CSIRO PUBLISHING

International Journal of Wildland Fire **2014**, *23*, 234–245
http://dx.doi.org/10.1071/WF13053

Fire regime shift linked to increased forest density in a piñon–juniper savanna landscape

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Abstract. Piñon–juniper (PJ) fire regimes are generally characterised as infrequent high-severity. However, PJ ecosystems vary across a large geographic and bio-climatic range and little is known about one of the principal PJ functional types, PJ savannas. It is logical that (1) grass in PJ savannas could support frequent, low-severity fire and (2) exclusion of frequent fire could explain increased tree density in PJ savannas. To assess these hypotheses I used dendroecological methods to reconstruct fire history and forest structure in a PJ-dominated savanna. Evidence of high-severity fire was not observed. From 112 fire-scarred trees I reconstructed 87 fire years (1547–1899). Mean fire interval was 7.8 years for fires recorded at ≥2 sites. Tree establishment was negatively correlated with fire frequency ($r = -0.74$) and peak PJ establishment was synchronous with dry (unfavourable) conditions and a regime shift (decline) in fire frequency in the late 1800s. The collapse of the grass-fuelled, frequent, surface fire regime in this PJ savanna was likely the primary driver of current high tree density (mean = 881 trees ha^{-1}) that is >600% of the historical estimate. Variability in bio-climatic conditions likely drive variability in fire regimes across the wide range of PJ ecosystems.

Additional keywords: fire scar, *Juniperus monosperma*, *Juniperus scopulorum*, *Pinus edulis*, PJ savanna, tree ring.

Received 31 March 2013, accepted 31 July 2013, published online 28 January 2014

Introduction

Piñon–juniper (PJ) ecosystems that are composed of a variety of *Pinus* and *Juniperus* species cover $\sim 30 \times 10^6$ ha in the western USA (West 1999*a*). For comparison, ponderosa pine covers $\sim 11 \times 10^6$–16×10^6 ha (Van Hooser and Keegan 1988). High variability among PJ ecosystems, driven in part by varying climate across a large geographic range, has resulted in an incomplete understanding of PJ ecosystem dynamics and fire regimes (see review by Romme *et al.* 2009). Romme *et al.* (2009) defined three fundamentally different PJ vegetation types: (1) persistent woodlands characterised by low 20 understorey plant cover and dominance by trees, (2) wooded shrublands that are shrub dominated with varying densities of trees and (3) savannas that have grass cover and low to moderate canopy cover. The proportion of annual precipitation in the growing season is thought to be one of multiple important climatic factors driving the variability among PJ ecosystems (Jacobs *et al.* 2008). For example, PJ ecosystems in the south-eastern portion of the geographic distribution (southern New Mexico and west Texas) receive the greatest proportion of precipitation in the growing season, which supports high native grass cover (fine fuels) compared to more northern PJ types on the Colorado Plateau (Jacobs *et al.* 2008). Climate-mediated variability in PJ vegetation cover and structure likely also contributes to variability in ecosystem processes (e.g. fire), which in turn affect PJ vegetation dynamics.

Fire is arguably the keystone ecological process in many ecosystems (Agee 1993). Fire is particularly important in the lightning-rich and drought-prone south-western USA (Allen 2002). Historical fire regimes in PJ ecosystems are best documented in persistent woodlands, where infrequent (>250-year fire rotation), high-severity fire regimes have been reconstructed using tree-ring age structure methods at multiple locations on the Colorado Plateau (Floyd *et al.* 2004; Huffman *et al.* 2008; Shinneman and Baker 2009). However, pre-1900 fire regimes and vegetation dynamics in PJ savannas are not well studied, and it is logical that the grass cover could support frequent, low-severity fire (Romme *et al.* 2009). Multiple tree-ring studies have documented evidence of low-severity fire at the PJ–ponderosa pine (*Pinus ponderosa* Laws., PIPO) ecotone from fire-scarred PIPO and occasionally from PJ species (Allen 1989; Brown *et al.* 2001; Huffman *et al.* 2008), but direct evidence of spreading low-severity fire in PJ ecosystems is not well documented. Evidence might include multiple cross-dated fire scars (on piñon and juniper trees) at multiple locations with age structure evidence that overstorey trees generally survived the fire (Baker and Shinneman 2004). The best evidence of low-severity fire in PJ ecosystems in the south-western USA may be from west Texas, where (Poulos *et al.* 2009) found multiple fire-scarred piñon (*Pinus cembroides* Zucc.) in two mountain ranges, but fire extent and relationships between fire and PJ age structure are not clear.

Piñon–juniper extent and tree density has increased in many locations across the western USA since the late 1800s (Leopold 1924; Tausch *et al.* 1981; Jacobs *et al.* 2008), but not others (Manier *et al.* 2005). Proposed mechanisms for increased density include: (1) recovery from disturbance, (2) natural range expansion, (3) livestock grazing, (4) climatic variability and

(5) fire exclusion (Romme *et al.* 2009). Untangling the competing hypotheses can be challenging, but it is important not to assume that all increases in woody plant density result from anthropogenic causes (Swetnam *et al.* 1999). Fire exclusion would lead to increased PJ tree density if frequent surface fires historically killed most seedlings and saplings (Leopold 1924; Burkhardt and Tisdale 1976; Miller and Rose 1999). Evidence supporting the fire exclusion hypothesis could include (1) increased tree establishment coinciding with the onset of surface fire exclusion and (2) low tree establishment during periods with high historical fire frequency. Alternatively, if climatic conditions favourable for PJ establishment were driving increased forest density then the period with the highest establishment rate would likely occur during wet conditions (Soulé *et al.* 2004; Gray *et al.* 2006). If increasing forest density was part of natural post-disturbance succession or 'recovery' (Floyd *et al.* 2004) then there should be evidence of high-severity fire (e.g. fire-killed snags and logs).

The goal of my research was to increase the understanding of historical fire regimes and vegetation dynamics for PJ ecosystems containing high grass cover (i.e. PJ savannas), where there is currently insufficient data for confident statements (see review by Romme *et al.* 2009). My specific research questions were as follows:

(1) Did the historical fire regime in a PJ savanna landscape include frequent, low-severity fires?
(2) Has PJ forest density changed following late 19th century Euro-American settlement, and if so, what were the influences of fire, grazing and climate?

Methods

Study area

Rowe Mesa is a ~31 000-ha, gently sloped mesa in north-central New Mexico (35°27′31″N; 105°43′33″W, Fig. 1). It is located at the nexus of the Southern Rocky Mountain, Southern Shortgrass Prairie and Arizona–New Mexico Mountains Ecoregions. Elevation on the mesa ranges from 1963 m to 2455 m above sea level and the mean slope is 4°. Half of the landscape (47%) is classified as PJ and the remainder is grassland (29%) and PIPO (24%, www.landfire.gov, 5 August 2012). Grassland valleys connect upland forest patches that are currently dominated by PJ species on xeric sites and PIPO on the more mesic north-facing sites and in drainages. Extensive young PJ regeneration (estimated to be $<$100 years old) is found within forest stands, at the grassland ecotone and throughout many of the grasslands. The PJ type is composed of Colorado piñon pine (*Pinus edulis* Engelm., PIED), Rocky Mountain juniper (*Juniperus scopulorum* Sarg., JUSC) and one-seed juniper (*Juniperus monosperma* [Engelm.] Sarg., JUMO), listed in decreasing order of abundance. The PIPO type is dominated by ponderosa pine (*Pinus ponderosa* Laws.). Grasslands are dominated by blue grama (*Bouteloua gracilis* [Willd. ex Kunth] Lag. ex Griffiths), which is also common throughout the PJ and PIPO forest understorey. Wavyleaf oak (*Quercus undulata* Torr.) is an understorey shrub present in varying densities in all vegetation types. Soils consisted of Typic Haplustalfs, Eutroboralfs and Ustochrepts derived from sandstone and mudstone parent material (USDA 1992).

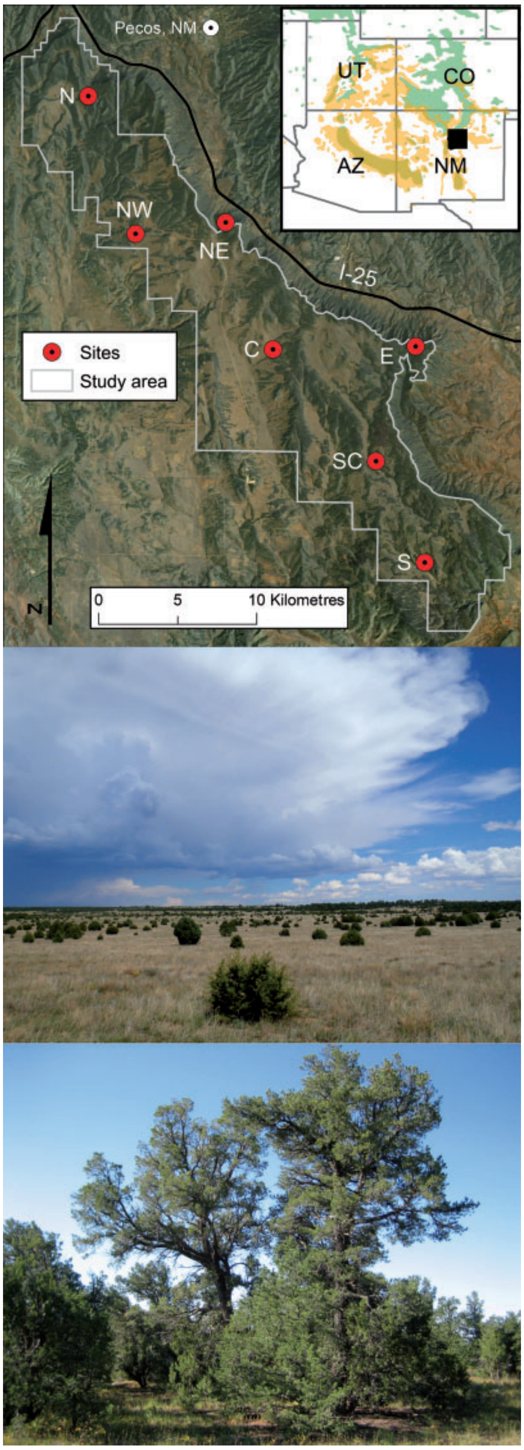

Fig. 1. (Top) Aerial photo of study area and sample sites on Rowe Mesa, north-central New Mexico (see Table 1 for site names). Light areas are grassland and dark areas are forest. Inset map illustrates the location of the study area within the south-western USA and the ranges of the dominant piñon–juniper (PJ) tree species in the study area; *Pinus edulis* (orange), *Juniperus scopulorum* (green) and both species (brown) (after Little 1971). (Middle) A PJ savanna grassland on Rowe Mesa infilling with young piñon and juniper trees. (Bottom) A typical open grassy old-growth PJ stand on Rowe Mesa that is being infilled by PJ tree species $<$130 years old.

Table 1. Fire and vegetation history sample site information

EVT, Existing Vegetation Type (see www.landfire.com); PJ, piñon–juniper; PIPO, ponderosa pine. Current and pre-settlement vegetation type determined by plurality of PJ or PIPO tree species at two vegetation plots within each fire scar site (see Methods for details)

Site	Site code	Elevation (m)	Area (ha)	Number of fire-scarred trees	EVT	Current vegetation	Pre-settlement vegetation
North	N	2356	1.6	11	PJ–PIPO	PJ	PJ–PIPO
North West	NW	2177	2.6	17	PJ–PIPO	PIPO	PIPO
North East	NE	2340	3.5	15	PJ–PIPO	PJ–PIPO	PJ–PIPO
Central	C	2234	5.4	21	PJ–PIPO	PJ	PJ
East	E	2329	4.0	11	PIPO	PIPO	PIPO
South Central	SC	2207	1.3	7	PIPO	PIPO	PIPO
South	S	2095	2.7	30	PJ	PJ	PJ–PIPO

The climate in the study area is continental and semi-arid, and annual precipitation is dominated by summer monsoon convective storms. Annual average precipitation at the Pecos Ranger Station (2125-m elevation, 10 km north of the study area) is 44.2 cm, with 38% occurring in July and August (1970–2000; Western Regional Climate Center; www.wrcc.dri.edu, accessed 6 June 2012). Annual average temperature is 9.6°C with an average maximum of 18.4°C and average low of 0.8°C (1970–2000). Forty five wildfires were reported in the study area between 1973 and 2009 (USFS, unpubl. data). All fires were suppressed and the largest fire burned 320 ha in 2007. Most fires (69%) were lightning-ignited; peak ignition occurred from May to July, and maximum area burned occurred in June during the pre-monsoon 'dry lightning' period (USFS, unpubl. data).

The Atchison, Topeka and Santa Fe transcontinental railroad arrived in Lamy, NM (south of Santa Fe, NM) in 1879, running <1 km north of Rowe Mesa through Glorieta Pass (Debuys 1985). The ability to transport livestock to pasture and to market by railroad enabled widespread and intense livestock grazing that dramatically reduced herbaceous vegetation in many locations throughout the south-western USA (Bailey 1980). Early 1900s surveys describe Rowe Mesa as '…very good grazing land but of recent years it has been severely overgrazed by sheep and goats' and 'sheeped to death' (Stabler 1906). Despite the presence of the large Puebloan community of Pecos just a few kilometres to the north that was occupied for many centuries before the late 1800s, there is little archaeological evidence of habitation or land use on Rowe Mesa in the centuries before railroad arrival in 1879. This is likely because there is not permanent water on Rowe Mesa. After 1879 the most common land use was grazing and selective tree harvesting, both of which continue today. I use the term 'pre-settlement' to describe the period before railroad arrival (pre-1879) and the associated intensive land-use changes associated with increased Euro-American settlement.

Study design

I used a 7-km grid to identify seven sites on Rowe Mesa that were spatially distributed across the study area (Fig. 1). Grid points that were located in grassland or young (<130 year old) forest were moved to the nearest forested patch >1 ha in area with live or dead trees estimated to be pre-settlement (>130 years old). The final sites were located 150 to 1300 m from the original grid points due to the extensive grassland and young (post-settlement) PJ cover. The final distance between adjacent sites ranged from 5.5 to 8.7 km (mean, 7.4 km). Site area ranged from 1.3 to 5.4 ha due to differences in the sizes of forested patches (Table 1).

Field methods

To reconstruct the fire history at each site I collected wedges or cross-sections from all fire-scarred *Pinus* spp. trees, stumps, snags and logs (Arno and Sneck 1977). Forty two fire-scarred JUSC were mapped across the study area, but samples were only collected from ten JUSC at three sites (C, S and NE). Fire-scarred JUSC were not sampled at all sites because it was uncertain whether the JUSC tree rings would crossdate (e.g. Huffman *et al.* 2008).

To assess the effects of fire on tree establishment and survival through time I quantified forest age structure associated with the fire scar record at 14 vegetation plots (two per fire scar site). The circular vegetation plots (0.2 ha, 25.2 m radius) were centred on two randomly selected fire-scarred trees separated by >100 m at each fire scar site. Within each vegetation plot, I cored the five trees with the largest diameter at breast height (DBH) of each of the three dominant species in the study area (JUSC, PIED and PIPO). All increment cores were collected as close to the base of the tree as possible (<0.3 m) and angled down to intersect the estimated location of the root crown in an attempt to sample all the years of tree growth. I re-sampled trees until I extracted a core containing rings estimated to be within 10 years of the pith. In addition to the age structure collected within the vegetation plots, I cored the two largest (DBH) trees within 10 m of all sampled fire scarred-trees at each study site.

To quantify tree density and composition of the contemporary (2011) and pre-settlement (1879) forest associated with the fire scar record I generally followed the methods of Fulé *et al.* (1997). These forest reconstruction methods have been shown to be highly accurate when tested against early 20th century forest surveys in wetter PIPO forests (Moore *et al.* 2004). I collected the following variables for all trees >5-cm DBH within each vegetation plot: species, diameter (DBH for live trees and DRC, diameter at root crown, 0.0 m, for dead trees) and condition class. Within a 1 by 25 m belt transect located along a randomly selected radius of the vegetation plot, I recorded species, height and condition class of all tree regeneration (<5-cm DBH). Density of charred live and dead trees has been used as evidence of fire in PJ ecosystems (e.g. Bauer and Weisberg 2009), so all live and dead trees within the vegetation plots were surveyed for char.

Laboratory methods

All tree-ring samples were sanded with progressively finer sandpaper until the ring structure was visible and then crossdated using skeleton plots (Stokes and Smiley 1968). Fire scars were dated to the calendar year and assigned seasonality by analysing the relative position of each scar within the annual growth ring. Fire scar seasonality classes include: dormant, early earlywood, middle earlywood, late earlywood, latewood or unknown (Baisan and Swetnam 1990). Fires that only scarred trees between the annual ring boundaries (dormant) were assigned to the year following the scar (i.e. spring or early summer fire that occurred before onset of cambial division). This was based on the dominant occurrence of earlywood fire scars (96%) among the reconstructed fires that burned during the growing season.

I estimated the first year of growth (pith) for both fire scar and age structure samples not containing the pith ring using a concentric circle method (Applequist 1958). Only samples that were estimated to be <25 years from pith were used in the age structure analysis (279 trees). The estimated number of years to pith was 3.9 ± 0.4 (mean $\pm$ standard error of the mean, s.e.). I corrected the fire scar samples for age to sample height by combining two estimates of growth rates for young trees in the study area. First, 15 PIPO (40–105 years old) growing in a range of conditions, from open to dense forest, were destructively sampled at 0.0, 0.3 and 0.6 m above root crown. Second, fire-scarred samples of all species collected from multiple heights on the same tree (ranging from 0.0 to 1.0 m) and containing the pith ring were used to derive an independent estimate of growth rates (cm year^{-1}). The mean growth rate was not different between the two estimates (*t*-test, $t = 0.58$ (d.f. $= 31$), $P = 0.57$), therefore they were combined to derive a mean growth rate of 5.9 ± 0.8 cm year^{-1} (mean $\pm$ s.e.) that was used to correct for age to sample height. Mean ($\pm$s.e.) sample height correction was 2.1 ($\pm$0.2) years.

Data analysis – fire history

The frequency of historical fires reconstructed from fire scars was analysed at three scales: (1) the landscape – all trees at all sites, (2) the site – all trees within a site and (3) among multiple sites (i.e. fire recorded by $\geq n$ of 7 sites) using FHX2 software (Grissino-Mayer 2001). The analysis period for the landscape and multiple-site fire intervals began on the first year that a fire scarred $\geq$10% of the recording trees in the study area and ended with the last fire. The analysis period for site fire intervals is presented for the full period of record at each site. Fire intervals calculated for the common period among sites (1711–1899) were similar to that of the full record (e.g. similar rank order of Weibull median probability interval (WMPI) among sites). WMPI is reported only when the Weibull model adequately fit the fire interval distribution. The landscape and site fire interval data were filtered by percentage of recording trees scarred to produce the following subsets of fires: all fires, fires scarring $\geq$10% of recording trees and fires scarring $\geq$25% of recording trees. Differences between mean fire interval of all fires (MFI_{ALL}) and mean fire interval of fires scarring $\geq$25% of recording trees ($MFI_{25\%}$) at the same site might indicate that fires were more patchy (i.e. fires scarred only a small proportion of the recording trees at a site). Trees were considered 'recording' after the first fire scar. Lastly, the density of charred trees at the 14 vegetation plots was tested for association with site time-since-fire, site MFI_{ALL} and site $MFI_{25\%}$ using the Pearson correlation coefficient (*r*).

Data analysis – forest reconstruction

To reconstruct historical tree density and composition, and test for changes following railroad arrival in 1879, I classified all 3023 measured trees ($n = 2645$ live and 378 dead) from the 14 vegetation plots as pre-1879 (inclusive) or post-1879. Using the diameter and crossdated tree ages of 30 JUSC, 48 PIED and 70 PIPO containing pith and cored at ground level I identified the diameter (DBH) of the smallest pre-settlement tree (i.e. pith year $\leq$1879) for each species. I chose this approach instead of a linear size-age regression because the 'DBH threshold' method was less likely to incorrectly classify fast-growing, large diameter post-settlement trees as pre-settlement. For example, 19% of crossdated PIED were incorrectly classified as post-settlement by the linear size-age model ($r = 0.77$, $P < 0.001$), whereas no trees were incorrectly classified as post-settlement by the DBH threshold method. As a result, the DBH threshold method consistently underestimated post-settlement tree density and overestimated pre-settlement tree density for all species. This conservative reconstruction approach likely compensates for pre-1879 trees that potentially died and decomposed and therefore would not be included in the historical density estimates based on static age structure (*sensu* Johnson *et al.* 1994).

The smallest DBH of trees establishing before 1879 were: 20 cm (PIED), 21 cm (JUSC) and 29 cm (PIPO). JUMO were not aged due to irregular tree rings, but were assumed to have a similar size-age relationship as JUSC. JUMO only accounted for 2% of the total live trees. To estimate the pre- and post-settlement status of dead trees that were not sampled, a linear relationship between DBH and DRC was used to set a similar pre- and post-settlement diameter (DRC) threshold for each species (PIED, $\geq$26 cm; JUSC, $\geq$26 cm and PIPO, $\geq$36 cm). All charred or fire-scarred dead or live trees were assumed to be pre-settlement as there was no field or documentary evidence of fires at the study sites since the late 19th century. To test for changes in tree density between the reconstructed (1879) and contemporary (2011) forest I used permutational multivariate analysis of variance (Anderson 2001; McArdle and Anderson 2001). This method is based on ecological distance or dissimilarity measures (Bray–Curtis in this study) and uses non-parametric permutation and Monte Carlo approaches to derive *P*-values.

Data analysis – relationships among tree establishment, climate, fire and grazing

To evaluate the hypothesis of fire exclusion as a possible mechanism for increased tree density I used multiple methods. Pearson correlation coefficient was used to test for association at the landscape-level between the number of trees recording fire (as fire scars) and the number of tree establishment dates through time (20-year bins, 207 trees). The analysis period began when both the number of trees recording fire and the number of tree establishment dates were >10 trees per 20-year bin (1681), and therefore did not include 60 trees that established between 1481 and 1680. A negative correlation between tree establishment and fire frequency would be expected if high fire frequency was limiting young tree establishment, and periods of reduced fire occurrence lead to increased tree establishment. To test whether changes in tree establishment and fire frequency were (1) coincident with railroad arrival and the onset of intensive livestock grazing in 1879 and (2) can be statistically classified as an abrupt change or an ecological 'regime shift', I applied a method that uses sequential *t* tests to identify the timing and magnitude of regime shifts in the fire and tree establishment data through time (Rodionov 2004). Threshold or regime shift detection methods are commonly used in climate science and have the potential for broader use in ecological studies (*see review by* Andersen *et al.* 2009). The minimum cut-off length of a regime was defined as 40 years (2 observations).

I used two approaches to evaluate the alternative hypothesis that favourable (wet) climate conditions were associated with the late 1800s increase in PJ tree establishment. First I determined whether tree-ring indices from a moisture-sensitive PIED chronology from the study area (Glorieta Mesa; ITRDB 2012) were above or below the long-term (492-year) mean during the period with the greatest increase in tree establishment (1881–1900). The nearest tree-ring reconstructed Palmer Drought Severity Index gridpoint (33, Cook and Krusic 2004) was also evaluated as being negative (dry) or positive (wet) during this period. Second, the PDSI and the PIED tree-ring chronology were tested for a regime shift with the threshold detection method described above using 20-year mean values over the same analysis period as the tree establishment and fire frequency data. The *a priori* level of significance for all statistical tests was set at $\alpha = 0.05$.

Results

Historical fire regime

Frequent, low-severity fires historically burned on the Rowe Mesa landscape, which is currently dominated by PJ vegetation. From 112 fire-scarred trees (9 JUSC, 19 PIED and 83 PIPO) I was able to crossdate 630 fire scars that burned during 87 unique fire years (1547–1899, Figs 2–3). The last fire recorded by multiple trees at $\geq$2 sites was 1870. Landscape composite mean fire interval of all fires (MFI_{ALL}) at all sites was 3.6 years and landscape $MFI_{25\%}$ was 26.9 years (1601–1899, Table 2). Composite $MFI_{25\%}$ at individual sites ranged from 9.9 years at a PIPO dominated site (SC) to 32.3 years at a PJ-dominated site (South site, Table 3). MFI of fires recorded at $\geq$2 sites was 7.8 years and at $\geq$4 sites (greater than half of the sampled landscape) was 23.7 years (Table 2). WMPI exhibited similar patterns among sites and filters, but was consistently lower than MFI (Tables 2, 3). The density of charred trees at the 14 vegetation plots was positively correlated with site MFI_{ALL} ($r = 0.62$, $P < 0.05$), but not time-since-fire ($r = -0.11$, $P = 0.70$) or site $MFI_{25\%}$ ($r = 0.03$, $P = 0.92$).

PIED or JUSC trees with multiple fire scars were crossdated at four of the seven sites (Figs 2–3). In total 71% (20 of 28) of fire-scarred PIED or JUSC had multiple fire scars. The oldest fire-scarred trees at three of the seven sites were PIED or JUSC. Twenty of the 30 fire-scarred trees at site S were PIED or JUSC (Fig. 2). In total 36 of the 87 unique fire years reconstructed in the study area were recorded as fire scars by PIED or JUSC trees (range of scar dates, 1601–1888). Of the fire years recorded by PIED or JUSC, 85% were recorded by at least one other tree at the same site and by additional trees at other sites separated by an average of 7.4 km (i.e. within- and between-site replication). For example, the 1812 fire was recorded by 22 trees at two sites, 5 of which were PIED at site S (Fig. 2). PJ-dominated sites generally had a greater difference between MFI_{ALL} and $MFI_{25\%}$ (e.g. $MFI_{ALL} = 10.6$ years and $MFI_{25\%} = 32.3$ years, site S), compared to PIPO-dominated sites (e.g. $MFI_{ALL} = 8.0$ years and $MFI_{25\%} = 9.9$ years, site SC, Table 3).

The seasonal position was determined for 367 out of 630 (58%) of the fire scars. Most (73%) fire scars that could be assigned seasonality ($n = 267$) occurred in the dormant season (between ring boundaries). Fire scars that occurred within the growing season ($n = 100$) predominantly occurred in the early earlywood (62%) and rarely (4%) in the latewood. For 28 fire years, both dormant and within-ring fire scars were recorded; in these cases, the most frequent within-ring scar position was early earlywood (89%), and no fire scars occurred in the latewood.

Contemporary and reconstructed forest composition, density and age structure

In 2011, 62% of all live trees ($n = 2467$) in the 14 vegetation plots were PJ tree species (i.e. PIED, JUSC or JUMO). In the contemporary forest, 94% of the trees were estimated to have established after 1879 (<130 years old). Contemporary mean ($\pm$ s.e.) tree density was 881 ($\pm$127) trees ha^{-1}, which was significantly greater than the reconstructed pre-settlement mean tree density of 135 ($\pm$15) trees ha^{-1} ($F = 11.87$; $P < 0.001$; Table 4). Increased tree density was observed at all sites. Mean tree regeneration density (<5-cm DBH) of PIED in 2011 was 1514 trees ha^{-1}, which accounted for 85% of all tree regeneration. Even-aged stands or groups of potentially fire-killed snags or logs were not present at any sites. A high proportion (95–100%) of the sampled pre-1879 trees ($n = 13$– 44 trees per site) survived two or more fires that were recorded as fire scars at the respective sites. Clusters of trees regenerated in the late 1700s at three sites (NW, C, and E) at the beginning of a site-specific, multi-decadal fire free period (Figs 2, 4). Overall, variability in tree establishment through time (1681–1940) had a strong negative correlation with fire frequency ($r = -0.74$, $P < 0.005$, $n = 206$ establishment dates, 442 fire scars; Fig. 4).

Late 19th century regime shifts

A regime shift occurred in both the number of trees recording fire (decrease) and the number of tree establishment dates (increase) in 1881 ($P < 0.05$, Fig. 4). A regime shift was not detected in the late 1800s for the reconstructed PDSI or the moisture sensitive PIED tree-ring chronology ($P > 0.05$). Nor was the timing of late 19th century fire exclusion and increased tree establishment associated with a wet climatic episode. This period of reduced fire and increased tree establishment (1881–1900), was the second lowest 20-year period of local PIED tree-ring growth (>1 s. d. below the 450-year mean), and contained two of the five single years with lowest tree-ring growth (i.e. dry conditions, Fig. 4). Similar patterns were observed with reconstructed PDSI.

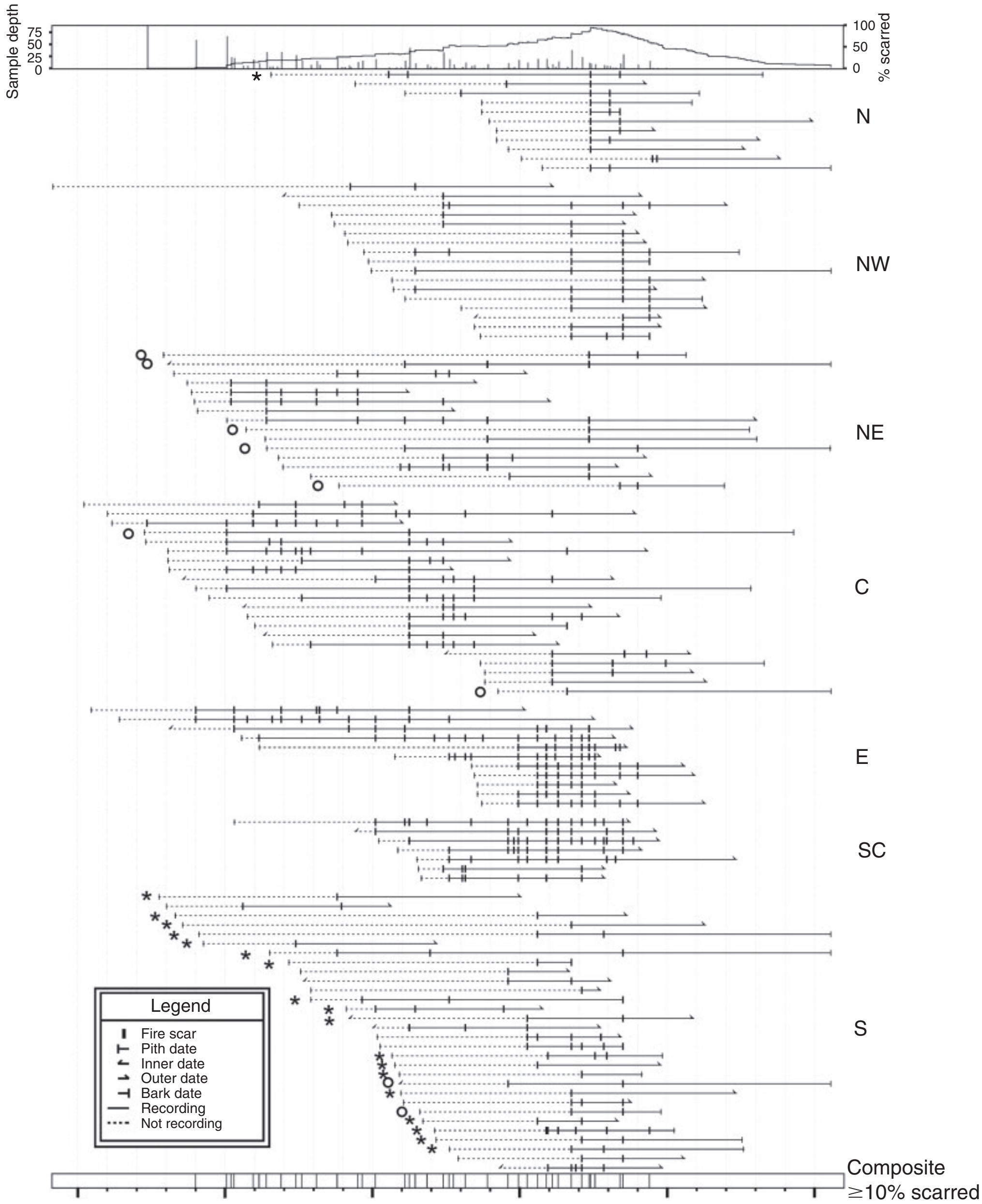

Fig. 2. Fire history chart for seven sites (e.g. N) on Rowe Mesa. Horizontal lines represent trees and vertical tick marks represent fire scars. Symbols to the left of horizontal lines indicate tree species: *, *Pinus edulis*; °, *Juniperus scopulorum*; and all others are *P. ponderosa*. Sample depth (continuous line) and percentage of recording trees scarred for each fire (vertical bars) included above. Site names listed in Table 1.

Discussion

Historical fire regime

There was evidence of frequent, low-severity surface fire at all sites on Rowe Mesa (Fig. 2, Tables 2, 3). Evidence included PIED and JUSC containing multiple fire scars that were synchronous within and among sites, and associated age structure indicating that overstorey trees generally survived the fires. This history of frequent, low-severity fire in a PJ savanna ecotone landscape in the south-western USA differs from reconstructed fire regimes in other PJ ecosystems in the western USA, where there is little evidence of low-severity fire (Floyd *et al.* 2004; Bauer and Weisberg 2009; Shinneman and Baker 2009). However, evidence of repeated low-severity fire (e.g. piñon or juniper trees with multiple fire scars) has also been documented in different PJ types from southern Arizona (*J. deppeana* Steud.; Leopold 1924) and west Texas (*P. cembroides*; Poulos *et al.* 2009). The current study provides the best evidence of historical repeated low-severity fire in the PIED-JUSC PJ type. The apparent range of historical fire regimes in PJ ecosystems likely reflects the large geographic and bio-climatic range of PJ

Fig. 3. Living *Pinus edulis* (left) and *Juniperus scopulorum* (right) with char and multiple fire scars. This direct evidence of repeated low-severity fire is rare in other piñon–juniper types.

Table 2. Fire interval statistics (years) for the landscape composite (*n* = 112 trees) and fires recorded at multiple sites (1601–2011)

WMPI, Weibull median probability interval. Data for 10% scarred were all fires recorded by $>$10% of all recording trees. Total number of sites = 7

Filter	Number of intervals	Mean	Median	WMPI	Minimum	Maximum
Landscape composite						
All fires	83	3.6	3	[A]	1	12
10% scarred	37	7.8	7	7.0	1	20
25% scarred	10	26.9	16	17.5	2	87
Multiple-site fires						
≥2 sites	34	7.8	7	6.6	2	25
≥3 sites	16	14.5	9	11.8	2	55
≥4 sites	7	23.7	23	18.7	4	72
≥5 sites	1	27	[B]	[B]	[B]	[B]

[A]WMPI is not shown where the Weibull model did not fit the fire interval data (Kolmogorov–Smirnov test, $P > 0.05$).

[B]Statistics can't be calculated.

ecosystems in the western USA. The climatic gradient of growing season monsoonal precipitation that increases from north-west to south-east across the south-western USA range of PJ ecosystems, and that corresponds to the abundance of warm-season grasses in more southerly PJ savannas, should be explicitly tested as a potentially important variable explaining the range of PJ fire regimes (Romme *et al.* 2009).

Although there is evidence of historically frequent surface fire throughout the Rowe Mesa study area ($MFI_{\geq 2\ sites} = 7.8$ years), fire was less frequent and more patchy in historically PJ-dominated sites. This is indicated by generally longer mean fire intervals and a greater difference between MFI_{ALL} and $MFI_{25\%}$ within a site, when compared to PIPO-dominated sites (Tables 1, 3; Fig. 2). Most fire-scarred PIED and JUSC on Rowe Mesa were located on upland sites, with thinner, more rocky soils compared to adjacent grass-dominated depositional sites containing the younger PJ trees (Jacobs 2011). However, even in these less productive upland sites, low intensity fires likely fuelled by grass were spreading within multiple PJ-dominated sites and were repeatedly scarring PIED and JUSC trees.

The high proportion of PIPO among the fire scarred trees in a landscape currently dominated by PJ trees was unexpected, and was likely a result of a combination of factors including: (1) a greater historical proportion of PIPO compared to contemporary conditions (Table 4), (2) the fire-scar prone topographic positions that support PIPO and (3) the tree physiognomy of PIPO bark structure and resin exudates compared to JUSC or PIED. Old (pre-1879), fire-scarred PIPO were most commonly found on the wetter north-facing slopes or in ephemeral drainage bottoms. In the later setting, woody debris and fine fuels were observed to accumulate on the 'upstream' side of the tree from ephemeral flows. Both topographic settings apparently caused sufficient fuel accumulation on the upslope or upstream side of the tree, which burned with sufficient intensity to create the initial fire scar and enabled the tree to record subsequent fires. Whereas older PJ trees were generally located on flat upland

Table 3. Fire interval statistics (years) for the full fire scar record at each site
WMPI, Weibull median probability interval

Site and analysis period	Filter	Number of intervals	Mean	Median	WMPI	Minimum	Maximum
North	All scars	8	22.8	17.5	19	3	57
1711–1893	10% scarred	2	10	10	[A]	7	13
	25% scarred	2	10	10	[A]	7	13
North-west	All scars	7	29.0	19.0	23.2	4	83
1685–1888	10% scarred	5	31.8	19.0	24.6	4	83
	25% scarred	5	31.8	19.0	24.6	4	83
North-east	All scars	17	16.2	14.0	13.4	2	52
1604–1880	10% scarred	11	25.1	24.0	22.4	4	69
	25% scarred	10	27.6	25.0	25.8	10	69
Central	All scars	30	11.7	9.0	9.3	2	54
1547–1899	10% scarred	16	16.4	10.0	13.8	4	53
	25% scarred	11	20.1	14.0	17.2	2	53
East	All scars	31	9.8	8.0	8.8	2	26
1580–1886	10% scarred	20	15.0	12.5	13.1	2	36
	25% scarred	20	15.0	12.5	13.1	2	36
South-central	All scars	22	8.0	6.5	7.1	2	25
1702–1877	10% scarred	17	9.9	8.0	8.4	2	27
	25% scarred	17	9.9	8.0	8.4	2	27
South	All scars	26	10.6	9	8.6	1	36
1612–1888	10% scarred	9	21.6	13	12.6	3	116
	25% scarred	6	32.3	18	21.8	7	116

[A]Statistics can't be calculated.

Table 4. Pre-settlement (1879) forest density (trees ha^{-1}) by species compared with the contemporary (2011) forest density
JUMO, one-seed juniper; JUSC, Rocky Mountain Juniper; PIED, Colorado piñon pine; PIPO, ponderosa pine
Sample size, $n = 14$, 0.2-ha plots. s.e., standard error of the mean

Species	Pre-settlement 1879		Contemporary 2011	
	Mean	s.e.	Mean	s.e.
JUMO	0.0	–	15.4	6.6
JUSC	21.8	6.7	131.8	27.7
PIED	20.4	7.5	397.1	128.3
PIPO	92.9	16.6	336.8	108.3
All species	135.1	15.3	881.1	127.0

sites with poor soils and less-dense vegetation cover. This physiographic location apparently resulted in less fuel accumulation around the base of the tree to create the initial scar and increase susceptibility to subsequent scarring, except on rare occasions. In addition, young PJ tree species are generally considered more susceptible to injury from even low intensity surface fire than PIPO due in part to (1) the comparatively thinner bark (e.g. PIED; Jackson *et al.* 1999), which increases the probability of fire-related cambial mortality (Ryan and Reinhardt 1988) and (2) lower crown base height of young PJ species compared to PIPO. On Rowe Mesa, the median age of PIPO when they first recorded a fire scar was 74 years ($n = 74$ trees), which was significantly younger than JUSC and PIED (103 years, $n = 27$ trees, Mann–Whitney test, $P < 0.01$). In addition, PIPO typically responds to stem injuries with greater secretions of flammable, but also wood-preserving, resin relative to PJ species. The resin increases both the sensitivity of PIPO to record damage from subsequent low-severity surface fires and the preservation of old pitchy fire-scar surfaces. This suggests that because of a greater ability for young PIPO to both survive and record fire scars they may be proportionally over-represented as fire-scarred trees compared to the actual proportion on the landscape. Studies designed to quantify fire mortality and scarring rates among PJ (and other) tree species are needed to improve the understanding of historical PJ fire regimes (Baker and Shinneman 2004).

Increased PJ forest density linked to fire exclusion

Fire exclusion, initiated by the reduction of fine fuels from intense livestock grazing (Savage and Swetnam 1990), was the most likely cause of the late 19th century increase in PJ density observed on Rowe Mesa. The alternative hypotheses considered include: (1) climatically favourable conditions for tree recruitment, (2) recovery from prior high-severity disturbance (e.g. fire) and (3) effects of grazing on tree establishment through reduced herbaceous competition. The late 19th century period of ecological change on Rowe Mesa was not associated with wet climatic conditions (Fig. 4), which have been shown to increase PJ establishment in other locations in the western USA (Swetnam *et al.* 1999; Soulé *et al.* 2004; Gray *et al.* 2006). Instead, local moisture sensitive tree-ring width measurements indicated that the 20-year period beginning in 1880 was the second driest in the last 500 years and was not associated with a climatic regime shift (Fig. 4).

Piñon–juniper woodlands that experience long interval (>250 years) high-severity fire would be expected to gradually increase in forest density as they recover from the last disturbance (e.g. Floyd *et al.* 2004). There was no evidence of

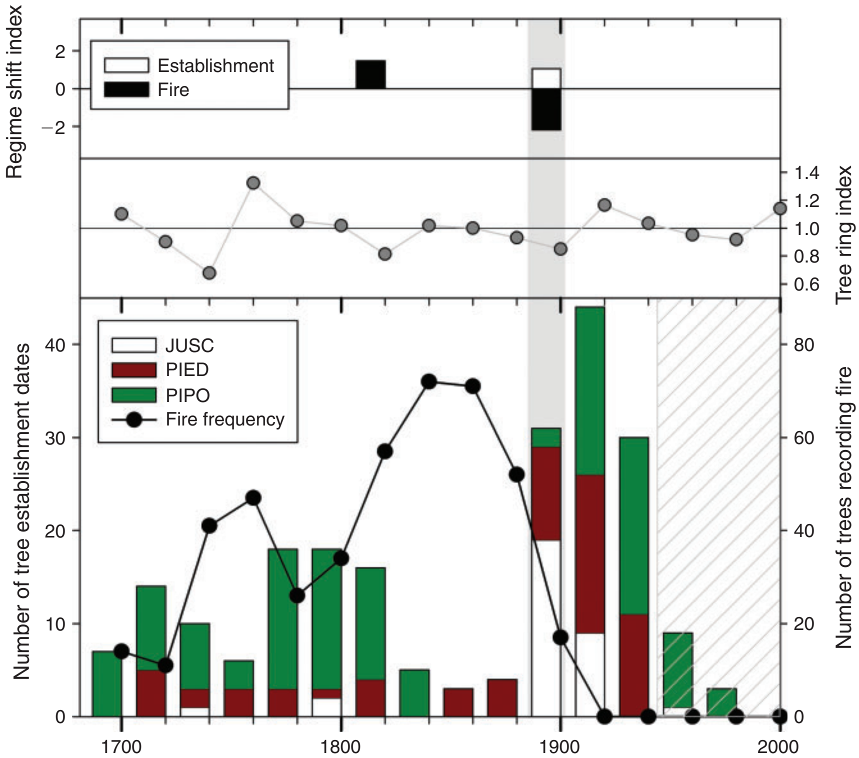

Fig. 4. Fire frequency (number of trees recording fire) and tree establishment (bottom), local precipitation sensitive tree-ring growth index (middle) and regime shift index (top). All data in 20-year bins, plotted on last year of bin. Vertical grey box highlights 1881–1900 regime shifts in fire occurrence (decrease) and tree establishment (increase) during below-average moisture conditions. Establishment dates not sufficiently sampled in crosshatched period.

high-severity fire at any of the study sites. Evidence might include: (1) even-aged stands that regenerated following fire or (2) groups of logs or snags that potentially represent a fire-killed forest. The age structure at all sites on Rowe Mesa was multi-aged, with no indication of a truncated age structure that might be evidence of partial or complete overstorey mortality from past fires. An early 20th century survey to include Rowe Mesa in the Pecos National Forest indicated that 'there have been no fires of any consequence … for a great many years' (Stabler 1906). Surveyors were often specifically looking for evidence of high-severity fire, because it would affect timber value. Therefore, it seems reasonable to interpret 'no fires of any consequence' as additional evidence for the lack of high-severity fire.

Heavy grazing may reduce grass cover, thereby reducing competition with tree seedlings and potentially leading to increased PJ tree species establishment (Johnsen 1962). Grazing has been associated with increased PJ tree establishment through comparisons of PJ density in grazed *v.* ungrazed sites (Gascho Landis and Bailey 2005; Shinneman and Baker 2009). However, in other locations grazing was not associated with increased PJ density (Soulé *et al.* 2004; Barger *et al.* 2009). It is possible that reduced grass competition from grazing on Rowe Mesa promoted increased tree establishment. However, the strong inverse relationship between fire occurrence and tree establishment suggests that before intensive grazing began in 1879 that fire alone was a primary determinant of forest age structure (Fig. 4). For example, the mid-1800 period of high fire occurrence was associated with the lowest number of trees established, and reduced fire occurrence *c.* 1800 was associated with a peak in tree establishment. Variability in fire occurrence alone, in the absence of livestock grazing, has been shown to be a primary determinant of variability in tree establishment in other frequent fire ecosystems (Brown and Wu 2005).

Forest density on Rowe Mesa increased dramatically and immediately following the collapse of the historically frequent fire regime in the late 19th century (Fig. 4). Both ecological regime shifts were coincident with the arrival of the transcontinental railroad <1 km north of the study area in 1879, which brought intensive livestock grazing (Debuys 1985). Fire exclusion initiated by reduction of fine fuels through intensive grazing has been shown to increase tree density in other frequent fire ecosystems of the region (Allen *et al.* 2002). Lastly, the strong inverse relationship between fire and tree establishment for multiple centuries before late 19th century grazing suggests that fire was the primary factor limiting tree establishment in this savanna landscape (Fig. 4; West 1999*b*; van Langevelde *et al.* 2003). Thus, of the multiple competing hypotheses for increased PJ tree density in the late 19th century on Rowe Mesa, the data suggest that fire exclusion was most likely the primary cause.

Landscape-scale ecological change and management implications

Rowe Mesa is a large savanna landscape that is currently dominated by PJ vegetation, which in some locations reach densities of >1000 trees ha^{-1}. However, multiple lines of evidence suggest that the landscape was an open PJ–PIPO savanna (<150 trees ha^{-1}) before ecological regime shifts catalysed by land use changes beginning *c*. 1879. The extent to which other areas currently dominated by PJ vegetation represent transitions from historically more-open savannas is unknown, but the potential is high in the summer monsoon precipitation-dominated range of PJ ecosystems (Jacobs 2011). In more-northern, PJ-dominated woodland ecotone sites on the Colorado Plateau that contained less grass and where surface fire was not historically widespread, such a shift apparently has not occurred (e.g. Huffman *et al.* 2008). However, piñon and juniper with multiple fire scars in grassy landscapes in southern New Mexico and west Texas (e.g. Brown *et al.* 2001; Poulos *et al.* 2009) suggest that other PJ ecosystems in the region could have historically burned with higher frequency and lower intensity (Romme *et al.* 2009).

As historical ecology is used to inform management, prioritise restoration and gain insights into future ecosystem trajectories it is important to recognise the potential for landscapes to undergo dramatic vegetation shifts as regulating processes change (e.g. fire exclusion or climatic change; Swetnam *et al.* 1999). Ecosystems that were historically maintained by frequent fire are perhaps most vulnerable to these anthropogenically induced shifts in density and fire regime (e.g. ponderosa pine in the south-western USA; Allen *et al.* 2002). Because savanna landscapes are particularly fire-prone they have high potential for vegetation shifts from grass to tree dominance (van Langevelde *et al.* 2003). Some sites may change so dramatically that recent conditions may not be recognisable without intensive paleo-ecological reconstructions. An example of such a dramatic shift occurred at the driest, lowest elevation (2095 m) site on Rowe Mesa (South site; Figs 1, 2; Table 1). Here, a ponderosa pine snag containing nine fire scars (point MFI = 22 years, 1676–1878) was hidden among a cluster of dense, young PIED and JUSC, all of which were currently surrounded by bare soil. Nearby, two metre deep headcuts signify the extent to which the removal of grass by intensive grazing catalysed severe erosion. Current tree density (>1000 trees ha^{-1}) is five times the historical estimate and the herbaceous layer that historically fuelled frequent surface fire has still not recovered, and may not in the near future with a predicted warmer and drier climate (Seager *et al.* 2007). Given the dramatic anthropogenically induced ecological changes documented on Rowe Mesa, it is clear that this and potentially other similar PJ savanna ecosystems would be ecologically justified for restoration, and differ greatly from the better-studied, persistent PJ woodlands (e.g. Floyd *et al.* 2004; Shinneman and Baker 2009).

Conclusions

I present direct tree-ring evidence from piñon and juniper trees that frequent, low-severity fire historically occurred in a PJ savanna landscape (i.e. with high grass cover). A strong inverse relationship between fire frequency and tree establishment, particularly after the last widespread fire in the late 1800s, provides support for the influence of fire exclusion on increased tree density in PJ savannas. The high variability in species assemblages and structure that exists among PJ ecosystems across a large geographic and bio-climatic gradient, suggests that an equally diverse range of fire regimes should also exist. Other ecosystems with large geographic and bio-climatic ranges (e.g. quaking aspen, *Populus tremuloides* Michx.) exhibit a similar wide range of fire regimes (Shinneman *et al.* 2013). Therefore, PJ ecosystems should not all be considered to have burned with infrequent, high-severity fire and ecological understanding and management should reflect local ecosystem processes functioning within the specific PJ type, which are likely driven by local bio-climatic conditions.

Acknowledgements

Funding provided by USFS Collaborative Forest Restoration Program Grant #34–10. Additional support provided by the University of Arizona Laboratory of Tree-Ring Research. I am grateful for discussions, field and laboratory help from T. W. Swetnam, C. D. Allen, M. Savage, C. Haffey, A. Zavelle, J. Danloe, J. Johnston, M. Villarreal and R. Brown. Comments from two anonymous reviewers improved the manuscript.

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