = 0.04$; $n = 112$)	<i>Abies lasiocarpa</i>	0.82a	0.91a	0.83b	0.85*
	<i>Picea engelmannii</i>	0.88a	0.85a	0.83b	0.86*
	<i>Pinus flexilis</i>	0.79a	0.85a	0.90a	0.85*
	<i>Pseudotsuga menziesii</i>	0.83a	0.93a	0.89a	0.86*
Invaded meadow (species, $P = 0.004$; species \times site, $P = 0.03$; $n = 91$)	<i>Pinus aristata</i>	0.90a	0.92b	0.89b	0.90*
	<i>Pinus flexilis</i>	0.93a	0.86b	0.95a	0.92*
	<i>Pinus ponderosa</i>	0.96a	0.99a	0.95a	0.97*
Subalpine (species, $P = 0.001$; site, $P < 0.001$; species \times site, $P = 0.08$; $n = 64$)	<i>Pinus aristata</i>	0.88	0.98	0.92	0.93b
	<i>Picea engelmannii</i>	0.92	1.00	1.00	0.97a

tions ($P < 0.05$) for pre-monsoon precipitation, but *Picea engelmannii* did not have a significant correlation.

Species at the invaded meadow community (Fig. 6e) had only a few significant correlations of RWI with climate variables, and those had low absolute r -values. In the subalpine forest (Fig. 6f), RWI–climate correlations for *Pinus aristata* were stronger than correlations for *Picea engelmannii* for winter precipitation, PDSI in all seasons, and for winter maximum temperature. *Pinus aristata* had significant correlations ($P < 0.05$) of RWI with annual and monsoon precipitation, and with annual maximum temperature, whereas *Picea engelmannii* did not. *Pinus aristata* was the only species at any community to have a negative correlation between RWI and monsoon precipitation.

DISCUSSION

The large amount of interannual variation in PDSI in the 51 years of our study revealed differences in sensitivity of tree radial growth to regional drought among species and forest communities over a gradient of precipitation and temperature represented by a change in elevation of 1500 m from the low-elevation pinyon-juniper/ponderosa pine ecotone forest to the

high-elevation subalpine forest. High values of $W : D$ indicate high sensitivity of tree radial growth to moisture conditions (Fekedulegn *et al.*, 2003). Separate analyses of RWI in wet years and dry years indicated that high $W : D$ was driven by both wide rings in wet years and narrow rings in dry years for most species at most sites.

Trees in low-elevation stands were more sensitive to regional drought than trees of the same species in high-elevation stands, and this difference was largest for *Picea engelmannii* and *Pinus ponderosa*. The large difference in $W : D$ between low- and high-elevation stands of these species could be due to their wide elevational range at our study sites (*c.* 430 m for *Picea engelmannii* and *c.* 600 m for *Pinus ponderosa*) that was associated with a large gradient in available soil water. In contrast, low- and high-elevation stands of *Pinus flexilis* and *Pseudotsuga menziesii* differed in elevation by only *c.* 340 m at our study sites, and differences in $W : D$ among elevations were smaller than for *Picea engelmannii* and *Pinus ponderosa*.

Regional drought sensitivity of *Pinus ponderosa* was greater than for a co-occurring conifer with a lower elevation range (*Pinus edulis*), but was lower than for co-occurring conifers with higher elevation ranges (such as *Pinus flexilis* and

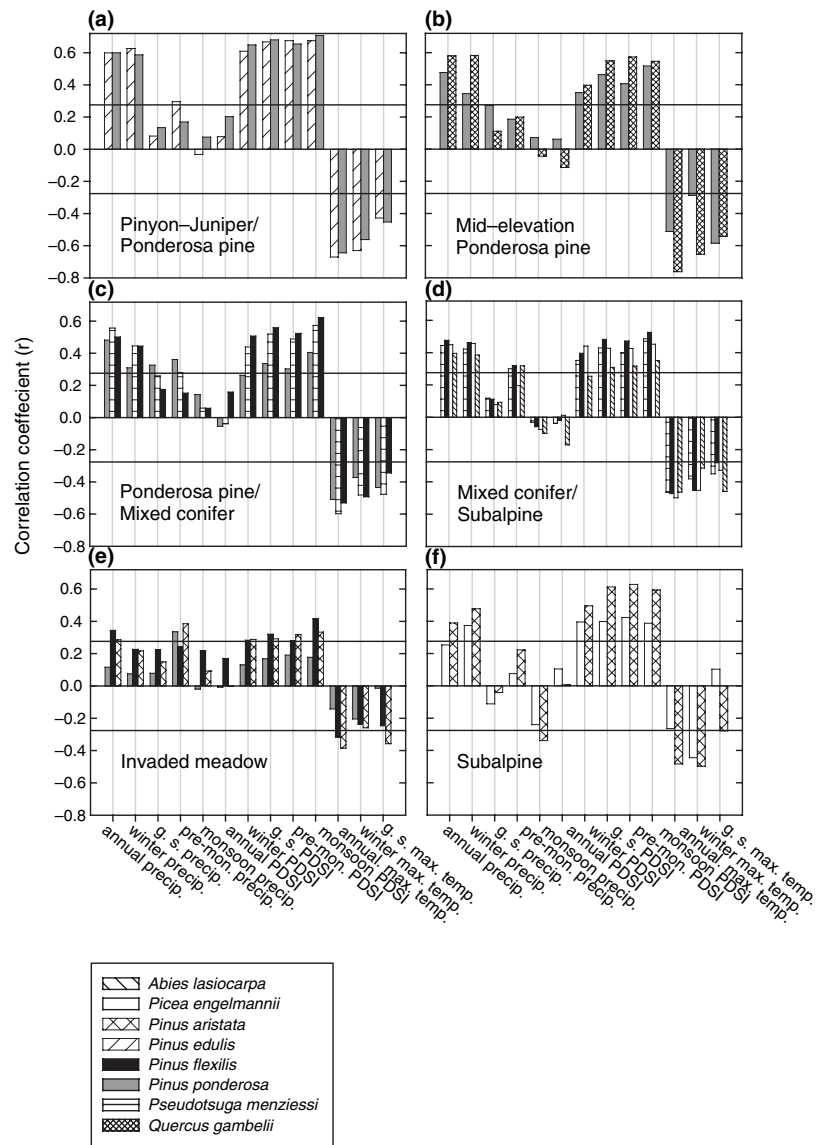


Figure 6 Correlations of 51-year RWI chronologies with climate variables at six communities: (a) pinyon-juniper/ponderosa pine ecotone, (b) mid-elevation ponderosa pine, (c) ponderosa pine/mixed conifer ecotone, (d) mixed conifer/subalpine ecotone, (e) invaded meadow and (f) sub-alpine. Annual values are for the hydrological year (October–September). Winter was defined as October–March, growing season (g.s.) as April–September, pre-monsoon (pre-mon.) as May–June, and monsoon as July–August. Horizontal lines at $r = 0.276$ and $r = -0.276$ form a 95% CI; significant correlations ($P < 0.05$, $n = 51$) extend outside the interval.

Pseudotsuga menziesii). This finding for *Pinus flexilis*, *Pinus ponderosa* and *Pseudotsuga menziesii* is consistent with the physiology of these species. In a seedling study, growth of *Pseudotsuga menziesii* was more responsive to watering than *Pinus ponderosa* (Zhang *et al.*, 1996). Although *Pinus ponderosa* is more prone to xylem cavitation during extreme water stress than *Pseudotsuga menziesii* (Piñol & Sala, 2000), *Pinus ponderosa* compensates by having greater stomatal control of water loss (Piñol & Sala, 2000) and by a greater capacity to store water (Stout & Sala, 2003). In an invaded meadow on the San Francisco Peaks, *Pinus ponderosa* had lower stomatal sensitivity to water vapour pressure deficit between the leaf and the atmosphere than did *Pinus flexilis* (Fischer *et al.*, 2002), suggesting greater photosynthesis by *Pinus ponderosa* than *Pinus flexilis* during drought.

There were no differences in W : D among species at the mixed conifer/subalpine forest ecotone. Separate analysis of RWI in wet and dry years helped explain this result. *Abies lasiocarpa* had a lower RWI in wet years than the other species

($P < 0.05$, $n = 112$, data not shown) at all three sites in this ecotone, indicating that it did not take advantage of favourable conditions in wet years for radial growth to the extent that other species did.

Although differences in W : D among species at the invaded meadow and subalpine forest communities were statistically significant, they were small compared to differences among species in lower elevation communities. At the invaded meadow communities, the white pines (subgenus *Haploxylon*) *Pinus flexilis* and *Pinus aristata* had greater W : D than did *Pinus ponderosa*; a finding that is consistent with differences in stomatal response to vapour pressure deficit between *Pinus ponderosa* and *Pinus flexilis* at a similar site (Fischer *et al.*, 2002). In the subalpine forest, *Pinus aristata* had a higher W : D than *Picea engelmannii*, a finding that is consistent with its greater occurrence on south-facing, dry ridges (Rominger & Paulik, 1983).

Growth of *Q. gambelii* was less sensitive to regional drought than growth of *Pinus ponderosa*. *Quercus gambelii* had lower

W : D than did *Pinus ponderosa* at the pinyon-juniper/ponderosa pine ecotone on sites with soil derived from sedimentary rocks and at the mid-elevation ponderosa pine forest. This result is consistent with *Q. gambelii*'s ability to avoid soil water stress (i.e. higher pre-dawn water potential) and to tolerate atmospheric water stress (i.e. higher photosynthesis at high vapour pressure deficit) better than *Pinus ponderosa* (Kolb & Stone, 2000). We caution against projecting the lack of a difference between *Q. gambelii* and *Pinus ponderosa* on the basalt-derived soil at the pinyon-juniper/ponderosa pine ecotone across similar sites, as this comparison was not replicated over sites.

Radial growth–climate correlations and W : D results in most communities were consistent in that species with low W : D had lower absolute r -values for most climate variables than did species with high W : D. This consistency indicates that species with low sensitivity of growth to severe regional drought (i.e. low W : D) also showed low sensitivity of growth to yearly variation in climate factors such as precipitation and temperature. One notable exception was at the mid-elevation ponderosa pine forest where *Q. gambelii* had higher r -values than *Pinus ponderosa* for every annual and seasonal climate variable, despite having a lower W : D than *Pinus ponderosa*. This result is interesting because others have not had much success at correlating *Q. gambelii* chronologies from very old trees with climate (Biondi, 1987). For the 51 years of our study (1950–2000), RWI of *Q. gambelii* growing near the San Francisco Peaks was clearly responsive to variation in precipitation and temperature.

Correlations of RWI with annual and seasonal precipitation and regional PDSI declined with increasing elevation from the pinyon-juniper/ponderosa pine forest ecotone to the subalpine/mixed conifer forest ecotone. This result is likely to reflect increasing water availability from low to high elevations. Low radial growth–climate correlations at invaded meadows suggest that growth of trees in this community was weakly coupled to variations in temperature and precipitation because there was little competition for water due to low tree density. Another potential reason for weak radial growth–climate correlations at the invaded meadows is that trees at these sites were generally younger than trees at other sites, as the strength of tree radial growth–climate relationships can increase with tree age for some species (Szeicz & MacDonald, 1994). In the subalpine forest, correlations of RWI with PDSI in the growing, pre-monsoon, and monsoon seasons were significant for *Pinus aristata* and *Picea engelmannii*, and were relatively high for *Pinus aristata* ($r = 0.61, 0.63$ and 0.59 , respectively, $n = 51$). These results, combined with a lack of positive correlations between RWI and temperature, and frequent negative correlations between RWI and maximum temperatures at the mixed conifer/subalpine forest ecotone, invaded meadow and subalpine forest communities, suggest that yearly growth in the high-elevation forests in our study was limited more by high temperatures and low water availability than by low temperatures.

Negative relationships between tree radial growth and temperature similar to our results have been reported before for subalpine tree species in the western USA (Villalba *et al.*, 1994; Ettl & Peterson, 1995; Peterson & Peterson, 2001). Increased carbon allocation to respiration during periods of high temperatures could cause a negative radial growth–temperature relationship (Dahl, 1951; Waring & Schlesinger, 1985). Huxman *et al.* (2003) measured net ecosystem CO₂ exchange using eddy flux towers of a subalpine forest at an elevation of 3050 m in the Colorado Front Range and found that low temperature in spring limited net CO₂ uptake, but high temperature in mid-summer increased ecosystem respiration, and thus decreased net CO₂ uptake. Low net CO₂ uptake of the forest at temperatures > 10 °C was partly attributed to increases in tree respiration with increasing temperature (Huxman *et al.*, 2003). At our study sites in northern Arizona located near the southern range limit of most of the species we studied, we speculate that high respiration resulting from high summer temperatures limits growth in warm years.

CONCLUSIONS

Severe regional drought reduced growth of all dominant tree species over a gradient of precipitation and temperature represented by a 1500-m change in elevation on the San Francisco Peaks in northern Arizona, but response to drought varied among species and sites. This variation suggests four rules that may be useful in understanding the effects of regional drought and climate change on tree growth for mountain landscapes that are characterized by pronounced gradients in precipitation and temperature. First, regional drought reduces tree growth more in drier, low-elevation forests than wetter, high-elevation forests. Second, regional drought reduces tree growth more for species that occur low in their elevational range in ecotones than co-occurring species that occur high in their elevational range, and this difference is more pronounced in low-elevation forests. Third, open-grown trees that have recently invaded meadows show little growth response to regional drought or yearly variation in precipitation and temperature. Fourth, constraints on tree growth from drought and high temperature are important for high-elevation subalpine forests located near the most southern range of the dominant species.

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BIOSKETCHES

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