Available online at www.sciencedirect.com

SCIENCE DIRECT®

Forest Ecology and Management 230 (2006) 107–118

Forest Ecology and Management

www.elsevier.com/locate/foreco

History of fire and Douglas-fir establishment in a savanna and sagebrush–grassland mosaic, southwestern Montana, USA

Emily K. Heyerdahl [a,*], Richard F. Miller [b,1], Russell A. Parsons [a]

[a] *USDA Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory,*
5775 West Highway 10, Missoula, MT 59808, United States
[b] *Oregon State University, Department of Rangeland Resources, 202 Strand Agriculture Hall,*
Corvallis, OR 97331-2218, United States

Received 13 January 2006; received in revised form 12 April 2006; accepted 13 April 2006

Abstract

Over the past century, trees have encroached into grass- and shrublands across western North America. These include Douglas-fir trees (*Pseudotsuga menziesii* (Mirb.) Franco var. *glauca* (Beissn.) Franco) encroaching into mountain big sagebrush (*Artemisia tridentata* Nutt. ssp. *vaseyana* (Rydb.) Beetle) from stable islands of savanna in southwestern Montana. Our objectives were to quantify the relative area occupied by mountain big sagebrush and grasslands versus Douglas-fir savanna in the Fleecer Mountains of southwestern Montana today and in the past, and to identify the historical role of fire and other factors in maintaining this distribution. To do this, we reconstructed a multicentury history of tree establishment and surface fires from 1120 trees sampled on a grid of 50 plots covering 1030 ha of a modern mosaic of sagebrush–grasslands and Douglas-fir trees. We compared these histories to time series of climate and land use, and to spatial variation in topography and soil moisture availability. Beginning in the mid-1800s, Douglas-fir trees established in areas in which trees did not persist historically. In 1855, less than half the plots (42%) had trees whereas today, most plots do (94%). This encroachment was synchronous with the cessation of frequent surface fires, likely caused by the advent of domestic livestock grazing, and perhaps by the start of several decades of relatively dry summers. Douglas-fir savannas historically occurred on fire-safe sites more often than did sagebrush–grass. Our inference that frequent fire excluded Douglas-fir in the past was supported by the results of a simulation model of fire and associated vegetation dynamics. In the continued absence of fire, mountain big sagebrush and grasslands in southwestern Montana are likely to become more homogeneous as Douglas-fir trees continue to encroach.

Keywords: Mountain big sagebrush; Douglas-fir; Montana; Encroachment; Fire history; Dendrochronology

1. Introduction

Tree and shrub encroachment into the grasslands and savannas of western North America over the past century may have global implications for land surface–atmosphere interactions and the carbon cycle (West, 1983; Houghton et al., 1999; Van Auken, 2000; Schimel et al., 2000; Huxman et al., 2005). During the twentieth-century, conifers, such as Douglas-fir, ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson var. *scopulorum* Engelm.), lodgepole pine (*Pinus contorta* Douglas ex Loudon var. *latifolia* Engelm.) and western juniper (*Juniperus occidentalis* Hook.) have encroached into shrub–grasslands at many sites in the Interior West (e.g., Patten, 1969; Vale, 1975; Burkhardt and Tisdale, 1976; Strang and Parminter, 1980; Young and Evans, 1981; Butler, 1986; Miller and Rose, 1995, 1999; Mast et al., 1997; Soulé and Knapp, 2000), including southwestern Montana (Sindelar, 1971; Houston, 1973; Arno and Gruell, 1983, 1986; Dando and Hansen, 1990; Hansen et al., 1995). This encroachment has generally been ascribed to factors that include some combination of a cessation of frequent fire, domestic livestock grazing (both directly and through its influence on fire) and climate. In the Fleecer Mountains of southwestern Montana, we observed many stands of

---

* Corresponding author. Tel.: +1 406 829 6939; fax: +1 406 329 4877.
E-mail addresses: eheyerdahl@fs.fed.us (E.K. Heyerdahl), richard.miller@orst.edu (R.F. Miller).
[1] Tel.: +1 541 737 1622.

0378-1127/$ – see front matter. Crown Copyright © 2006 Published by Elsevier B.V. All rights reserved.
doi:10.1016/j.foreco.2006.04.024

apparently young Douglas-fir, both within and outside areas with sparse, old trees. In addition, dead stems of mountain big sagebrush, a species that is quickly out-competed by trees, were common in the understories of these young stands of Douglas-fir. Some combination of the factors that control tree encroachment elsewhere is likely to have maintained sagebrush–grasslands in the Fleecer Mountains in the past. However, these factors can interact in complex ways and not all factors operate everywhere encroachment has occurred (Butler, 1986). Tree rings contain proxy records of Douglas-fir dynamics and some of the factors that may control them, e.g., climate and fire. In addition, simulation modeling allows us to test hypotheses about the relative impact of fire on vegetation dynamics and can indicate the potential consequences of different fire regimes (Turner et al., 1993; He and Mladenoff, 1999; Gustafson et al., 2000).

Our objectives were to quantify the relative area occupied by sagebrush–grasslands versus Douglas-fir savanna today and in the past and to identify the historical role of fire and other factors in maintaining this distribution.

2. Study area

The study area is north of the Big Hole River near the town of Wise River, Montana, which lies east of the continental divide (45.83°N, 112.94°W; Fig. 1). Elevation ranges over 325 m (1900–2225 m) and includes several gentle north-south drainages (slopes less than 55%). The climate is continental, with cold winters and warm summers (average minimum in January −13 °C, average maximum in July 27 °C; 1951–2003 at Wise River; NCDC, 2004). Annual precipitation is low (mean 30 cm) and monthly precipitation peaks in May and June. Modern lightning-ignited fires generally occur in July and August, after the peak in precipitation (98% of 8228 ha burned in July and August in Beaverhead, Deer Lodge and Silver Bow counties, 1986–1996; Schmidt et al., 2002; Gisborne, 1931).

Starting in the mid-1850s, land use changed dramatically in this region as a result of the restriction of Native Americans to reservations, the discovery of placer gold and the introduction of domestic livestock. The study area is in the traditional territory of the Flathead and Pend d'Oreille tribes (Malouf, 1998). Although local native culture and populations had already been altered by introduced diseases, guns and horses prior to this time, native use of the region was further reduced when the territorial governor of Washington signed treaties with the Flathead, Pend d'Oreille and other tribes in the 1850s, followed by their removal to reservations (Haines, 1938; Malone et al., 1991). Also in the 1850s, several cattle herds were wintered in what is now southwestern Montana, to re-supply emigrants on the Oregon Trail (Osgood, 1929; Malone et al., 1991). However, in 1862, the first Montana discovery of placer gold about 70 km south of the study area, started a mining boom in southwestern Montana and brought the first major influx of non-native people, namely prospectors and those who supplied them (Malone et al., 1991; Paul, 1963). The open-range domestic livestock industry was established in southwestern Montana at this time to supply the prospectors, and the population of these animals increased rapidly in the following decades (Osgood, 1929; Wentworth, 1948; Malone et al., 1991).

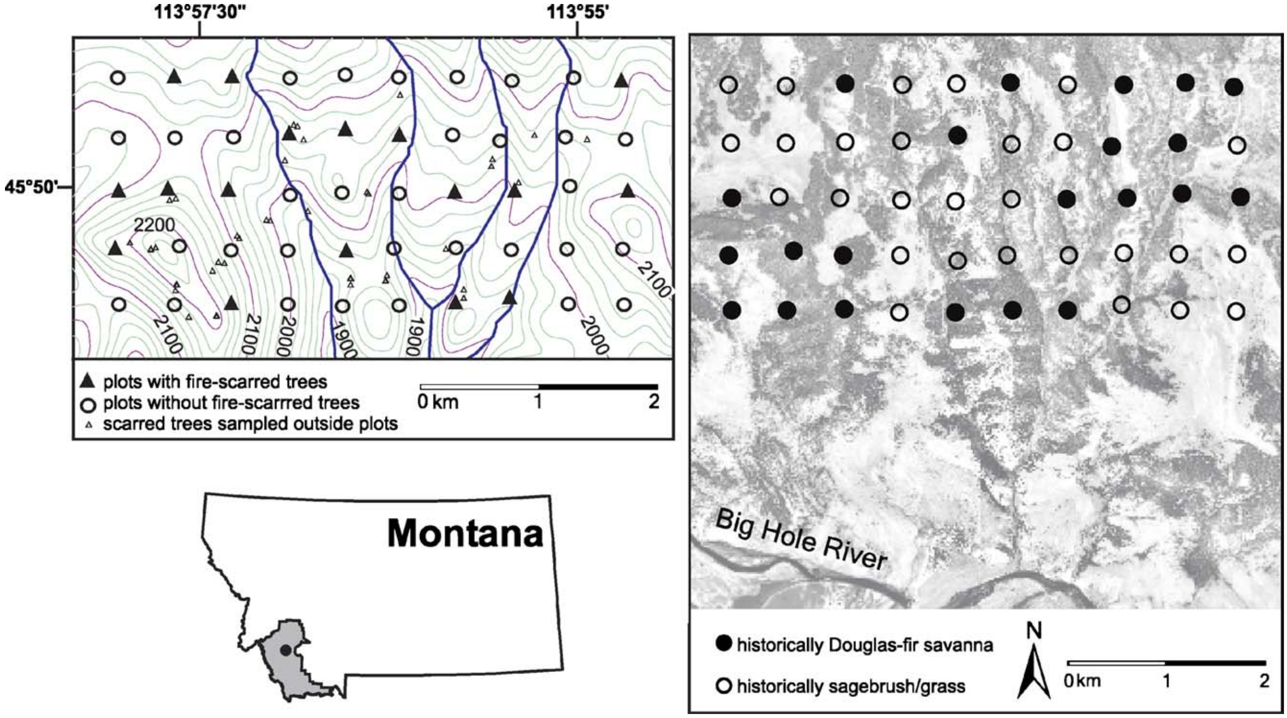

Fig. 1. Location of the study area and Silverbow, Deer Lodge and Beaverhead counties (shaded region), and the sampled plots, showing the location of fire-scarred trees sampled within and outside of plots (left) and location of plots that were historically Douglas-fir savanna (i.e., at least three Douglas-fir trees established before 1855) vs. those that were historically sagebrush–grass (right). The orthophoto was taken in August 1995 (USGS, 1995).

There is no record of pre-1900 logging in the study area, although a few of the plots we sampled had been logged since the 1960s and a few were burned by manager-ignited fires since 1989. The study area is currently managed by the Bureau of Land Management—Butte Field Office, and abuts land managed by the Wise River Ranger District of the Beaverhead-Deerlodge National Forest.

3. Methods

We sampled a grid of 50 variable-radius plots (described below), spaced 500 m apart, covering 1030 ha of the modern mosaic of forest and sagebrush–grass in the study area (Fig. 1). To avoid roads, streams, rock outcrops and the boundaries between vegetation types, we moved the center of 15 plots 36 m (on average) along a randomly chosen azimuth. At each plot, we measured slope, aspect, elevation and location, and took one photograph in each cardinal direction. We computed an index of relative soil moisture among our plots by summing assigned values for categories of the following slope parameters: slope steepness, slope aspect, topographic position (valley bottom, lower slope, middle slope, upper slope or ridge top) and slope configuration (concave, straight or convex; Parker, 1982).

3.1. History of surface fires

To reconstruct a history of surface fires, we sampled 83 fire-scarred trees within and between plots. We searched for fire-scarred trees within a radius of 80 m (corresponding to approximately 2 ha) of each plot center and found one to four trees with well-preserved scars at only 17 of them. We used a chain saw to remove fire-scarred partial cross-sections from these trees (33 trees sampled; Arno and Sneck, 1977). In addition, we removed sections from 50 fire-scarred trees that we encountered between plots. We sanded the scarred sections until the cell structure was visible with a binocular microscope and assigned calendar years to tree rings using a combination of visual crossdating of ring widths and cross-correlation of measured ring-width series (Holmes, 1983; Grissino-Mayer, 2003). In addition to fire scars, we obtained a small amount of supporting evidence of surface fires (12% of fire dates at plots) from abrupt changes in the width of annual rings (Landsberg et al., 1984; Sutherland et al., 1991). However, because factors other than surface fires can cause abrupt changes in cambial growth, we used such a change in a given sample as evidence of a surface fire only when it was synchronous with a fire scar in other samples.

We identified the calendar year in which each scar formed to determine the year of fire occurrence (Dieterich and Swetnam, 1984). In the northern hemisphere, the season of cambial dormancy (i.e., the period corresponding to the ring boundary) spans two calendar years—from the time the cambium stops growing in the summer or fall of 1 year until it resumes in the spring of the following year. For this study, we assigned ring-boundary scars to the *preceding* calendar year because modern fires near the study area generally burn in mid- to late summer (Schmidt et al., 2002). We were unable to determine the intra-ring position of some scars because they were obscured by rot or insect galleries, or the rings were very narrow.

To compute fire intervals at the plots, we composited the fire dates from all trees sampled at a plot into a single record of fire occurrence for that plot (composited over approximately 2 ha; Dieterich, 1980) and computed the intervals between years in which a fire scarred at least one tree. We estimated the area burned in a given year as the area of a convex hull surrounding any trees with evidence of fire for that year, including trees in and between plots. We computed fire intervals and fire size from 1700 to 1860, the period after which at least 41% of the 17 plots with fire-scarred trees were recording fires (i.e., trees were present on the plot and had been scarred at least once) and before the recent abrupt cessation of surface fires in the study area.

3.2. History of tree establishment

To reconstruct the history of tree establishment at each plot, we used an *n*-tree density-adapted sampling method (Jonsson et al., 1992; Lessard et al., 2002). We removed samples (increment cores or cross-sections) from those trees that were closest to plot center but within a radius of 30 m, up to a maximum of 30 trees. Consequently, the plots varied in size with tree density and three plots did not include any trees. For each tree within a plot, we determined species and diameter at breast height (dbh, 1.4 m). From live trees, we removed increment cores approximately 15 cm above the ground. We did not remove increment cores from live saplings (trees less than 15 cm dbh and greater than 30 cm tall), but tallied them by species. From dead trees that were sound enough to crossdate, we used a chain saw to remove a section, including the pith, from what would have been approximately 15 cm above the ground. We did not remove sections from dead trees that were not sound enough to crossdate, but tallied them instead. Trees had been recently harvested from seven of our plots, but we obtained establishment dates from the stumps and remaining live trees.

For each plot, we computed several tree densities. We tallied modern and historical trees (alive in 2003 and 1855, respectively) and modern saplings, and divided by plot size. Plot size was computed as the area of a circle with radius equal to the distance between plot center and the tree sampled farthest from plot center (range 11–30 m, average 25 m) and ranged from 0.04 to 0.28 ha (average 0.20 ha).

We mounted the increment cores on wooden holders. All cores and sections were sanded and crossdated using the methods employed for fire-scarred sections. We estimated the establishment date of each tree as its pith date. Most increment cores (83%) did not intersect the pith. To estimate the pith date of these trees, we estimated the number of years to pith from the curvature of the innermost rings sampled (average years to pith: 7 years; Applequist, 1958; Duncan, 1989) and subtracted this estimate from the innermost ring date. We did not correct for the number of years it took the trees to reach the height at which we cored them (approximately 15 cm above ground). However, Douglas-fir trees in other open forests near the study area took about 5–10 years to reach this height (Monserud, 1984; Dando and Hansen, 1990; Hansen et al., 1995). Consequently, we assume that the true establishment dates in our study area are 5–10 years earlier than we report.

3.3. Drivers of recent tree establishment

To identify potential drivers of the recent increase in establishment of trees in the study area, we compared our time series of tree establishment to fire size, domestic livestock grazing and climate. From our record of fire scars, we reconstructed fire size for a given year as the area of the smallest convex polygon containing all the plots or trees with evidence of fire in that year (1700–2003; Sedgewick, 1988). Our time series of domestic livestock grazing is the number of sheep and cattle in Montana (1867–2004; MASS, 2004). The county in which the study area lies (Silver Bow) lacks grazing records before 1881, the year it was established. However, the number of animals for the state of Montana probably captures the number near the study area before 1880 because the livestock industry was confined to the area surrounding the study area at that time (Osgood, 1929; Malone et al., 1991). Our time series of climate is the summer Palmer Drought Severity Index (PDSI; Palmer, 1965, June–August), reconstructed from tree rings (1700–2003, grid point 84; Cook et al., 1999).

To model the effect of fire on the dynamics of Douglas-fir establishment and persistence in our study area, we used a landscape fire succession model (LANDSUM; Keane et al., 2002, 2004). In this spatially explicit model, we stratified the landscape into zones of potential vegetation and deterministically modeled changes in vegetation composition and structure through time, based on established transition times between successional stages and the effects of stochastically modeled fires (Kessell and Fischer, 1980). We modeled vegetation dynamics in the study area under two scenarios. For the historical fire scenario, we based our model of fire occurrence and size on the distributions that we reconstructed from tree rings in our study area, and tree-ring reconstructed PDSI (Cook et al., 1999; Appendix A). For the fire exclusion scenario, fires burned only a short distance from their origin. We summarized Douglas-fir dynamics at the locations of our field-sampled plots and across the entire 1030 ha study area. From the modeled time series (5000 years long), we identified the historical range of variation in percentage of plots with Douglas-fir trees, in the presence and absence of fire.

3.4. Characteristics of historical Douglas-fir savanna versus sagebrush–grass plots

Based on the establishment dates of live and dead trees, we placed the plots into one of two categories of historical vegetation. We categorized plots as historically Douglas-fir savanna if at least three trees had established by 1855, the year of the last large surface fire we reconstructed in the study area and the beginning of a period of major change in land use in southwestern Montana. We categorized plots with fewer than three trees in 1855 as historically sagebrush–grass. While the presence of trees before 1855 in a plot is sufficient to characterize it as historically Douglas-fir savanna, the absence of such trees is not, because trees may have established before 1855 but died since then. Therefore, to confirm our categorization of plots, we determined the establishment dates of dead trees in our plots and if these trees were too decayed to

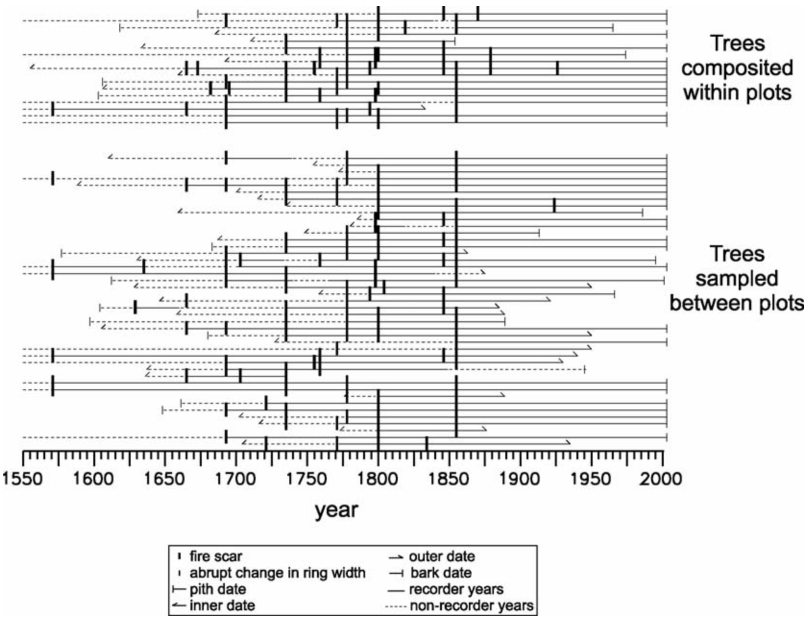

Fig. 2. Chronology of surface fire occurrence in the study area. Each horizontal line shows either the composite fire-scar record for a plot (i.e., fire-scar dates composited for all trees within a plot, specifically one to four trees sampled over approximately 2 ha), or the record from a single tree sampled opportunistically between plots. Non-recorder years precede the formation of the first scar on each tree but also occur when subsequent fires or rot consume that record. Inner and outer dates are the dates of the earliest or latest rings sampled for trees where pith or bark was not sampled.

yield an establishment date, we noted their presence. The presence of large undatable trees in a plot may indicate that the plot supported Douglas-fir trees in the past.

Soil moisture is a factor in the establishment and persistence of trees elsewhere in the Interior West (e.g., Sindelar, 1971). To assess whether soil moisture may have influenced the spatial distribution of Douglas-fir trees in our study area in the past, we computed the topographic relative moisture index for each plot (TRMI, Parker, 1982). This index is the sum of indices of four slope parameters that we measured in the field: aspect, slope, topographic position and slope configuration. We tested for differences in mean soil moisture index between plots that were historically Douglas-fir savannas versus those that were sagebrush–grass (equal variances, SAS Proc TTEST; SAS Institute, 2001), excluding three plots dominated by lodgepole pine.

4. Results

4.1. History of surface fires

We removed fire-scarred sections from a total of 83 trees. All were Douglas-fir, except for five lodgepole pine that had charred triangular basal catfaces and multiple scars. About half (48%) the fire-scarred trees, we sampled were logs, snags or stumps. We were unable to crossdate sections from a few of the sampled trees (8%). Those that crossdated yielded 192 fire scars, and 26 abrupt changes in ring width between 1571 and 2003 (Fig. 2; Dieterich, 1980; Grissino-Mayer, 1995, 2001). We were able to assign an intra-ring position to only 36% of the fire scars due to rot and insect galleries. Of these, almost all were formed on the boundary between two rings (97% of scars, 1571–2003). The surface fires we reconstructed burned from 9 to 302 ha within the study area (Fig. 3) and burned the sampled plots once every 2–84 years during the analysis period (1700–1860; Fig. 2). From 1860 to the present, only a single small fire (32 ha) was documented in the study area.

4.2. History of tree establishment

To estimate establishment dates, we removed samples from 1 to 30 trees per plot (22 on average), for a total of 1037 trees across the study area, mostly Douglas-fir (94%). However, three plots were dominated by lodgepole pine and three plots

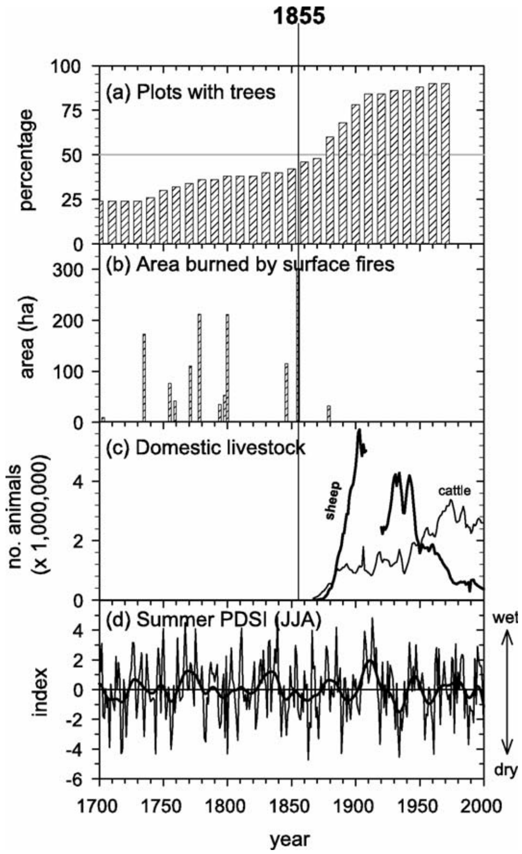

Fig. 3. Synchrony of a recent increase in the rate of establishment of Douglas-fir trees in the study area (a) with an abrupt decline in relative area burned by surface fires in the study area (b), the rise of domestic livestock grazing in Montana (c) and the start of 20 years of relatively dry summers (June through August) (d). For Palmer Drought Severity Index (PDSI), the thin line shows yearly variation, the thick line is the yearly data filtered with a 20-year low-pass filter to emphasize decadal variation (Cook et al., 1999).

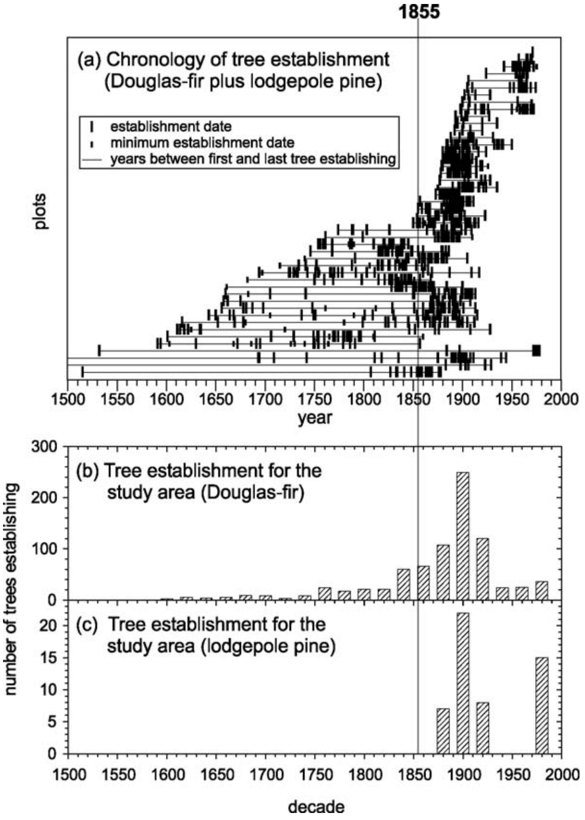

Fig. 4. History of tree establishment (trees >15 cm dbh) by plot for Douglas-fir plus lodgepole pine (a), and across the study area, by species (b and c). In (a), each horizontal line shows the establishment history of Douglas-fir and lodgepole pine trees at a single plot. Each long vertical line shows a year during which at least one tree established. Short vertical lines indicate an innermost ring date for trees with rotten centers. Only one tree established for most vertical lines (66% of establishment dates). However, a few vertical lines represent the establishment of two (24%) or more trees (10%). The lodgepole pine trees that established in the 1970s likely did so in response to logging.

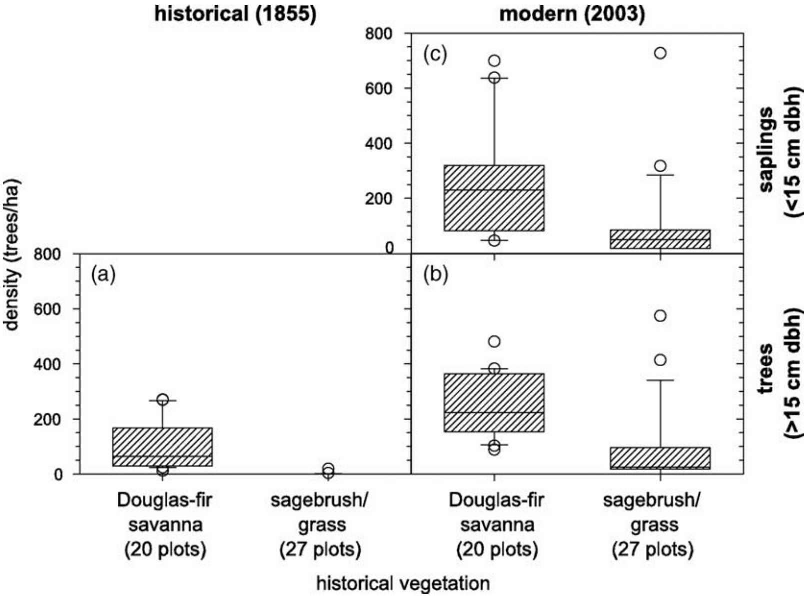

Fig. 5. Density of live Douglas-fir trees in plots that were historically Douglas-fir savanna (i.e., at least three trees established before 1855) vs. plots that were historically sagebrush–grass. Historical density of trees (a) vs. modern density of trees (b) and modern density of saplings (c). The boxes enclose the 25th to 75th percentiles, the whiskers enclose the 10th to 90th percentiles of the distribution of densities among plots. The horizontal line across each box indicates the median and all values falling outside the 10th to 90th percentiles are shown as circles.

lacked live or dead trees in 2003. In addition, we tallied 112 trees that were too decayed to crossdate and 1234 saplings (trees less than 15 cm dbh and greater than 30 cm tall). For some of the 1037 trees we sampled (11%), we could not determine the pith date because the center of the tree was rotten. For these trees, we determined the date of the innermost ring sampled. For other trees, (5%) we could not obtain even minimum establishment dates because they did not crossdate. We tallied these with the other undatable trees (i.e., those not sampled because they were too decayed to crossdate).

Douglas-fir trees have established in all but six plots since the last large surface fire in 1855. Tree density has increased both in plots that were historically sagebrush–grass and those that were Douglas-fir savannas (Fig. 4). Although some trees have persisted in the study area for many hundreds of years, most are young. The majority of trees in the study area established after 1855 (76% of all dated trees, 70% of Douglas-fir trees), and likely all of the 1234 undated saplings (indicating that 89% of the trees established after 1855). However, the oldest establishment date we estimated was 1515 and one tree sampled for fire scars had an inner-ring date of 1388. A post-harvest cohort of lodgepole pine trees appears to have established in one of the three plots harvested since the 1960s (Fig. 4). Trees are currently denser, both at plots that historically supported Douglas-fir savannas and at those that supported sagebrush–grass (Fig. 5).

4.3. Drivers of recent tree establishment

The increase in establishment of trees across the study area after 1855 was synchronous with the cessation of surface fires in the study area, an increase in the number of sheep and cattle in southwestern Montana, and the beginning of 20 years of relatively dry summers (Fig. 3). The recent increase in establishment likely occurred somewhat before our estimate, because we underestimated establishment dates.

The simulated dynamics of Douglas-fir support our inference from tree rings that in the past fire likely excluded Douglas-fir from plots which could support this species. Douglas-fir occurred at fewer plots under the historical fire scenario than under the fire exclusion scenario (59%,

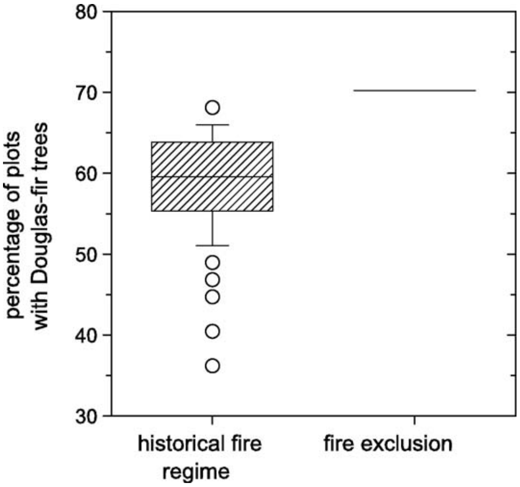

Fig. 6. Presence of Douglas-fir trees simulated with a landscape fire succession model for the plots sampled for tree rings in this study, for a fire regime that mimics that reconstructed from tree rings vs. one in which fires were excluded. The box encloses the 25th to 75th percentiles and the whiskers enclose the 10th to 90th percentiles of the distribution of percentage of plots with Douglas-fir trees over the 5000 years of the simulation. The horizontal line indicates the median and all values falling outside the 10th to 90th percentiles are shown as circles. For the fire exclusion scenario, the percentage of plots with Douglas-fir was constant through time.

range 36–68% versus 70%, no range, respectively; Fig. 6). The simulated results for trees under the historical fire scenario was nearly identical to the study area as a whole (59%, range 36–68% versus 61%, range 40–70%, respectively) indicating that vegetation dynamics at our plots were representative of those simulated for the study area.

4.4. Characteristics of historical Douglas-fir savanna versus sagebrush–grass plots

We categorized 20 plots as historical Douglas-fir savannas (i.e., more than three trees established by 1855) and 27 as sagebrush–grass. The remaining three plots are currently dominated by lodgepole pine. Consistent with our categorization, undatable trees were uncommon at plots that were historically sagebrush–grass. Of the 221 undatable trees, only 42 (19%) occurred at plots that were historically sagebrush–grass, with an average of 2 undatable trees per plot (range 1–3). In contrast, such trees were common in historical Douglas-fir savanna plots (average 5, range 1–9 trees).

Soil moisture availability may have been a driver of the spatial distribution of Douglas-fir trees in our study area in the past. Plots that supported Douglas-fir savannas in the past have significantly lower soil moisture availability than those that did not ($p = 0.02$), although there is considerable overlap in moisture availability between the two categories of plots (Fig. 7). Taking a closer look at the parameters of the index, savanna plots tend to lie on middle (65% of plots) to upper slopes or ridges (25%) and on convex landforms (55%). In contrast, most sagebrush–grass plots lie on middle (56%) to lower slopes or valley bottoms (30%), and on concave landforms (63%).

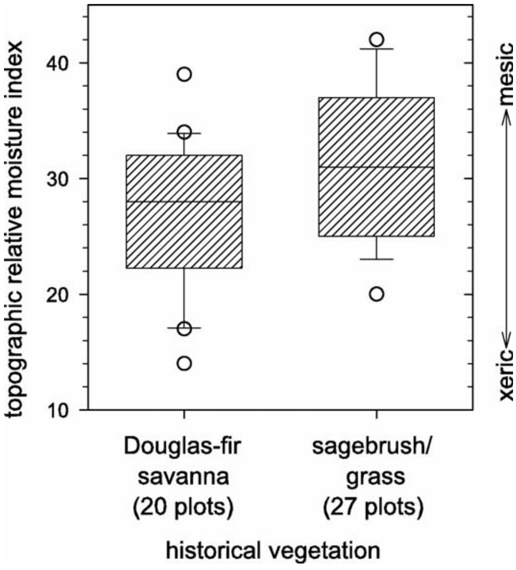

Fig. 7. Relative soil moisture availability (topographic relative moisture index; Parker, 1982). The three plots dominated by lodgepole pine are not included here (topographic relative moisture indices of 34, 36 and 39). The boxes enclose the 25th to 75th percentiles and the whiskers enclose the 10th to 90th percentiles of the distribution of the topographic relative moisture index among plots. The horizontal line across each box indicates the median and all values falling outside the 10th to 90th percentiles are shown as circles.

5. Discussion

5.1. Douglas-fir trees are more abundant now than in the past

The distribution of vegetation in the study area has changed dramatically since 1855. In the past, a mosaic of sagebrush–grasslands with stable islands of Douglas-fir savanna probably dominated the study area much of the time, whereas today it is dominated by Douglas-fir forest. The establishment of trees after 1855 was not simply a matter of treeline moving up or down hill. Rather, Douglas-fir trees have encroached into sagebrush–grasslands from historically stable tree islands and tree density has increased on the tree islands. In 1855 less than half the study area sustained trees whereas all but six plots have trees today and average tree density at plots has increased from 45 trees/ha in 1855 to 166 trees/ha today. This pattern of high modern tree density is strengthened when we consider that there are now also an average of 123 saplings/ha. We did not obtain establishment dates for these saplings, but the median establishment date is 1891 for the 44 Douglas-fir trees we sampled that are less than 16 cm dbh, suggesting that most of these trees established after 1855. This pattern of recent tree encroachment is similar to that documented elsewhere in southwestern Montana (Sindelar, 1971; Arno and Gruell, 1983, 1986; Dando and Hansen, 1990; Hansen et al., 1995).

In general, our categorization of plots as historically savanna versus shrub–grassland was consistent with the presence of undatable trees. Such trees were present in some of the shrub–grassland plots. However, while we did not measure the diameters of all the undatable trees, a review of the plot photographs shows that these trees were generally small in diameter and therefore likely to have established and died since 1855.

5.2. Fire, interacting with climate and soils, likely maintained past sagebrush–grasslands

Douglas-fir trees undoubtedly encroached into sagebrush–grasslands at various times in the past. However, surface fires were frequent enough to kill many of these trees before they reached fire-resistant size. Indeed, the increase in tree establishment in the mid-1800s is synchronous with the cessation of the surface fires that likely excluded such establishment.

When Douglas-fir is in the pole and sapling stages, it is readily killed by fire because it has thin resinous bark and its small crown is near the ground (Turner and Krannitz, 2001; Steinberg, 2002). Mature trees can survive surface fires because the lower bole develops thick corky bark that insulates the cambium, and the crowns are large and can be far from the ground. This occurs by about 40 years of age for Douglas-fir trees on moist sites in the Northern Rocky Mountains (Steinberg, 2002). We suggest that it may take longer for this species to become fire-resistant at our relatively dry site in southwestern Montana, and this is supported by the relatively long fire interval we reconstructed. Surface fires occurred in our plots every 37 years on average (range 2–84 years; composited over approximately 2 ha, 1700–1860), and so would often have been frequent enough to kill young Douglas-fir trees.

Our fire and establishment histories are consistent with the limited existing data on the size of Douglas-fir trees that survive fire. In several studies of tree mortality after prescribed fire in the Rocky Mountains, mortality was high among Douglas-fir trees that averaged 15–20 cm dbh and was complete for trees less than 8 cm dbh (Wyant et al., 1986; Ryan et al., 1988; Kalabokidis and Wakimoto, 1992). In our study area, trees that are less than 40 years old today average 20 cm dbh and so many of these trees would likely have been killed by the surface fires that occurred every 37 years on average. However, the range of variation in fire occurrence under this regime (2–84 years) would likely allow some trees to establish during the longer fire intervals. This frequency is also comparable to the frequency estimated by modeling studies to exclude Douglas-fir (approximately 30 years; Keane et al., 1990), and to that reconstructed from tree rings in Douglas-fir/mountain big sagebrush elsewhere in southwestern Montana (20–40 mean intervals; Houston, 1973; Arno and Gruell, 1983; Littell, 2002) where frequent past fires are also thought to have prevented the establishment of Douglas-fir. All of the surface fires that we reconstructed burned in at least one and sometimes many plots across the study area. Consequently, we believe that fires likely burned the area between plots with evidence of fire in the same year, including across historical sagebrush–grass plots.

Our simulation model of Douglas-fir dynamics with and without fire supported our inference that fire was a likely driver of these dynamics in the past. Both the tree-ring reconstruction and the model indicate that roughly half of the landscape was forested in the past (42% versus 61% of plots, respectively), and that Douglas-fir trees occupy previous unforested plots in the absence of fire. However, our tree-ring reconstruction shows that nearly all of the landscape supports Douglas-fir in the absence of fire (94% of plots have Douglas-fir trees today) whereas the model suggests a much smaller proportion (71% of plots). This difference is likely to due to the limited spatial resolution of the model inputs (generally 30 m cells). Given the difficulties of parameterizing simulation models at fine spatial scales, our model results are best interpreted as relative, rather than quantitive, dynamics of Douglas-fir in the presence versus absence of frequent fires (Pennanen and Kuuluvainen, 2002).

Why were surface fires excluded from the study area after 1855? We suggest that it was likely due to a reduction of fine fuel and/or ignitions. Two factors may have reduced the fine grassy fuels that carry surface fires. The first, domestic livestock grazing, increased dramatically in the study area in the mid-1800s. Such grazing reduces fine fuel loads and has been implicated in fire exclusion elsewhere (e.g., Ellison, 1960; Savage and Swetnam, 1990; Baisan and Swetnam, 1997; Miller and Rose, 1999). Grazing was likely heavy in the study area. In fact, by the mid-1860s, the Montana territorial legislature enacted several laws regulating cattle (Osgood, 1929; Malone et al., 1991) and by the early 1870s, overcrowding and overgrazing in southwestern Montana forced cattle growers to move their herds out of the area (Osgood, 1929; Malone et al., 1991). Several decades of relatively low summer precipitation (i.e., low PDSI 1840–1870; Fig. 3) is the second factor that may have encouraged the establishment of Douglas-fir trees in our study area in the mid-1800s by encouraging the growth of shrubs and discouraging the growth of grass and forbs. This period of relatively dry summers is consistent with climate reconstructed from other networks of tree rings near the study area. The region experienced above-average summer temperatures and below-average stream flow during this period (reflecting below-average winter precipitation and likely lower snow packs; Kipfmueller, 2003; Graumlich et al., 2003). Mountain big sagebrush growth is enhanced during dry periods because it has deep roots, over-wintering foliage and persistent litter that increases soil organic matter and thus water holding capacity (West, 1983; Perfors et al., 2003). While the growth of stress-tolerant shrubs is enhanced during dry periods, less-tolerant perennial grasses and forbs experience considerable mortality during these periods (Anderson and Inouye, 2001). Thus, we expect that extended periods of dry summers in our study area, such as the one that occurred in the mid-1800s, would enhance the establishment of Douglas-fir by encouraging the establishment of mountain big sagebrush that are nurse plants for conifers on semi-arid sites in the West (Cooper, 1953; Sindelar, 1971; Miller and Rose, 1995). At the same time, the decrease in grasses and forbs during this dry time would have resulted in a decrease in the fine fuels that carry the surface fires that would have killed any recently established Douglas-fir. Therefore, dry periods and grazing likely had synergistic effects on tree encroachment in the study area (Pechenac et al., 1937). Lastly, the Native Americans that historically lived in southwestern Montana were restricted to reservations by the mid-1800s (Malone et al., 1991). If native ignition was a significant source of surface fires in the past, a decrease in such ignitions may also have contributed to the exclusion of surface fires from the study area.

Crown fires were probably not common in overstory Douglas-fir tree islands in the study area. Overstory tree density was probably too low to carry active crown fires, as most plots had fewer than 127 Douglas-fir trees/ha (Fig. 5). Prior to 1855, there are a few short pulses of tree establishment among or within plots that might indicate a post-fire cohort (Fig. 4). However, Rocky Mountain Douglas-fir can establish in the understory, so these pulses are not necessarily the result of overstory crown fires.

Although frequent surface fires killed young Douglas-fir trees encroaching into sagebrush–grasslands in many parts of study area in the past, other parts of the study area sustained tree islands over many centuries in the presence of these same frequent fires. We believe that this complex mosaic of patches of Douglas-fir savanna and mountain big sagebrush–grasslands resulted from spatial variation in soil moisture, through its influence on the amount of fine fuel. Our index of soil moisture indicates that Douglas-fir savannas occupied drier microsites than sagebrush–grasslands. We infer that these microsites likely had less fine fuel to carry surface fires. The persistence of trees in historically fire-safe sites in our study area is consistent with findings for Douglas-fir and other species elsewhere in the

Interior West (Burkhardt and Tisdale, 1976; Arno and Gruell, 1983, 1986; Miller and Rose, 1995) and with fire-driven differences in vegetation between habitat islands and the surrounding matrix elsewhere (Clarke, 2002).

Prior to 1855, fires occurred frequently enough in the study area to limit Douglas-fir establishment, but not so frequently that they eliminated mountain big sagebrush. This species is killed by surface fires and does not sprout, but re-establishes from seed (Daubenmire, 1975; Morris et al., 1976). Although the seeds are short-lived (Stevens et al., 1981) and likely do not form persistent seedbanks (Young and Evans, 1989), it was likely that sagebrush quickly re-established from seed sources within our study area because none of the surface fires that we reconstructed burned the entire area (Fig. 3). If fire does not recur too quickly, mountain big sagebrush can return to its pre-burn abundance (Akinsoji, 1988). For example, after fire, mountain big sagebrush at sites near our study area, and in the Great Basin, required up to 30 years to return to >20% cover (Wambolt et al., 2001; Ziegenhagen, 2003). Thus, sagebrush abundance would have had time to recover after fire. However, fire intervals varied in the past, as did climate, so the distribution of trees and shrubs across the study area likely varied as well. Furthermore, Douglas-fir establishment immediately following fire was likely limited by low shrub density because this species establishes preferentially in shaded microsites in this region (Sindelar, 1971; Coffman, 1975; Ryker, 1975), as does western juniper in the northern Great Basin (Burkhardt and Tisdale, 1976; Miller and Rose, 1995). The lengthening of the fire interval after 1855 increased the abundance of Douglas-fir, which reduced the abundance of understory species. Elsewhere, mountain big sagebrush cover decreases rapidly as juniper dominance increases (Miller et al., 2000). We assume that sagebrush was similarly killed by a Douglas-fir overstory in our study area, where we observed dead stems of mountain big sagebrush under the canopy of young Douglas-fir stands.

The sagebrush shrub steppe is among the most endangered in the United States (Noss et al., 1995). Among other perturbations, altered fire regimes have resulted in the encroachment of conifers into the wetter and more productive plant associations within the biome (Miller and Tausch, 2001). The loss of sagebrush communities throughout the West has resulted in the loss of valuable wildlife habitat (Maser et al., 1984) and the potential listing of a number of sagebrush obligate species (Connelly and Braun, 1997; Knick et al., 2005). In response, land-management agencies are attempting difficult and expensive restoration programs (Hemstrom et al., 2002). These programs often lack a spatially and temporally dynamic description of the historical plant communities or guidelines for application of treatments to maintain or restore these communities. Our data suggest that in the past, fire was important in creating heterogeneous landscapes of savannas, mountain big sagebrush and grasslands. In the continued absence of fire, these landscapes are likely to become more homogeneous as trees dominate much of the landscape.

Acknowledgements

This work was funded by the Bureau of Land Management, Butte Field Office; USDA Forest Service, Rocky Mountain Research Station; and Oregon State University. We thank Lindsey Goetz, Cara Greger, Richard Greger, Karl Hopkins, Kathy Krauel, Kristy Miller, Eric O'Neil, Dave Pacioretty and Marc Weber for help in the field; Joslin Heyn, Don Long, Jim Menakis, Mo Mislivets, Denny Simmerman, Tom Thompson and Marc Weber for help with the figures and GIS mapping; the USDA Forest Service, Wise River Ranger District for logistical support; and Rudy King for guidance on the statistical analyses. We thank Gerad Dean, Don Gayton, Bob Keane, Jeremy Littell, Kevin Ryan, Elizabeth Reinhardt, James Riser, Marc Weber and two anonymous reviewers for reviews of the manuscript. The fire-scar and establishment dates and associated metadata are available through the International Multiproxy Paleofire Database (http://www.ncdc.noaa.gov/paleo/impd/paleofire.html).

Appendix A

The LANDSUM model uses probability distribution functions in simulation of fire occurrence and fire size. As these parameters can significantly affect the outcome of the simulation (Keane et al., 2003) it is important to use parameters that based as much as possible on real data. However, as there were too few observed fires in the tree-ring reconstructed fire history to robustly estimate the maximum likelihood estimator, we used theoretical distributions that fit what data we had, evaluated with the Kolmogorov's D statistic. For the fire size probability density function, we assumed that a fair number of small fires that might have occurred would have been unrecorded in the historical record, and that the mean observed value of the theoretical distribution was reasonably captured by the observed fire history. For the fire size distribution, we used a two-parameter Weibull, probability density function (Grissino-Mayer, 1995) with a scale parameter of 120 ha and a shape parameter of 1.2, resulting in a generally negative exponential shaped curve. For fire occurrence we used the three-parameter Weibull hazard function described in Keane et al. (2002).

The influence of climate in the LANDSUM model is primarily through an increase in fire size for dry years and smaller fires for wet years. The proportion of dry, wet and normal years was estimated from a PDSI time series, which was reconstructed via simple linear regression from composited annual tree ring widths ($r^2 = 0.6537$). To reduce the chances of an undue influence from this parameter, we defined dry years as those years for which the PSDI lay ≥ 0.5 standard deviations above the mean, and wet years lay ≥ 0.5 standard deviations below the mean. This resulted in a distribution of climate influences that was generally weighted towards normal years, and with equal chance of either dry or wet years. In the version of LANDSUM used here, climate influences are stochastically modeled based on these weights, but are independent, rather than temporally autocorrelated. There is thus little likelihood for extended periods of either drought or moist years in this simple model.

Simulation of landscape dynamics for small landscapes, such as our study area, is problematic because, if modeled only at small spatial extents, it becomes increasingly likely that significant influences that lie outside, but would ordinarily impact the area of interest, such as large fires originating outside and burning through the study area, are not included in the simulation. Simulation of small areas thus tends to underestimate fire occurrence (Keane et al., 2002). To mitigate this problem, we simulated landscape dynamics for a much larger area, roughly 30 times the size of our study area, and extracted the area of interest from the larger set, post-simulation.

References

Akinsoji, A., 1988. Postfire vegetation dynamics in a sagebrush steppe in southeastern Idaho, USA. Vegetatio 78, 151–155.

Anderson, J.E., Inouye, R.S., 2001. Landscape-scale changes in plant species abundance and biodiversity of a sagebrush steppe over 45 years. Ecol. Monogr. 71, 531–556.

Applequist, M.B., 1958. A simple pith locator for use with off-center increment cores. J. For. 56, 141.

Arno, S.F., Sneck, K.M., 1977. A method for determining fire history in coniferous forests of the mountain west. General Technical Report GTR-INT-42. U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT, p. 28.

Arno, S.F., Gruell, G.E., 1983. Fire history at the forest-grassland ecotone in southwestern Montana. J. Range Manage. 36, 332–336.

Arno, S.F., Gruell, G.E., 1986. Douglas-fir encroachment into mountain grasslands in southwestern Montana. J. Range Manage. 39, 272–276.

Baisan, C.H., Swetnam, T.W., 1997. Interactions of fire regimes and land use in the central Rio Grande valley. Research Paper Rocky Mountain-RP-330. United States Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO, p. 20.

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

Butler, D.R., 1986. Conifer invasion of subalpine meadows, central Lemhi Mountains, Idaho. Northwest Sci. 60, 166–173.

Clarke, P.J., 2002. Habitat islands in fire-prone vegetation: do landscape features influence community composition? J. Biography 29, 677–684.

Coffman, M.S., 1975. Shade from brush increases survival of planted Douglas-fir. J. For. 73, 726–728.

Connelly, J.W., Braun, C.E., 1997. Long-term changes in sage grouse *Centrocercus urophasiamus* populations in western North America. Wildl. Biol. 3, 229–234.

Cook, E.R., Meko, D.M., Stahle, D.W., Cleaveland, M.K., 1999. Drought reconstructions for the continental United States. J. Climate 12, 1145–1162 (Data archived at National Geophysical Data Center [online, Cook E.R., et al., 2004, North American summer PDSI reconstructions. IGBP PAGES/World Data Center for Paleoclimatology, data contribution series #2004-45. NOAA/NGDC Paleoclimatology Program, Boulder CO, USA]. Available from http://www.ngdc.noaa.gov/paleo/pdsi.html [cited 8 September 2004]).

Cooper, H.W., 1953. Amounts of big sagebrush in plant communities near Tensleep, Wyoming, as affect by grazing treatment. Ecology 34, 186–189.

Dando, L.M., Hansen, K.J., 1990. Tree invasion into a range environment near Butte, Montana. Great Plains-Rocky Mountain Geographer 18, 65–76.

Daubenmire, R., 1975. Ecology of *Artemisia tridentata* subsp. *tridentata* in the state of Washington. Northwest Science 49, 24–35.

Dieterich, J.H., 1980. The composite fire interval: a tool for more accurate interpretation of fire history. In: Stokes, M.A., Dieterich, J.H. (technical coordinators), Proceedings of the Fire History Workshop, 20–24 October 1980, Tucson. General Technical Report RM-81. U.S. Department of Agriculture Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO, pp. 8–14.

Dieterich, J.H., Swetnam, T.W., 1984. Dendrochronology of a fire-scarred ponderosa pine. Forest Sci. 30, 238–247.

Duncan, R.P., 1989. An evaluation of errors in tree age estimates based on increment cores in kahikatea (*Dacrycarpus dacrydiodes*). N. Z. Nat. Sci. 16, 31–37.

Ellison, L., 1960. Influence of grazing on plant succession of rangelands. Bot. Rev. 26, 1–78.

Gisborne, H.T., 1931. A fire-year record of lightning storms and forest fires. Monthly Weather Rev. 59, 139–150.

Graumlich, L.J., Pisaric, M.F.J., Waggoner, L.A., Littell, J.S., King, J.C., 2003. Upper Yellowstone River flow and teleconnections with Pacific basin climate variability during the past three centuries. Climatic Change 59, 245–262.

Grissino-Mayer, H.D., 1995. Tree-ring reconstructions of climate and fire history at El Malpais National Monument, New Mexico. Ph.D. dissertation. University of Arizona, Tucson, p. 407.

Grissino-Mayer, H.D., 2001. FHX2—Software for analyzing temporal and spatial patterns in fire regimes from tree rings. Tree-Ring Res. 57, 115–124.

Grissino-Mayer, H.D., 2003. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. Tree-Ring Res. 57, 205–211.

Gustafson, E., Shifley, S.R., Mladenoff, D.J., Nimerfro, K.K., He, H.S., 2000. Spatial simulation of forest succession and timber harvesting using LANDIS. Can. J. Forest Res. 30, 32–43.

Haines, F., 1938. The northward spread of horses among the Plains Indians. Am. Anthropol. 40, 429–437.

Hansen, K., Wyckoff, W., Banfield, J., 1995. Shifting forests: historical grazing and forest invasion in southwestern Montana. Forest Conserv. History 39, 66–76.

He, H.S., Mladenoff, David J., 1999. Spatially explicit and stochastic simulation of forest-landscape fire disturbance and succession. Ecol. Soc. Am. 80, 81–99.

Hemstrom, M.A., Wisdom, M.J., Hann, W.J., Rowland, M.M., Wales, B.C., Gravenmier, R.A., 2002. Sagebrush-steppe vegetation dynamics and restoration potential in the interior Columbia Basin, USA. Conserv. Biol. 16, 1243–1255.

Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bull. 43, 69–78.

Houghton, R.A., et al., 1999. The US carbon budget: contributions from land-use change. Science 285, 574–578.

Houston, D.B., 1973. Wildfires in northern Yellowstone National Park. Ecology 54, 1111–1117.

Huxman, T.E., Wilcox, B.P., Breshears, D.D., Scott, R.L., Synder, K.A., Small, E.E., Hultine, K., Pockman, W.T., Jackson, R.B., 2005. Ecohydrological implications of woody plant encroachment. Ecology 86, 308–319.

Jonsson, B., Holm, S., Kallur, H., 1992. A forest inventory method based on density-adapted circular plot size. Scand. J. Forest Res. 7, 405–421.

Kalabokidis, K.D., Wakimoto, R.H., 1992. Prescribed burning in uneven-aged stand management of ponderosa pine/Douglas-fir forests. J. Environ. Manage. 34, 221–235.

Keane, R.E., Arno, S.F., Brown, J.K., 1990. Simulating cumulative fire effects in ponderosa pine/Douglas-fir forests. Ecology 71, 189–203.

Keane, R.E., Parsons, R.A., Hessburg, P.F., 2002. Estimating historical range and variation of landscape patch dynamics: limitations of the simulation approach. Ecol. Modell. 151, 29–49.

Keane, R.E., Cary, G.C., Parsons, R.A., 2003. Using simulation to map fire regimes: an evaluation of approaches, strategies, and limitations. Int. J. Wildland Fire 12, 309–322.

Keane, R.E., Cary, G.J., Davies, I.D., Flannigan, M.D., Gardner, R.H., Lavorel, S., Lenihan, J.M., Li, C., Rupp, T.S., 2004. A classification of landscape fire succession models: spatial simulations of fire and vegetation dynamics. Ecol. Model. 179, 3–27.

Kessell, S.R., Fischer, W.C., 1980. Predicting postfire plant succession for fire management planning. General Technical Report INT-94. Intermountain Forest and Range Experiment Station, U.S. Department of Agriculture, Forest Service, Ogden, UT, p. 19.

Kipfmueller, K.F., 2003. Fire–climate–vegetation interactions in subalpine forests of the Selway-Bitterroot Wilderness Area, Idaho and Montana, USA. Ph.D. dissertation. University of Arizona, Tucson, AZ, p. 322.

Knick, S.T., Holmes, A.L., Miller, R.F., 2005. The role of fire in structuring sagebrush habitats and bird communities. Stud. Avian Biol. 30, 63–75.

Landsberg, J.D., Cochran, P.H., Finck, M.M., Martin, R.E., 1984. Foliar nitrogen content and tre growth after prescribed fire in ponderosa pine. Research Note PNW-412. USDA Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, OR, p. 15.

Lessard, V.C., Drummer, T.D., Reed, D.D., 2002. Precision of density estimates from fixed-radius plots compared to *N*-tree distance sampling. Forest Sci. 48, 1–5.

Littell, J.S., 2002. Determinants of fire regime variability in lower elevation forests of the northern Greater Yellowstone Ecosystem. M.S. thesis. Montana State University, Bozeman, MT, p. 121.

Malone, M.P., Roeder, R.B., Lang, W.L., 1991. Montana: A History of Two Centuries, revised ed. University of Washington Press, Seattle, p. 466.

Malouf, C.I., 1998. Flathead and Pend d'Oreille. In: Walker, Jr., D.E. (Ed.), Handbook of North American Indians, vol. 12. Smithsonian Institution Plateau, Washington, DC, pp. 297–312.

Maser, C., Thomas, J.W., Anderson, R.G., 1984. Wildlife habitats in managed rangelands—the Great Basin of southeastern Oregon: The Relationship of Terrestrial Vertebrates To Plant Communities And Structural Conditions. USDA Forest Service General Technical Report PNW-172. Pacific Northwest Forest and Range Experiment Station, Portland, OR, p. 262.

Mast, J.N., Veblen, T.T., Hodgson, M.E., 1997. Tree invasion within a pine/grassland ecotone: an approach with historic aerial photography and GIS modeling. Forest Ecol. Manage. 93, 181–194.

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

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

Miller, R.F., Svejcar, T., Rose, J.A., 2000. Impacts of western juniper on plant community composition and structure. J. Range Manage. 53, 574–585.

Miller, R.F., Tausch, R.J., 2001. The role of fire in pinyon and juniper woodlands: a descriptive analysis. In: Galley, K., Wilson, T. (Eds.), Fire Conference 2000: The First National Congress On Fire Ecology, Prevention And Management. Tall Timbers Research Station, Tallahassee, FL, pp. 15–30.

Monserud, R.A., 1984. Height growth and site index curves for inland Douglas-fir based on stem analysis data and forest habitat type. Forest Sci. 30, 943–965.

Montana Agricultural Statistics Service (MASS), 2004. Cattle and calves inventory and value; and sheep and wool: inventory, production and value [online]. Available from http://www.nass.usda.gov/mt/livestock/cattle%26c.htm and http://www.nass.usda.gov/mt/livestock/shp%26wool.htm [cited 10 April 2004].

Morris, M.S., Kelsey, K.G., Griggs, D., 1976. The geographic and ecological distribution of big sagebrush and other woody *Artemisia*s in Montana. Proc. Montana Acad. Sci. 36, 56–79.

National Climatic Data Center (NCDC), 2004. Climate data for Wise River, Montana [online]. Available from http://www.wrcc.dri.edu/cgi-bin/cliRECtm.pl?mtwise [cited 13 December 2003].

Noss, R.F., LaRoe, E.T., Scott, J.M., 1995. Endangered Ecosystems of the United States: A Preliminary Assessment of Loss and Degradation. Biological Report 28. USDI National Biological Service, Washington, DC.

Osgood, E.S., 1929. The Day of the Cattleman. University of Minnesota Press, Minneapolis, MN, p. 283.

Palmer, W.C., 1965. Meteorological drought, Research Paper Number 45. United States Department of Commerce, Weather Bureau, Washington, DC.

Parker, A.J., 1982. The topographic relative moisture index: an approach to soil-moisture assessment in mountain terrain. Phys. Geo. 3, 160–168.

Patten, D.T., 1969. Succession from sagebrush to mixed conifer forest in the northern Rocky Mountains. Am. Midland Natural. 82, 229–240.

Paul, R.W., 1963. Mining Frontiers of the Far West, 1848–1880. Holt, Rinehart and Winston, New York, p. 236.

Pechenac, J.F., Pickford, G.D., Stewart, G., 1937. Effects of the 1934 drought on native vegetation of the upper Snake River Plains, Idaho. Ecology 18, 490–505.

Pennanen, J., Kuuluvainen, T., 2002. A spatial simulation approach to natural forest landscape dynamics in boreal Fennoscandia. Forest Ecol. Manage. 164, 157–175.

Perfors, T., Harte, J., Alter, S.E., 2003. Enhanced growth of sagebrush (*Artemisia tridentata*) in response to manipulated ecosystem warming. Global Change Biol. 9, 736–742.

Ryan, K.C., Peterson, D.L., Reinhardt, E.D., 1988. Modeling long-term fire-caused mortality of Douglas-fir. Forest Sci. 34, 190–199.

Ryker, R.A., 1975. A survey of factors affecting regeneration of Rocky Mountain Douglas-fir. Research Paper INT-174. USDA Forest Service, Intermountain Forest and Range Experiment Station, Odgen, UT, p. 19.

SASSSSS, 2001. SAS Institute. 2001. SAS Release 8.02. Campus Drive, Cary, North Carolina 27513, USA.

Savage, M., Swetnam, T.W., 1990. Early 19th-Century fire decline following sheep pasturing in a Navajo ponderosa pine forest. Ecology 71, 2374–2378.

Schimel, D., Melillo, J., Tain, H., McGuire, A.D., Kicklighter, D., Kittel, T., Rosenbloom, N., Running, S., Thornton, P., Ojima, D., Parton, W., Kelly, R., Sykes, M., Neilson, R., Rizzo, B., 2000. Contribution of increasing CO_2 and climate to carbon storage by ecosystems in the United States. Science 287, 2004–2006.

Schmidt, K., Menakis, J., Hardy, C., Hann, W., Bunnell, D., 2002. Development of coarse-scale spatial data for wildland fire and fuel management. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. RMRS GTR-87, Fort Collins, CO.

Sedgewick, R., 1988. Algorithms, second ed. Addison-Wesley, Reading, MA, p. 657.

Sindelar, B.W., 1971. Douglas-fir invasion of western Montana grasslands. Ph.D. dissertation. University of Montana, Missoula, MT, p. 130.

Soulé, P.T., Knapp, P.A., 2000. *Juniperus occidentalis* (western juniper) establishment history on two minimally disturbed research natural areas in central Oregon. Western North Am. Natural. 60, 26–33.

Steinberg, P.D., 2002. *Pseudotsuga menziesii* var. *glauca*. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory, (Producer). Available: http://www.fs.fed.us/database/feis/ [accessed 2004. December 17].

Stevens, R., Jorgensen, K.R., Davis, J.N., 1981. Viability of seed from thirty-two shrub and forb species through fifteen years of warehouse storage. Great Basin Natural. 41, 274–277.

Strang, R.M., Parminter, J.V., 1980. Conifer encroachment on the Chilcotin grasslands of British Columbia. For. Chronicle 56, 13–18.

Sutherland, E.K., Covington, W.W., Andariese, S., 1991. A model of ponderosa pine growth response to prescribed burnind. Forest Ecol. Manage. 44, 161–173.

Turner, M.G., Romme, W.H., Gardner, R.H., O'Neill, R.V., Kratz, T.K., 1993. A revised concept of landscape equilibrium: disturbance and stability on scaled landscapes. Landscape Ecol. 8 (3), 213–227.

Turner, J.S., Krannitz, P.G., 2001. Conifer density increases in semi-desert habitats of British Columbia in the absence of fire. Northwest Sci. 75, 176–182.

United States Geological Survey (USGS), 1995. Digital orthophoto, Wise River, Montana, from aerial photos of 8/14/1995 and 8/20/1995 [online]. Montana State Library, Helena, MT. Available from http://nris.state.mt.us/nsdi/doq.asp?Srch24=4511278 [cited February 2004].

Van Auken, O.W., 2000. Shrub invasions of North American semiarid grasslands. Ann. Rev. Ecol. System. 31, 197–215.

Vale, T.R., 1975. Invasion of big sagebrush (*Artemisia tridentata*) by white fire (*Abies concolor*) on the southeastern slopes of the Warner Mountains, California. Great Basin Natural. 35, 319–324.

Wambolt, C.L., Walhof, K.S., Frisina, M.R., 2001. Recovery of big sagebrush communities after burning in south-western Montana. J. Range Mange. 61, 243–252.

Wentworth, E.N., 1948. America's Sheep Trails: History, Personalities. The Iowa State College Press, Ames, IA, p. 667.

West, N.E., 1983. Western intermountain sagebrush steppe. In: West, N.E. (Ed.), Temperate Deserts and Semi-deserts. Ecosystems of the World 5. Elsevier Scientific Publishing Company, New York, pp. 351–374.

Wyant, J.G., Omi, P.N., Laven, R.D., 1986. Fire induced tree mortality in a Colorado ponderosa pine/Douglas-fir stand. Forest Sci. 32, 49–59.

Young, J.A., Evans, R.A., 1981. Demography and fire history of a western juniper stand. J. Range Manage. 34, 501–505.

Young, J.A., Evans, R.A., 1989. Dispersal and germination of big sagebrush (*Artemisia tridentata*) seeds. Weed Sci. 37, 201–206.

Ziegenhagen, L.L., 2003. Shrub reestablishment following fire in the mountain big sagebrush (*Artemisia tridentata* Nutt. ssp. *vaseyana* (Rydb.) Beetle) alliance. M.S. thesis. Oregon State University, Corvallis, OR.