CLIMATE AND DISTURBANCE FORCING OF EPISODIC TREE RECRUITMENT IN A SOUTHWESTERN PONDEROSA PINE LANDSCAPE

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Abstract. Strong but relatively short (annual to decadal length) climate change can have broad-scale and long-lasting effects on forest communities. Climate impacts forests through direct effects on tree demography (mortality and overstory recruitment) and indirect effects on disturbance regimes. Here, we compare multicentury chronologies of tree recruitment from a 307-ha ponderosa pine forest in southwestern Colorado to reconstructions of fire years, hydroclimate, and the El Niño-Southern Oscillation (ENSO). Few trees predate a regional multiyear megadrought centered in the 1580s. A prolonged pluvial in the early1600s resulted in a pulse of tree recruitment that corresponds to recruitment seen over much of the Southwest. Other cohorts in the early 1700s and mid-1800s established during multidecadal fire-quiescent periods. These periods correspond to shifts in ENSO that apparently resulted in dampening of interannual wet/dry oscillations responsible for fuel buildup and drying. Fires, mediated by stochastic climate variation, acted as a density-independent regulation on tree populations since establishment was not limited by overstory tree density, but rather by fire-caused mortality of seedlings and saplings during periods of more frequent fires. Even-aged cohorts in ponderosa pine forests likely have little if anything to do with episodic mortality caused by more severe fires, but rather relate mainly to episodic recruitment opportunities. Fire cessation after Euro-American settlement in the late 1800s resulted in an increase in tree density and changes in forest composition, which are major factors that have contributed to recent severe wildfires in other Southwestern forests. Our results document clear linkages between synoptic climate forcing, fires, and recruitment episodes, and highlight the importance of regional historical processes on contemporary forest composition and structure.

Key words: dendroecology; density-independent population dynamics; drought; El Niño-Southern Oscillation; fire regimes; tree demography; tree recruitment.

INTRODUCTION

Strong but relatively short (annual to decadal length) climatic anomalies can result in broad-scale effects that persist for decades to centuries in long-lived forest ecosystems (Allen and Breshears 1998, Swetnam and Betancourt 1998). Climate change impacts forest structure through both direct effects on tree demography and indirectly through effects on disturbance regimes (Overpeck et al. 1990). Since climate changes and resulting effects are nonstationary and probably nonlinear, prediction of vegetation dynamics is difficult without basic understanding of past transient versus persistent climatic effects on plant community composition and structure.

Dendrochronological analysis of static (i.e., present-day) tree ages combined with disturbance and climate histories can elucidate long-term climate/vegetation/disturbance coupling (Mast et al. 1998, Swetnam and Betancourt 1998, Villalba and Veblen 1998, Heyerdahl et al. 2001). Static age structure reflects tree survivorship resulting from the combination of natality and mortality over time. Climate directly affects age structure through favorable conditions for tree establishment or through unfavorable conditions (e.g., droughts) that result in mortality. Climate indirectly affects age structure through control of both disturbance severity, which influences scale and magnitude of mortality, and disturbance frequency, which limits establishment to periods between disturbance events. Disturbances of varying scales also are crucial processes in many forests to open up canopy space for new canopy recruitment to occur.

Confounding effects may limit inferences that can be made about climatic vs. disturbance forcing of forest patterns. In closed-canopy forests, the presence of even-aged tree cohorts is often evidence of past severe crown fires (Agee 1993, Johnson and Gutsell 1994). This evidence relies on coupled but distinct ecological/demographic processes: fire that kills trees followed by synchronous tree recruitment into canopy openings. However, in open-canopy or climatically marginal forests and savannas, episodic recruitment also occurs as a result of transient moisture or temperature conditions optimal for new recruitment to occur (e.g., Peet 1981).

PLATE 1. Old-growth ponderosa pine forest and gamble oak community on Archuleta Mesa, southwestern Colorado. Photo credit: P. M. Brown.

Climatic vs. disturbance effects should tend to be scale-dependant. Fire-caused cohorts are more likely to be relatively local in size (only a few stands burned catastrophically in a past fire, while others were not affected or burned less intensively), while climatically forced recruitment should be synchronous across larger areas because of the broader-scale "footprints" of climatic anomalies.

The dominant historical disturbance regime in ponderosa pine (*Pinus ponderosa* Laws) forests across western North America consisted of recurrent surface fires (Covington and Moore 1994, Mast et al. 1998, Swetnam and Betancourt 1998, Brown et al. 1999, Heyerdahl et al. 2001, Allen et al. 2002, Ehle and Baker 2003, Friederici 2003, Swetnam and Baisan 2003, Grissino-Mayer et al. 2004). Mature ponderosa pine trees are well adapted to survive surface burning, with thick bark that protects vascular cambium from girdling and high crowns that reduce the likelihood of fatal crown scorch. Ponderosa pine also has relatively large, heavy seeds that are not well adapted to rapid recolonization after extensive crown fires. Dates and locations of surface burning are reconstructed from proxy fire-scar records, distinctive injuries caused by localized cambial death from heating and recorded in tree-ring series. Networks of fire-scar chronologies document regionally synchronous fire years that correspond to seasonal droughts induced by interhemispheric synoptic climate forcings, such as the El Niño-Southern Oscillation (ENSO; Swetnam and Betancourt 1998, Heyerdahl et al. 2002, Westerling and Swetnam 2003).

Less clear is how demographic patterns in ponderosa pine forests relate to climate variation. Most seedlings and smaller saplings were killed during recurrent fires, and forests were generally open as a result (White 1985, Covington and Moore 1994, Allen et al. 2002). Overstory recruitment in many ponderosa pine forests was apparently highly episodic, related both to optimal climate conditions for seed production, seedling germination, and sapling growth (e.g., Pearson 1933, Savage et al. 1996) and to longer intervals between surface fires, which allowed more seedlings and saplings to reach a stage where they were relatively immune from subsequent burns (White 1985, Grissino-Mayer and Swetnam 2000). These factors are correlated, since extended wet periods would have resulted in more years conducive to seedling germination and tree growth in typically xeric ponderosa pine forests and fewer years during which fuels were dry enough for fire ignition and spread. However, other studies suggest that even-age cohort structure in at least some ponderosa pine forests was the result of severe fires opening up canopies for new recruitment to occur (Ehle and Baker 2003). Unfortunately, few tree-ring studies in ponderosa pine forests have collected the tree-establishment data needed to assess regional climatic vs. local disturbance effects on recruitment patterns.
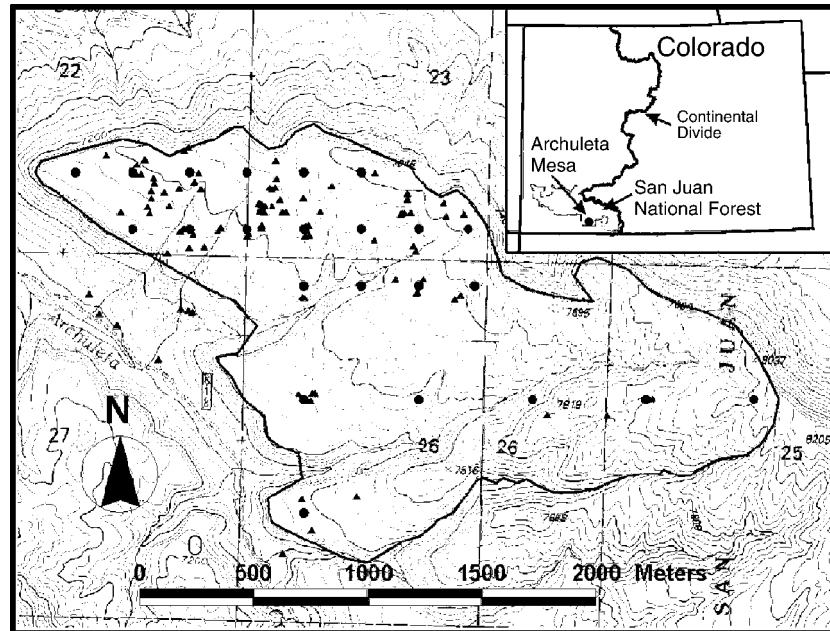
FIG. 1. Location of tree recruitment plots (circles) and fire-scarred trees (triangles) sampled on Archuleta Mesa.

In this study, we constructed chronologies of tree recruitment dates and compared them to proxy reconstructions of fire years, hydroclimate, and ENSO indices to provide inferences about historical climate, fire, and vegetation dynamics across a ponderosa pine landscape in southwestern Colorado. The climate reconstructions document large annual- and decadal-scale variations over the past five centuries, the period covered by fire year and tree recruitment chronologies. Our objectives are to compare timing of tree recruitment to variations in climate forcing and fire years, and to provide inferences about the contribution of both to development of forest structure over time.

METHODS

Study area

Archuleta Mesa is an isolated mesa in southwestern Colorado ~25 km southwest of Pagosa Springs (see Plate 1, Fig. 1). Elevations range from 2225 m to 2450 m, sloping down from the southeast to the northwest. Soils are sandy clays. The forest on the mesa top is an unlogged, old growth forest of mainly ponderosa pine. Other tree species include Rocky Mountain juniper (*Juniperus scopulorum*), Utah juniper (*J. osteosperma*), piñon (*Pinus edulis*), and Douglas-fir (*Pseudotsuga menzesii*). There is abundant oak (*Quercus gambelii*) shrub cover in patches of typically <0.1 ha in size. Ground cover consists of grasses and herbaceous species. Instrumental climate averages from nearby Pagosa Springs (elevation 2200 m) for the period 1906 to 1998 were: January maximum temperature, 3.3°C, minimum −17.0°C; July maximum temperature, 28.4°C, minimum 7.3°C; annual precipitation, 513 mm.

Reconstructing tree recruitment dates and fire years

We designated a 307-ha study landscape on the mesa top, within which we established a 500-m grid for tree recruitment sample plot locations (Fig. 1). We use the term "tree recruitment" to refer to trees that established in the overstory and have persisted to the present. We increased plot density to a 250-m grid on the northwestern tip of the mesa to increase sampling of larger ponderosa pine trees in this area. A total of 23 plots were sampled. We used *n*-tree density-adapted sampling methods (Jonsson et al. 1992, Lessard et al. 2002) to sample the nearest 30 remnant (logs and snags) or living trees ≥20 cm diameter at breast height (dbh) to each plot center. The maximum plot radius was set at 40 m (~0.5 ha in area) and most plots were <0.25 ha in size. Increment cores were removed from 10 cm height above ground level on living trees and cross sections were cut from logs and snags such that one surface was 10 cm above the estimated root–shoot boundary. Sampled cores were no more than a field-estimated 10 yr from pith to minimize pith offset when assessing pith date. Tree diameters at 10 cm height were measured on living trees or estimated for remnant trees missing bark, sapwood, and often heartwood.

We collected cross sections from an additional 70 fire-scarred trees for reconstruction of fire frequency and timing (Fig. 1). We collected samples from living trees, logs, and snags that both exhibited sequences of multiple fire scars and from which we were able to obtain a usable cross section (many fire-scarred logs were too decayed for sampling). Multiple-scarred trees were selected to maximize the time span of fire years (Swetnam and Baisan 2003). While this is not a com-

plete spatial census of fire-scarred trees, we assumed this dataset to be representative of temporal patterns of past fire years across the study landscape for comparison to climate reconstructions and tree recruitment dates.

We used standard dendrochronological methods to crossdate all cores and cross sections against a master chronology for Archuleta Mesa. We used visual matching of ring characteristics and correlated measured ring widths to assure absolute pith and fire-scar dates. Questionable dates were not used in subsequent analyses. Intra-annual positions of fire scars also were noted to assess season of fire occurrence. On increment cores and cross sections that did not include pith but inside ring curvature was visible, pith dates were estimated using overlaid concentric circles of varying diameters that take into account both average inside ring widths and an estimated distance to pith. Pith dates at 10 cm height were corrected to germination dates by subtracting 5 yr, the average time we estimated for seedlings to grow from germination to 10 cm height (P. M. Brown, *unpublished data*). Tree germination dates (referred to as tree recruitment dates in this paper) and fire-scar dates were compiled into chronologies using program FHX2, an integrated package for graphing and statistical analyses of fire and forest histories (Grissino-Mayer 2001).

Evaluating fire frequency

We determined mean, median, and Weibull median fire intervals to describe and compare fire frequency using different subsets of fire years. Fire frequency analysis is based on composited fire years (Dieterich 1980) derived from fire scars recorded on all trees. We consider fire scars only as proxy evidence (i.e., the event recorded in a natural archive) for dates of fire events, and not as a true representation of burning across the landscape (sensu Baker and Ehle 2001). We assume that during any fire year there were many trees that had fire at their base but did not record a fire scar (Falk 2004) that invalidate assessment of precise spatial patterns of burning from fire-scar evidence. However, we assume that percentages of trees recording fire scars during fire years are representative of the relative spatial scales of burning for those years (Swetnam and Baisan 2003).

Evaluating tree recruitment, fire year, and climate relationships

We graphically and statistically compared tree recruitment and fire year chronologies with independently derived tree-ring based reconstructions of precipitation, drought, and ENSO to assess climatic forcing of fire years and recruitment episodes. We used superposed epoch analysis (SEA; Swetnam 1993) to compare average annual climate conditions for the set of fire years recorded on two or more trees to climate for the entire period of record. We also used SEA to compare climate during years prior to fire years to assess antecedent climate conditions. Significant climate conditions were determined using bootstrapped confidence intervals based on average annual climate values with the same number of years as fire year data sets. We exclude fire years recorded on only one tree from this analysis since there also may be false positives, scars not caused by fire but assumed to be fire scars (Falk 2004), when assigning fire years. We assume that use of fire-scar dates recorded on two or more trees minimizes the likelihood of false positives since it is less likely that other possible scarring mechanisms (e.g., lightning, fell-tree abrasions) affected more than one tree during the same year. We used four independently derived tree-ring based climate reconstructions in SEA: (1) annual precipitation from northern New Mexico (Grissino-Mayer 1996); (2) summer Palmer drought severity indices (PDSI) from the four-corners area (Cook et al. 2004); (3) Southern Oscillation Index (SOI; Stahle et al. 1998), and (4) Niño3 sea surface temperature (SST) index (Cook 2000). SOI is a commonly used measure of ENSO, and is the difference in surface air pressure between Darwin, Australia, and Tahiti. The Niño3 SST index is also a measure of ENSO and is the average sea surface temperature from mid-tropical Pacific recording stations, the region that has the largest variability in sea-surface temperature on El Niño (3–4 yr) time scales. The SOI reconstruction only goes back to 1706 and we used the SST index reconstruction to extend our inferences about ENSO forcing of fire years for the entire 500-yr tree-ring record.

RESULTS AND DISCUSSION

We were able to crossdate 574 of 730 trees collected, of which 515 had pith or on which a pith date could be estimated with confidence. Many of the trees we were not able to crossdate were juniper (65 trees, 37% of the total juniper trees collected), mainly because of false and missing rings. Other samples had too few rings, were too complacent (i.e., not enough variability in ring patterns to cross-match against the master chronology), were too slow growing (i.e., rings too tight), or contained injuries, branches, or decay that made accurate crossdating impossible.

Recruitment dates are summarized and graphically compared with fire years and reconstructions of annual precipitation, PDSI, and ENSO indices in Fig. 2. Very few trees (almost all ponderosa pine) predate a multiyear megadrought centered in the 1580s (Fig. 2b, d). This prolonged drought, the most severe in at least the last 1000+ years in this region (Grissino-Mayer 1996), has been identified in tree-ring chronologies from throughout the western United States and northern Mexico (Stahle et al. 2000). Some seedlings established shortly before or during the megadrought, but these were very slow growing until moisture regimes became more favorable during a prolonged pluvial in the early 1600s. Abundant ponderosa pine recruitment also oc-
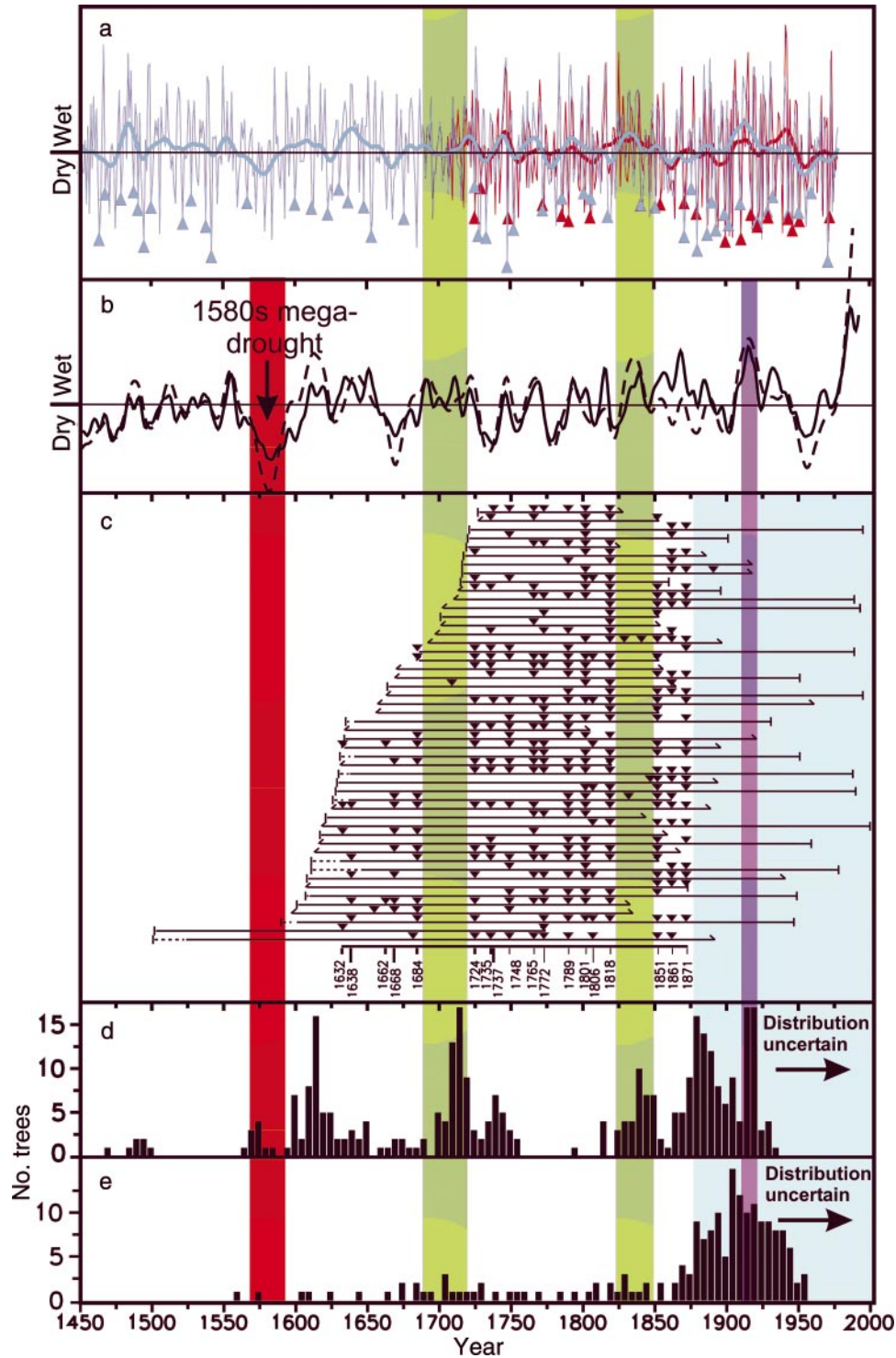
FIG. 2. Comparison of ENSO, hydroclimate, fire-year, and tree recruitment chronologies. (a) ENSO time series (blue, Niño3 SST index [Cook 2000]; red, SOI [Stahle et al. 1998]). SOI is reversed to be consistent with other moisture indices. Heavy lines are annual series smoothed with 20-yr cubic smoothing splines. Years of significant triennial wet/dry oscillations $(y_t - y_{t-2})$ identified by superposed epoch analyses (SEA) in Fig. 3c, d are shown by arrows centered on the drought years. Biennial oscillations $(y_t - y_{t-1})$ also were tested and found to be largely absent during the fire-quiescent periods of 1684–1724 and 1818–1851. (b) Reconstructed hydoclimate time series, smoothed with 20-yr cubic splines. The solid line shows the annual precipitation in northeastern New Mexico (Grissino-Mayer 1996), and the dashed line shows the Palmer drought severity index for the four-corners area (Cook et al. 2004). (c) Fire-year chronology for Archuleta Mesa. Horizontal lines mark time spans of individual trees, with fire scars designated by inverted triangles. Fire years at bottom are those recorded

curred during the early 1600s and likely was a result of the combination of openings from drought-caused tree mortality as well as moisture conditions optimal for seedling germination and sapling growth in this dry ponderosa pine forest. The effects of the 1580s megadrought and following pluvial on forest age structure in the Southwest have been noted elsewhere (Swetnam and Brown 1992). Comparatively few trees in forests throughout Arizona and New Mexico predate the late 16th century but it is easy to find trees that established during the early 17th century.

It is doubtful that severe fires were responsible for stand opening during the megadrought, since we found no fire scars on any trees surviving from this period. It is, however, possible that other disturbance factors, such as bark beetles, contributed to widespread and synchronized mortality during the megadrought. Massive forest dieback occurred in many forests of the four-corners region during 2002–2004 as a combined result of severe drought and extensive beetle outbreaks (USDA Forest Service 2004). However, no evidence of bark beetles, such as blue stain in sapwood, persists from the megadrought period. Any trees that would have died in the megadrought have long since decayed from the landscape.

In addition to an extended pluvial, the early 17th century also was a period with few fires (Fig. 2c). Seedlings and smaller saplings are readily killed by surface burns, and longer intervals between fires would have allowed more trees to grow to a height where they could survive subsequent fires. After the early 1600s, two distinct pulses of tree recruitment occurred during extended fire-quiescent periods, the first from 1684 to 1724 (40 yr) and the second from 1818 to 1851 (33 yr). Excluding these two periods, fires occurred on average every 11 yr (range 2 to 24 yr) from 1632 to 1871 (Table 1).

It appears that climate change likely affected fuel conditions that were less favorable for burning during the fire-quiescent periods. SEA documents that fires occurred predominately during dry years, and were preceded by one to three wet years (Fig. 3a, b). Fire years, on average, also were La Niña years, which are typically dry years in the Southwest, and often preceded by El Niño years, which typically are wet (Fig. 3c, d). This pattern has been interpreted as a buildup of surface fuels (grasses and forbs) during exceptionally wet years which then burn more extensively and readily during subsequent drought years (Swetnam and Baisan 1996, Swetnam and Betancourt 1998, Brown et al. 2001, Wes-

TABLE 1. Fire frequency estimates for fire years at Archuleta Mesa, southwestern Colorado, USA.

Period	Fire interval (mean ± SE)	Median	WMI†	Range
1632–1871	14.1 ± 10.1	11	12.4	2–40
1632–1871‡	11.1 ± 5.7	10	10.6	2–24

Note: All values are in years.
† Weibull median interval.
‡ Excluding the two fire-quiescent intervals from 1684–1724 and 1818–1851.

terling et al. 2003). This pattern has been found in both tree-ring and modern fire-atlas data sets. Coupled interannual oscillations of El Niño/La Niña years of the magnitudes apparently necessary for a pattern of fuel buildup and drying were notably absent during the 1684–1724 and 1818–1851 fire-quiescent periods (Fig. 2a). These results suggest that a dampening of interannual moisture and ENSO variability was as crucial a factor for modifying fire occurrence and causing tree recruitment as extended wet conditions, depending on the period in question. Contemporaneous fire-quiescent periods and tree cohorts occurred in other ponderosa pine forests in the Southwest (White 1985, Swetnam and Betancourt 1998, Mast et al. 1999; T. W. Swetnam, *personal communication*) providing supporting evidence for a hypothesis of regional climate synchronization of fire timing and related episodes of successful tree recruitment. However, more recruitment and fire year data sets from throughout the Southwest are needed to better assess broad-scale direct and indirect (mediated by fire timing) effects of climate on recruitment patterns.

Climate forcing of recurrent surface fires affected density-independent control on tree recruitment in ponderosa pine forests. Recruitment in many forests tends to be density limited because of competitive limitations for light, nutrients, water, and space imposed on seedlings by the existing overstory. However, at Archuleta Mesa, recruitment occurred largely during periods when surface fires were restricted by climate conditions less conducive to burning. Fires burned mainly in understory grasses and herbaceous fuels and, since they were affected by seasonal weather conditions, would have occurred irregardless of overstory tree or seedling density at the time of burning. During periods of shorter-interval fires, most seedlings and saplings were killed before they had a chance to establish and forests were typically open as a result. Historic accounts and early settlement photographs of ponderosa pine forests

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on ≥2 trees and used for SEA in Fig. 3. (d, e) Tree recruitment dates by 5-yr periods for (d) ponderosa pine and (e) other tree species. Recruitment dates are truncated toward the present, since we only collected data on trees >20 cm. The red vertical bar marks the 1580s megadrought, green bars mark fire-quiescent periods, the blue bar marks recent decades of fire exclusion after Euro-American settlement, and the purple bar marks the early 20th-century wet period and pulse of recruitment in ponderosa pine centered on 1919 (Savage et al. 1996).
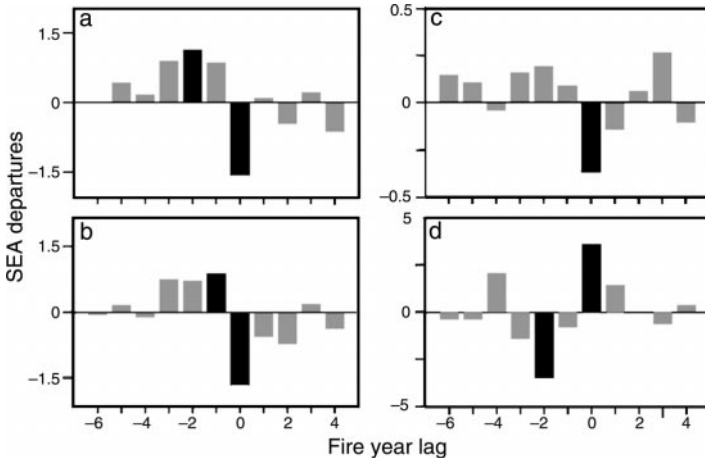
FIG. 3. Superposed epoch analyses of hydroclimate and ENSO anomalies for fire years in Fig. 2c: (a) precipitation in northern New Mexico (Grissino-Mayer 1996); (b) PDSI from the four-corners region (Cook et al. 2004); (c) Niño3 SST index (Cook 2000); and (d) SOI (Stahle et al. 1998). Black bars mark significant departures ($P < 0.01$) based on bootstrapped confidence intervals. SOI is reversed in terms of moisture relative to other proxies (dry years are high SOI). Fire year lag 0 is the average climate anomaly for all fire years, with antecedent conditions indicated by negative lags.

throughout the West document often "park-like," open, multi-aged forest stands, composed of mainly large trees scattered across grassy understories (Covington and Moore 1994, Allen et al. 2002, Friederici 2003). Timing of fire intervals and recruitment suggests that trees had to have been on the order of 10–40 yr old before they experienced their first surface fire to successfully recruit into the overstory and survive to the present (Fig. 2d).

Density-independent recruitment in ponderosa pine forests contrasts with density-dependent recruitment in closed-canopy forests. Cohorts of even-aged trees in closed-canopy forests are often evidence of severe crown fires or other major disturbance events (Heinselmann 1973, Agee 1993, Johnson and Gutsell 1994). However, even-aged cohorts in ponderosa pine forests likely have little to do with episodic mortality in the overstory (sensu Baker and Ehle 2002, Ehle and Baker 2003), but rather relate primarily to extended fire-quiescent periods and favorable climatic episodes. White (1985) proposed that spatially episodic recruitment in ponderosa pine forests was restricted to "safe sites," locations missed by burning during patchy surface fires. Our results suggest that more important effects on broader-scale forest structure were "safe periods," extended fire-quiescent intervals that resulted in temporally distinct recruitment episodes. Regional differences in ponderosa pine forests make generalizations difficult (Allen et al. 2002), but since virtually all ponderosa pine forests show evidence of surface fires in the form of fire scars it is likely that cohort structures in many areas were more dependent on episodic recruitment opportunities rather than episodic mortality events that reduced overstory density.

In addition to surface fires, is it possible that so-called mixed- or variable-severity fires also occurred on Archuleta Mesa? Mixed-severity fires were primarily surface burns that contained patches of fire-caused tree mortality (Agee 1993, Ehle and Baker 2003). A few stands exhibit "truncated" recruitment dates (i.e., the oldest trees in the stand are much younger than the oldest trees present on the landscape; Table 2), and it has been suggested that such variation in stand ages provides evidence for mixed-severity fires (Ehle and Baker 2003). However, it is impossible to know why some portions of the forest are older than others. Variation in ages of surviving trees in any one stand is the result of hundreds of years of patch dynamics that included both chronic as well as episodic tree mortality by any number of factors, only one of which may have been lethal fire but also including drought stress or other disturbances such as insects, pathogens, windthrow, or lightning. What is clear from our results is that by scaling up from individual plots to the entire landscape an emergent pattern appears in which cohort structure is uncoupled from any single mortality event and instead appears to be the result of broader scale climate forcing of fire timing that resulted in successful recruitment episodes (Fig. 2). This conclusion, furthermore, suggests that there are minimum spatial and temporal scales over which tree recruitment and fire histories must be assessed to adequately encapsulate relevant patterns and develop robust inferences (see also Falk 2004). Cohesive patterns resulting from climate forcing only emerge at broader spatial and longer temporal scales. While this study does not address what minimal scales for fire and recruitment histories should be, our data strongly suggest that such scales should encompass more than only a few stands and one to two

TABLE 2. Spatial variation in oldest recruitment dates in plots.

Oldest date	No. plots
Before 1600	13
1601–1650	6
1651–1700	2
1701–1750	1
1751–1800	0
1801–1850	0
1851–1900	1

hundred years of tree recruitment and fire history data (e.g., Ehle and Baker 2003).

Land use changes that accompanied Euro-American settlement in the latter half of the 1800s led to cessation of surface fires from virtually all ponderosa pine forests across the western United States (Covington and Moore 1994, Swetnam and Betancourt 1998, Brown et al. 2001, Friederici 2003: Fig. 2c). The proximal cause of fire cessation in the late 19th century was widespread sheep and livestock grazing that was later followed by active fire suppression in the 20th century (Allen et al. 2002). The 135 yr long fire-free period from 1871 to 2005 is more than three times as long as the longest historical fire-quiescent period of 40 yr from 1684 to 1724. Establishment of both ponderosa pine and less fire-tolerant species has been unchecked by fire-caused mortality of seedlings with the result that current forests are much denser than in the past (Covington 2000: Fig. 2d, e). Optimal climatic conditions for ponderosa pine regeneration and establishment in the early 20th century also contributed to denser forests, especially during 1919 when a tremendous pulse of seedlings established across apparently much of the Southwest (Pearson 1933, Savage et al. 1996: Fig. 2d). Increased post-settlement tree density has resulted in altered canopy fuel structures, including formation of ''ladder'' fuels that allow wildfires to burn more severely. Crown fire has largely replaced surface fire in many ponderosa pine forests (Covington 2000, Allen et al. 2002). Record-setting fire sizes and severities in ponderosa pine and closely related forests during fire seasons in 1996, 2000, 2002, and 2003 have been attributed in large part to changes in forest structure and fuel conditions over the period of fire exclusion (Covington 2000, Romme et al. 2003).

Previous modeling of forest dynamics has tended to discount rates of tree recruitment relative to rates of tree mortality (e.g., Shugart 1998). Climatically forced mortality can cause rapid changes in forest structure or composition while recruitment has been viewed as a much slower process (Allen and Breshears 1998). Yet, after the 1580s megadrought, southwestern ponderosa pine forests were able to recover fairly rapidly in following decades that were both relatively climatically optimal for seedling establishment and growth and that saw few fires. This has important implications for prediction of vegetation response after recent massive mortality caused by interactions between drought and insect populations over millions of hectares of piñon and ponderosa pine forests in the southwestern United States (USDA Forest Service 2004). Over multicentury time scales, broad-scale dynamics in the Southwest have included abrupt and synchronized mortality that, as least once before in the relatively recent past, was followed by fairly rapid community recovery. Recruitment data highlight the importance of historically contingent events in formation of forest structure and composition, and the dynamic interaction of climate, dis-

turbances such as fire, and forest structure over both short and long time scales. Historical data aid in modeling possible future responses of plant communities to climate change and accompanying effects in disturbance regimes (Overpeck et al. 1990).

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