Ecological Applications, 19(5), 2009, pp. 1231–1245

Historical fire and multidecadal drought as context for piñon–juniper woodland restoration in western Colorado

DOUGLAS J. SHINNEMAN[1,3] AND WILLIAM L. BAKER[2]

[1]*Department of Botany, University of Wyoming, Laramie, Wyoming 82071 USA*
[2]*Ecology Program and Department of Geography, Department 3371, 1000 East University Avenue, University of Wyoming, Laramie, Wyoming 82071 USA*

Abstract. Fire is known to structure tree populations, but the role of broad-scale climate variability is less clear. For example, the influence of climatic "teleconnections" (the relationship between oceanic–atmospheric fluctuations and anomalous weather patterns across broad scales) on forest age structure is relatively unexplored. We sampled semiarid piñon–juniper (*Pinus edulis–Juniperus osteosperma*) woodlands in western Colorado, USA, to test the hypothesis that woodland age structures are shaped by climate, including links to oceanic–atmospheric fluctuations, and by past fires and livestock grazing. Low-severity surface fire was lacking, as fire scars were absent, and did not influence woodland densities, but stand-replacing fires served as long-rotation (>400–600 years), stand-initiating events. Old-growth stands (>300 years old) were found in 75% of plots, consistent with a long fire rotation. Juniper and piñon age structures suggest contrasting responses during the past several centuries to dry and wet episodes linked to the Atlantic Multidecadal Oscillation (AMO) and Pacific Decadal Oscillation (PDO). Juniper density increased slightly during periods of drought, positive (warm) AMO (after ~10-year lag), and negative (cool) PDO. In contrast, piñon populations may still be recovering from a long, drought-filled period (AD 1620–1820), with pulses of recovery favored during cool AMO, warm PDO, and above-average moisture periods. Analysis of 20th-century tree establishment and instrumental climate data corroborate the long-term relationships between age structure and climate. After Euro–American settlement (AD 1881), livestock grazing reduced understory grasses and forbs, reducing competition with tree seedlings and facilitating climate-induced increases in piñons. Thus tree populations in these woodlands are in flux, affected by drought and wet periods linked to oceanic–atmospheric variability, Euro–American livestock grazing, and long-rotation, high-severity fires. Reductions in livestock grazing levels may aid ecological restoration efforts. However, given long-term fluctuations in tree density and composition, and expected further drought, thinning or burning to reduce tree populations may be misdirected.

Key words: Atlantic Multidecadal Oscillation; climate teleconnections; disturbance dynamics; ecological restoration; Juniperus osteosperma; *Pacific Decadal Oscillation; piñon–juniper woodland;* Pinus edulis; *regeneration.*

INTRODUCTION

Piñon–juniper and juniper woodlands cover ~30 million ha in semiarid western North America (West 1999*a*) and have been altered by land uses, leading to ecological restoration programs across large land areas (e.g., Eastern Nevada Landscape Coalition, Uncompahgre Plateau Project; information *available online*).[4,5] However, successful landscape-level restoration will require strategies based on both an adequate understanding of the historical dynamics of these woodlands and compatibility with expected future climate–disturbance interactions.

A common view is that piñon–juniper woodlands were open and savanna-like but became unnaturally dense and invaded shrublands and grasslands after Euro–American settlement (e.g., West 1999*b*, Brockway et al. 2002). Evidence for increased density and invasion is from repeat photography (Gordon et al. 1992, Johnson et al. 1999) and dendroecological research in the Great Basin (Tausch et al. 1981, Burwell 1998), Southwest (Landis and Bailey 2005), and Oregon (Miller and Rose 1995, Soulé et al. 2004). Causes may include livestock grazing, which reduced competition for tree seedlings, and control of low-severity surface fires that historically maintained savanna-like conditions and confined old woodlands to fire-safe sites (Miller and

---

Manuscript received 5 May 2008; revised 15 September 2008; accepted 12 November 2008. Corresponding Editor: R. A. Hufbauer.

[3] Present address: U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, Snake River Field Station, 970 Lusk St., Boise, Idaho 83706 USA.
E-mail: dshinneman@usgs.gov

[4] ⟨http://www.envlc.org⟩

[5] ⟨http://www.upproject.org⟩

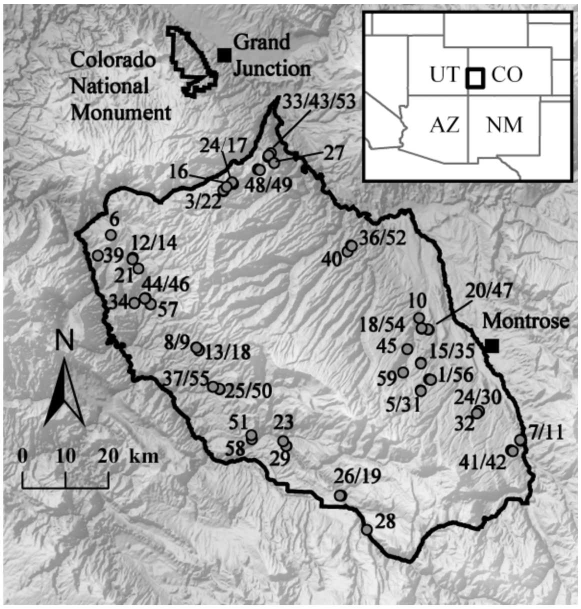

FIG. 1. The Uncompahgre Plateau and study area with numbered sample locations (see Table 1 for plot information).

Rose 1999, West 1999*b*, Miller and Tausch 2001). Tree expansion and increased density may reduce understory plant cover, plant diversity, and water release, and increase soil erosion, severe fires, or insect outbreaks (Davenport et al. 1998, Tausch 1999, Nabhan et al. 2004).

However, recent reviews of fire in these woodlands concluded that stand-replacing fires dominated in the pre-Euro–American period, and there is little or no evidence that low-severity surface fire played a role (Baker and Shinneman 2004, Romme et al. 2008). Long-rotation (400+ years), stand-replacing fires supported dense, mixed-age woodlands in southwestern Colorado (Eisenhart 2004, Floyd et al. 2004) near our study area. Yet more research is needed to determine the relative role of fire and other factors, including climatic variability and land use, in shaping piñon–juniper stand age structures and tree population dynamics (Romme et al. 2008).

Tree species' range expansion and demography have been linked to multidecadal climate patterns (Swetnam and Betancourt 1998, Gray et al. 2006). Some recent changes in piñon–juniper woodlands likely are a continuation of postglacial, early-Holocene expansion, aided by above-average moisture in the early 20th century, rather than being entirely land-use driven (Miller and Wigand 1994, Swetnam et al. 1999). In contrast, expansion of junipers north into Wyoming over the last millennium was induced by periods of drought (Lyford et al. 2003). In the Southwest, severe drought historically killed trees directly and created conditions favoring bark beetle outbreaks and fire (Swetnam and Betancourt 1998, Grissino-Mayer and Swetnam 2000). However, drought-induced tree mortality in Southwest woodlands over the past several years, particularly of piñons, is generally viewed as more extensive than in historical events (Nabhan et al. 2004, Mueller et al. 2005, Shaw et al. 2005; but see Romme et al. 2003).

Anomalous moisture that could affect piñon–juniper dynamics has been linked to oceanic–atmospheric conditions. In the western United States, interannual moisture variability is strongly influenced by El Niño Southern Oscillation (ENSO) events (Swetnam and Betancourt 1998), while extended droughts are linked to multidecadal patterns in sea surface temperatures (SSTs) (McCabe and Dettinger 1999). Historically severe, extended droughts in the western United States are linked to an interaction of the negative (cool) phase of the Pacific Decadal Oscillation (PDO) and the positive (warm) phase of the Atlantic Multidecadal Oscillation (AMO), including a severe drought in the 1950s (McCabe et al. 2004) and a megadrought in the late 16th century (Gray et al. 2003).

Few studies (e.g., Alftine et al. 2003) have directly examined the relationship between these oscillatory, broad-scale climate patterns and tree population age structures. Long-lived trees, such as piñon and juniper, whose contemporary age structures reflect cumulative regeneration and mortality dynamics over long time periods, may be particularly suited to comparisons with multidecadal climate patterns. Thus we sampled stand age structures across a two-needle piñon–Utah juniper (*Pinus edulis–Juniperus osteosperma*) woodland landscape on the Uncompahgre Plateau in western Colorado, USA. Our large data set of piñon–juniper age structure is the only one we are aware of that includes extensive Utah juniper ages. We evaluated the hypothesis that variability in age structures strongly reflects climatic fluctuations, but fire suppression and livestock grazing may also have affected these structures. We discuss potential restoration options in light of our findings.

METHODS

To evaluate our primary hypothesis, we (1) used standard dendroecological techniques to date stand origins and age structures, (2) measured tree density and composition, (3) studied evidence of pre-Euro–American fire, (4) explored potential relationships between population age structures and multidecadal climate patterns linked to oceanic–atmospheric fluctuations that influence moisture availability, and (5) employed statistical techniques to investigate the influence of climate variables and livestock grazing upon recent (20th-century) tree recruitment.

Study area

The Uncompahgre Plateau in western Colorado (Fig. 1) is transitional between the Colorado Plateau and the Southern Rockies. Its otherwise moderate relief is dissected by many canyons, including Unaweep Canyon, the northern border of the study area. Geologic substrata include sandstone, siltstone, mudstone, and shale formations of the Cretaceous, Jurassic, and Triassic, and occasional Precambrian outcrops (Scott et al. 2001). Sandy soils are generally shallow to moderately deep and well drained (USDA Natural Resource Conservation Service 1995), but patches of deeper aeolian, colluvial, and alluvial soils may occur on level to gentle slopes and along cliff-bottoms, while high clay content is common in soils of the slope-forming Morrison formation and some Cretaceous formations (Scott et al. 2001).

A semicontinuous zone of piñon–juniper woodlands, with scattered grasslands and shrublands, occurs between 1800 m and 2300 m elevation on ~240 000 ha of the study area. Between 1400 m and 1800 m elevation, scattered woodlands occur in a mosaic with semidesert grasslands and shrublands (e.g., sagebrush, *Artemisia tridentata*). Winters are cool and summers typically hot, with mean July temperatures reaching 34°C at low elevations. Precipitation increases from ~20 cm annually at the lowest elevations to >40 cm at upper elevations of the piñon–juniper zone with precipitation peaks occurring in late summer and early fall because of monsoon thunderstorms and local convection (Western Regional Climate Center, data *available online*).[6]

The Ute Indians used the Uncompahgre Plateau for hunting, fuelwood gathering, and collection of piñon nuts and other foods, possibly since AD 1100, but had few permanent settlements (Cassells 1997, Simmons 2000). After Euro–American settlement in 1881, intense and unregulated livestock grazing persisted until the 1940s, followed by regionally extensive clearing of woodlands to increase livestock forage. There is currently widespread interest in restoring the region's ecosystems (Uncompahgre Plateau Project web site [see footnote 5]). Most of the plateau is publicly owned (~75% of the study area), managed by the U.S. Forest Service and Bureau of Land Management (BLM).

Site selection, sampling, and sample processing

We used a geographic information system (GIS) to generate a stratified, random sample of potential plots within piñon–juniper woodlands in the study area. Plots were selected only on BLM land, and strata included elevation, geologic substrate, slope, and aspect. In 2002, 59 plots were sampled (Fig. 1), including (1) a "main" random sample of 28 "age-structure" plots, (2) three random plots that fell within stands that were mechanically cleared, and (3) 28 "companion" plots selected near each random sample point based on stand structures (e.g., tree size and density) that were clearly different from those of the nearest main plot. A "stand" is a relatively uniform area of forest. The 28 main age-structure plots were used for all analyses, and the 28 companion and three mechanically cleared plots were used for stand origin and stand structure analyses. We included mechanically cleared plots because we wanted to sample the range of contemporary stand conditions in the study area, reflecting a diversity of past and current land uses (e.g., livestock grazing, fire suppression). Companion plots were strategically sampled because remote and difficult access limited random sites. Although companion plots are not fully random, their general location is, and they represent a broad spectrum of stand ages and densities (Table 1).

In each plot, located using a global positioning system, we recorded slope, aspect, elevation, geology (Appendix A), and signs of past disturbance, including charred wood or burned snags (Table 1). Live and dead trees within 10 m of a 50-m plot center line were tallied by species, stem diameter (measured above root collar due to low branching), standing/down wood, and evidence of fire (scars). The first 15 trees <5 cm in diameter (collar diameter [cd]) and ~50 trees >5 cd, closest to the origin, were tallied, each within a corresponding rectangular plot whose area was calculated for the density estimate.

Age samples (cores) were obtained from live piñon and juniper trees >5 cd using increment borers at 10 cm in height on the main stem whenever possible, while trees <5 cd were cut at the base. Three age-sampling procedures were used: (1) in 28 main plots, the first 15 trees <5 cd were collected in all stands, and cores were collected from the first 30–40 and 20–25 trees >5 cd in older and younger stands, respectively; (2) in three plots recovering from mid-1900s mechanical clearing, a single core from the largest tree was collected to corroborate treatment dates on record; and (3) in 28 companion plots, only the ~10 largest trees were cored to estimate stand age. This latter procedure provided a reliable estimate, as tree sizes were modestly correlated with age (Appendix B), and in all but one main plot the oldest tree was among the largest 10 in diameter. Collectively, 1180 cores and 382 cut trees were collected. See Table 1 for sample sizes.

Samples, including both cores and cross sections from seedling/saplings, were processed and dated using standard methods (Stokes and Smiley 1968). A subsample of juniper cores was cross-dated with a nearby established chronology, showing that false and missing rings occurred, but raw ring counts yielded a small average net error (+0.5 yr/100 yr); thus ring counts were considered reasonably accurate estimates of age. Piñons could often be cross-dated with a nearby master chronology (Harlan 1978). Two age-correction procedures were used. A missing pith correction (Norton et al. 1987) was required for 68% of cores and, afterwards, cores were within 10 years of the pith for 60% of piñons and 57% of junipers. A coring height correction employed age vs. height regressions for 32 piñons and 22 junipers selected randomly from the entire seedling–

---

[6] ⟨http://www.wrcc.dri.edu/climsum.html⟩

TABLE 1. Sample sizes, elevation, stand characteristics, and fire evidence for the 59 plots.

Plot				Oldest tree (years)		Density of live trees (trees/ha)			Fraction of trees (>25 cm cd) dead			
No.	Type	No. ages	Elev. (m)	Piñon	Juniper	Piñon	Juniper	Understory (piñon fraction)	Piñon	Juniper	Evidence of fire	Century of origin
1	T	1	2200	56	···	714	143	1048 (0.64)	0.25	0.33	···	20th
2	T	1	2275	81	···	288	26	254 (0.81)	0.33	0.00	···	20th
3	M	32	2401	93	66	467	13	160 (1.00)	0.00	···	···	20th
4	T	1	2319	94	···	133	117	250 (0.80)	0.38	0.60	...	20th
5	C	10	2347	113	109	340	10	90 (1.00)	0.00	···	···	19th
6	C	10	2254	116	···	344	10	386 (1.00)	···	···	···	19th
7	C	10	2175	126	···	1067	0	600 (1.00)	···	···	···	19th
8	C	10	2088	131	···	340	64	1636 (1.00)	1.00	0.17	yes	19th
9	M	37	2094	140	110	178	110	3000 (1.00)	···	0.50	yes	19th
10	C	10	1802	105	149	40	75	130 (0.38)	···	0.00	···	19th
11	M	27	2185	103	153	700	20	300 (0.80)	···	···	yes	19th
12	C	10	2005	122	154	127	324	625 (0.87)	···	0.33	near	19th
13	M	31	2093	98	159	8	83	30 (1.00)	0.14	0.46	yes	19th
14	M	39	2022	112	163	542	146	1231 (0.81)	···	0.00	yes	19th
15	M	49	2125	186	162	371	129	938 (0.87)	0.25	···	yes?	19th
16	C	10	2364	222	223	926	185	800 (1.00)	1.00	0.00	···	18th
17	C	10	2303	232	285	706	206	235 (0.75)	0.25	0.60	yes	18th
18	M	39	1868	116	304	31	59	33 (0.30)	0.00	1.00	···	17th
19	C	10	2205	203	311	1000	556	1333 (0.75)	0.00	0.25	near	17th
20	M	48	1826	98	314	13	75	71 (0.07)	···	1.00	yes	17th
21	M	48	2108	253	327	1625	312	15000 (0.87)	0.00	0.00	···	17th
22	C	10	2412	358	···	464	0	214 (1.00)	0.00	···	yes?	17th
23	C	10	1859	359	343	211	329	79 (0.49)	0.50	0.00	yes?	17th
24	M	52	2130	366	358	210	150	1600 (0.83)	0.50	0.25	···	17th
25	C	11	1837	377	326	288	173	577 (0.73)	0.14	0.00	···	17th
26	M	49	2189	212	400	500	467	300 (0.89)	0.40	0.00	near	17th
27	C	11	1953	307	416	224	431	86 (0.80)	0.33	0.67	···	16th
28	M	51	2208	409	422	327	77	327 (0.82)	0.50	0.59	···	16th
29	M	51	1900	268	429	275	510	3333 (0.87)	0.25	0.09	yes?	16th
30	C	11	2122	326	430	909	182	1364 (0.87)	0.00	0.00	···	16th
31	M	38	2336	434	310	467	144	356 (0.53)	0.50	0.29	yes?	16th
32	M	50	2170	285	386	260	100	1250 (0.95)	0.00	0.00	···	16th†
33	C	10	1923	391	387	196	161	333 (0.87)	0.50	0.60	yes?	16th†
34	M	49	1716	388	444	125	208	216 (0.56)	0.00	0.71	···	16th
35	C	10	2138	463	132	348	61	288 (0.74)	0.33	0.50	yes	16th
36	M	46	1797	100	477	18	339	45 (0.20)	0.50	0.00	···	16th
37	C	10	1802	92	480	183	300	217 (0.92)	0.00	0.40	···	16th
38	C	11	2086	427	490	464	393	536 (0.73)	0.22	0.25	···	16th
39	M	48	2020	494	341	515	91	3333 (0.93)	0.00	0.38	···	16th
40	M	49	1874	228	509	320	340	556 (0.67)	···	0.40	···	15th
41	M	49	2351	522	368	272	49	340 (0.88)	0.50	0.67	yes	15th
42	C	4	2372	294	···	193	88	480 (1.00)	0.22	···	···	15th‡
43	C	11	1964	440	522	255	255	938 (1.00)	0.33	0.00	···	15th
44	M	48	1884	459	474	733	1267	1444 (0.92)	0.00	0.50	···	15th†
45	M	51	2007	179	525	114	568	318 (1.00)	···	0.43	···	15th
46	C	10	1890	255	526	375	175	1875 (0.87)	0.00	0.43	···	15th
47	C	10	1823	···	534	0	317	144 (0.47)	···	0.00	···	15th
48	C	12	1995	547	269	200	133	283 (1.00)	0.56	0.71	···	15th
49	M	50	2126	476	552	176	132	400 (0.81)	0.20	0.45	···	15th
50	M	53	1850	454	555	364	81	507 (0.95)	0.11	···	···	15th
51	C	9	1926	315	559	1167	444	556 (0.90)	0.00	0.29	yes?	15th
52	C	8	1761	94	566	54	296	27 (0.33)	0.50	0.29	near	15th
53	M	53	1917	491	562	63	110	643 (0.94)	0.60	1.00	···	14th†
54	C	11	1863	159	578	151	302	105 (0.89)	0.00	0.00	···	14th†
55	M	44	1825	375	591	74	382	59 (1.00)	0.50	0.69	yes	14th†
56	C	11	2182	677	401	537	268	268 (0.73)	0.20	0.00	yes	14th
57	C	10	1814	331	699	100	180	160 (0.81)	0.00	0.67	···	14th
58	M	46	1878	230	655	188	359	109 (1.00)	0.00	0.43	yes?	13th†
59	M	51	2157	339	666	329	657	1154 (0.80)	0.43	0.58	yes	13th†

Notes: Key to plot types: M, main; T, treated (mechanically cleared); C, companion. For fire evidence, yes = fire char or burned snag; yes? = small amounts of fire-char; near = fire char or burned snag within 100 m. For fraction of trees dead, cd is collar diameter.

† Partial cores yielded oldest tree dates from early in a century, and thus stand origin dates were assigned to the previous century.

‡ Stand origin date estimated because large, old junipers could not be cored; origin date estimated from successfully dated, similarly sized junipers located nearby (within ~500 m).

sapling collection, using dated cross sections at 5 cm height intervals. Slope, aspect, and elevation were explored via multiple regression as potential predictors of age at various heights, revealing that piñon height growth is slower on steeper slopes and juniper height growth is slower on steeper, southwest-facing slopes, and yielding the following coring height corrections ($n = 166$ and 119 for piñon and juniper cross sections, respectively): piñon age = 4.5 + 0.707 (height in cm) − 0.15 (slope in degrees) ($R^2 = 44.0\%$, $P < 0.001$); juniper age = 13 + 1.1 (height in cm) − 0.229 (slope in degrees) − 4.74 (cosine-transformed aspect) ($R^2 = 42.7\%$, $P < 0.001$).

After corrections, samples were assigned to one of four quality ranks based on ring quality (e.g., obscure rings), years added through corrections, and whether successfully cross-dated: (1) "high" were estimated to be within 20 years of actual age (45% of junipers, 87% of piñons); (2) "good" were considered to be within 40 years of actual age (24% of junipers, 7% of piñons); (3) "fair" were considered to be within 80 years of actual age (15% of junipers, 2% of piñons); and (4) "partial" showed no signs of the pith and were included in stand age structures only by the date of their earliest ring (16% of junipers, 4% of piñons). After corrections, 98% of samples ($n = 1547$) collected were retained for analysis.

Analysis

Age structures were graphed for each main plot and a composite of all main plots by tree density (no./ha) in 20-year age classes. Partial cores were not used in the composite. Stand ages were estimated using oldest trees, with adjustments in nine plots having partial cores or oldest trees that could not be dated (see Table 1). Dead trees were not dated, and lags may occur before tree regeneration after disturbance (Erdman 1970); thus some stand ages may be underestimated. Fire evidence could not be dated, but its abundance and pattern were considered, along with stand origin dates, stand structures, and abundance of postfire seral shrubs, to evaluate if fire was likely a stand-initiating event. For all analyses, the 1881 Euro–American settlement date was rounded to 1880 to match 20-year tree age classes, and trees <5 cd were classified as an understory component, as few reach canopy height; trees >5 cd were considered overstory.

We assessed climate effects using two procedures. First, to determine the potential influence of historical climate on woodland age structures, we qualitatively compared age structures with three climate indices. Smoothed (10-year running means) Pacific Decadal Oscillation (PDO) reconstructions were from MacDonald and Case (2005) and Atlantic Multidecadal Oscillation (AMO) from Gray et al. (2004), each derived from tree ring chronologies from multiple locations. A 20-year low pass filter of the Palmer Drought Severity Index (PDSI), a relative measure of moisture availability calculated from instrumental climate data and reconstructed from local tree ring chronologies (Cell ID118; Cook et al. 2004), was used as a measure of drought in west-central Colorado. Given the imprecision in older tree dates, statistical analysis is inappropriate for these comparisons, and the effects of interannual variability, reflected in El Niño Southern Oscillation (ENSO) patterns, also cannot be assessed. Moreover, because we analyzed both relatively accurately dated piñons and coarsely dated older junipers, our comparison is intended to explore a working hypothesis that climate is a critical driver of population age structures, but with contrasting effects on junipers and piñons.

Second, we analyzed relationships between five-year piñon and juniper establishment totals (standardized as $\text{trees}\cdot\text{ha}^{-1}\cdot\text{five years}^{-1}$) from AD 1900–2000 and key climate variables (see Soulé et al. 2004). Analysis was restricted to younger trees with more accurate origin dates, as many were derived from full cross sections at the base. Climate data began in AD 1900 (Montrose, Colorado; Williams et al. 2004) and included mean maximum/minimum temperature, seasonal/annual totals for precipitation, and two previous five-year precipitation values combined to determine potential lag effects, such as delayed regeneration response after drought-induced overstory mortality. We assessed relationships using Spearman's rank correlation, because of nonnormal distributions and to minimize skew toward recent establishment periods with lower cumulative mortality. After determining correlation significance, we standardized scores to facilitate graphical comparisons. We then performed a best-subsets regression using these correlated variables and other climate variables to examine potential multivariate relationships with tree establishment and to investigate potential multicollinearity.

To determine the influence of livestock grazing on extant tree density, we used a two-sample t test of the null hypothesis that seedling–sapling density does not differ between reference areas and grazed areas with similar environmental conditions. Reference areas were inside Colorado National Monument, a nearby protected area (Fig. 1) not grazed by livestock since the early 1900s, or were within the study area on isolated mesas seldom, if ever, subjected to livestock grazing. The maximum possible subset of reference-area piñon–juniper plots ($n = 17$) and grazed plots ($n = 28$) that matched in geologic substrate, elevation, slope, and aspect was used in the comparison. Seedling–sapling density (trees/ha) was estimated using 20 m × 50 m plots from this study and from reference areas elaborated in another study (Shinneman et al. 2008).

RESULTS

Stand origins and structures

There is little difference in the distribution of stand origins for main and companion plots (Fig. 2), suggesting the companion plots, although not completely random, were a relatively unbiased sample and will

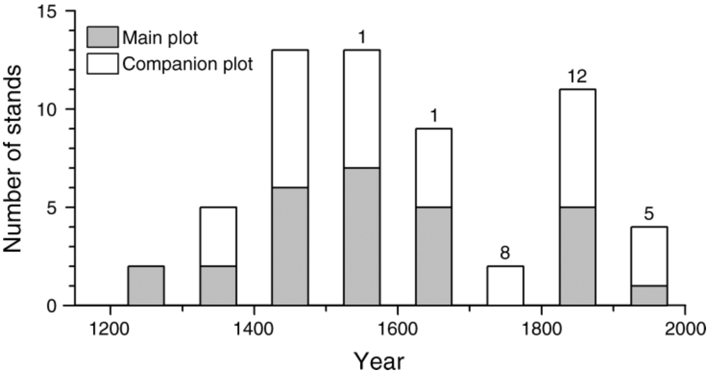

FIG. 2. Number of stands originating in each century for all 59 plots. Numbers above bars indicate the number of stands for each century in which relatively continuous piñon recruitment (i.e., no more than two consecutive age-class gaps) began (27 of 28 plots with age structures; see also Appendix C).

not likely skew the findings. Thus we included them in stand origin and stand structure analyses. Few of the 59 sampled stands originated from recent human activities: 53 stands (89.8%) originated before Euro–American settlement (AD 1881), and 42 (71.2%) established 400–700 years before the present (Fig. 2, Table 1). The AD 1400s and 1500s were a peak period for stand establishment, with 13 stands (22.0%) each century (Fig. 2). Of six stands (10.2%) that originated after Euro–American settlement, three were mechanically cleared by the Bureau of Land Management and contained large-diameter (35–52 cm) down trees that would have significantly predated Euro–American settlement (Appendix B).

Tree age and density patterns varied among stands, were often unique between junipers and piñons, and were likely influenced in part by elevation. Junipers were the oldest trees in 21 of 28 main, uncleared plots, outdating the oldest piñons by an average of 127 years in main plots that originated before 1800 (Table 1), and comprising 71.9% of all trees >300 years old. Mean stand age, often skewed by abundant young trees, ranged from 67–210 years for piñons and 66–377 years for junipers (Table 2). There was modest correlation between older stands and low-elevation slopes (Fig. 3a), and the fraction of piñons per stand increased significantly with elevation (Fig. 3b). Although underrepresenting pre-Euro–American density because of mortality, overstory trees established before AD 1880 demonstrated considerable variability in density, ranging from 0–1176 trees/ha (Table 2; only one main stand contained no trees this old). Total tree densities today were also quite variable among stands but generally high, ranging from 88 to 2000 trees/ha for live overstory

TABLE 2. General woodland stand conditions, by plot averages.

Stand traits and species	Mean	SD	Median	Range	No. plots
Fraction overstory post-Euro–American					
Juniper	0.25	0.32	0.11	0.00–1.00	28
Piñon	0.67	0.29	0.75	0.17–1.00	28
Both	0.47	0.28	0.36	0.10–1.00	28
Overstory age (yr)					
Juniper	221.7	82.9	254.1	66.0–376.8	28
Piñon	123.4	47.2	108.8	66.5–209.6	28
Live overstory density (trees/ha)					
Juniper	223.4	210.9	161.0	0–1267	59
Piñon	366.3	323.1	288.0	0–1625	59
Both	589.6	411.7	462.0	88–2000	59
Live understory density (trees/ha)					
Juniper	115.5	269.3	50.0	0–2000	59
Piñon	782.2	1764.2	300.0	5–13000	59
Both	897.8	2015.8	340.0	27–15000	59
Post-Euro–American overstory density (trees/ha)					
Juniper	29.2	37.8	16.5	0–157	28
Piñon	188.5	192.1	137.5	13–900	28
Both	217.6	195.0	145.6	36–900	28
Pre-Euro–American overstory density (trees/ha)					
Juniper	117.1	119.5	59.5	0–485	28
Piñon	128.4	212.5	46.0	0–1000	28
Both	245.4	252.1	198.5	0–1176	28

Note: Density range values are rounded to the nearest whole number. Partial cores are not used in this assessment.

and 27 to 3333 trees/ha (with one outlier = 15 000 trees/ha) for live understory, which also had a median 300 and 50 trees/ha of piñons and junipers, respectively (Table 2). Live overstory trees originating after Euro–American settlement in a stand averaged 66.9% for piñons and 24.7% for junipers (Table 2).

Evidence of past fire regimes

No fire-scarred trees were found in any plots, or while traveling during three years of research on the Uncompahgre Plateau; since both tree species are capable of scarring (Baker and Shinneman 2004), this lack of evidence suggests low-severity surface fires were rare or did not occur. Moreover, 39 plots contained at least 100 snags or down and dead trees per hectare, and 78% of all plots contained dead trees ≥25 cd (Table 1). These larger dead trees, many of which likely predate Euro–American settlement (Appendix B) and the era of fire suppression, would not have accumulated, especially scar-free, if surface fires were common (Eisenhart 2004).

High-severity fire was likely a stand-initiating event in many stands, as charred snags or charcoal were found in or near (<100 m) 41% of all plots, though 67% of this evidence was found at >2000 m elevation (Table 1 and Appendix C have individual plot characteristics and stand age structures, respectively). Of eight stands originating in the early to mid-1800s (plots 8–15), all but one (plot 10) contained or were near evidence of past high-severity fires, including large charred snags, burned logs, or surface charcoal. All main plots in this group (plots 9, 11, 13–15) demonstrated similar oldest tree dates for piñons and junipers, suggesting a stand-initiating event in the late 1700s to early 1800s. Of 11 stands established between AD 1600 and 1800 (plots 16–26), fire or possible fire evidence was found in six. In another stand, similar ages between oldest piñon and juniper trees and high densities of piñons early in development (plot 24) also suggest postfire origin. Of 33 plots established before 1600 (plots 27–59), five contained definite fire evidence (plots 35, 41, 55, 56, 59), five had small amounts of charcoal (plots 29, 31, 33, 51, 58), and one had charred juniper snags nearby (plot 52).

Fire evidence was also lacking in many stands. None of three untreated stands originating after AD 1880 (plots 3, 5, 6) or two of four stands originating within 30 years of Euro–American settlement (plots 7, 10) had evidence of fire. Two of these woodland plots (3, 10) occurred in the ecotone with grasslands–shrublands, possibly reflecting some dynamism in these ecotones or land-use driven invasion. Among 27 stands originating before AD 1800 that had no fire evidence, most had badly weathered deadwood that provided little evidence for other stand initiation events, and several (e.g., plots 18, 47, 54) had almost no deadwood at all.

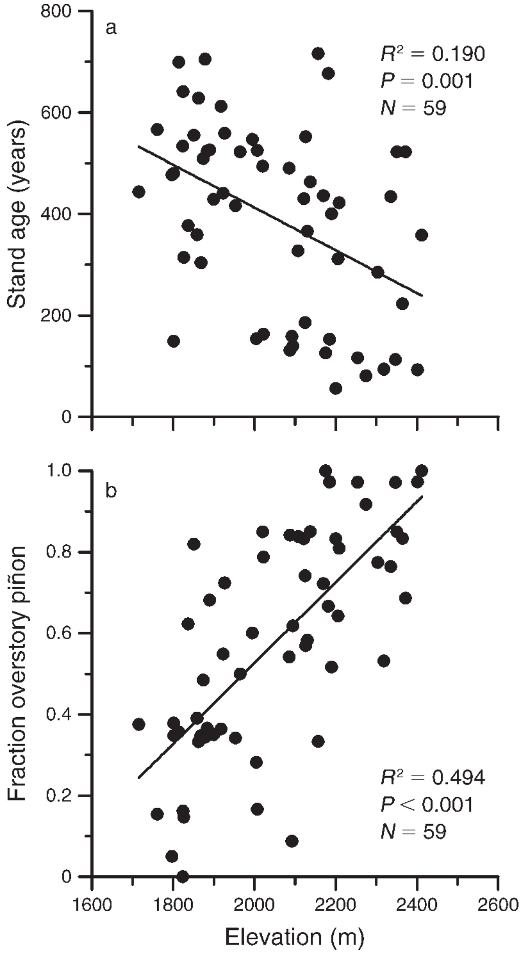

FIG. 3. Significant relationships with elevation for (a) stand age and (b) piñon fraction of trees in stand overstory.

Fire rotation is the expected time to burn an area equal to a study area (Romme 1980). A set of point estimates of stand origin after high-severity fire also provides a valid estimate of fire rotation, estimated by the time period divided by the fraction of sampled stands burned (Baker, *in press*). Considering only the 14 untreated, younger (<300 years) stands for which fire evidence is more reliable, and bell-shaped age structures or seral mountain-shrub understories that suggest high-severity fire (Erdman 1970), eight (57%) likely originated after stand-replacing fire (Table 1). Dividing the 300-year period by 0.57 yields an estimated mean fire rotation of ~526 years. If we assume all 56 untreated stands originated after fire, and use origin dates for the 48 stands established from AD 1400–1900, the most reliable 500-year period for stand ages, the fraction is 0.86 and fire rotation is ~580 years (e.g., Floyd et al. 2000, 2004). If only the fully random main plots (Fig. 2) are used, the fraction is 0.82 (23 of 28 plots) and the rotation ~610 years. Thus a range for fire rotation of ~500–600 years is a rough estimate, as exact dates of fires are unknown, some stand ages may be underestimated, and not all stands may have initiated after fire while others may have burned more than once. A broader fire rotation range of 400–600+ years additionally compensates for half the

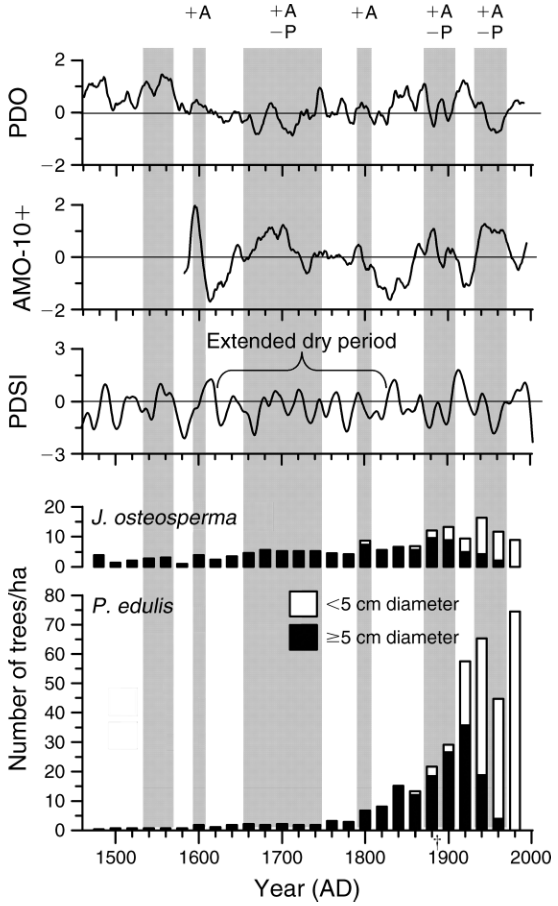

FIG. 4. Composite age structure for piñons (*Pinus edulis*) and junipers (*Juniperus osteosperma*) for all 28 main, uncleared plots, compared to three climate indices. Bars represent 20-year age classes (e.g., 1900 = 1900–1919). Palmer Drought Severity Index (PDSI) values represent a 20-year low pass filter from Cooke et al. (2004); Atlantic Multidecadal Oscillation (AMO) values are 10-year running means from Gray et al. (2004) placed 10 years in advance of actual dates; and Pacific Decadal Oscillation (PDO) values are 10-year running means calculated from MacDonald and Case (2005). Gray shading is centered on juniper population pulses, roughly coinciding with periods of drought (low PDSI), with −P and +A indicating observable correlations with negative (cool) PDO and positive (warm) AMO (with 10-year lag), respectively. The dagger (†) along the bottom *x*-axis indicates the date of Euro–American settlement (AD 1881). The bars placed before AD 1500 represent the total number of piñon and juniper trees established prior to that date.

stands burning twice as often (i.e., every 300 years) and the possibility that some stands rarely burned.

Relationship between age structures and multidecadal, broad-scale climate variables

Individual stand age structures (Appendix C) and a composite of age structure (using 20-year age classes) across stands (Fig. 4) provide evidence about population change. Age structures result from mortality and natality over centuries; thus only qualitative analysis is warranted. Although older juniper tree samples (>300 years old) were often coarsely dated, the composite age data provide a reasonable depiction of stand age structures at the population level. Six slight juniper increases (higher density relative to previous and later age classes), highlighted by shading (Fig. 4), are suggested from AD 1500–2000: in the mid-1500s, ~1600, centered on the late 1600s, in the early 1800s, near the turn of the 19th century, and during the mid- to late 1900s. Piñon samples were generally accurately dated, especially those established after AD 1700. A substantial and sustained increase of piñons within the study area began ~80 years prior to Euro–American settlement (~AD 1800), with additional pulses in the mid-1800s, the early- to mid-1900s, and 1980–2000 (Fig. 4). At the individual stand level, all but one had at least semicontinuous piñon recruitment (i.e., no gaps greater than two consecutive age classes) beginning at different times after AD 1700, while junipers had little age-class continuity (Appendix C).

All three piñon pulses that occurred during the overall increase in population after AD 1800 coincide with positive (warm) Pacific Decadal Oscillation (PDO), negative (cool) Atlantic Multidecadal Oscillation (AMO) after a 10-year lag, and sustained periods of above-average moisture indicated by positive Palmer Drought Severity Index (PDSI) values (Fig. 4). A possible exception for piñon was in 1940–1960, but drought occurred late in this period, peaked in the late 1950s, and continued into the 1970s. Thus the AD 1960–1980 piñon age class better corresponds with this drought. An extended dry period (AD 1620s to 1820s) preceded most of the dramatic increase in piñon population that began around AD 1800 and continued throughout most of the 1900s (Fig. 4). This ~200-year dry period contained several consecutive droughts without intervening, persistent high-moisture periods. The piñon population increase may have been supported by rising moisture levels during the last decade of the 1700s, followed by less-severe drought and then a lengthy wet period in the 1830s and 1840s that probably aided survival of recently established, young (<50 years old by AD 1840) trees (Fig. 4). The start of the piñon population increase around AD 1800 also coincided with a rapid decrease in, and sustained negative values of the AMO index, and a simultaneous increase in PDO values (Fig. 4). In contrast to piñons, each of the six slight juniper increases (Fig. 4) either directly centers on or overlaps a severe, prolonged drought period evident in low PDSI values (Cook et al. 2004). Also in contrast to piñons, after AD 1500, all five juniper increases coincide with all five periods of high (warm) AMO values after a 10-year lag, and three also coincide with three periods of low (cool) PDO values.

Relationships between post-1910 piñon and juniper establishment and climate

Comparing climate data with five-year establishment totals (based on extant trees of post-AD 1900 origin)

TABLE 3. Spearman's rank correlations (r_s) between five-year piñon establishment totals and climate variables.

Variable	Time period	n	r_s
Piñon			
Precipitation total	spring, previous 10 yr	18	0.569
Mean maximum temperature	summer, 5 yr	20	0.511
	annual, 5 yr	20	0.638
Mean minimum temperature	summer, 5 yr	20	0.507
	fall, 5 yr	20	0.564
	annual, 5 yr	20	0.645
Juniper			
Precipitation total	summer, 5 yr + previous 10 yr	18	−0.517
	annual, 5 yr + previous 10 yr	18	−0.482
Mean maximum temperature	winter, 5 yr	20	0.510

Notes: Only variables with >0.4 correlation and significant at $\alpha = 0.05$ are shown. Sample size is smaller ($n = 18$) with lagged 10-yr analysis because climate data were not available before 1900.

further clarified these relationships. Spearman's rank analyses revealed that both temperature and precipitation were significantly ($\alpha = 0.05$) related to the number ($n = 518$) of piñon trees established (Table 3). The strongest relationships included positive correlations between five-year establishment and mean five-year minimum temperature, maximum temperature, and total spring (March–May) precipitation in the previous two five-year periods (Table 3). Minimum and maximum temperatures and piñon establishment values all trended upward over time, suggesting autocorrelation, and potentially confounding other causes of continuous periods of tree recruitment (e.g., widespread reduction in interspecific competition) with climate-induced variability. However, standardized scores reveal the positive covariance between all the variables, including downward-trending 10-year spring precipitation (Fig. 5), and suggest causative relationships between tree establishment and climate variables. For junipers established after AD 1900 ($n = 111$), correlation analysis at $\alpha = 0.05$ revealed that total winter precipitation (December–February) during the same five-year period was positively correlated with establishment, and that the sums of current five-year and previous ten-year values for total annual precipitation and total summer precipitation were both negatively correlated with establishment (Table 3). Best subsets regression confirmed these relationships for each species. The final equations are:

$$\begin{aligned}\text{Five-year piñon establishment totals} \\ &= -97.7 + (0.603 \times \text{sum of previous 10-year spring precipitation}) \\ &\quad + (2.41 \times \text{five-year mean temperature minimum}) \\ &\quad + (1.62 \times \text{sum of five-year winter precipitation})\end{aligned}$$

($R^2 = 59.9\%$; $P = 0.004$, $n = 18$ five-year periods from 1910–2000) and

$$\begin{aligned}\text{Five-year juniper establishment totals} \\ &= 1.87 - (0.076 \times \text{sum of five-year and previous 10-year precipitation}) \\ &\quad + (0.236 \times \text{five-year mean winter temperature maximum}) \\ &\quad + (0.282 \times \text{sum of five-year winter precipitation})\end{aligned}$$

($R^2 = 54.6\%$; $P = 0.01$, $n = 18$ five-year periods from 1910–2000).

The final piñon model predicts that higher establishment follows 10-year periods of wetter springs, and temporally corresponds with wetter winters (significant only in the presence of other variables) and higher

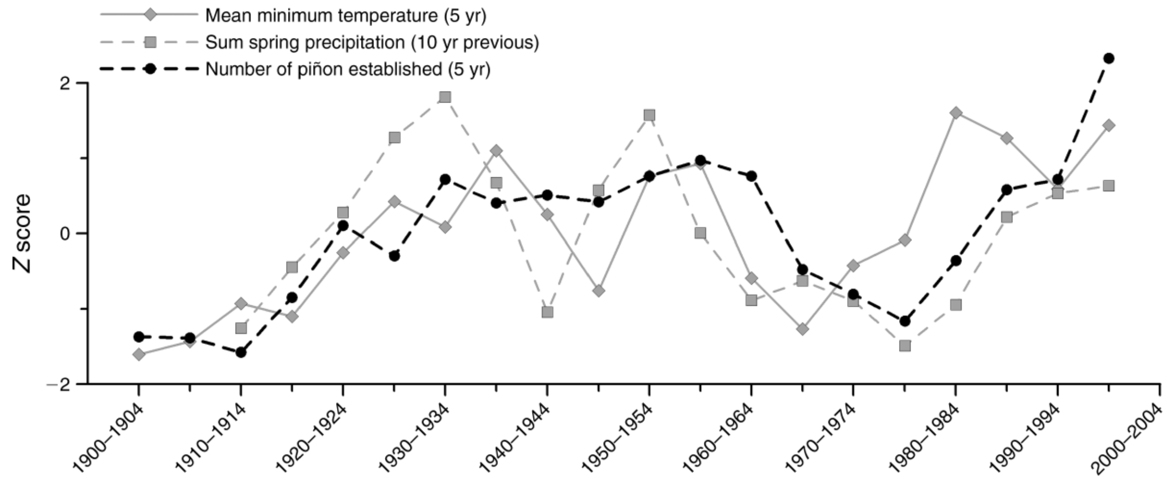

FIG. 5. Standardized scores for five-year piñon establishment totals, spring (March, April, May) precipitation total of the two previous five-year periods (i.e., 10 years total, adjusted temporally in graph to align with correlated piñon pulses), and mean minimum temperature for each five-year period. Winter (December, January, February) precipitation totals were significant only in the presence of the other two predictors in the final best subsets regression model and thus are not shown here. The analysis follows Soulé et al. (2004).

minimum annual temperatures. The juniper and piñon models are similar, in that greater establishment is predicted during periods with warmer and wetter winters, but in contrast to piñons, juniper establishment is predicted to decline when the establishment period and the previous 10-year period are wetter.

Seedlings–sapling density in grazed and ungrazed areas

The null hypothesis of no difference in mean seedling–sapling density between livestock-grazed (outside reference areas) plots and ungrazed (inside reference areas) plots can be rejected for pooled piñon and juniper (ungrazed = 262 trees/ha, grazed = 684 trees/ha, $t(43) = 2.39$; $P = 0.023$) and for piñon alone (ungrazed = 191 trees/ha, grazed = 579 trees/ha, $t(43) = 2.41$; $P = 0.022$), but not for juniper alone (ungrazed = 70 trees/ha, grazed = 105 trees/ha, $t(43) = 1.21$, $P = 0.234$).

Discussion

Variability in stand origins and age structures

With ~75% of the uncleared sampled stands reaching ages of >300 years old (Table 1), our data do not support models in which low-severity surface fire historically maintained savanna-like conditions and restricted old-growth woodlands to fire-safe sites (e.g., West 1999*b*, Miller and Tausch 2001). Old-growth woodlands on the Uncompahgre Plateau occur across all elevations, substrata, and topographic positions (Appendix A), and range from relatively open and juniper dominated at low elevations to closed canopied and piñon dominated at higher elevations (Table 1, Fig. 3, Appendix C), similar to patterns found elsewhere (Martens et al. 2001). The oldest woodlands (e.g., plots 58, 59) have juniper-dominated overstories and are associated with lower elevation (Table 2, Fig. 3).

Stand ages (Fig. 2, Table 1) are comparable to those found elsewhere on the Colorado Plateau. Floyd et al. (2004) estimated 75% of piñon–juniper stands on the Mesa Verde cuesta in Colorado were >400 years old before recent fires, and Floyd et al. (2008) determined that more than half a study area in southern Utah was 300–600 years old based on oldest piñon ages. Eisenhart (2004) found ~57% of stands on and near the Uncompahgre Plateau were ≥300 years old, with peak stand establishment 200–250 years ago, and numerous piñons >500 years old. Our peak establishment age of 400–600 years is substantially older, but Eisenhart dated only piñons and excluded some older trees in estimating stand age, reasoning they could be survivors from a previous stand. However, our age structures show that junipers tend to pre-date piñons by >100 years (Table 1), and no oldest tree in any plot was sufficiently discontinuous in age to likely be a remnant of a former stand (Table 1). Similarly, in a *Pinus edulis–Juniperus osteosperma* woodland on the Colorado Plateau in Arizona, the oldest junipers established in the early to late 1400s and the oldest piñons in the mid-1500s to mid-1700s (Landis and Bailey 2005).

Other studies, in contrast, found young stands dominate some elevation zones. In the Great Basin, Tausch et al. (1981) found ~30% of sampled *P. monophylla–J. osteosperma* woodland stands were >300 years old (estimated from their Appendix C), generally at midelevations, with much younger stands above and below, ostensibly from human land use. Other research focused specifically on tree invasion into nonwoodland ecosystems (e.g., Burkhardt and Tisdale 1976). We did not find an elevation zone entirely composed of young trees, and only two stands (plots 3, 10) of 59 were young enough (<150 years old), had no fire evidence or large dead trees, and were adjacent to openings, to possibly represent invasion caused by Euro–American land use.

Nevertheless, nearly half of the trees in main untreated plots, mostly piñons, originated after Euro–American settlement. Moreover, in several stands near or <2000 m elevation, there is a young piñon component within older juniper stands that completely or nearly lack large dead or older piñons (e.g., plots 18, 20, 36, 40, 45, 58 in Table 1 and age structures in Appendix C). This suggests piñons only recently prospered at low elevations, were only present in the distant past, or were previously culled as young cohorts by frequent disturbance.

Role of fire in woodland dynamics

We found no fire-scar evidence for low-severity surface fires, suggesting they were rare or lacking in these woodlands, as elsewhere in piñon–juniper (Baker and Shinneman 2004, Romme et al. 2008). Nearby, Floyd et al. (2000, 2004) discovered no fire scars in Mesa Verde, and Eisenhart (2004) also found no scars and suggested that accumulation of abundant deadwood in advanced stages of decay and numerous old snags were unlikely under a surface-fire regime. In contrast, evidence for high-severity fires was not uncommon and occurred across a wide elevation range, although 67% of stands with fire evidence occurred above 2000 m (Table 1). Similarly, Eisenhart (2004) found direct evidence of stand-replacing fire in 38% of piñon–juniper stands in and around the Uncompahgre Plateau, mostly at high elevations. Higher elevations coincide with conditions conducive to fire, including greater canopy continuity and increased lightning (Eisenhart 2004), which could maintain generally younger stand ages (Fig. 3b).

Floyd et al. (2000, 2004) used direct evidence of large stand-replacing fires that burned 41% of the area of Mesa Verde National Park in 1700–1900 to estimate a high-severity fire rotation of ~400 years. Our estimate is longer (400–600+ years), perhaps because our study area, about 150 km north of theirs, includes more elevational range. In fact, Floyd et al. (2004) suggested longer rotations for the entire Mesa Verde cuesta, which includes more low-elevation and drier sites with fewer documented fires. Old, low-elevation, open-canopied, juniper-dominated stands on the Uncompahgre Plateau may have rarely experienced fire, and may persist in quasi-steady states, influenced by drought-induced, selective mortality and slow tree regeneration (Floyd et al. 2004). Some higher-elevation, piñon-dominated stands also lacked fire evidence and were possibly initiated by other disturbances, shifting ecotones, or severe fires during extended drought that greatly protracted successional recovery to woodlands and left little fire evidence. Evidence of past stand-initiating fire can be difficult to detect in older stands, as postfire seral stages recede, burned wood becomes highly weathered or decomposed, and charcoal remnants break down in the topsoil.

Climate forcing of population age structures

Our results indicate piñon age structure corresponds to alternating periods of above-average moisture and drought that, in turn, are influenced by Atlantic and Pacific sea surface temperatures (SSTs). Although somewhat out of synch with the generally low Palmer Drought Severity Index (PDSI) values toward the end of the extended dry period, the population-wide increase in piñons beginning about AD 1800 coincides with the most substantial and extended decrease in Atlantic Multidecadal Oscillation (AMO) (Gray et al. 2004) and simultaneous increase in Pacific Decadal Oscillation (PDO) values over the period of record (Fig. 4). All three piñon pulses after AD 1800 also coincided with periods of simultaneous negative AMO (after a 10-year lag) and positive PDO, a combination linked to extended periods of above-average moisture in the Southwest (McCabe 2004). An inverse relationship is suggested for juniper age structures and climate patterns. Most notably, there is consistent correspondence between slight to modest juniper increases and positive (warm) AMO (after a 10-year lag), and three of these periods also coincide with negative (cool) PDO. Five of six of these juniper increases occurred during severe droughts indicated by the PDSI, including the extended dry period of the AD 1620s–1820s (Fig. 4).

Given the coarseness of older (>300 years) juniper tree ages, vs. more accurately dated younger piñons, we present the contrasting relationships between the two species and broad-scale climate patterns as an exploration of a working hypothesis. However, this hypothesis is supported by our understanding of the relationship between anomalous periods of moisture availability and multidecadal patterns in SSTs (McCabe and Dettinger 1999), our understanding of contrasting responses between piñons and junipers to moisture availability and drought-induced disturbance, and our subsequent analysis of 20th-century establishment patterns and climate. We discuss these issues in support of our hypothesis.

McCabe et al. (2004) demonstrated that broad-scale droughts in the United States were associated with a positive (warm) AMO and a negative (cool) PDO. A positive AMO is particularly associated with drought in the midwestern and northwestern United States, extending southward to most of Colorado (McCabe et al. 2004). Moreover, co-occurrence of positive AMO and negative PDO may prolong severe drought conditions in the southwestern United States, in part by enhancing El Niño Southern Oscillation (ENSO) events (McCabe et al. 2004) which, in the La Niña phase, can cause severe drought in the Southwest (Swetnam and Betancourt 1990). Atlantic SSTs, relative to other SSTs, also had the most effect on water flow of the Upper Colorado River Basin (McCabe et al. 2007), within which our study area lies, and a positive AMO is correlated with above-average temperatures in North America (Sutton and Hodson 2005).

The relatively low density of piñons during most of the AD 1620s to 1820s dry period (Fig. 4) suggests that piñons were not producing seed, not successfully germinating, or not surviving to maturity, and likely were disproportionately affected by direct drought mortality. Severe water stress can lead to xylem cavitation and eventual death in both piñons and junipers (Linton et al. 1998), but dense stands of piñons, having shallow roots, are particularly vulnerable to drought compared to deep-rooted junipers, which can acquire deeper soil moisture (Foxx and Tierney 1987, Williams and Ehleringer 2000). Moreover, the seasonality of moisture availability affects the growth and persistence of the two species differently, as two-needle piñon is adapted to maximally utilize moisture during periodic, summer-monsoonal rainfall, especially following wet winters, but is highly vulnerable to summer drought; Utah juniper maximally utilizes moisture during both wet winters and summer drought conditions, allowing it to more readily survive droughts than do piñons (West et al. 2008). Drought tolerance may be lowest for sensitive young and less-vigorous mature piñon trees (Ogle et al. 2000, Martens et al. 2001).

Severe and prolonged drought can also cause extensive mortality from subsequent fire or insect outbreaks in these woodland systems (Betancourt et al. 1993, Swetnam and Betancourt 1998, Nabhan et al. 2004), especially within denser, piñon-dominated stands (Breshears et al. 2005, Mueller et al. 2005, Shaw et al. 2005). In the Southwest, lack of piñons and junipers >400 years old has been attributed to extensive mortality from a sustained, severe "megadrought" in the late 1500s (Swetnam and Betancourt 1998), also evident in the PDSI record for southwestern Colorado (Fig. 4) and other regional proxy climate data (Gray et al. 2003, Piechota et al. 2004). However, the megadrought of the late 1500s and the subsequent prolonged dry period probably had patchy and selective effects across the Uncompahgre Plateau. Similar to elsewhere on the Colorado Plateau (Betancourt et al. 1993), our study area contains many piñons and junipers >400 years old (Table 1). Extreme SST phase combinations that provide above-average moisture, similar to the wet conditions in the mid-to late 1800s after the extended dry period (Fig. 4), likely reduce drought-related disturbance, such as fire (e.g., Sibold and Veblen 2006).

Relative moisture availability was not only likely responsible for differential rates and patterns of mortality between the two species, but also for differential rates of regeneration. Analysis of 20th-century tree regeneration indicates that five-year piñon establishment totals increased with less-cold, wet winters following 10 years of wet springs, while juniper establishment totals increased after warmer, wetter winters, but decreased when there were antecedent wet periods (Table 3, Fig. 5). Wet winters and mild temperatures may be crucial to germination of short-lived (<2 years) piñon seeds and provide optimal conditions for seedling growth, although mechanisms for successful piñon germination are poorly understood (Gottfried et al. 1995). Similar relationships with winter climate may also exist for junipers (Chambers et al. 1999, West et al. 2008), but increases in disturbed and relatively open conditions would have favored juniper seedling survival and development, given its greater drought tolerance and ability to obtain water in open interspace environments, while discouraging piñon seedlings more dependent on shade and nurse plants (Meagher 1943, Miller et al. 1992, Chambers et al. 1999, Nowak et al. 1999). The unique relationship between establishment and antecedent wet/dry periods for each species may also be related to the apparent 10-year lag in population responses to extreme AMO values (Fig. 4). Specifically, the noticeable lag in juniper increases after warmer or drier (positive-AMO) periods might represent extensive piñon mortality that eventually created open environments favoring regeneration of junipers over piñons.

Euro–American influence on stand age structures and woodland dynamics

In the Great Basin, livestock reduction of fine fuels that once supported frequent surface fires was thought to explain woodland expansion into sagebrush after Euro–American settlement (e.g., Miller and Rose 1995). However, recent research has shown that fires were not historically frequent in sagebrush (Baker 2006), so this mechanism could not explain tree invasions. Reduction in surface fire by livestock grazing also could not explain tree density increases in piñon–juniper in our study area, as these woodlands lacked surface fires.

Livestock reduction of grasses and forbs (Shinneman et al. 2008), and the competition they provide to tree seedlings more likely explain increased small piñons in grazed areas. Our comparison data suggest livestock grazing roughly triples seedling–sapling density, almost entirely through greater piñon establishment. Juniper seedlings better tolerate competition from grasses than do piñons, so reduction in grass by livestock grazing may especially favor piñons (Chambers et al. 1999). Piñon regeneration may also have been aided by favorable moisture in the early 1900s and the 1980s to mid-1990s (Fig. 4). Thus peak levels of livestock grazing after settlement likely increased seedling–sapling survivorship (Nabhan et al. 2004). Grazing may also be partly responsible for tree invasion, albeit quite limited, into adjacent nonwoodland communities (Appendix C, plots 3, 10), and possibly for some invasion of piñons into older juniper stands (e.g., plot 18). Increased atmospheric CO_2 concentrations could also be affecting stand structures through enhanced tree growth and increased seedling survival (Knapp et al. 2001, Soulé et al. 2004), yet this is not apparent in the juniper population (Fig. 4).

Summary and implications for restoration

Although highly variable (Table 2, Appendix C), piñon–juniper woodland stand age structures on the Uncompahgre Plateau appear strongly influenced by broad-scale, multidecadal climate patterns forced by Atlantic and Pacific sea surface temperatures that foster periods of severe, prolonged drought and above-average moisture (Fig. 4). The striking absence of piñon age classes in many stands during the extended dry period from the AD 1620s to 1820s strongly suggests drought can cause substantial changes in stand age structures. These changes likely accrue from lack of tree regeneration, direct mortality of drought-sensitive piñons, and drought-induced disturbances (e.g., piñon needle scale, piñon ips beetle), as was found with southwestern piñon ips beetle (*Ips confusus*) outbreaks during AD 2003–2005 (Mueller et al. 2005). In contrast, the juniper population increased slightly during dry periods, but generally maintained a relatively steady density over the 500-year record, despite fluctuating climate (Fig. 4). This stability implies a relative balance between juniper regeneration and mortality at the landscape scale that stems from longevity, resistance to drought-induced mortality (Mueller et al. 2005, West et al. 2008), an ability to more quickly establish after fire (Tausch and West 1988), and temporally asynchronous production of long-lived seeds (Chambers et al. 1999). These characteristics are congruent with the northward migration of junipers during dry, warm periods of the late Holocene (Lyford et al. 2003) and piñon migration into the far northern Colorado Plateau during periods of above-average moisture (Gray et al. 2006).

Correspondence with climate indices investigated here (Palmer Drought Severity Index, Atlantic Multidecadal Oscillation, Pacific Decadal Oscillation) suggests that the two centuries of piñon population increase that began around AD 1800 represent a release or recovery from previously constraining drought-induced conditions. The increase in piñons, often within woodlands containing older junipers, was aided by periods of above-average moisture. The timing of this population trend is similar in other research in western Colorado (Eisenhart 2004, Floyd et al. 2004) and in *Pinus edulis–Juniperus monosperma* woodlands in eastern Colorado (Tonnesen and Ebersole 1997).

After Euro–American settlement, livestock grazing and possibly also increased atmospheric CO_2 (Soulé et al. 2004) likely added to expanding tree densities and may have caused limited invasions into adjacent sagebrush and grasslands. However, fire exclusion likely did not affect woodland structures, given the short duration of effective fire exclusion, historically long fire rotation, and lack of low-severity surface fires, as observed elsewhere (Floyd et al. 2004). Moreover, if our sampled reference areas indicate pre-Euro–American conditions, abundant seedling–sapling establishment (>250 trees/ha) may have been common before livestock grazing.

Ecological restoration should reflect broad-scale variability in stand conditions and be based on the century-scale variability in disturbance dynamics and climate that we have shown, especially given predicted climate change (e.g., Seager et al. 2007). Since fire exclusion did not contribute to increased piñons in old woodlands, prescribed, low-severity surface fires will not aid restoration. Ecological restoration might appropriately include reducing livestock grazing levels and restoring understory grasses and forbs, before selectively thinning a fraction (up to two-thirds) of small-diameter piñons in dense stands (rather than indiscriminate clearing). However, thinning may be ill-advised in many areas, because piñon densities are already being reduced by drought, insects, and disease, perhaps as in the 17th–18th centuries. If sufficient moisture returns, a multi-century piñon recovery may once again follow, while under a drought-filled future-climate scenario predicted for the interior West of the United States (McCabe et al. 2004, Seager et al. 2007), juniper-dominated woodlands may prevail (West et al. 2008). Since tree populations have long been in flux and may change further, a more sensible focus is to reduce livestock grazing to facilitate restoring woodland understory grasses and forbs.

Acknowledgments

This study was supported by the U.S. Department of Interior, Bureau of Land Management, under Agreement No. ESA020016. We appreciate the assistance of Bob Welch and Amanda Clements at the Uncompahgre Field Office and Harley Metz with the Grand Junction Field Office. We also acknowledge support provided by the USDA Forest Service Northern Research Station, Grand Rapids, Minnesota, USA.

Literature Cited

Alftine, K. J., G. P. Malanson, and D. B. Fagre. 2003. Feedback-driven response to multidecadal climatic variability at an alpine treeline. Physical Geography 24:520–535.

Baker, W. L. 2006. Fire and restoration of sagebrush ecosystems. Wildlife Society Bulletin 34:177–185.

Baker, W. L. *In press*. Fire ecology in Rocky Mountain landscapes. Island Press, Washington, D.C., USA.

Baker, W. L., and D. J. Shinneman. 2004. Fire and restoration of piñon–juniper woodlands in the western United States: a review. Forest Ecology and Management 189:1–21.

Betancourt, J. L., E. A. Pierson, K. A. Rylander, J. A. Fairchild-Parks, and J. S. Dean. 1993. Influence of history and climate on New Mexico piñon–juniper woodlands. Pages 42–62 *in* E. F. Aldon and D. W. Shaw, editors. Managing piñon–juniper ecosystems for sustainability and social needs. USDA Forest Service General Technical Report RM-236. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.

Breshears, D. D., et al. 2005. Regional vegetation die-off in response to global-change-type drought. Proceedings of the National Academy of Sciences (USA) 102:15144–15148.

Brockway, D. G., R. G. Gatewood, and R. B. Paris. 2002. Restoring grassland savannas from degraded pinyon–juniper woodlands: effects of mechanical overstory reduction and slash treatment alternatives. Journal of Environmental Management 64:179–197.

Burkhardt, J. W., and E. W. Tisdale. 1976. Causes of juniper invasion in southwestern Idaho. Ecology 57:472–484.

Burwell, T. 1998. Successional patterns of the lower montane treeline, eastern California. Madroño 45:12–16.

Cassells, E. S. 1997. The archaeology of Colorado. Johnson Books, Boulder, Colorado, USA.

Chambers, J. C., S. B. Vander Wall, and E. W. Schupp. 1999. Seed and seedling ecology of piñon and juniper species in the pygmy woodlands of western North America. The Botanical Review 65:1–38.

Cook, E. R., C. A. Woodhouse, C. M. Eakin, D. M. Meko, and D. W. Stahl. 2004. Long-term aridity changes in the western United States. Science 306:1015–1018.

Davenport, D. W., D. D. Breshears, B. P. Wilcox, and C. D. Allen. 1998. Viewpoint: Sustainability of piñon–juniper ecosystems: a unifying perspective of soil erosion thresholds. Journal of Range Management 51:231–240.

Eisenhart, K. S. 2004. Historic range of variability and stand development in piñon–juniper woodlands of western Colorado. Dissertation. University of Colorado, Boulder, Colorado, USA.

Erdman, J. A. 1970. Pinyon–juniper succession after natural fires on residual soils of Mesa Verde, Colorado. Brigham Young University Science Bulletin Biological Series XI:1–26.

Floyd, M. L., D. D. Hanna, and W. H. Romme. 2004. Historical and recent fire regimes in piñon–juniper woodlands on Mesa Verde, Colorado, USA. Forest Ecology and Management 198:269–289.

Floyd, M. L., W. H. Romme, and D. D. Hanna. 2000. Fire history and vegetation pattern in Mesa Verde National Park, Colorado, USA. Ecological Applications 10:1666–1680.

Floyd, M. L., W. H. Romme, D. D. Hanna, M. Winterowd, D. Hannah, and J. Spence. 2008. Fire history of piñon–juniper woodlands on Navajo Point, Glen Canyon National Recreation Area. Natural Areas Journal 28:26–36.

Foxx, T. S., and G. D. Tierney. 1987. Root patterns in the pinyon–juniper woodland. Pages 69–79 *in* R. L. Everett, editor. Proceedings: Pinyon–juniper conference (Reno, Nevada, USA, January 13–16, 1986). USDA Forest Service General Technical Report INT-215. Intermountain Research Station, Ogden, Utah, USA.

Gordon, B. R., G. P. Parrott, and J. B. Smith. 1992. Vegetation changes in northern Arizona: the Alexander Gardner photos. Rangelands 14:308–320.

Gottfried, G. J., T. W. Swetnam, C. D. Allen, J. L. Betancourt, and A. L. Chung-Maccoubrey. 1995. Pinyon–juniper woodlands. Pages 95–132 *in* D. M. Finch and J. A. Tainter, editors. Ecology, diversity, and sustainability of the Middle Rio Grande Basin. USDA Forest Service General Technical Report RM-268. Rocky Mountain Research Station, Fort Collins, Colorado, USA.

Gray, S. T., J. L. Betancourt, C. L. Fastie, and S. T. Jackson. 2003. Patterns and sources of multidecadal oscillations in drought-sensitive tree ring records from the central and southern Rocky Mountains. Geophysical Research Letters 30:491–494.

Gray, S. T., J. L. Betancourt, S. T. Jackson, and R. G. Eddy. 2006. Role of multidecadal climate variability in a range extension of pinyon pine. Ecology 87:1124–1130.

Gray, S. T., L. J. Graumlich, J. L. Betancourt, and G. T. Pederson. 2004. A tree ring based reconstruction of the Atlantic Multidecadal Oscillation since 1567 A.D. Geophysical Research Letters 31:LL12205.

Grissino-Mayer, H. D., and T. W. Swetnam. 2000. Century-scale climate forcing of fire regimes in the American Southwest. Holocene 10:213–220.

Harlan, T. P. 1978. International Tree Ring Data Bank: Dolores, USA, 37N,108W. ⟨http://hurricane.ncdc.noaa.gov/pls/paleo/fm_createpages.treering⟩

Johnson, A. R., B. T. Milne, and P. Hraber. 1999. Analysis of change in pinyon–juniper woodlands based on aerial photography, 1930s–1980s. Pages 106–111 *in* D. M. Finch, J. C. Whitney, J. F. Kelly, and S. R. Loftin, editors. Rio Grande ecosystems: linking land, water, and people: toward a sustainable future for the middle Rio Grande Basin. USDA Forest Service Proceedings RMRS-P-7. Rocky Mountain Research Station, Fort Collins, Colorado, USA.

Knapp, P. A., P. T. Soule, and H. Grissino-Mayer. 2001. Detecting potential regional effects of increased atmospheric CO_2 on growth rates of western juniper. Global Change Biology 7:903–917.

Landis, A. G., and J. D. Bailey. 2005. Reconstruction of age structure and spatial arrangement of piñon–juniper woodlands and savannas of Anderson Mesa, northern Arizona. Forest Ecology and Management 204:221–236.

Linton, M. J., J. S. Sperry, and D. G. Williams. 1998. Limits to water transport in *Juniperus osteosperma* and *Pinus edulis*: implications for drought tolerance and regulation of transpiration. Functional Ecology 12:906–911.

Lyford, M. E., S. T. Jackson, J. L. Betancourt, and S. T. Gray. 2003. Influence of landscape structure and climate variability on a late Holocene plant migration. Ecological Monographs 73:567–583.

MacDonald, G. M., and R. A. Case. 2005. Variations in the Pacific Decadal Oscillation over the past millennium. Geophysical Research Letters 32:L08703.

Martens, S. N., D. D. Breshears, and F. J. Barnes. 2001. Development of species dominance along an elevational gradient: population dynamics of *Pinus edulis* and *Juniperus monosperma*. International Journal of Plant Science 162:777–783.

McCabe, G. J., J. L. Betancourt, and H. G. Hidalgo. 2007. Associations of decadal to multidecadal sea-surface temperature variability with Upper Colorado River flow. Journal of the American Water Resources Association 43:183–192.

McCabe, G. J., and M. D. Dettinger. 1999. Decadal variations in the strength of ENSO teleconnections with precipitation in the western United States. International Journal of Climatology 19:1399–1410.

McCabe, G. J., M. A. Palecki, and J. L. Betancourt. 2004. Pacific and Atlantic Ocean influences on multidecadal drought frequency in the United States. Proceedings of the National Academy of Sciences (USA) 101:4136–4141.

Meagher, G. 1943. Reaction of pinyon and juniper seedlings to artificial shade and supplemental watering. Journal of Forestry 41:480–482.

Miller, R. F., L. E. Eddleman, and J. M. Miller. 1992. The seasonal course of physiological processes in *Juniperus occidentalis*. Forest Ecology and Management 48:185–212.

Miller, R. F., and J. A. Rose. 1995. Historic expansion of *Juniperus occidentalis* (western juniper) in southeastern Oregon. Great Basin Naturalist 55:37–45.

Miller, R. F., and J. A. Rose. 1999. Fire history and western juniper encroachment in sagebrush steppe. Journal of Range Management 52:550–559.

Miller, R. F., and R. J. Tausch. 2001. The role of fire in juniper and pinyon woodlands: a descriptive analysis. Pages 15–30 *in* K. E. M. Galley and T. P. Wilson, editors. Proceedings of the invasive species workshop: the role of fire in the control and spread of invasive species. Tall Timbers Research Station Miscellaneous Publication No. 11, Tallahassee, Florida, USA.

Miller, R. F., and P. E. Wigand. 1994. Holocene changes in semiarid pinyon–juniper woodlands. BioScience 44:465–474.

Mueller, R. C., C. M. Scudder, M. E. Porter, R. T. I. Trotter, C. A. Gehring, and T. G. Whitham. 2005. Differential tree mortality in response to severe drought: evidence for long-term vegetation shifts. Journal of Ecology 93:1085–1093.

Nabhan, G. P., M. Coder, and S. J. Smith. 2004. Woodlands in crisis: a legacy of lost biodiversity on the Colorado Plateau. Bilby Research Center Occasional Papers No. 2. Ralph M. Bilby Research Center, Northern Arizona University, Flagstaff, Arizona, USA.

Norton, D. A., J. G. Palmer, and J. Ogden. 1987. Dendroecological studies in New Zealand 1: An evaluation of tree age estimates based on increment cores. New Zealand Journal of Botany 25:373–383.

Nowak, R. S., D. J. Moore, and R. J. Tausch. 1999. Ecophysiological patterns of pinyon and juniper. Pages 35–46 *in* S. B. Monsen and R. Stevens, editors. Ecology and management of pinyon–juniper communities within the interior West. USDA Forest Service Proceedings RMRS-P-9, Rocky Mountain Research Station, Fort Collins, Colorado, USA.

Ogle, K., T. G. Whitham, and N. S. Cobb. 2000. Tree ring variation in pinyon predicts likelihood of death following severe drought. Ecology 81:3237–3243.

Piechota, T., J. Timilsena, G. Tootle, and H. Hidalgo. 2004. The western U.S. drought: How bad is it? EOS 85:301–308.

Romme, W. H. 1980. Fire history terminology: report of the ad hoc committee. Pages 135–140 *in* M. A. Stokes and J. H. Dieterich, editors. Proceedings of the fire history workshop. USDA Forest Service General Technical Report RM-81, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.

Romme, W., et al. 2008. Historical and modern disturbance regimes, stand structures, and landscape dynamics of piñon–juniper vegetation in the western U.S. Colorado Forest Restoration Institute, Fort Collins, Colorado, USA.

Romme, W. H., L. Floyd-Hanna, and D. D. Hanna. 2003. Ancient piñon–juniper forests of Mesa Verde and the West: a cautionary note for forest restoration programs. Pages 335–350 *in* P. N. Omi and L. A. Joyce, editors. Fire, fuel treatments, and ecological restoration.USDA Forest Service Proceedings RMRS-P-29 (Fort Collins, Colorado, April 16–18, 2002). Rocky Mountain Research Station, Fort Collins, Colorado, USA.

Scott, R. B., A. E. Harding, W. C. Hood, R. D. Cole, R. F. Livaccari, J. B. Johnson, R. R. Shroba, and R. P. Dickerson. 2001. Geologic map of Colorado National Monument and adjacent areas, Mesa County, Colorado. U.S. Geological Survey Geologic Investigations Series I-2740, U.S. Geological Survey, Denver, Colorado, USA.

Seager, R., et al. 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. Science 316:1181–1184.

Shaw, J. D., B. E. Steed, and L. T. DeBlander. 2005. Forest inventory and analysis (FIA) annual inventory answers the question: What is happening to pinyon–juniper woodlands? Journal of Forestry 103:280–285.

Shinneman, D. J., W. L. Baker, and P. Lyon. 2008. Ecological restoration needs derived from reference conditions for a semiarid landscape in Western Colorado, USA. Journal of Arid Environments 72:207–227.

Sibold, J. S., and T. T. Veblen. 2006. Relationships of subalpine forest fires in the Colorado Front Range with interannual and multidecadal-scale variation. Journal of Biogeography 33:833–842.

Simmons, V. M. 2000. The Ute Indians of Utah, Colorado, and New Mexico. University Press of Colorado, Boulder, Colorado, USA.

Soulé, P. T., P. A. Knapp, and H. D. Grissino-Mayer. 2004. Human agency, environmental drivers, and western juniper establishment during the late Holocene. Ecological Applications 14:96–112.

Stokes, M. A., and T. L. Smiley. 1968. An introduction to tree-ring dating. University of Chicago Press, Chicago, Illinois, USA.

Sutton, R. T., and D. L. R. Hodson. 2005. Atlantic Ocean forcing of North American and European summer climate. Science 309:115–118.

Swetnam, T. W., C. D. Allen, and J. L. Betancourt. 1999. Applied historical ecology: using the past to manage for the future. Ecological Applications 9:1189–1206.

Swetnam, T. W., and J. L. Betancourt. 1990. Fire–Southern Oscillation relations in the southwestern United States. Science 249:1017–1020.

Swetnam, T. W., and J. L. Betancourt. 1998. Mesoscale disturbance and ecological response to decadal climatic variability in the American Southwest. Journal of Climate 11:3128–3147.

Tausch, R. J. 1999. Historic pinyon and juniper woodland development. Pages 12–19 *in* S. B. Monsen and R. Stevens, editors. Ecology and management of pinyon–juniper communities within the interior West. USDA Forest Service Proceedings RMRS-P-9, Rocky Mountain Research Station, Fort Collins, Colorado, USA.

Tausch, R. J., and N. E. West. 1988. Differential establishment of pinyon and juniper following fire. American Midland Naturalist 119:174–184.

Tausch, R. J., N. E. West, and A. A. Nabi. 1981. Tree age and dominance patterns in Great Basin pinyon–juniper woodlands. Journal of Range Management 34:259–264.

Tonnesen, A. S., and J. J. Ebersole. 1997. Human trampling effects on regeneration and age structures of *Pinus edulis* and *Juniperus monosperma*. Great Basin Naturalist 57:50–56.

USDA Natural Resource Conservation Service. 1995. Soil survey of Uncompahgre National Forest area, Colorado: parts of Mesa, Montrose, and San Miguel Counties. USDA Forest Service and Soil Conservation Service. ⟨http://soils.usda.gov/survey/online_surveys/colorado/⟩

West, A. G., K. R. Hultine, J. S. Sperry, S. E. Bush, and J. R. Ehleringer. 2008. Transpiration and hydraulic strategies in a piñon–juniper woodland. Ecological Applications 18:911–927.

West, N. E. 1999*a*. Distribution, composition, and classification of current juniper–pinyon woodlands and savannas across western North America. Pages 20–23 *in* S. B. Monsen and R. Stevens, editors. Ecology and management of pinyon–juniper communities within the interior West. USDA Forest Service Proceedings RMRS-P-9, Rocky Mountain Research Station, Fort Collins, Colorado, USA.

West, N. E. 1999*b*. Juniper–piñon savannas and woodlands of western North America. Pages 288–308 *in* R. C. Anderson, J. S. Fralish, and J. M. Baskin, editors. Savannas, barrens and rock outcrop plant communities of North America. Cambridge University Press, New York, New York, USA.

Williams, C. N., Jr., R. S. Vose, D. R. Easterling, and M. J. Menne. 2004. United States historical climatology network daily temperature, precipitation, and snow data. ORNL/CDIAC-118, NDP-070. ⟨http://cdiac.ornl.gov/ftp/ndp070/ndp070.txt⟩

Williams, D. G., and J. R. Ehleringer. 2000. Intra- and interspecific variation for summer precipitation use in pinyon–juniper woodlands. Ecological Monographs 70:517–537.

APPENDIX A

The environmental settings of the 59 plots on the Uncompahgre Plateau in western Colorado (*Ecological Archives* A019-047-A1).

APPENDIX B

The relationship between tree size class and age (years) (*Ecological Archives* A019-047-A2).

APPENDIX C

Age-structure graphs for all 28 main, untreated (not mechanically cleared) woodland plots (*Ecological Archives* A019-047-A3).