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Research Article

Arizona pine (*Pinus arizonica*) stand dynamics: local and regional factors in a fire-prone madrean gallery forest of Southeast Arizona, USA

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Abstract

In southwestern North America, large-scale climate patterns appear to exert control on moisture availability, fire occurrence, and tree demography, raising the compelling possibility of regional synchronization of forest dynamics. Such regional signals may be obscured, however, by local, site-specific factors, such as disturbance history and land use. Contiguous sites with similar physical environments, lower and middle Rhyolite Canyon, Arizona, USA, shared nearly the same fire history from 1660-1801, but then diverged. For the next 50 years, fires continued to occur frequently in lower Rhyolite, but, probably as result of flood-induced debris deposition, largely ceased in middle Rhyolite. We related stand dynamics of Arizona pine (*Pinus arizonica*) to fire history and drought severity and compared the dynamics in the two sites before and after the divergence in fire frequency. Fires occurred during unusually dry years, and possibly following unusually moist years. Arizona pine exhibited three age structure peaks: two (1810–1830 and 1870–1900) shared by the two sites and one (1610–1640) only in middle Rhyolite. The latter two peaks occurred during periods of unusually low fire frequency, suggesting that fire-induced mortality shapes age structure. Evidence was mixed for the role of favorable moisture availability in age structure. As expected, moisture availability had a prominent positive effect on radial growth, but the effect of fire was largely neutral. The two sites differed only moderately in stand dynamics during the period of divergence, exhibiting subtle age structure contrasts and, in middle Rhyolite only, reduced growth during a 50-year fire hiatus followed by fire-induced release. These results suggest that, despite local differences in disturbance history, forest responses to regional fire and climate processes can persist.

Introduction

Recent studies have demonstrated the powerful influence of regional scale climate patterns on forests (e.g., Neilson 1986; Johnson and Wowchuck 1993; Condit et al. 1995; Szeicz and MacDonald 1995; Kitzberger et al. 1997; Villalba and Veblen 1997a, 1998; Swetnam and Betancourt 1998; Veblen et al. 1999; Wright et al. 1999). For example, in southwestern North America, interannual variation in moisture availability has been shown to synchronize regional fire occurrence (Swetnam and Betancourt 1990; Swetnam 1993; Fulé and Covington 1996; Villanueva-Díaz and McPherson 1996; Grissino-Mayer and Swetnam 2000). Wet winters, often resulting from El Niño-Southern Oscillation (ENSO) events, followed by dry years appear to create conditions of sufficient fine fuel load and combustibility to foster regionally-synchronized years of major fires. Studies in other regions are also beginning to uncover similar relationships between fire, regional climate, and ENSO-related synoptic air mass dynamics (e.g., Johnson and Wowchuck 1993; Kitzberger et al. 1997; Veblen et al. 1999).

Interannual and decadal-scale variation in regional climate can also exert potent control over forests through direct effects on tree populations by controlling moisture availability and the levels of conditions such as temperature. The dependence of radial growth on variation in these factors has long been known (e.g., Glock 1955; Fritts 1976). Recent work has also revealed striking connections between synoptically-driven climate variation and regional episodes of mortality and recruitment in the Southwest (e.g., Neilson 1986; Betancourt et al. 1993; Savage et al. 1996; Swetnam and Betancourt 1998) and elsewhere (Condit et al. 1995; Villalba and Veblen 1997a, b, 1998; Allen and Breshears 1998).

These recent discoveries suggest the compelling possibility that forest dynamics may be highly synchronized at a regional scale. The degree of such synchrony has fundamental implications for forest structure, function, and equilibrium, as well as for forest management (see Allen and Breshears 1998; Swetnam and Betancourt 1998; Swetnam et al. 1999). High levels of synchrony in the Southwest would imply, for example, that the shifting mosaic model of landscape equilibrium is invalid for forests in that region (Turner et al. 1993). An evaluation of the synchronizing effects of regional climate on forests requires an assessment of the degree to which local responses of plant populations are driven by these large-scale controls versus local factors specific to the site. Although the potential role of regional, synchronizing climate and associated fire patterns is compelling, local differences between sites in natural disturbance history, human land use, and other factors could obscure or modify community responses to regionally-synchronized fire and climate patterns.

The last two decades have seen a flurry of research on fire history in the U.S. Southwest border region, producing one of the most complete regional records of fire history in the world (Baisan and Swetnam 1990; Fulé and Covington 1994, 1996; Swetnam and Baisan 1996; Swetnam et al. 2001). This record typically reveals frequent, moderate-intensity, highly-synchronized fires occurring until the late 19th century, when intensive livestock grazing and then active fire suppression began (e.g., Swetnam and Baisan 1990; Bahre 1991; Swetnam and Basin 1996; Swetnam et al. 2001). Many of the tree species in this border region are distributed primarily in the Sierra Madre Occidental of Mexico, occurring in the United States only in the southern parts of Texas, New Mexico, and Arizona (Perry 1991). Despite the extensive fire history record that has been developed, other aspects of fire ecology research on these Madrean tree species lag far behind that for other common southwestern species, such as ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) (but see Barton 1993, 1999; Fulé and Covington 1994, 1996, 1998; Villanueva-Díaz and McPherson 1995, 1996).

The fire history of Rhyolite Canyon, in the Chiricahua Mountains of southeastern Arizona, USA, is known in great detail (Swetnam et al. 1989, 1992, 2001; Swetnam and Baisan 1996; 'Fire History' section below), and provides an excellent opportunity for examination of the role of fire in Madrean tree dynamics (see Barton 1995, 1999). Until the 20th century, fires occurred frequently and most fires probably burned throughout the length of the canyon, as indicated by highly synchronous dates recorded on widely distributed fire scarred trees (see 'Fire history' section below; Figures 1 and 2). During the first half of the 19th century, however, fires ceased in the middle canyon, but continued to occur in the lower canyon (Figure 2A). This natural experiment provides a unique opportunity to investigate the effects of differences in fire history between two areas that are otherwise nearly identical in terms of physiography and microclimate. Hargrove and Pickering (1992) argue that, because true landscape-level experiments are often not possible, such 'quasi-experiments' can be productive, even if they fall short of being as fully controlled and replicated as field experiments. This is especially true in studies of long-term dynamics, such as the case described here, in which data are available for before, during, and after 'treatments' occurring over time periods of decades and centuries.

We investigated patterns of age structure and radial growth over a three century-period in Arizona pine (*Pinus arizonica*; sensu Bailey and Hawksworth 1983) in a gallery forest in lower and middle Rhyolite Canyon. If these patterns were molded by local differences in fire regime rather than by regional fires, we would expect to find differences in the timing of recruitment pulses and subsequent survival between the two sites during the fire-free period in middle Rhyolite (1802–1850). Because fires can increase the availability of light, moisture, and nutrients, Arizona pine may exhibit increases in radial growth after fire; conversely, after long fire-free periods, trees might exhibit radial growth decreases from increased competition. Thus, if local differences in fire regime were important in population dynamics, then we would also expect tree growth rates to be relatively low in middle

Rhyolite during the fire-free period compared to lower Rhyolite, where fires continued to occur.

We assess relationships among four time series: Arizona pine age structure and radial growth and fire history and drought severity. A large body of literature has focused attention on fire and drought severity as the predominant factors controlling forest communities in the Southwest (Barton 1993, 1994, 1999; Covington and Moore 1994a, b; Fulé and Covington 1998; Swetnam and Betancourt 1998; Mast et al. 1998, 1999). Although many studies have addressed the singular effects of either of these factors on some aspect of population dynamics, very few have examined fire and drought severity simultaneously, especially on radial growth as well as recruitment and mortality (see Mutch 1994; Villalba and Veblen 1997a; Mast et al. 1998, 1999). As a result, ecologists continue to have only a rudimentary understanding of the independent and interacting effects of these two factors on the dynamics of tree populations.

Study area

This study was carried out in the Chiricahua Mountains, which are located in southeastern Arizona in Cochise County (31°52′ N, 109°15′ W), and are considered part of the Sierra Madre 'archipelago' (DeBano et al. 1995). The mountains extend southeast to northwest for about 80 km and rise from about 1100 to 3000 m altitude. A wide array of species and communities is supported, including from low to high elevations, desert scrub, desert grassland, open oak woodland, pine-oak woodland, pine-oak forest, canyon gallery forest (spanning the entire lower half of the gradient), pine forest, montane fir forest, and subalpine forest (Whittaker and Niering 1965; Niering and Lowe 1984; Barton 1994).

The study site was in Rhyolite Canyon (Figure 1), which drains westward into the Sulfur Springs Valley and is the largest canyon in Chiricahua National Monument. The stream channel, which runs intermittently, is well-developed and boulder-strewn for much of its length. Elevations in the canyon range from about 1640 to 2229 m. We worked in a gallery Arizona pine (*P. arizonica*) forest from about 1700–1900 m elevation in the canyon bottom and sideslopes, below (lower Rhyolite) and above (middle Rhyolite) the intersection with Sarah Deming Canyon. *P. arizonica* (Engelm. var *arizonica*; Bailey and Hawksworth 1983), which is distributed from southern Arizona and New Mexico to the Sierra Madre of Mexico, appears to be similar to *P. ponderosa* var. *scopulorum* (Southwestern ponderosa pine) in habit and ecology, and is often subordinated to subspecific status (*P. ponderosa* var. *arizonica* Shaw; e.g., Carter 1997).

The climate of the Chiricahua Mountains is semiarid, with two wet seasons, one between July and September, when more than 50% of total precipitation falls, and the second between December and March. A pronounced dry season usually occurs between the final winter storms in March or April and the onset of the rainy season in July (Sellers et al. 1985). In Rhyolite Canyon, January average minimum and maximum temperatures are −0.2 °C and 14.7 °C, respectively. For July, average minimum and maximum temperatures are 17.4 and 32.8 °C, respectively.

Fire history

The fire history of Rhyolite Canyon was reconstructed by sampling and crossdating 62 fire scarred trees along the length of the canyon (Figures 1, 2A, 2B; see Swetnam et al. 1989, 1992, 2001; Swetnam and Baisan 1996). The fire scarred trees were primarily ponderosa (*P. ponderosa*) and Arizona pines (*P. arizonica*), but a few were Chihuahua pine (*P. leiophylla*) and Apache pine (*P. engelmannii*). Both living and dead trees with fire scars were sampled. The samples were distributed over more than four km in linear distance from the mouth of the canyon near the Chiricahua National Monument headquarters to the pine covered uplands above the head of the canyon (Figures 1 and 2B). Additionally, a small set of fire scarred trees was sampled in Surprise Canyon located immediately to the north of the mouth of Rhyolite Canyon.

Comparison of synchronous fire events among the widely distributed fire scarred trees and sites indicates that many fires were very extensive, burning the full length of the canyon from its mouth to its head (or *vice versa*), and including the pine forests in the uplands. These extensive fires are indicated as continuous vertical lines in the master fire chronology chart (Figure 2A). It is possible that some of these fires were separate burns that were ignited in different events that occurred during the same year. However, since the fuels are more-or-less continuous between the sites (today), and these distances are not very great (<5 or 6 km), it is most likely that the synchronous fire scar dates represent continuous burns.

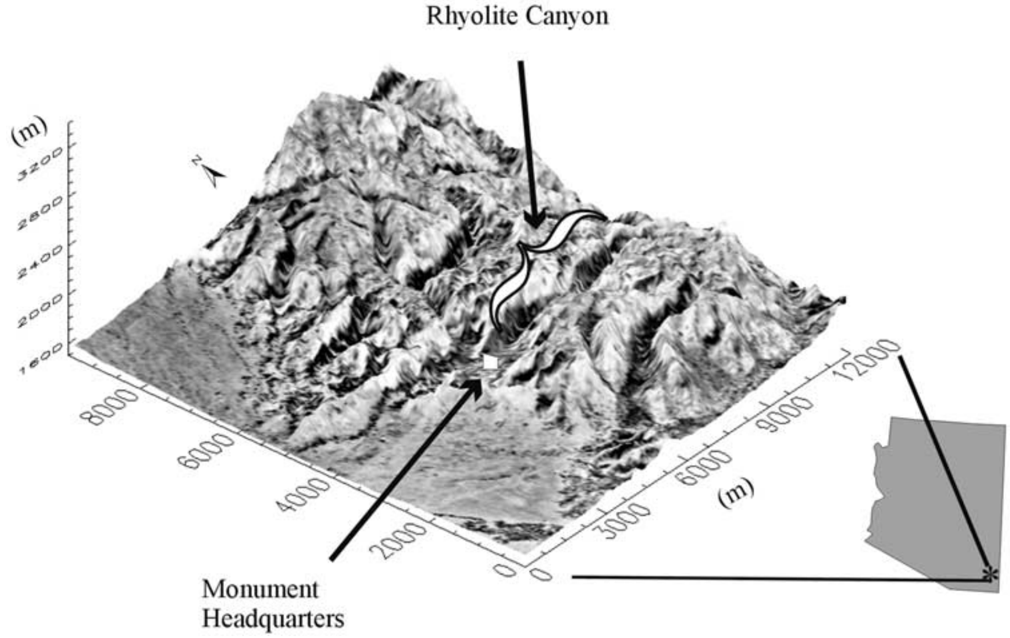

Figure 1. Chiricahua National Monument shown as a digital orthophoto overlay on a 30 m DEM. Monument location in SE Arizona, USA, is shown on the inset map. Mexico lies to the south of the Arizona border.

The inferred canyon-wide fire events were evidently interrupted during the first half of the 19th century. After a fire in 1801, no fires were recorded in most of the middle part of the canyon (site 4) until 1851. Only one fire (1820) was recorded during the period 1801 to 1851 by any fire scarred trees above the confluence of Sarah Deming Canyon with Rhyolite Canyon. Such a long fire-free interval (50 years) is rare in Southwestern ponderosa pine forests (Swetnam et al. 1992, 1999, 2001; Covington and Moore 1994b; Swetnam and Baisan 1996; Fule et al. 1997; Mast et al. 1999). We suspect that this long interval may be related to flood events within Rhyolite Canyon (Swetnam et al. 1991). This is a very flood-prone canyon with evidence of multiple floods in the past, including flood scarred trees and old debris flow fans. A flood in August 1993, for example, scoured the canyon bottom in several places, removed surface fuels, and deposited sand and gravel bars that would probably serve as barriers to effective fire spread for years to decades.

Methods

Increment core collection, preparation, and measurement

We sampled 124 Arizona pines (*P. arizonica*) from middle Rhyolite Canyon and 105 from lower Rhyolite Canyon. Trees were rejected if they were <35 cm diameter at breast height (DBH) or >5 m upslope from the canyon bottom; all other Arizona pines were sampled beginning at the Sarah Deming Canyon junction and moving downstream (lower Rhyolite) and upstream (middle Rhyolite) until the final sample size was attained. Sampling distance along the canyon was about 400–500 m in each direction. For each tree, DBH was measured and two to four cores were extracted at 1.4 m height.

Binocular microscopes were used to crossdate and age trees from sanded, polished, unstained cores, using standard procedures (Stokes and Smiley 1968). Of the 229 cored trees, 211 were datable, 92 of which were cored to the pith, and 40 of which were cored to within an estimated 3 years of the pith. For cores in which the pith was missed, the pith date at coring height was estimated with a circle gauge: distance from innermost ring to pith was estimated by the innermost ring's arc and number of missing rings was calculated according to the width of the innermost

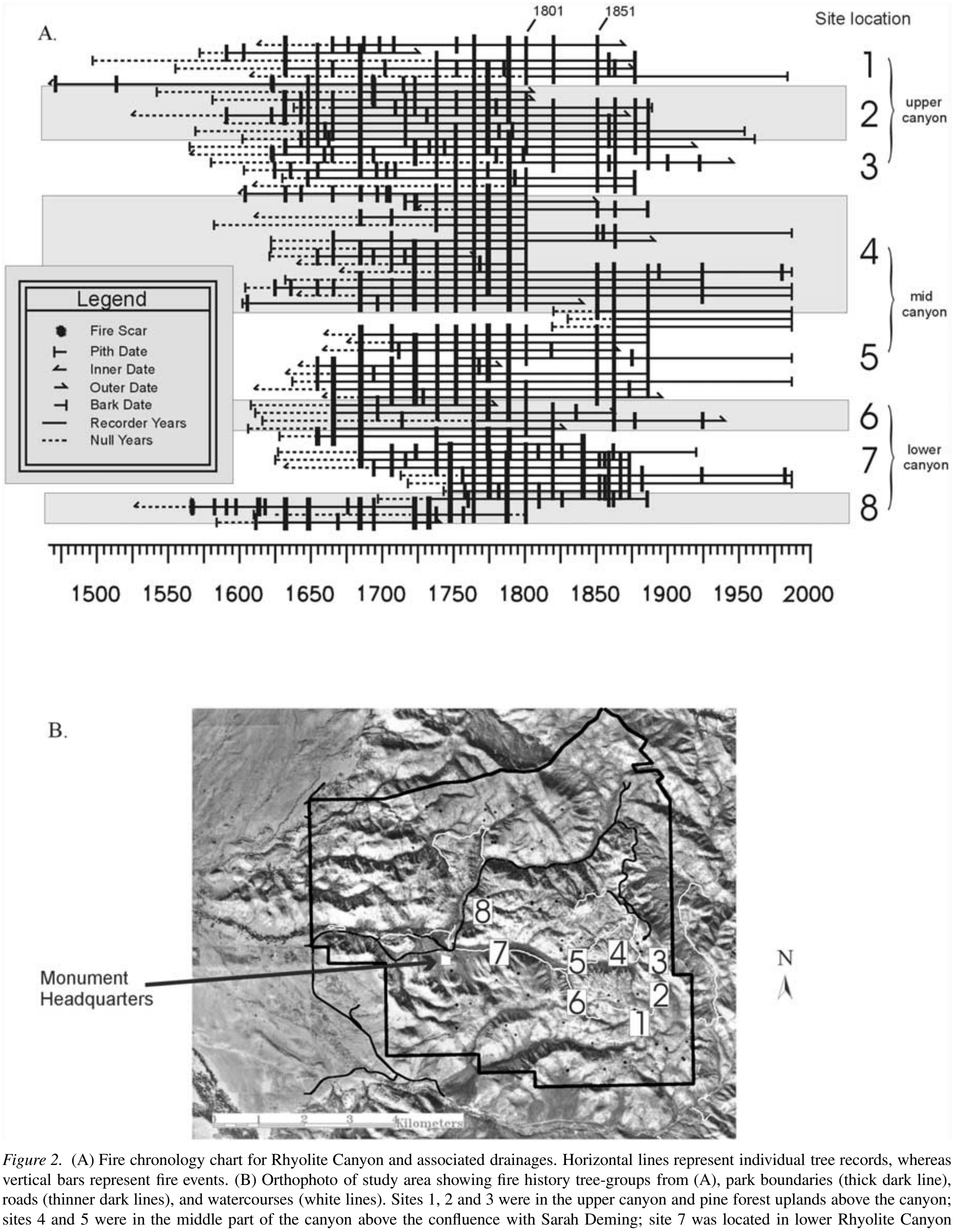

Figure 2. (A) Fire chronology chart for Rhyolite Canyon and associated drainages. Horizontal lines represent individual tree records, whereas vertical bars represent fire events. (B) Orthophoto of study area showing fire history tree-groups from (A), park boundaries (thick dark line), roads (thinner dark lines), and watercourses (white lines). Sites 1, 2 and 3 were in the upper canyon and pine forest uplands above the canyon; sites 4 and 5 were in the middle part of the canyon above the confluence with Sarah Deming; site 7 was located in lower Rhyolite Canyon between park headquarters and Sarah Deming Canyon; site 6 was located in Sarah Deming Canyon, which is continuous with lower Rhyolite Canyon in terms of fuel and topography; site 8 was in Surprise Canyon, also continuous with lower Rhyolite Canyon.

rings. To estimate germination dates, the approximate age in years at coring height was subtracted from each pith date. The age at coring height was estimated by constructing growth curves from height growth data for 138 Arizona pines varying in size from 3–140 cm tall. These young pines were growing in relatively open canopy conditions. Growth rates of cored mature trees were generally rapid during their juvenile stages, suggesting that they were also initially growing in open conditions, justifying our use of juveniles from open canopy locations for estimating ages at coring height. We found that juvenile age at coring height (1.4 m) was 13 years, with a range of 11–15 years (A.M. Barton, unpublished data). Therefore, we subtracted 13 years from the estimated pith dates of sampled mature trees. Ring widths were measured for the 77 trees that germinated before 1860, to the nearest 0.01 mm with computerized Bannister incremental measuring machines.

Data sets

Four primary sets of time series were used in the study: (1) number of trees germinating in each decade from 1600 to 1910 (age structure) for middle and lower Rhyolite, (2) ring widths for each site, (3) fire years for each site, and (4) estimates of past drought severity.

Because precise years of germination could not be determined in this study (see Villalba and Veblen 1997c), establishment dates were classified into decadal groups for examination of relationships of age structure with fire history and climate. To remove age-related trends in declining ring width, the data were standardized by fitting a negative exponential curve to the ring-width series for each core and dividing the ring widths by the values of the fitted curve (see Fritts and Swetnam 1989). Thus, values greater than 1 represent relatively high growth (greater than average) and values less than 1 represent low growth. For each tree, values for all cores were averaged together. For each of the two study areas, all trees were averaged for each year to develop a site ring-width index series.

For analyses in which fire years were used as an independent variable, we included fires that scarred at least 50% of the trees (and at least two trees). We consider these fires because they were most likely to have burned extensively over the sampled area. Including fires scarring at least 25% of the trees did not change the results of analyses, and we do not present those data. Drought severity was estimated for the years 1693–1978 using the mean June-August Palmer Drought Severity Index (PDSI) estimates of Cook et al. (1996, 1999; data at http://www.ngdc.noaa.gov/paleo/usclient2.html) for the four geographical grid points (42, 43, 52, 53) surrounding the study area. Their calculations are based on multiple site tree ring indices from drought sensitive trees and sites. Each grid point reflects subregional to regional climate patterns as verified by a set of rigorous statistical tests (Cook et al. 1999).

Statistical analyses

Fire occurrence and drought severity

The relationship between estimated June-August PDSI and the timing of fires was examined using superposed epoch analysis (SEA; Lough and Fritts 1987; Swetnam 1993), which uses a Monte Carlo approach to statistically examine departures in a time series (e.g., PDSI) from expected values for time periods prior to and subsequent to a set of events (e.g., fire). We tested whether drought was significantly less or more severe than expected to occur by chance during extensive fire years ($\geq$50% of trees scarred), and in the five years prior to fire year.

Recruitment, fire occurrence, and drought severity

We visually assessed relationships between the time series of number of Arizona pines germinating in each decade and the time series of fire years and reconstructed PDSI. The relationships between number of stems in a decade and mean decadal PDSI was statistically examined with simple linear regression separately for each site, and differences in PDSI between periods with age structure peaks and other periods were assessed with ANOVA. The relationships between age structure and fire history was investigated by determining for each decade, the number of trees recruiting, the number of fires that occurred in the previous 10, 20, 30, and 40 years (starting with the 4th year of the decade and counting back), and the number of fires that occurred in the subsequent 10, 20, 30, and 40 years (starting with the 5th year of the decade and counting forward). For each site separately, we tested four regression models: the relationships between the number stems in a given decade and the number of fires in (1) the past 10 years and the subsequent 10 years, (2) the past 20 years and the subsequent 20 years, (3) the past 30 years and the subsequent 30 years, and (4) the past 40 years and the subsequent 40 years. Because the independent variables in these analyses are autocorrelated, we report only the strength of these relationships (r) and not the F-values and P-values.

Radial growth, fire occurrence, and drought severity

We examined, separately for each site, relationships among radial growth (ring indices), fire history, and drought severity. First, to test whether radial growth was higher during years of lower drought severity, ring indices were regressed against reconstructed PDSI for the dates 1693–1899 for middle Rhyolite and 1777–1899 for lower Rhyolite. Second, superposed epoch analysis was used to test whether radial growth was significantly higher than expected in the year of fire and in the post-fire years one to eight. Because such analyses might be confounded by climate patterns associated with fire years, we also used methods developed for isolating the effects of defoliating insects on host tree growth from the effects of climate (see Swetnam et al. 1985). In this case, we wished to remove climate but not fire signals from the Arizona pine ring indices (for a slightly different approach, see Kitzberger et al. 1995). This procedure uses a 'control' tree-ring chronology that is unaffected by the signal of interest (fire in this case) to aid in the identification of the signal in the 'affected' chronology. A 'corrected' index is calculated by subtracting PRI (predicted residual indices) from the affected index, where PRI = (control standard deviation/affected standard deviation)∗(control index − control mean).

Because of the pervasiveness of fire in the borderland region, no perfect control ring index could be found (i.e., a site in a fire-free area with a closely correlated climate signal). We used Douglas-fir (*P. menziesii*) from upper Rhyolite Canyon, which should represent closely the climate patterns experienced by the affected population but may share responses to some of the fires occurring in the lower elevation Arizona pine, where fires were more frequent. We also used a Douglas-fir ring index from the Animas Mountains, a range about 100 km to the east of Rhyolite Canyon; this series should have experienced a similar climate signal to the Arizona pine population, but a largely different set of fires (Swetnam et al. 2001). These two populations, although not ideal, are reasonable choices given the lack of available controls.

In the third set of analyses, an examination of the simultaneous effects of fire and drought severity on radial growth, we used a General Linear Model with PDSI as a continuous variable and fire as a categorical variable (fire in the 5 years previous to a given date vs. no fire).

Radial growth during different periods

To test for a growth reduction in middle Rhyolite during the fire-free period, we used an ANOVA of three time periods separately for the two sites. The time periods were pre-fire-free (1777–1801), fire-free (1811–1850), and post-fire-free (1851–1899). We did not include the years 1801–1810 as fire-free years because of the possible post-fire effects of the 1801 fire. Expecting a post-fire growth release after the fire-free period in middle but not lower Rhyolite, we also compared ring indices for before (1831–1850) versus after (1852–1862; another fire occurred in 1863) the 1851 fire in the two sites ANOVA. In these analyses of differences in radial growth among time periods, we also used estimated PDSI as a covariate to remove the possibility that the resulting patterns were caused by coincidental drought severity patterns rather than fire.

Because tree rings of time series are usually autocorrelated, which violates assumptions of parametric statistics, degrees of freedom in calculating F-values were decreased in accordance with degree of first-order autocorrelation (see Fritts 1976).

Results

Fire and PDSI

For middle and lower Rhyolite combined, years in which fires occurred exhibited significantly drier estimated June-August PDSI than expected ($P < 0.01$; Figure 3). Fire years were also drier for each site analyzed separately, significantly for middle Rhyolite ($P < 0.05$) but marginally insignificant for lower Rhyolite ($0.05 < P < 0.10$). Drought severity was lower than expected in all five years prior to fires, but this was significant only for year t_{-5} ($P < 0.05$; Figure 3). Similarly, drought severity was lower than expected during most years prior to fire for each site analyzed separately, but these deviations were not significant for any year for either site ($P > 0.10$; Figure 3)

Age structure, fire, and drought severity

Figure 4 presents the number of Arizona pine (*P. arizonica*) stems in decades from 1600 to 1920 in relation to fire history and estimated PDSI. For the period of overlap (1680–1900), the decadal time series of stems recruiting for the two sites are strongly correlated ($r = 0.92$, $P < 0.0001$). Both sites exhibit a peak of stems

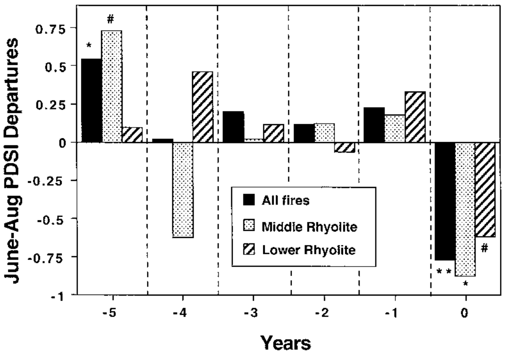

Figure 3. Results of superposed epoch analysis for mean tree-ring reconstructed June-August PDSI for years before and after fires. Years represent fire year (0) and years prior to fire (−1 to −5). Data are the mean departures for each year based on a Monte Carlo simulation of expected values using the appropriate entire tree ring data set (see Methods). Mean departures that were significantly different than expected are indicated (# $P < 0.10$, * $P < 0.05$, ** $P < 0.01$).

late in the 1800s, especially in the 1880s through the first decade of the 1900s. Because stems >35 cm DBH only were sampled, the data set is incomplete for the 1900s. Both sites also exhibit a peak of stems from about 1810–1830, continuing for approximately two additional decades in lower Rhyolite.

There were important differences between the sites as well. In middle but not lower Rhyolite, a cohort of stems germinated and survived from about 1610–1640 (Figure 4). In fact, the oldest sampled tree in the middle canyon was 140 years older than that for the lower canyon (1547 versus 1687). Second, although the late 1800s irruption of trees begins in middle Rhyolite in the 1850s, albeit at a low level, in lower Rhyolite, no trees occurred from the 1850s or 1860s, during a period of very high fire frequency (Figure 4).

Contrary to expectations, there were no clear differences between the two sites in the number of stems remaining from the period (1802–1850) in which middle Rhyolite was largely fire-free and lower Rhyolite recorded three extensive fires; as described previously, in both sites a large number of stems occur from the early part of this period (Figure 4).

The number of stems remaining from each decade corresponds to fire history in both middle and lower Rhyolite. The two peaks common to both sites occur during periods of relatively low fire frequency, preceded by periods of much higher fire frequency (Figure 4). For example, the late-1800s cohort occurs after a period of especially high fire frequency and during a period of very low fire frequency. In general, relatively low establishment and survival are

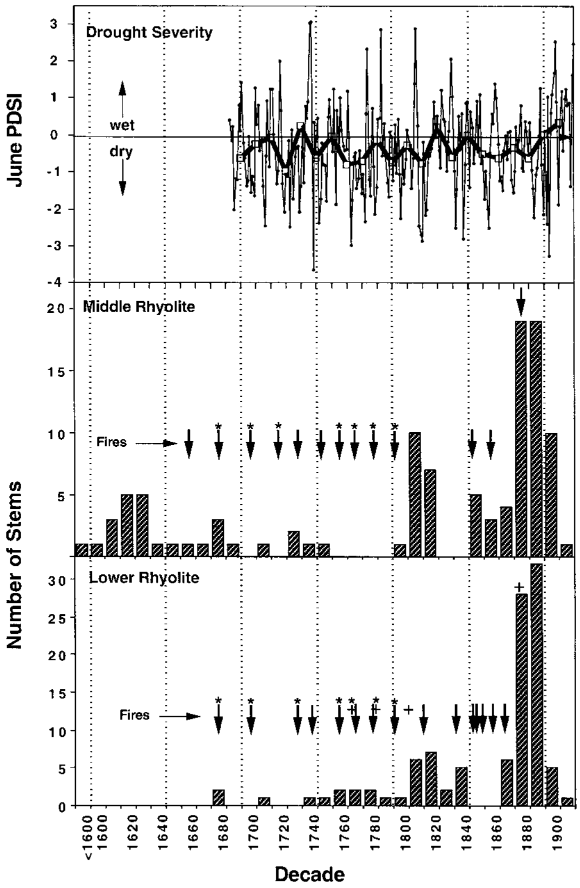

Figure 4. Number of Arizona pine stems in decade age classes for lower and middle Rhyolite Canyon. At the top is presented the tree-ring reconstructed regional annual June–August PDSI (light line, small points) and the decadel mean estimated June-August PDSI (thick line, large squares). Dates of major fires (scarring ≥ 50% of trees) from the late 1600s to the early 1900s are shown as arrows for each site. Plus signs indicate fires scarring 25–49% of trees. Asterisks indicate fires common to both areas.

associated with periods of high fire frequency (e.g., 1750s–1780s in middle Rhyolite and 1840s–1850s in lower Rhyolite).

Statistical analysis of the influence of fire frequency on the number of stems surviving from given decades corroborates these apparent patterns. The number of stems in a given decade was negatively related to the number of fires in subsequent decades, with the highest correlation coefficients for periods of 20 years and 30 years for both middle and lower Rhyolite (Table 1). In other words, more stems remained from a given decade when fires were relatively infrequent in the following two and three decades. These modest correlation coefficients, however, might be in-

Table 1. Correlation coefficients for lower and middle Rhyolite between number of Arizona pine stems in a given decade and number of fires in previous and subsequent decades. Sample size for the number of decades is given in parentheses.

Time period	Middle rhyolite		Lower rhyolite	
	Previous	Subsequent	Previous	Subsequent
10 years	−0.14 (22)	−0.13 (22)	−0.35 (22)	−0.38 (22)
20 years	−0.35 (21)	−0.47 (21)	−0.34 (21)	−0.46 (21)
30 years	−0.27 (20)	−0.47 (20)	0.01 (20)	−0.36 (20)
40 years	−0.09 (22)	−0.29 (22)	0.31 (19)	−0.32 (19)

flated by autocorrelation (see Section Radial growth during different periods).

Given the low and negative correlation coefficients for the relationships between number of stems in a decade and the number of fires in previous decades, the results do not point to a positive relationship between these two variables. Because of the lack of sufficient fire data prior to the second half of the 17th century, the peak of stems from the early part of that century in middle Rhyolite could not be included in these analyses.

There was no general relationship apparent between the timing of peaks in the age structure record and either decadal mean estimated PDSI or Arizona pine radial growth. Regressions of decadal frequencies of stems on PDSI were insignificant for middle and lower Rhyolite ($F_{1,18} < 0.2$, $P > 0.05$). PDSI and radial growth during the two 19th century peaks of stems were not significantly different from other periods ($P > 0.05$). For the early 17th century peak of stems in middle Rhyolite, however, radial growth was higher during this time than for other periods ($F_{1,401} = 2985$, $P = 0.004$). Estimated PDSI data were not available for this period.

Radial growth, fire, and drought severity

For lower Rhyolite, ring widths were only slightly higher than expected in the year after fire ($0.05 < P < 0.10$; Figure 5). For middle Rhyolite, ring widths were lower than expected in the year of fire ($P < 0.01$; Figure 5). As shown previously, fire years were drier than expected ($P < 0.01$), suggesting that lower growth in these years likely resulted from climate not fire. When potentially confounding effects of climate were removed, patterns for both the fire year and the year after fire disappeared (Figure 5). Correction with Douglas-fir (*P. menziesii*) from either Rhyolite Canyon or from the Animas Mountains produced results exhibiting higher than expected growth in most years after fire, but this was significant only for year t_{+5} for the Animas correction ($P < 0.05$; Figure 5).

For both lower and middle Rhyolite, ring indices were strongly positively associated with estimated June-August PDSI ($P < 0.0001$, $r = 0.65$ and $r = 0.59$, respectively). When PDSI and fire were used as independent variables in a General Linear Model, ring widths were significantly related to PDSI but not to fire (fire vs. no fire in the 5 years previous for each ring index value): for lower Rhyolite, PDSI $F_{1,173} = 81.1$ and $P < 0.0001$, Fire $F_{1,173} = 0.3$ and $P > 0.05$; for middle Rhyolite, PDSI $F_{1,204} = 109.0$ and $P < 0.0001$, Fire $F_{1,204} = 0.9$ and $P > 0.05$.

Variation in the standardized tree-ring indices over time are shown in Figure 6 and differences between the two sites (middle minus lower Rhyolite) are shown in Figure 7. Although the two ring indices varied similarly for much of the chronology ($r = 0.82$, $P < 0.0001$), important differences occurred. In middle Rhyolite, there were detectable differences among the three periods identified to examine the effects of lack of fire in the first-half of the 19th century ($F_{2,120} = 9.2$, $P < 0.0001$): ring widths during the fire-free period were significantly lower compared to both the prior period (1777–1801; $t_{72} = 43.5$, $P < 0.001$) and the subsequent period (1851–1899; $t_{87} = 81.0$, $P < 0.001$). In contrast, lower Rhyolite did not exhibit significant differences among these periods ($F_{2,120} = 0.3$, $P > 0.10$). These patterns were not altered when the data were analyzed using estimated PDSI as a covariate to remove the possible confounding effects of climate or when corrected (with Douglas-fir) ring indices were used (data not shown). Ring widths for the fire-free period were also lower for middle than for lower Rhyolite (paired t-test, $t_{38} = 3.3$, $P = 0.002$). In an analysis of the effects of the 1851 fire, tree ring indices were larger after the 1851 fire than before for middle but not for lower Rhyolite (Figure 8). Again, this pattern remained unaltered when using estimated PDSI as a covariate or using corrected ring indices (data not shown).

Discussion

Fire occurrence and drought severity

An increasing number of studies have shown that the timing of local fires is in part controlled and synchronized by regional climate patterns, some of which

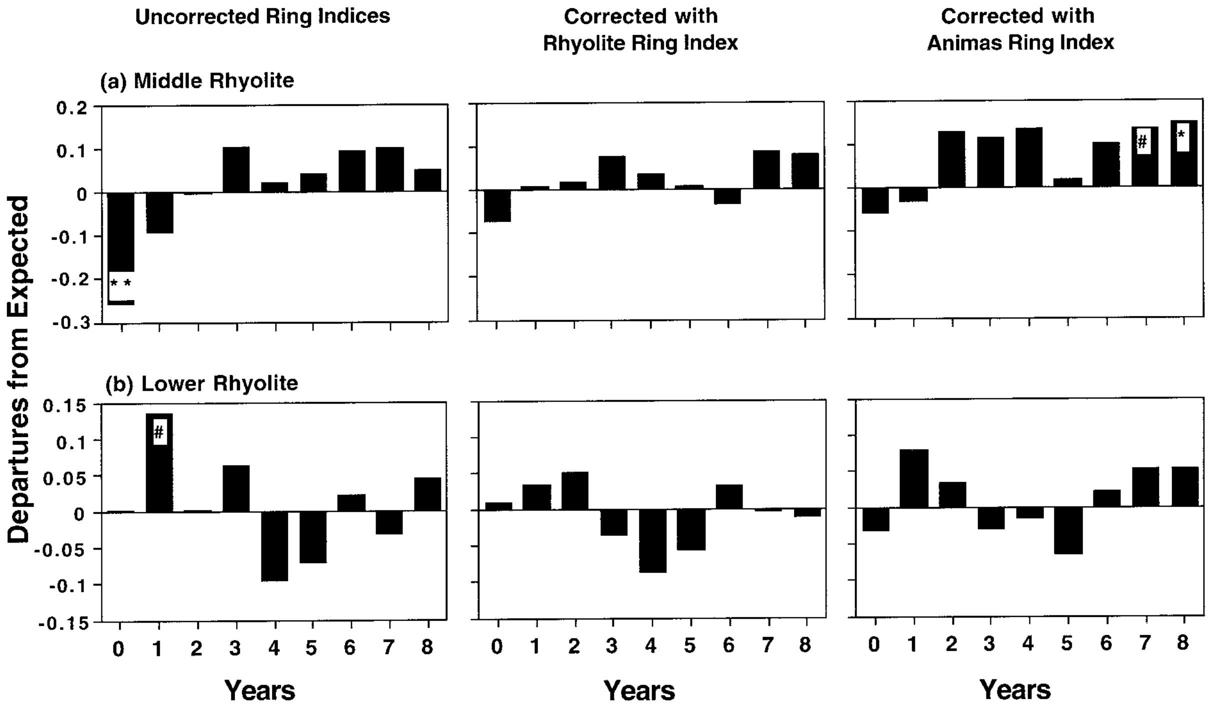

Figure 5. Results of superposed epoch analysis for (a) middle Rhyolite and (b) lower Rhyolite for mean uncorrected Arizona pine tree-ring index, corrected index using Douglas-fir index from Rhyolite Canyon as 'non-host', and corrected index using Douglas-fir index from the Animas Mountains as 'non-host' (see Methods). Years represent fire year (0) and years after fire (1 to 8). Data are the mean departures for each year based on a Monte Carlo simulation of expected values using the appropriate entire tree-ring data set (see Methods). Mean departures that were significantly different than expected are indicated (# $P < 0.10$, * $P < 0.05$, ** $P < 0.01$).

are in turn driven by global climate patterns such as the El Niño-Southern Oscillation (ENSO) (Swetnam and Betancourt 1990; Johnson and Wowchuck 1993; Swetnam 1993; Fulé and Covington 1996; Kitzberger et al. 1997; Swetnam and Betancourt 1998; Veblen et al. 1999; Grissino-Mayer and Swetnam 2000). Dry years, often associated with the La Niña phase of ENSO, appear to be crucial for the effective ignition and spread of fires, especially in mesic environments (e.g., canyons, mixed conifer forest). Some studies have also demonstrated the importance of El Niño-associated moist years prior to fire, which lead to accumulation of fine fuels that promote fire spread and intensity (Swetnam and Betancourt 1990; Swetnam 1993; Villanueva-Díaz and McPherson 1996; Kitzberger et al. 1997; Veblen et al. 1999; Grissino-Mayer and Swetnam 2000). Our results indicate that dry years were especially important to fire occurrence in Rhyolite Canyon. For fires occurring in lower and middle Rhyolite separately or combined, fire years were drier than expected ($P < 0.01$, Figure 3). Evidence for unusually moist years prior to fire was weak: the five years prior to fire were all moister than usual for all fire years, but significantly only for year t_5 ($P < 0.05$, Figure 3).

Relationships of climate and fire were less pronounced for lower than for middle Rhyolite (Figure 3), and lower Rhyolite exhibited an overall higher fire frequency. Lower Rhyolite is in close proximity to an area apparently used as a 'rancheria' by indigenous people, the Chiricahua Apaches, at least during the 19th century (Kaib 1998). Human-ignited fires associated with this rancheria, especially during times of warfare (e.g., 1850s; Bahre 1991; Wilson 1995), may account for the higher fire frequency and the reduced connection between natural climate patterns and fire occurrence (Kaib 1998). Accumulating evidence suggests that modification of fire regime by the Apaches was variable in both time and space, occurring episodically in some local sites but not in others (Morino 1996; Seckleki et al. 1996; Kaib 1998; Kaye and Swetnam 1999; Swetnam et al. 2001). The fire history results for Rhyolite Canyon are consistent with this view.

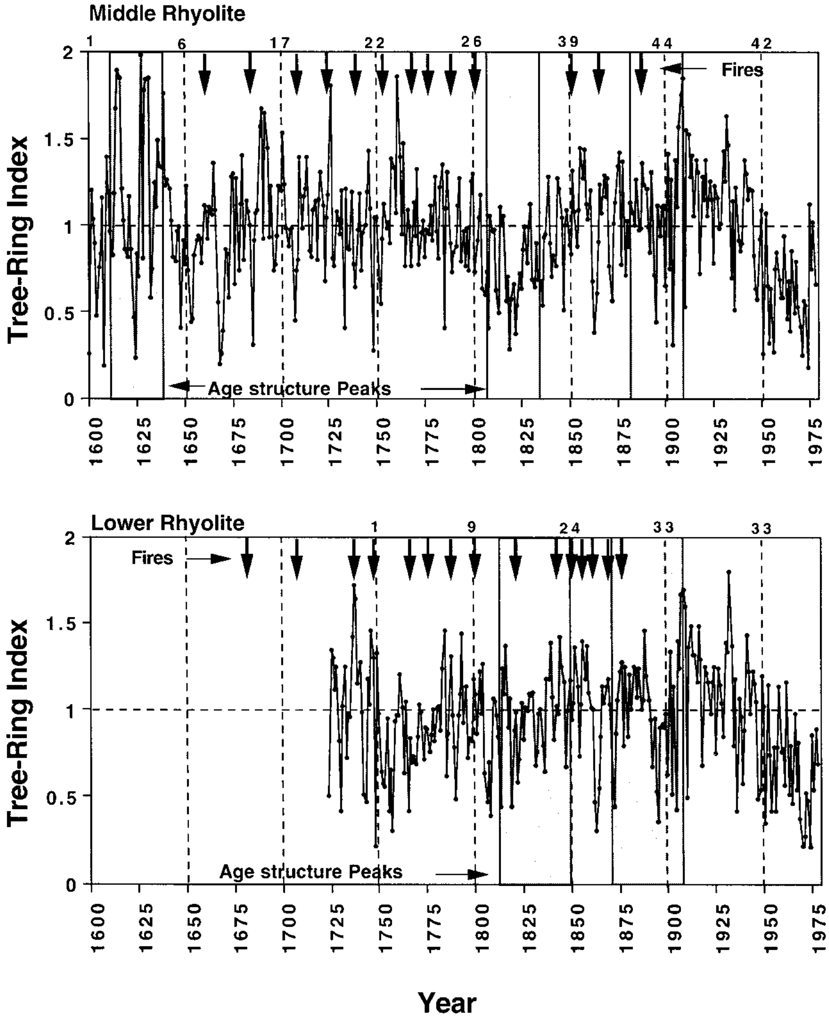

Figure 6. Tree-ring indices of Arizona pine for lower and middle Rhyolite from 1600–1978. Sample sizes are given for every half-century. Arrows above the ring index data represent the dates of fires (scarring ≥50% of the trees). Peaks of stems in the age structure record are indicated by shaded regions.

Age structure, fire, and drought severity

The Arizona pine (*P. arizonica*) age structure record exhibited three prominent peaks. Two peaks – 1810–1830 and 1870–1900 – were shared by the two sites (Figure 4). The third peak, 1610–1640, occurred only in middle Rhyolite, which supported much older trees than did lower Rhyolite. We can not account for this discrepancy, but offer two speculations. First, older trees might have been logged out of lower Rhyolite, an area more accessible than middle Rhyolite to late 19th century European settler communities at lower elevations. There is little evidence supporting this hypothesis, however. Historical records mention several canyons in the western Chiricahua Mountains as logging or sawmill sites during the late 1800s, but not Rhyolite Canyon (Kellogg 1902 cited in Bahre 1995; Bahre 1995; Wilson 1995). During this period, soldiers from Fort Bowie chose to log trees from canyons farther afield rather than from the relatively small and inaccessible Rhyolite Canyon (Wilson 1995). Stumps are very rare in the canyon, in contrast to other canyons in the Chiricahua Mountains with documented logging operations (e.g., Turkey and Rucker Canyons) (Bahre 1995; Kaib 1998). The 1600s cohort in middle Rhyolite arose just after what appears to have been a stand replacement fire in 1591 (T.W. Swetnam, unpublished data). Lower Rhyolite but not middle Rhyolite today supports a high density of silverleaf oak (*Quercus hypoleucoides*), a small

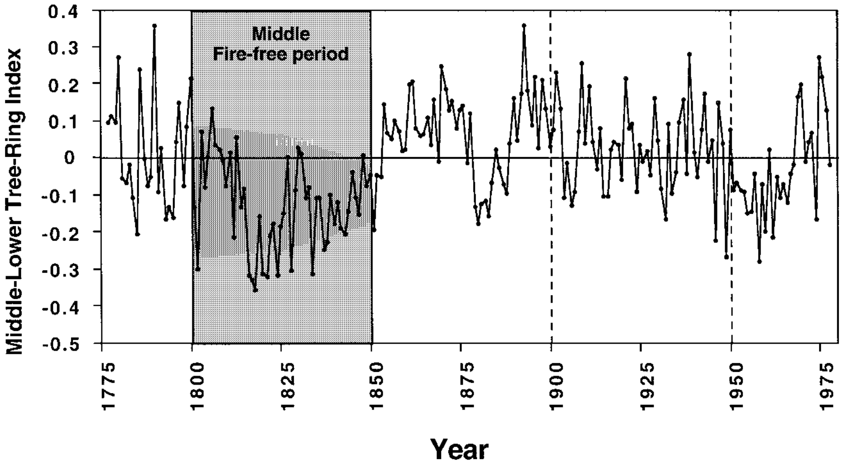

Figure 7. Differences between the Arizona pine tree-ring indices of middle minus lower Rhyolite. The fire-free period in middle Rhyolite is shown as a shaded area. Sample sizes are given in Figure 6.

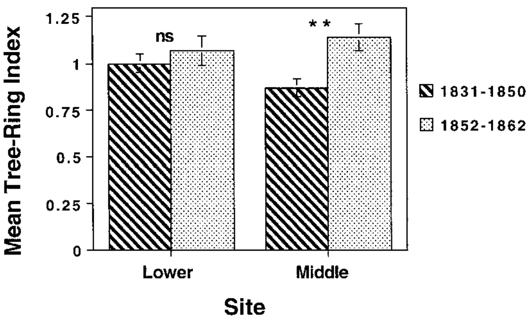

Figure 8. Mean (with standard error bars) ring widths of Arizona pine for lower and middle Rhyolite for before the 1851 fire (1831–1850) versus after the 1851 fire but before the next fire (1852–1862). Asterisks indicate significant differences (** $P < 0.01$, ns – not significant) between the two periods.

tree capable of prolific post-fire sprouting, spread, and eventual dominance at the expense of pines. This is especially the case where largely seed-dependent pines have been locally exterminated by fire (Barton 1999, in review; see also Fulé and Covington 1998). Therefore, a second hypothesis for the lack of the 17th century cohort in lower Rhyolite is that suppression by silverleaf oak thwarted recovery of Arizona pine in this area for more than a century after the 1591 fire.

Our results show a strong correlation between the Arizona pine age structure and fire occurrence. The 1810–1830 and 1870–1900 age structure peaks occur during periods of very low fire frequency preceded by periods of much higher and consistent fire occurrence. For both sites, the number of stems occurring in a decade is negatively related to the number of subsequent fires, especially over periods of 20 and 30 years (Table 1). In contrast, there is no clear relationship between the number of stems in a decade and number of prior fires (Table 1). Comparison of the two sites further points to the role of mortality from fire in age structure. During the 1850s and 1860s, middle Rhyolite exhibited a moderate fire frequency and a moderate number of trees survive from that time. In contrast, lower Rhyolite exhibited an extremely high fire frequency and no stems remain from those two decades.

These results are consistent with the idea that in Rhyolite Canyon fire-induced mortality played a crucial role in shaping Arizona pine age structure. This scenario posits that long-term survival of recruits is enhanced by fire-free periods of sufficient length to permit them to attain a height at which they are relatively resistant to fire. Height growth projections for *P. arizonica* show that the average juvenile attains a height of 3–4 m in 25 years (A.M. Barton, unpublished data). Fire-induced mortality is strongly size-dependent for other pines in the Chiricahua Mountains

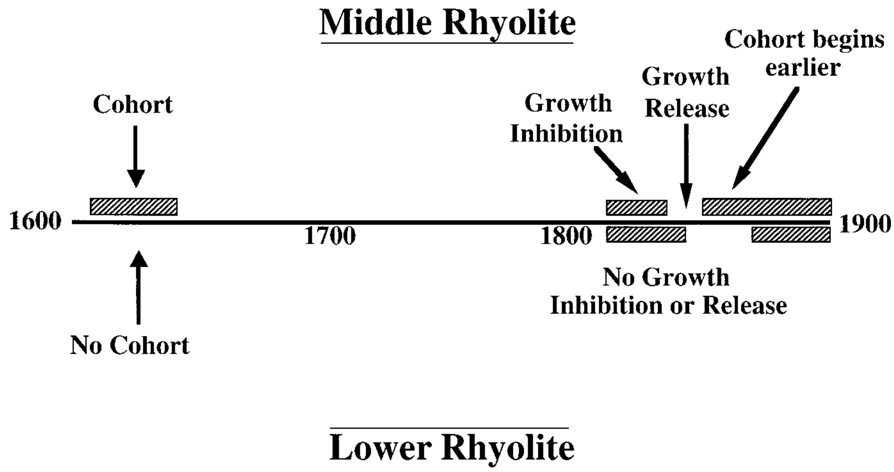

Figure 9. Summary of differences and similarities in population dynamics between lower and middle Rhyolite.

(A.M. Barton, unpublished data), a general pattern for tree species (e.g., Peterson and Ryan 1986; Ryan and Reinhardt 1988). It is plausible, therefore, that fire-free periods lasting two or more decades, such as in the early and late 1800s, are particularly important for survival of age-class cohorts to maturity.

A dominant role for fire-free periods in shaping age structure may account for the lack of difference in age structure between the two sites despite the divergence in fire history from 1802–1850. Close inspection of the fire chronology reveals that even in lower Rhyolite fire frequency was relatively low during 1802–1850 compared to periods both before and after this period. Thus, the 50-year fire-free period in middle Rhyolite and the nearly 20-year fire-free periods in lower Rhyolite may have all been sufficiently long to allow recruits to survive to a size at which they could survive subsequent surface fires. In long-needled pines in the Sierra Madre, a 29-year period without fire was apparently sufficient to allow the survival of newly-recruited stems not found in a site with fires at shorter intervals (Fulé and Covington 1998).

White (1985) and Mast et al. (1998, 1999) also argue that a lack of surface fires may be important in producing periods of pronounced ponderosa pine (*P. ponderosa*) recruitment because of reduced seedling mortality. Perhaps the most prominent example of this phenomenon is the peak in age structure in the late 19th century and early 20th century shown here and in many studies of ponderosa pine throughout the southwestern USA. This dramatic increase in recruitment and stand density has been attributed to a reduction in grass competition and surface fires resulting from heavy livestock grazing, as well as favorable cone crop and seedling survivorship associated with warm, wet summers (Cooper 1960; White 1985; Covington and Moore 1994a, b; Savage and Swetnam 1990; Savage et al. 1996; Swetnam et al. 2001).

In southeastern Arizona, intensive livestock grazing was introduced in the 1870s (Bahre 1995; Wilson 1995), but arrived in different mountain ranges at different times – by as much as 30 years (Swetnam et al. 2001). Fire history records consistently reveal cessation of fire within individual ranges closely coinciding with the timing of livestock introductions (Swetnam et al. 2001). Livestock grazing in the Chiricahua Mountains and surrounding valleys increased dramatically in the early 1880s (Bahre 1995; Wilson 1995). This coincides with reduced fire frequency (Figure 2A) and age structure peaks in Arizona pine (Figure 4) and other pines and oaks in Rhyolite Canyon (Barton 1999). Fire suppression by government fire fighters, in contrast, was not common in the Chiricahua Mountain region until about 1920 (Wilson 1995). These results point clearly to a prominent role of livestock grazing in the initial reduction of fire frequency and massive regeneration of trees in Rhyolite Canyon in the late 19th century (see Bahre 1995; Swetnam et al. 2001).

Despite the apparent role of fire-induced mortality in age structure and the lack of correlation between age structure peaks and prior fire events, fire was likely of central importance in Arizona pine recruitment. A large literature has demonstrated that successful recruitment requires fire-induced seed bed preparation and reduction of competition in ponderosa pine (e.g., Cooper 1960; White 1985; Covington et al. 1994b) and other long-needled pines (Barton 1993, 1999; Fulé and Covington 1998). Fires, therefore, likely promoted Arizona pine germination and establishment, and subsequent fires shaped age structures by selectively eliminating particular cohorts. A complete long-term view of the relationship between fire and Arizona pine recruitment must also recognize that, even in widespread fires, some recruits are likely to persist, imposing additional variability in time and space (see Brown et al. 1999).

The results provide conflicting evidence for the alternative hypothesis that favorable moisture availability, rather than reduced fire frequency, accounts for the age structure peaks in Arizona pine. The early 1600s peak occurred during a period of radial growth that was significantly higher than for the rest of the tree-ring record, suggesting higher than usual moisture availability. In fact, regional reconstructions have revealed relatively moist conditions (e.g., Fritts 1991; Grissino-Mayer 1996) and major recruitment of trees for this period across the Southwest (Swetnam and Brown 1992). However, neither reconstructed decadal-mean June–August PDSI or radial growth rate was significantly correlated with number of stems in a decade. Mean PDSI and mean growth rate also were not unusually high during the age structure peaks of 1810–1830 and 1870–1900. Other studies have shown, however, that the early 1800s in the Southwest were characterized by wet winters and springs (Fritts 1991; Meko et al. 1993; see also Swetnam and Betancourt 1998 and Grissino-Mayer and Swetnam 2000, for a discussion of the changing relationship between climate and fire during this period). In fact, 1815–1816 was the second wettest pair of consecutive years in the entire 286-year reconstructed PDSI record for the Chiricahua Mountains region, and 1815–1817 was the third wettest consecutive trio of years. This short moist period could have been instrumental in the age structure peak of Arizona pine from 1810–1830. On the other hand, the wettest three consecutive years (1745–1747) and other unusually moist periods in the PDSI record did not produce age structure peaks that remain today, and unusually moist years did not occur in 1870–1900, during the most recent age structure peak. These results, then, provide evidence for the potential of enhanced moisture in recruitment during two of the three age structure peaks, but also the likelihood that moist conditions are often not sufficient alone to produce recruitment.

Enhanced moisture availability plays a crucial role in recruitment in many arid region tree species, including ponderosa pine (Pearson 1923; Savage et al. 1996) and other pines in the Chiricahua Mountains (Barton 1993; Barton and Teeri 1993). It would be surprising if it were not connected to recruitment in Arizona pine in Rhyolite Canyon. Although some studies have demonstrated relationships between decade-long periods of relatively high moisture availability and recruitment in ponderosa pine (Mast et al. 1998), single years or 2–3 year periods of high rainfall often are sufficient for establishment in this species (Pearson 1923; Savage et al. 1996). Thus, more complete tests of the role of moisture availability on recruitment and age structure may require tree germination dates on an annual rather than decadal scale (see Savage et al. 1996; Villalba and Veblen 1997c), a common problem encountered in similar studies (e.g., White 1985; Mast et al. 1998, 1999). Additionally, summer moisture might be more important than winter moisture. The reconstructed June-August PDSI values probably do not separate monsoon moisture from winter-spring carry over moisture very well. New techniques involving the measurement of ring growth before and after false rings in southern Arizona, and isotopic analyses, however, have promise for separately reconstructing cool season and summer precipitation.

Even with accurate annual data on germination and climate, plant ecologists must face at least three major challenges in their effort to disentangle the effects of fire and climate on age structure in species like Arizona pine. First, periods of high moisture availability and low fire frequency may be closely linked, making statistical separation of effects on age structure very difficult (see Villalba and Veblen 1997a; Mast et al. 1998, 1999). Second, especially for long age structure records, distant recruitment events can be largely obscured by subsequent mortality episodes, erasing connections between past environmental conditions and stand dynamics (White 1985; Johnson et al. 1994; Villalba and Veblen 1997a; Mast et al. 1998). Conjectures based on static age structures, like those presented here, are always subject to such caveats. Finally, the coincidence of several conditions may be required for successful plant establishment in arid ecosystems subject to fire. Conditions for recruitment in Arizona pine, for example, may be stringent and episodic in a manner similar to that for ponderosa pine in northern Arizona (see Peet 1981; White 1985), requiring (1) large seed crops, (2) prior seed bed preparation and reduction of competition by fire,

(3) consecutive moist years to foster germination and establishment, and (4) a subsequent fire-free period to allow growth to a size relatively resistant to subsequent periodic fires. Such a scenario poses challenges to revealing the intricate connections between climate patterns, the proximal environmental events, and successful establishment. Progress will likely require both the methods of historical ecology employed here, as well as multifactoral experimental approaches.

Radial growth, fire, and drought severity

The long-term connections between drought severity, fire, and tree radial growth in arid environments are complex, with climate directly influencing growth through its control of moisture availability and indirectly influencing growth through its control of fire (Sutherland et al. 1991; Mutch and Swetnam 1995; Villalba and Veblen 1997b). Increased moisture availability, inferred from tree-ring reconstructed PDSI, strongly enhanced growth. Initial analyses using uncorrected ring widths indicated negative effects of fire during fire years in middle Rhyolite and positive effects in the year after fire in lower Rhyolite. When the potentially confounding effects of climate were removed, however, these apparent patterns disappeared. This contrast clearly demonstrates the crucial role of ‘correction’ in separating the effects of fire versus climate on tree growth. The ‘corrected’ results did reveal a possible weak positive effect of fire in middle Rhyolite, although this was significant only for post-fire year eight. These results suggest that fire plays a largely neutral role in radial growth of Arizona pine surviving fires in Rhyolite Canyon. Simultaneous analysis of the two factors, an approach rarely pursued in past studies (but see Mutch 1994; Mutch and Swetnam 1995), revealed similar results: strong effects of drought severity but no influence of fire.

The prominent role of drought severity in radial growth is typical of ponderosa pine and other tree species in the southwestern USA and other arid regions (Glock 1955; Fritts 1976, 1991; Villanueva-Díaz and McPherson 1996; Villalba and Veblen 1997b). In contrast, past studies have found positive (Morris and Mowat 1958), negative (Wooldridge and Weaver 1965), and ambiguous or no effects (Lynch 1959; Sutherland et al. 1991) of fire on radial and height growth in ponderosa pine, as well as other species (Abbott and Loneragan 1983; Reinhardt and Ryan 1988; Mutch 1994). Most studies have examined only one or a few, usually recent, fires; few have taken the approach here, of examining the impacts of a long series of typical, periodic presettlement fires on radial growth of surviving trees (but see Brown et al. 1992). Given the potentially large role of growth rate in population dynamics, understanding the effects of fire on growth rates (in addition to age structure) appears to be an important understudied aspect of fire ecology.

Despite the apparent negligible effect of fire on radial growth in the immediate post-fire environment, fire likely plays an important long-term role in maintaining growth conditions for Arizona pine. As with recruitment, there is a large literature demonstrating positive effects of fire in southwestern ponderosa pine habitats on soil resource availability, litter accumulation, and levels of competition (e.g., Morris and Mowat 1958; Covington and Sackett 1984, 1986; Sackett et al. 1996). The contrasting fire history during the first-half of the 19th century in middle versus lower Rhyolite provides a unique opportunity to test the long-term effects of periodic fire on radial growth. As expected, growth of Arizona pine in middle Rhyolite, which was fire-free during this period, was significantly lower compared to that in lower Rhyolite and compared to that in middle Rhyolite during the periods prior to and subsequent to these fire-free years. In contrast to the lack of a clear post-fire growth release for all fires analyzed together, the 1851 fire alone was associated with a strongly significant post-fire increase in radial growth in middle but not lower Rhyolite. These results together are consistent with the following scenario for middle Rhyolite: lack of fire from 1802–1850 led to increased resource competition and depressed radial growth, but the 1851 fire decreased competition, and thereby increased radial growth. Importantly, these growth patterns were unchanged when the potential effects of drought severity were removed using corrected indices or PDSI as a covariate. Fulé and Covington (1994), working in a similar long-needle pine ecosystem in the Sierra Madre, also attributed relatively low height and radial growth in a site to a lack of fire and increased competition since 1945 compared to an otherwise similar site experiencing frequent fire.

Conclusions: Regional and local factors

Fire and drought severity exerted overarching control in the population dynamics of Arizona pine in Rhyolite Canyon. Drought severity was largely responsible for variation in radial growth. Periods of higher than usual moisture availability may also have served as important times of recruitment, although such effects were not conclusive here. Fire in presettlement times played a crucial role in promoting a relatively open forest structure, and probably maintaining soil and light conditions required for recruitment and growth (Marshall 1962; Fulé and Covington 1996; Barton 1999; Swetnam et al. 2001). Fires were sufficiently frequent and Arizona pine seedlings sufficiently fire-sensitive that fire-free periods were also crucial for long-term survival of seedling cohorts. Fire also appeared to be sufficiently frequent, and perhaps of sufficiently low intensity, that immediate post-fire years differed little from pre-fire years in terms of radial growth and growing conditions, except after a long hiatus of fire. These results raise the possibility that, in this presettlement system, the notion of perturbation of ecosystem and population processes applies less to fire events than to unusually long fire-free periods (see Fulé et al. 1997; Platt 1997). This conclusion probably does not apply, however, to modern-day crown fires outside the boundaries of presettlement reference conditions (Fulé and Covington 1998; Moore e tal. 1999; Barton in review).

Synoptic climate processes, such as those connecting climate and fire in the southwestern USA, are likely to exert strong control on forest patterns at continental spatial (and long temporal) scales. At increasingly more local spatial (and shorter temporal) scales, we would expect these processes to be obscured and superceded by site-specific processes and land use (see Villalba and Veblen 1997a; Huston 1999; Heyerdahl et al. 2001). Some of the contrasts in population dynamics between lower and middle Rhyolite (Figure 9) are probably attributable to site-specific differences, such as fire occurrence. For example, during the 1802–1850 fire-free period in middle Rhyolite, this site only exhibited relatively low radial growth and a growth release in response to the 1851 fire. Local differences in fire frequency in 1850–1870 – much higher fire frequency in lower versus middle Rhyolite – may also have led to the larger number of stems surviving from those two decades in middle Rhyolite. However, age structures remaining from the 18th and 19th century were surprisingly similar between the two sites, especially from the 1802–1850 period (Figure 9). These results demonstrate that, even at a very local spatial scale, prominent responses to regional processes imposed by climate can persist.

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