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Fire and stand history in two limber pine (*Pinus flexilis*) and Rocky Mountain bristlecone pine (*Pinus aristata*) stands in Colorado

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Abstract. We developed fire-scar and tree-recruitment chronologies from two stands dominated by limber pine and Rocky Mountain bristlecone pine in central and northern Colorado. Population structures in both sites exhibit reverse-J patterns common in uneven-aged forests. Bristlecone pine trees were older than any other at the site or in the limber pine stand, with the oldest tree dating to 780 AD and several dating to the 1000s and 1100s. The oldest trees in the limber pine stand date to the 1400s, with a majority of recruitment after an apparent bark beetle outbreak in the early 1800s. Spatial patterning in the limber pine suggests that the oldest trees established from seed caches left by corvid birds. Fire scars present in the early part of each chronology document that surface fire regimes dominated during certain periods. Decreased fire frequency, increased tree recruitment, and changes in species composition from the 1600s to1800s in the bristlecone pine may be reflective of cooler and wetter conditions during the Little Ice Age. Results suggest that a recent (1978) severe fire in the bristlecone pine stand that caused complete tree mortality was outside the historical range of variability in fire severity for at least the past ~1000 years.

Additional keywords: climate forcing of fire and tree recruitment, crossdating, dendrochronology, fire regimes, Little Ice Age, spatial patterning.

Introduction

Limber pine (*Pinus flexilis* James) and Rocky Mountain bristlecone pine (*P. aristata* Engelm.) are two often very long-lived, five-needle white pine species that grow in the southern Rocky Mountains of Colorado. Limber pine is widely distributed from northern Mexico to southern Canada, found mainly in dry woodland sites but occasionally intermixed with other conifer species in more mesic forests. Limber pine also has the broadest elevational distribution of any tree species in Colorado, ranging from isolated stands in the short-grass steppe of eastern Colorado at ~1600 m to treeline stands growing at over 3400 m (Schoettle and Rochelle 2000). Rocky Mountain bristlecone pine has a more restricted distribution, found mainly in dry sites at higher elevations (above 2750 m) primarily in Colorado with localised populations in northern Arizona and northern New Mexico. Both species are often very slow growing and can attain great ages, possibly because of their locations in mainly open stands in climatically stressed sites (e.g. Schulman 1954). The oldest known Rocky Mountain bristlecone pine tree is over 2400 years old (Brunstein and Yamaguchi 1992) and limber pine trees are known to be over 1600 years old (OLDLIST 2006).

Chronologies from both species have been compiled for use in dendroclimatic studies because of their great ages and typical locations in climatically stressed sites (ITRDB 2006). However, little research has been conducted into the species' population age structures and historical disturbance dynamics (Schoettle 2004*a*). Such information is of particular importance in light of recent invasion by white pine blister rust (WPBR; *Cronartium ribicola* J.C. Fisch.), an introduced pathogen that has had devastating effects on white pine populations throughout North America (e.g. Tomback *et al*. 2001). WPBR was first found on limber pine in northern Colorado in 1998 (Johnson and Jacobi 2000) and was recently found in Rocky Mountain bristlecone pine stands in the Sangre de Cristo Mountains in southern Colorado (Blodgett and Sullivan 2004). Better understanding of these species' colonisation dynamics and disturbance histories is urgently needed to inform future management decisions and possible ecological restoration efforts in response to probable impacts from WPBR mortality (Schoettle 2004*b*; Schoettle and Sniezko 2007).

Here we describe fire and stand histories from two stands dominated by limber and bristlecone pine in central and northern Colorado. We use both fire-scar and tree-recruitment data to reconstruct fire timing and spatiotemporal dynamics in population structure over the past several centuries. Our results provide some of the longest such histories yet compiled for this region of the southern Rocky Mountains. In addition to providing basic historical data on fire and stand history in the two stands we sampled, our results suggest that the potential length of fire-scar and tree-recruitment chronologies that could be derived from especially bristlecone pine make these valuable species to sample in further studies to examine multi-decadal to multi-centennial climate forcing of fire and tree recruitment in this region over the past millennium.

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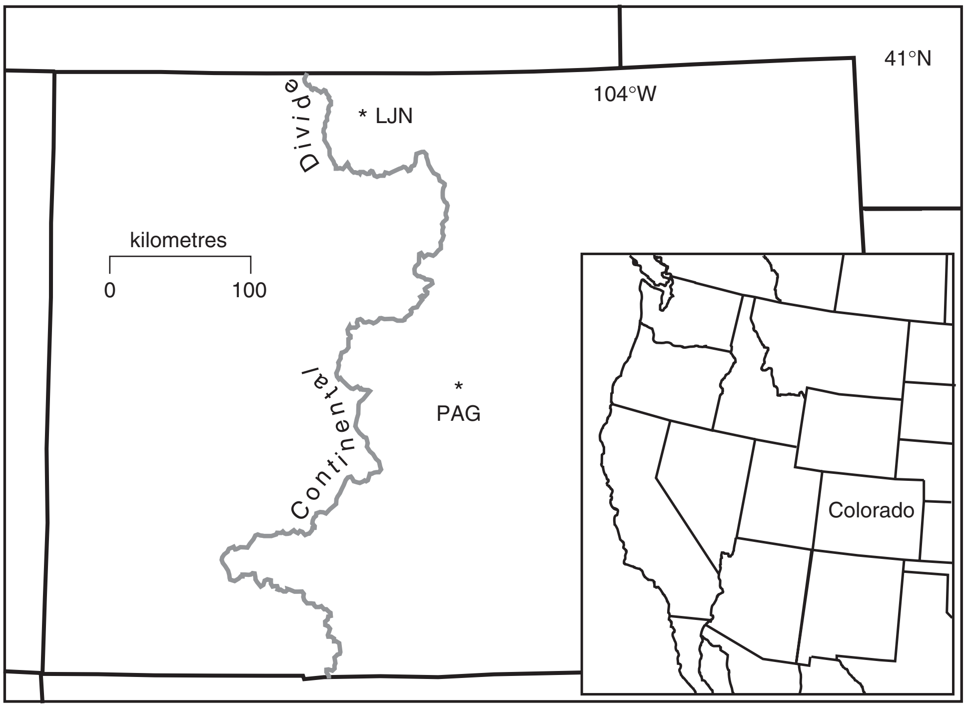

Fig. 1. Location map of sites Lake John (LJN) and Packer Gulch (PAG) in Colorado.

Methods

Study sites

We reconstructed fire and stand history in two stands, Lake John (LJN) and Packer Gulch (PAG; Fig. 1). LJN and PAG were selected for dendroecological study because they are locations of ongoing genetic, ecological, demographic, and physiological studies of the two species (Schoettle 2004*a*, 2004*b*). LJN is an isolated limber pine woodland located on a ridge in the north-eastern corner of North Park, a large, high-elevation montane grassland in northern Colorado (site location: 40°47.86′N, 106°30.25′W; elevation 2658–2665 m). Understorey vegetation in and surrounding the woodland is a mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana* (Rydb.) Beetle)–bunchgrass shrub steppe. Aspen (*Populus tremuloides* Michx.) is the only other tree species present. PAG is located on the south-eastern edge of South Park (another high-elevation montane grassland) in central Colorado (site location: 39°12.23′N, 105°36.28′W; elevation 2890–2920 m). The site is located on a steep slope in an ~400 m-wide stringer of residual forest that was left after the Packer Gulch Fire that caused complete canopy mortality on both sides of the stand in 1978. The forest at PAG is dominated by bristlecone pine and contains lesser amounts of limber pine, Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), Engelmann spruce (*Picea engelmannii* Perry ex Engelm.), and aspen. Understoreys at PAG consist of sparse herbaceous cover and abundant needle litter, which is likely the natural condition given the density of the current overstorey. Both stands are representative of the biophysical conditions under which the two species occur in Colorado (Schoettle 2004*a*). Neither stand has evidence of past timber harvest, although cattle grazing is occurring in both areas and may have been present in the stands since ~the 1860s when widespread Euro-American settlement began in Colorado.

Reconstruction of fire and stand histories

Tree-ring evidence is central to documenting historical fire regimes and patterns in tree recruitment and mortality affected by climate variations or disturbances (e.g. Heyerdahl *et al*. 2002; Swetnam and Baisan 2003; Hessl *et al*. 2004; Brown and Wu 2005; Brown 2006; Sibold and Veblen 2006). Fire history reconstructions rely on proxy evidence of fire timing and behaviour recorded in long-lived trees. We reconstructed fire and stand history using three types of tree-ring proxy evidence: (1) fire scars created during surface burning; (2) recruitment dates of trees that potentially post-date crown-opening fires or were affected by climate changes (see Brown and Wu 2005; Brown 2006); and (3) death or outside dates of trees killed by fire or other disturbances.

We systematically sampled trees to reconstruct patterns of tree recruitment and mortality in four plots at PAG and three plots at LJN (Table 1). Initial plots in each stand were subjectively located in the vicinity of on-going studies (Schoettle 2004*a*, 2004*b*) with subsequent plots spaced at a 250-m distance from each other across and down the slope at PAG or a 250-m distance along the crest of the ridge at LJN. We used an *n*-tree density-adapted sampling method (Jonsson *et al*. 1992; Lessard *et al*. 2002) to sample the nearest 30 living and remnant (logs and snags) trees to each plot centre. This sampling design has been used in numerous recent studies in multiple forest types across the western US (Brown and Wu 2005; Brown 2006; Heyerdahl *et al*. 2006; Brown *et al*. 2008). We collected increment cores from 10-cm height above ground level on living

Table 1. Site and stand characteristics of bristlecone pine and limber pine plots

Plot	Aspect (degrees)	Slope (%)	Density (trees ha^{-1})	Basal area (m^2 ha^{-1})	Plot area (ha)
Packer Gulch (PAG)					
PAG1	252	53	508	28.6	0.045
PAG2	242	51	824	29.8	0.034
PAG3	230	47	469	18.8	0.049
PAG4	229	51	419	20.8	0.057
Lake John (LJN)					
LJN1	73	7	905	39.1	0.032
LJN2	40	8	193	18.0	0.129
LJN3	120	4	454	29.3	0.057

trees, and cross-sections were cut from logs and snags such that one surface was a 10-cm height above the estimated root-shoot boundary. Tree distances and azimuths from plot centres were measured for stand mapping and calculation of tree densities, stocking, and spatial patterning. Living tree diameters were measured at 10-cm diameter at sample height (DSH) and breast heights (DBH). Ten-cm-height diameters were measured on remnant trees with an accompanying designation of state of decay, whether bark, sapwood, or heartwood was present. We also searched for and collected cross-sections from additional fire-scarred trees in each stand to aid in the reconstruction of fire frequency and timing.

We used standard dendrochronological methods to crossdate all cores and cross-sections against a master chronology developed for each stand. Visual matching of ring characteristics and correlated measured ring widths were used 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 possible seasons of fire occurrence. On increment cores and cross-sections that did not include pith but where 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. We did not attempt to make any correction from 10-cm pith dates to germination dates because we have no information on how long it can take for seedlings to grow from germination to 10-cm height in the various species we sampled. Part of the on-going study in the burned stand at PAG is documenting both bristlecone and limber pine seedling regeneration timing and growth rates, and these data should be available in the future. Time spans of individual trees and fire-scar dates were compiled into chronologies using the program *FHX2*, an integrated package for graphing and statistical analyses of fire and forest histories (Grissino-Mayer 2001).

Stand structure and spatial patterning

Tree densities (stems ha^{-1}) and basal areas (m^2 ha^{-1}) were determined for each plot from field measurements. The radius of each plot was first calculated as the distance from plot centre to centre of the farthest tree of the 30 measured. Plot area was determined as a circular plot of the calculated radius and using a bias correction derived by Moore (1954; see also Lessard *et al*. 2002; Lynch and Wittwer 2003). Total stem basal area and number of living trees within the plot were then scaled to determine stand density and tree basal area on a per hectare basis.

Tree azimuths and distances from plot centres were converted to x,y coordinates to examine spatial patterning of trees by recruitment dates in each plot using Ripley's $L(t)$ function (Ripley 1981). The $L(t)$ function produces a cumulative distribution function that represents the expected number of trees within a given distance of an individual tree. We computed 95% confidence intervals using a Monte Carlo simulated Poisson process to define when observed patterns of spacing of older and younger trees in each plot (defined in the results for the different sites) differed from random ($P < 0.05$). Clustered arrangements representing significant spacing of trees within 10 m of each other are indicated by an $L(t)$ above the confidence interval, and regular (or random) tree spacing occurs where $L(t)$ falls below the interval.

Assessing relationships between climate, fire, and tree recruitment

We compared fire-scar and tree-recruitment chronologies with independently derived tree-ring based reconstructions of precipitation and temperature to assess possible climate forcing of fire occurrences and tree recruitment patterns. We used superposed epoch analysis (SEA; Swetnam 1993) to compare average annual climate conditions for the set of fire years from LJN with climate for the period of record of each reconstruction. We did not use SEA to test fire years at PAG as 5 or fewer fire years overlapped with climate reconstructions. Significant climate anomalies were determined in SEA using bootstrapped confidence intervals based on average annual climate values with the same number of years as the LJN fire-year dataset. We used two climate reconstructions in SEA: (1) reconstructed summer temperature for the southern Rocky Mountains (C. Woodhouse, P. Brown and M. Hughes, unpubl. data); and (2) summer Palmer drought severity indices (PDSI) from northern Colorado (grid point 131 from Cook *et al*. 2004).

Results and discussion

Patterns in tree recruitment and fire timing

We collected 138 trees from PAG and 111 trees from LJN. We successfully crossdated 115 trees (83% of total) from PAG, of which 82 (71% of total dated) had pith or on which a pith date could be estimated with confidence. We successfully crossdated 96 trees (86% of total) from LJN and 77 (80% of total crossdated) of these had pith or a pith date could be estimated.

Tree-recruitment and fire-scar data from LJN and PAG are summarised in Figs 2 and 3. Recruitment data from both stands exhibit 'reverse-J' patterns found in uneven-aged forests, with fewer old trees and more abundant recruitment closer to the present. Bristlecone pine trees at PAG were older than any other species found in the stand or at LJN. The oldest remnant bristlecone pine at PAG (a log) had an inside date of 780 AD, and several living and remnant trees extended back to the 1000s and 1100s (Fig. 3). All species at PAG other than bristlecone pine were established after ~1700, with the majority of recruitment dating from the 1700s and 1800s. In contrast, the oldest limber pine individuals at LJN established in the 1400s, followed by

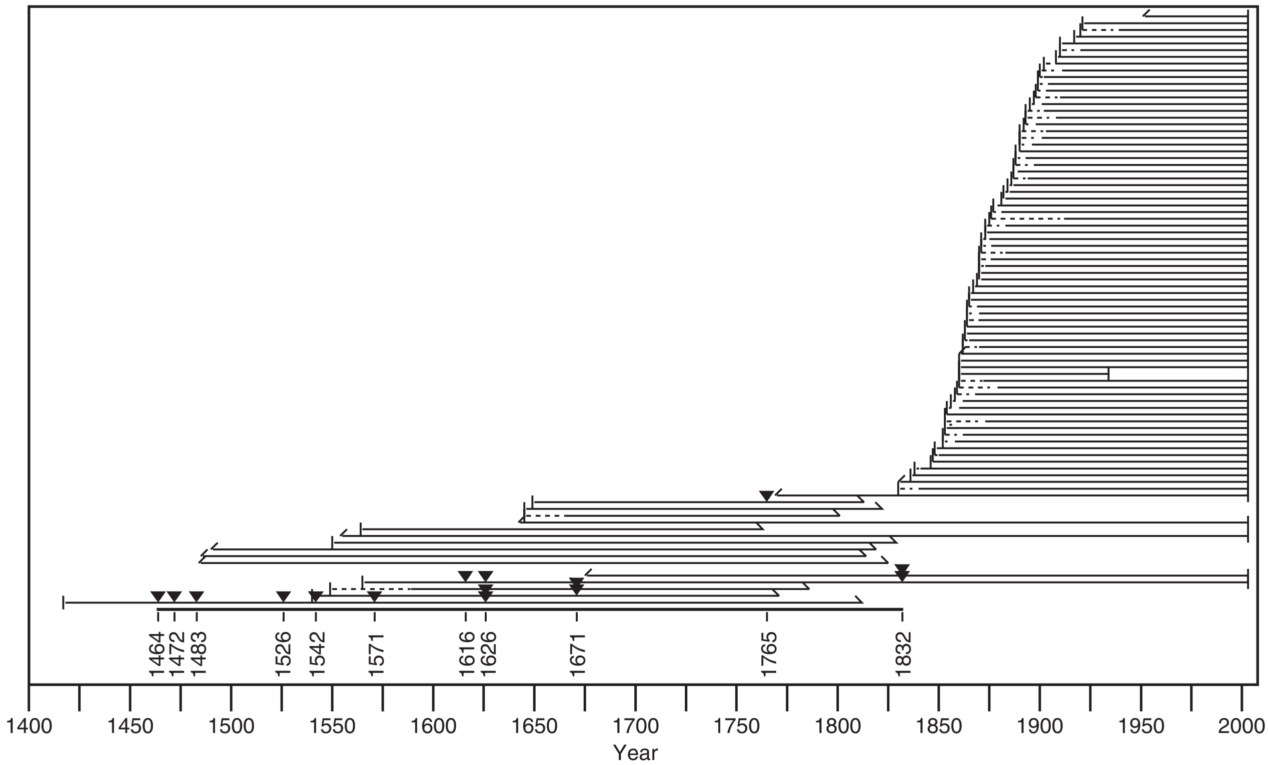

Fig. 2. Tree-recruitment and fire-scar chronology from Lake John (LJN). Only limber pine were sampled at the site. Horizontal lines mark time spans of individual trees with dates of fire scars marked by inverted triangles. Dashed lines are estimated number of years to pith dates on cores or cross-sections that did not intersect pith but inside ring curvature was visible. Vertical lines to left on each tree chronology are pith dates with inside dates (i.e. unknown number of years to pith) marked by slanted lines. Vertical lines to right are bark dates (= death dates in remnant trees) with outside dates (i.e. unknown number of years to death date) marked by slanted lines. Top tree chronologies are from plot trees, with additional trees collected for fire scars at the bottom (see Methods).

abundant limber pine recruitment beginning in the mid-1800s (Fig. 2).

Both stands contain evidence of surface fires over the past several centuries in the form of fire scars. Fire scars in both limber pine and bristlecone pine were recorded either in the latewood or dormant season (between two rings), and likely represent fires that occurred between August to late September or early October when winter snows usually begin. At LJN, fire scars were recorded from the beginning of the chronology in the 1400s to a fire recorded in 1832 (Fig. 2; Table 2). Fire frequency shifted from more frequent fires from the beginning of the record in the late 1400s to the late 1600s, to only two fires recorded in the 1700s and early 1800s. Several older trees appeared to have died just before the last fire recorded in the stand in 1832, although all of these trees had eroded outside surfaces and their exact death dates could not be confirmed (Fig. 2). These trees likely did not die as a result of the fire in 1832 as sapwood was present on several and contained evidence of blue stain fungi. Blue stain is an indicator of possible mortality from bark beetles, likely *Dendroctonus ponderosae* (mountain pine beetle), which is known to infect limber pine in Colorado (Furniss and Carolin 1977). We interpret this evidence to suggest that a bark beetle outbreak killed trees in the stand in the middle to late 1820s, which was followed by a fire in 1832 that may have been fuelled by dead stems and branches from beetle-killed trees and may have caused additional mortality.

A majority of trees in the stand established after this possibly combined beetle- and fire-caused stand-opening episode. Relatively dense stands of trees that established post-1832 (Table 1) have persisted to the present because of a lack of fires since that time. Fire cessation was likely affected – at least later in the 19th century – by changes in land use that include livestock grazing. Cessation of surface fires is seen in many forests around the western US beginning in the middle to late 1800s (e.g. Heyerdahl *et al*. 2002; Hessl *et al*. 2004; Brown and Wu 2005; Kitzberger *et al*. 2007). In contrast to probable native grazers before Euro-American settlement, early settlement livestock grazing was thought to be especially intensive and reduced fine fuels (grasses and herbaceous plant cover) below a point that allowed fires to spread past a point of ignition (e.g. Swetnam and Betancourt 1998). Changes in the competitive relationships between grasses and woody plants also accompanied grazing, with the result that woody plants were able to establish in what were formerly sagebrush- or grass-dominated communities.

PAG also shows apparent shifts in fire frequency and patterns of tree recruitment from the early to latter parts of the chronology (Fig. 3). Fire scars recorded on multiple trees from 1106 to 1557 suggest that the stand was open enough to support surface fires through this period. Fire frequency in the early part of the chronology was less than at LJN (Table 2) but the presence of fire scars argues that a surface fire regime was present for several centuries at the site. Tree recruitment

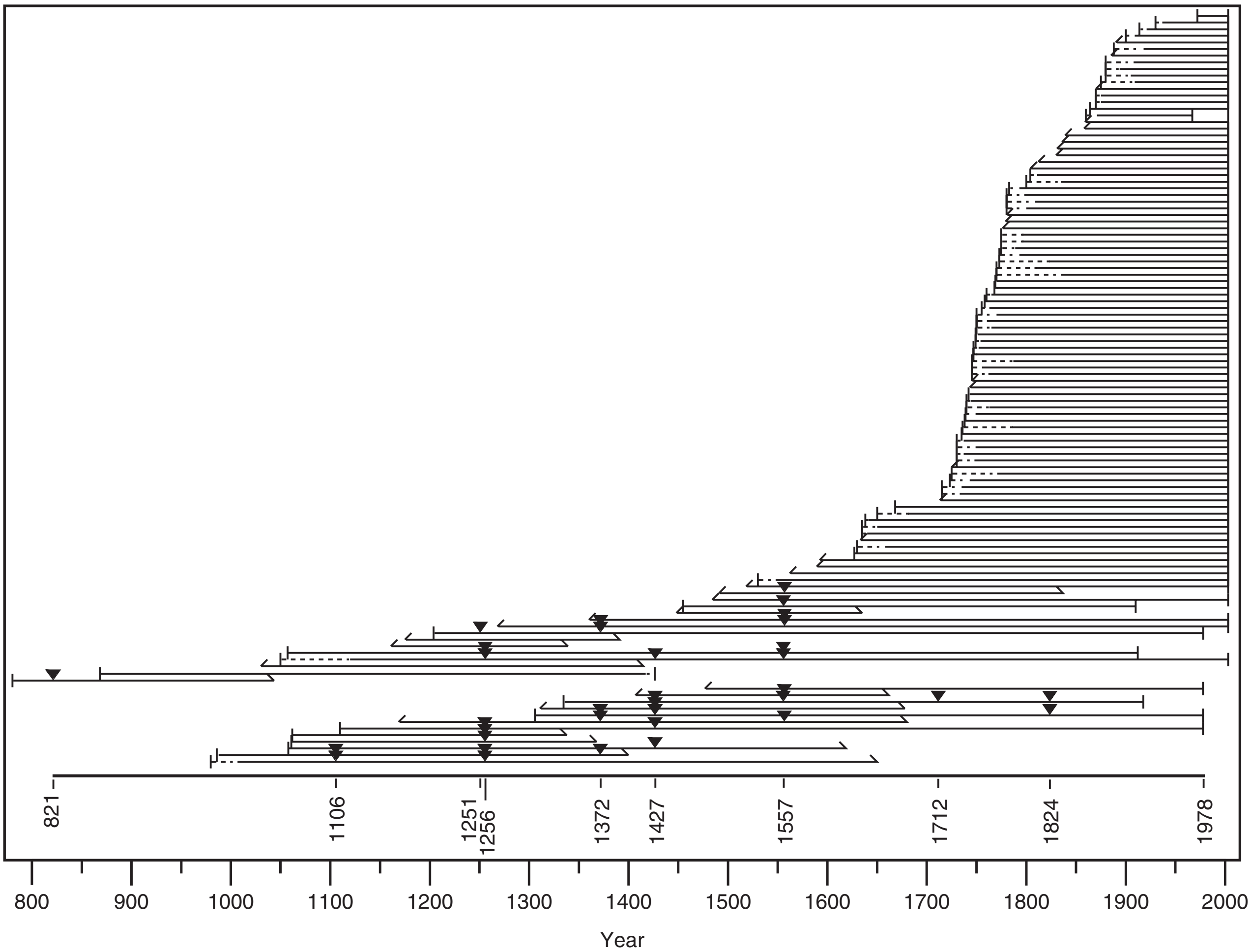

Fig. 3. As in Fig. 2 for trees collected at Packer Gulch (PAG). Graph includes all species sampled at the site, including Rocky Mountain bristlecone pine, limber pine, Engelmann spruce, and Douglas-fir.

Table 2. Fire frequency in limber pine and bristlecone pine stands based on intervals between fire scars (dates shown in Figs 1 and 2)
MFI, mean fire interval

Site	Period of analysis	No. of intervals	MFI ± s.d. (years)	Median (years)	Range (years)
Lake John (LJN)	1464 to 1832	9	40.9 ± 47.6	29	8 to 161
Packer Gulch (PAG)	1106 to 1824	7	102.6 ± 53.8	116	5 to 155

appears to have largely occurred between fires, such as a pulse of bristlecone pine that established in the early 1600s. Some time after the 1600s, however, it appears the fire regime shifted to less frequent fires with accompanying greater tree recruitment. A possibly ‘mixed-severity’ fire (i.e. that included both surface and crown burning) in 1712 scarred at least one tree and may have killed several others, although death dates on these again cannot be confirmed because of missing sapwood (Fig. 3). Abundant recruitment occurred after 1712, perhaps because of stand opening by the 1712 fire and probable shifts in regional climate forcing or changes in Native American burning habits (see further discussion below). This later recruitment also included Engelmann spruce and Douglas-fir in addition to bristlecone and limber pine, which may indicate stand succession from a predominately bristlecone pine stand to more of a mixed-conifer forest. It is also possible that the stand has always contained these other species but their populations turn over faster than the longer-lived bristlecone pine. However, as we did not find any logs or snags of these other species in the stand, we suspect that these are relatively recent arrivals compared with the length of time that the bristlecone pine trees have occupied the site. Fire in 1824 appears to have been mainly a patchy surface fire as evidenced by fire scars recorded on two trees and no apparent mortality of overstorey trees. The final fire recorded in the

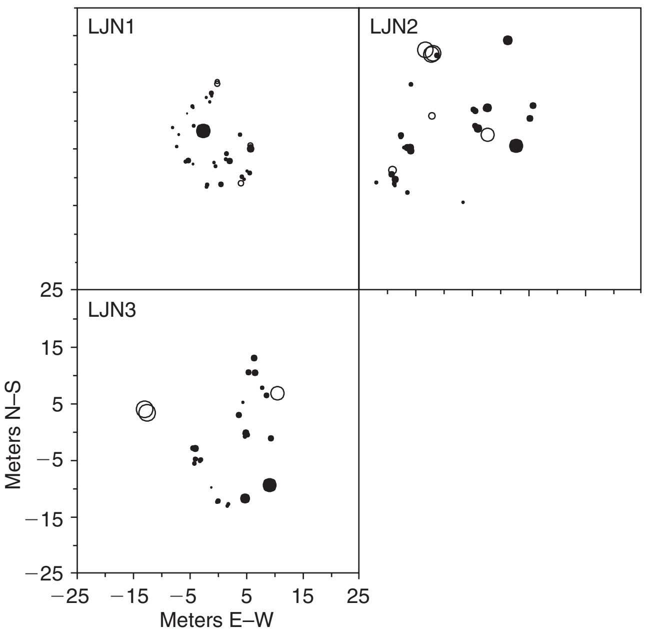

Fig. 4. Spatial patterning and relative sizes of living (filled circles) and remnant (open circles) limber pine trees at Lake John (LJN) plots. Size exaggeration on tree diameters is 5×.

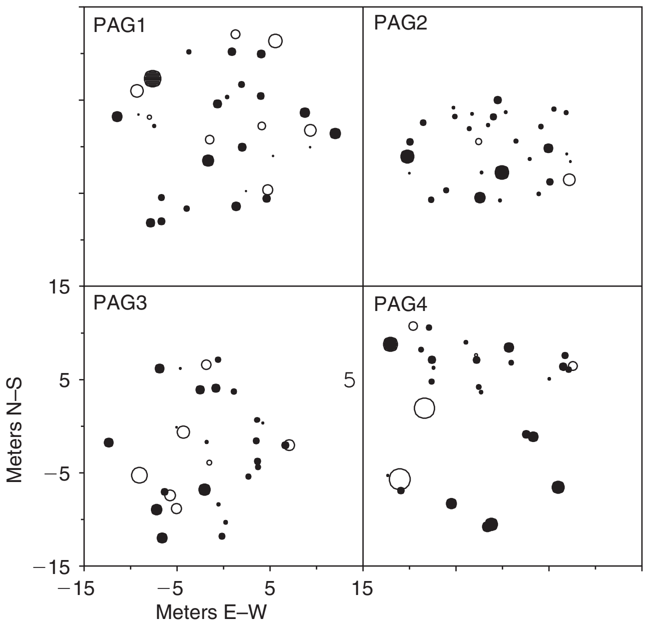

Fig. 5. As in Fig. 4 for trees in Packer Gulch (PAG) plots. Graphs include all species sampled in each plot, including Rocky Mountain bristlecone pine, limber pine, Engelmann spruce, and Douglas-fir.

stand was the recent severe crown fire in 1978 that caused complete tree mortality on both sides of the plots where we sampled. Crown mortality in the 1978 fire was extensive, killing ~110 ha of forest overstorey surrounding the unburned island of ~30 ha that we sampled. Several of the fire-scarred trees we sampled, including some of the oldest (Fig. 3), were killed in the 1978 fire, suggesting that in terms of overstorey mortality, this fire was outside the range of severity of any fire that the stand had seen for at least the past ~1000 years.

Spatial patterning of tree recruitment

Stem maps of trees and $L(t)$ functions document differing spatiotemporal distributions of trees in the limber and bristlecone pine plots (Figs 4 and 5). Both older and younger stems (defined as those that recruited before and after 1712) in the bristlecone plots are largely randomly spaced with no apparent clumping (Fig. 5). In contrast, older limber pine trees (defined as those that recruited before 1832) in two of the LJN plots (LJN2 and LJN3; Fig. 4) show significant clumping based on their $L(t)$ distributions. This is likely due to seed caching by corvid birds, which is a common means of limber pine colonisation, especially after stand-opening disturbance events (Lanner and Vander Wall 1980). Several of the older stems at LJN were found growing from the same base, and if pith was present on both stems, they dated to roughly the same origin dates. In contrast, spatial patterning of younger trees in the stand (those established after 1832) showed largely random distributions. Our interpretation of these patterns is that initial establishment of the oldest trees at LJN was in seed caches left by corvids, and that more recent establishment after 1832 was from seed fall or short-distance dispersal of the wingless seeds by rodents (Tomback *et al.* 2005) from the surrounding older parent cohort. The random, non-clustered tree distribution in the bristlecone stand implies that tree recruitment was largely the result of wind dispersal of the winged seeds, even among the oldest individuals. This also provides supporting evidence that the bristlecone pine forest at this site has been fairly stable for many centuries.

Climate forcing of past fires and recruitment episodes

Fire years at LJN were found to be on average associated with cool summers in northern Colorado (Fig. 6). Reconstructed PDSI did not show any significant relationships with LJN fire dates in SEA. It is unclear from the limited data we have from this one stand why cooler summer temperatures would be associated with increased fire occurrence. It is also possible that human ignitions were more important to fire occurrence in this stand than were natural ignitions, which would show less response to climate forcing. However, additional regional fire data are needed that may show significant relationships with both drought indices and possible synoptic climate forcing such as El Niño–Southern Oscillation (ENSO) and Pacific Decadal Oscillation (PDO), as has recently been shown in subalpine forests farther east in central Colorado (e.g. Sibold and Veblen 2006).

In contrast to high-frequency (annual) trends tested by SEA, low-frequency (multi-decadal to multi-centennial) trends in fire timing and tree recruitment at PAG provide possible evidence for longer-term forcing of fire and recruitment patterns by climate change. Reconstructions of global and regional climate regimes demonstrate that the period from roughly the late 17th to 19th centuries, often referred to as the Little Ice Age, was generally cooler and had fewer regional droughts than previous centuries, notably the period from the 10th through the 14th centuries (e.g. Cook *et al.* 2004; Moberg *et al.* 2005). Cooler and wetter conditions during the Little Ice Age would have

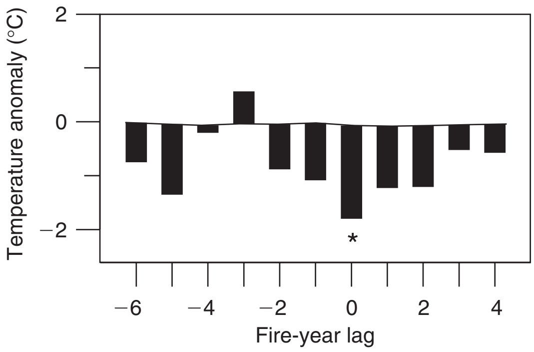

Fig. 6. Superposed epoch analyses of average summer temperature anomalies in northern Colorado (C. Woodhouse, P. Brown and M. Hughes, unpubl. data) for Lake John (LJN) fire years listed in Fig. 1. Fire year lag '0' is the average climate anomaly for fire years, with antecedent conditions indicated by negative lags. Asterisk marks significant departure in average climate conditions based on bootstrapped confidence intervals ($P < 0.05$).

contributed to generally fewer years when fires were able to ignite and spread. The shift to lessened fire frequency in the 1700s and 1800s found at both LJN and PAG is synchronous with patterns seen in fire histories reconstructed from both ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson) forests in the Colorado Front Range (Brown *et al.* 1999; Donnegan *et al.* 2001) and in regional fire histories reconstructed from giant sequoia (*Sequoiadendron giganteum* (Lindl.) J. Buchholtz) forests in the Sierra Nevada in California (Swetnam 1993). Fire chronologies from the Front Range document a shift from higher fire frequency and patchier spatial extent from the beginning of the chronologies to the middle 1600s, to less frequent but more spatially extensive fires during the 1700s to latter part of the 1800s, after which surface fires ceased because of changes in land use and fire suppression. This period was the coolest and wettest of the Little Ice Age period (e.g. Salzer and Kipfmueller 2005). Giant sequoia chronologies also show increased regional synchrony and frequency of fires during the period from ~900 to 1500 relative to the period from 1700 to the latter half of the 1800s (Swetnam 1993). Although giant sequoia chronologies are from sites that are quite far west of our study area, they are likely reflective of subcontinental patterns in multi-decadal to multi-centennial temperature effects on fire occurrences during that time period (Swetnam 1993).

More favourable climate conditions during the Little Ice Age also would have contributed to greater tree recruitment and faster tree growth in typically dry bristlecone pine forests, leading to denser forests and more even-aged forest structures. This appears to have happened at PAG with abundant recruitment and an apparent shift in species composition during the 1700s and 1800s. We interpret evidence at PAG to suggest that the stand experienced a shift from a relatively open bristlecone pine stand that supported surface fires in the early part of the chronology to a prolonged, mostly fire-quiescent period during the cooler and wetter Little Ice Age that resulted in greater tree recruitment and a change to a denser mixed-conifer forest. This finding is in contrast to that by Baker (1992), who, in a regional study of bristlecone pine populations in Colorado, suggested that regionally synchronous cohorts of bristlecone pine appear to have established in response to fire events during what he suggested was a warmer and drier Little Ice Age period. However, he did not date any fires from any of the stands he examined in his study. Moreover, tree recruitment data reported by Baker (1992) are largely contemporaneous with data from PAG, which strongly suggests climate synchronisation in regional tree recruitment patterns (see Brown 2006).

Based on results from the present study, we hypothesise that favourable climate conditions for bristlecone pine recruitment during the Little Ice Age coupled with a general lack of fires during this period resulted in denser forest stands and a succession to mixed-conifer forests with the addition of species such as Douglas-fir and Engelmann spruce. Several studies have found that limber pine is the first tree species to colonise high-elevation burns in the Colorado Front Range and, in the absence of fire, it gradually facilitates its own replacement by more shade-tolerant species such as spruce and fir (Veblen 1986; Rebertus *et al.* 1991). The rate of colonisation and subsequent succession following limber pine establishment may decline with increasing site elevation (Shankman and Daly 1988; Donnegan and Rebertus 1999). It is unclear, however, if this same process occurs in bristlecone pine forests. The geographic distribution of bristlecone coincides with high-elevation areas within the North American monsoon, suggesting that bristlecone pine establishment to the north may be limited by summer moisture availability. Consequently, past wetter periods at the northern edge of the monsoon region in central Colorado may have been favourable for bristlecone recruitment. A recent study of bristlecone pine conducted in the San Francisco Peaks in northern Arizona (well within the monsoon region) found nearly continuous recruitment over the last 400 years, including the last century of fire exclusion (Cocke *et al.* 2005). Timing of this recruitment also fits well with the abundant recruitment we found in site PAG, and provides support for a likelihood of regional climate synchronisation. Our limited data would suggest that bristlecone pine forests in Colorado may have sustained post-disturbance pine recruitment concurrent with a slow successional trajectory during moist periods. The observed changes in stand density, species composition, and fuel structure that we have reconstructed may have, in turn, contributed to more severe fire behaviour such as the extensive crown mortality that occurred in the forest at PAG in 1978.

Conclusions

The limber pine woodland at LJN appears to have been a relatively open stand that supported a surface fire regime up until 1832, after which time fires ceased and tree density increased. A fire in 1832 may have contributed to stem mortality, but bark beetles – as evidenced by blue stain in the sapwood of several trees that died about this time – probably were the more likely cause of stand opening in the early 19th century. Fire cessation after this likely was at least partially the result of changes in land use, including livestock grazing in the surrounding sage–grassland prairie beginning in the ~1860s and later fire suppression by land management agencies in the 20th century.

Fire scars and less tree recruitment in the bristlecone pine stand at PAG during the early part of the record from ~1100 to 1500 suggest that the forest was open enough to support surface fires during this period. Tree recruitment may have been restricted during the early part of the chronology by generally warmer and drier conditions less conducive to seedling establishment and growth. The early period was followed by a change to cooler and wetter conditions during the Little Ice Age that apparently led to lessened fire frequency and more favourable conditions for tree recruitment. Increased tree growth driven largely by climate change rather than changes in human land use appear to be the main reason for shifts in the fire regime at PAG. The 1978 fire that caused extensive tree mortality in the nearby forest was likely more severe than any fire recorded during the past 1000+ years.

However, the above observations and inferences must all be considered as hypotheses to test with additional fire-scar and tree-recruitment data from other limber and bristlecone pine populations in this region. Climate forcing of tree recruitment and fire regimes should have resulted in contemporaneous patterns in other sites across the region. This is the first detailed assessment of fire and stand histories in these forests in Colorado, and without corroborating data, it is difficult to assess the relative strength of forcing factors such as climate or shifts in fire frequency and timing on tree recruitment patterns. However, the potential length of fire and tree recruitment chronologies from limber and bristlecone pine stands make them valuable species to target for future study, not only for understanding community and population dynamics in these forests but also for placing fire and forest histories from this region into the context of longer-term climatic and land-use effects.

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