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ORIGINAL ARTICLE

Fire, fuels and restoration of ponderosa pine–Douglas fir forests in the Rocky Mountains, USA

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ABSTRACT

Aim Forest restoration in ponderosa pine and mixed ponderosa pine–Douglas fir forests in the US Rocky Mountains has been highly influenced by a historical model of frequent, low-severity surface fires developed for the ponderosa pine forests of the Southwestern USA. A restoration model, based on this low-severity fire model, focuses on thinning and prescribed burning to restore historical forest structure. However, in the US Rocky Mountains, research on fire history and forest structure, and early historical reports, suggest the low-severity model may only apply in limited geographical areas. The aim of this article is to elaborate a new variable-severity fire model and evaluate the applicability of this model, along with the low-severity model, for the ponderosa pine–Douglas fir forests of the Rocky Mountains.

Location Rocky Mountains, USA.

Methods The geographical applicability of the two fire models is evaluated using historical records, fire histories and forest age-structure analyses.

Results Historical sources and tree-ring reconstructions document that, near or before AD 1900, the low-severity model may apply in dry, low-elevation settings, but that fires naturally varied in severity in most of these forests. Low-severity fires were common, but high-severity fires also burned thousands of hectares. Tree regeneration increased after these high-severity fires, and often attained densities much greater than those reconstructed for Southwestern ponderosa pine forests.

Main conclusions Exclusion of fire has not clearly and uniformly increased fuels or shifted the fire type from low- to high-severity fires. However, logging and livestock grazing have increased tree densities and risk of high-severity fires in some areas. Restoration is likely to be most effective which seeks to (1) restore variability of fire, (2) reverse changes brought about by livestock grazing and logging, and (3) modify these land uses so that degradation is not repeated.

Keywords
Douglas fir, ecosystem restoration, fire ecology, historical accounts, *Pinus ponderosa*, ponderosa pine, *Pseudotsuga menziesii*, Rocky Mountains.

INTRODUCTION

In the Southwestern United States of America, the structure and composition of ponderosa pine (*Pinus ponderosa* P. and C. Lawson) forests are thought to have been altered by fire exclusion, leading to increases in tree density and a host of associated ecological changes (Covington & Moore, 1994). A formalized restoration model (Friederici, 2003) suggests that restoration of pre-fire exclusion forest conditions and a low-severity fire regime is also consistent with a reduction in the risk of crown fires in ponderosa pine ecosystems. Thus, this low-severity model has contributed to the widespread assumption that ecological restoration and fire hazard mitigation can be simultaneously achieved in most low-elevation, dry forest ecosystems of the western United States (e.g. Covington, 2000), which is a major driving force behind

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US national fire policy (United States Department of Agriculture, 2002; White House, 2002). Ecologists have devised detailed proposals for restoring Southwestern ponderosa pine forests and reintroducing fire (Allen *et al.*, 2002; Friederici, 2003). Do these proposals, however, apply to related forests of the Rocky Mountains? Ecologists have cautioned that evidence about the applicability of the low-severity model should be examined before restoration (Gutsell *et al.*, 2001; Veblen, 2003; Brown *et al.*, 2004; Odion *et al.*, 2004; Schoennagel *et al.*, 2004).

In this article, we draw upon some previously unused historical sources and other evidence to assess the applicability of the low-severity model, and an alternative variable-severity model, throughout the ponderosa pine–Douglas fir (*Pseudotsuga menziesii* (Mirbel) Franco) forests of the US Rocky Mountains. The primary focus of this paper is on forests dominated by ponderosa pine, either solely or in mixtures with Douglas fir within the Rocky Mountains (Fig. 1). However, because succession can result in the replacement of ponderosa pine by Douglas fir, we also include some information from forests where ponderosa pine occurs, but Douglas fir is dominant. In this gradient from ponderosa pine-dominated to Douglas fir-dominated forests, other conifers (e.g. *Larix* and *Abies*) or aspen (*Populus tremuloides* (Michx.)) may also be found but are not dominants. The questions addressed about Rocky Mountain ponderosa pine–Douglas fir forests, in assessing these models, include: (1) was the pre-20th century fire regime (i.e. prior to fire exclusion) dominated by low-severity surface fire or by variable-severity fire (i.e. with a significant role played by severe fires); (2) was tree density generally low and comparable to density expected under the low-severity model, or variable as under the variable-severity model; (3) under the variable-severity model, how did fires of different severity affect spatial and temporal variation in tree density; (4) under the variable-severity model, how did variable fire affect fuels; and (5) under the variable-severity model, what have been the effects of fire exclusion, logging and livestock grazing on tree density and fuels?

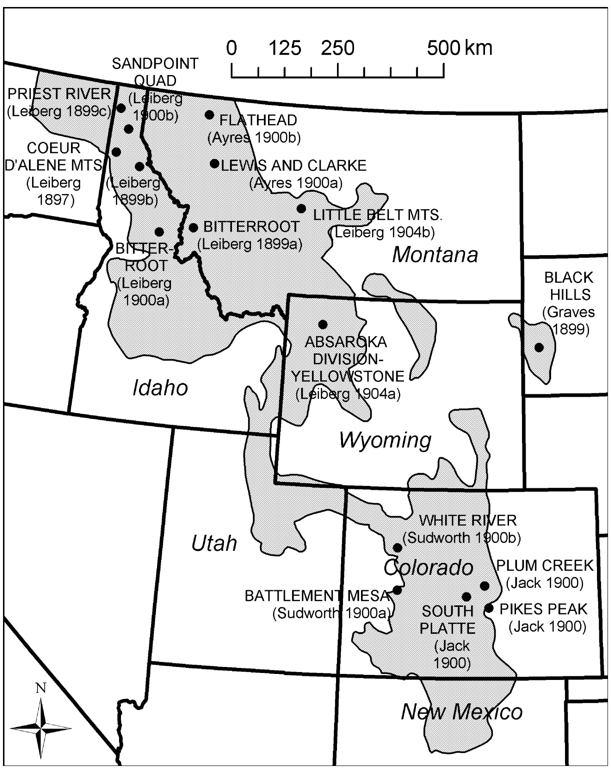

Figure 1 Location of forest reserves and the reports used in this study. The boundary of the Rocky Mountains is shaded as a backdrop.

The low-severity and variable-severity restoration models

Many forest restoration proposals are based on models (or restoration frameworks) derived from an assessment of historical variability. The idea in using historical variability as a model is not to exactly re-create the past, but to restore enough forest structure, and the processes that maintain it, to put the forest back on a track congruent with its history (Landres *et al.*, 1999). These models are derived using historical ecology – analysis of accounts and photographs by early explorers and settlers, as well as tree-ring based reconstructions of tree density and fire history before EuroAmerican settlement (White & Walker, 1997; Egan & Howell, 2001).

The central image in the low-severity model (Table 1) is a pre-20th century forest with widely spaced, mature trees (often old growth) over a grassy or herbaceous forest floor (Fig. 2a). Low-severity fires are thought to have burned frequently through these fine surface fuels, leaving most larger trees alive, but killing small trees and maintaining low tree density, while preventing fuel buildup. Excluding fires, under this model, leads to increased survival of small trees and a buildup of fuels, which may then cause uncharacteristic high-severity fires. This summary of the low-severity model is necessarily simplified, emphasizing the central features. Variation from this central concept has been elaborated and detailed in a recent collection (Friederici, 2003).

Recent research has concluded that the low-severity model is inappropriate for most ponderosa pine forests in the Colorado Front Range (Veblen *et al.*, 2000; Huckaby *et al.*, 2001; Ehle & Baker, 2003; Sherriff, 2004). Based on the ideas and evidence in this research, we make an initial formulation of a variable-severity model as a coherent alternative to the low-severity model. The new model (Table 1) is based around a variable-severity fire model, often also called mixed severity (Agee, 1993). In this model, natural fires vary in severity and frequency, sometimes burning at low severity in surface fuels and sometimes burning as high-severity fires in the crowns of trees, or with a mixture of surface and crown fire. In the variable-severity model, most of the landscape historically experienced or is capable of supporting high-severity fire and most stands (i.e. 1–100 ha areas of forest) have evidence of mixed- or high-severity fire over the last few centuries. Patches

Table 1 Comparison of two models of fire and forest structure in ponderosa pine and ponderosa pine–Douglas fir forests

Low-severity model	Variable-severity model
Old-growth trees dominant	Old-growth patches common, but patches of other ages occur
Low-severity surface fires only	Variable fire severity: low-severity surface fires, mixed severity, and high severity
Trees widely spaced, tree density low	Trees varying from dense to widely spaced
Low-severity fires kill few canopy trees	Moderate and high-severity fires kill canopy trees in groups or over large areas
Tree regeneration commonly linked to climate	Tree regeneration enhanced after fires and sometimes linked to climate
Frequent surface fires	Surface fires
1. kill most small trees	1. kill some small trees, leaving some patches
2. prevent fuel buildup	2. have varied effects on fuels
	3. enhance tree regeneration
Fire exclusion leads to	Fire exclusion leads to
1. high tree regeneration	1. low tree regeneration
2. fuel buildup	2. varied fuel effects
3. uncharacteristic high-severity fires	3. decrease in natural high-severity fires

of high-severity fire probably exceeded 100 ha but continuous mapping of past fire severity has not been conducted at broader spatial scales. The central landscape image from this model is of patches of forest varying in tree age and density, including some young, dense patches (Fig. 2b) and some older, lower-density patches (Fig. 2a). Variability in tree age and density comes in part from variation in environment (dry, south-facing slopes vs. moister, north-facing slopes) but also from variation in fire severity within each environment. As fires vary in severity, the number of surviving trees and density of post-fire regeneration also vary, as do snags and dead wood. Not all regenerating young trees are killed by fires. Tree regeneration is also favoured after fires, especially high-severity fires. Thus, the exclusion of fire may have different effects than under the low-severity model, leading in some cases to decreased tree regeneration and other processes that produce fuels thought to lead to subsequent high-severity fire. These two models can and should be revised or replaced with other models as new knowledge of local conditions accumulates, but at the present time these two models are the only models with a substantive body of evidence.

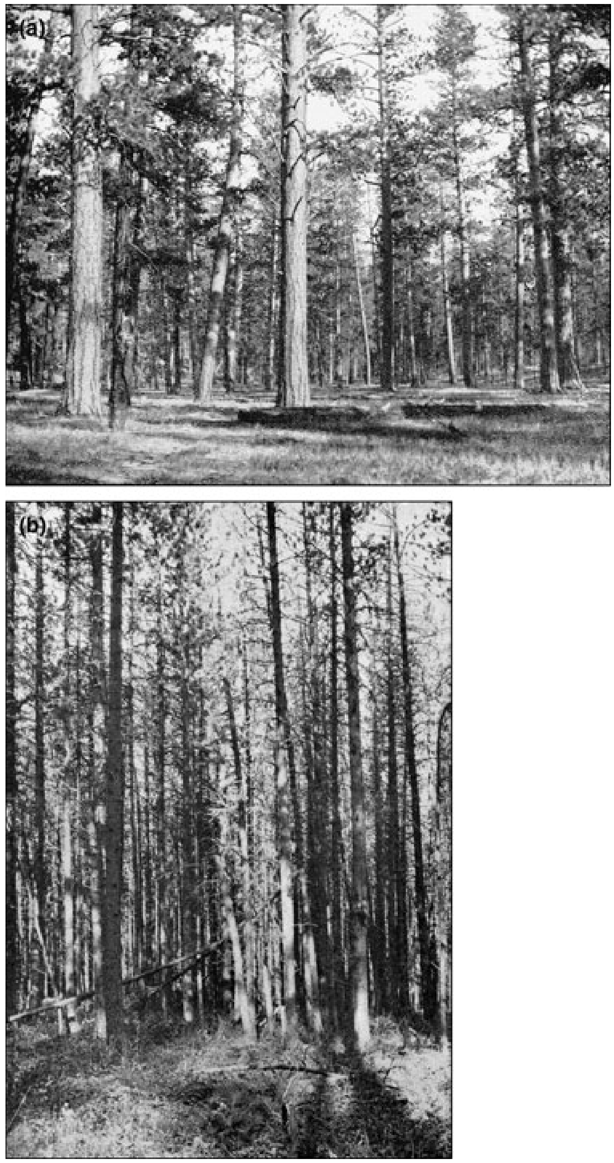

Figure 2 (a) Old-growth ponderosa pine forest is the restoration target under the Southwestern model. This is an example of an open, park-like, old-growth stand in the Bitterroot forest reserve in the late 1800s (reproduced from Leiberg, 1899a, plate LXX). Patches of these old, low-density trees and (b) young, high-density trees in the late 1800s (reproduced from Graves, 1899, plate XXXIV) are included in the restoration target under the Rocky Mountain model.

SOURCES OF EVIDENCE

Evidence about the relevance of these two models in the Rocky Mountains is in part from early reports on forest reserves, which later became National Forests, but also from the available scientific literature. The forest reserve reports were conducted by government scientists in the late 1800s. If these scientists had an agenda that affected their observations, it was that they were instructed to document the extent of human-set fires and unregulated logging and grazing thought to be affecting resources in the reserves (Pinchot, 1898). However, these were not early explorers in the usual sense, as they were trained scientists who made systematic observations and estimates of area burned and the severity of fires, tree density, tree regeneration, and effects of logging and livestock grazing. We focused on evidence from unlogged portions of the reserves. We extracted all quotes and data relevant to the questions posed in the introduction and

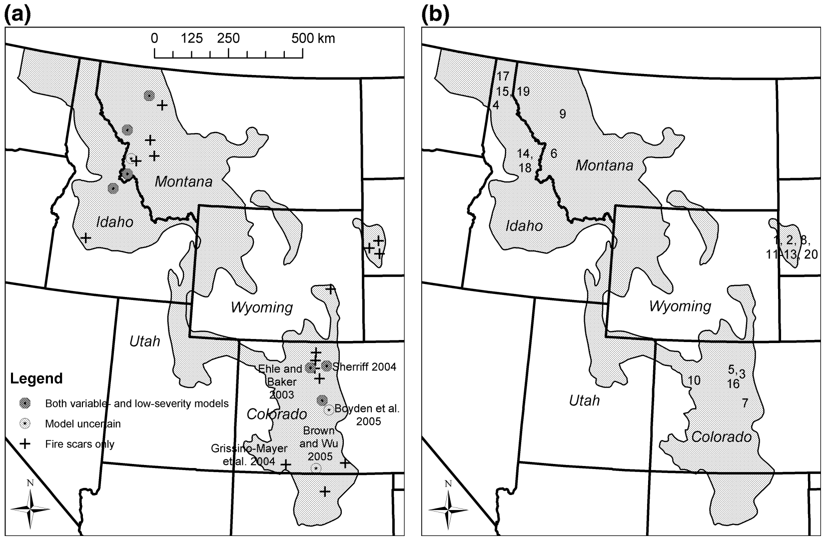

Figure 3 Data sources include (a) tree-ring studies of fire history and (b) direct measurements and tree-ring reconstructions of tree density near AD 1900. In (a) fire-history studies that lack age structure and include only fire scar data are not used, as they do not provide evidence about fire severity; citations for those studies not identified on the map are in Baker & Ehle (2003). Eight of the 10 studies that do include both age structure and fire scars document stands in each sample area in which both the variable- and the low-severity models apply, but two other studies are here considered uncertain (see text); in (b) see Table 2 for the data corresponding to each number.

placed this evidence in tables (see Tables S1–S4 in Supplementary Material) or have reviewed it in the text.

Researchers have generally considered AD 1900 to be sufficiently early in the Rocky Mountain region to provide suitable reference conditions from which to gauge natural fire regimes and forest structure (Arno *et al.*, 1995a,b, 1997; Kaufmann *et al.*, 2001), although climatic conditions and fire regimes may have changed during the 20th century. Forest reserve reports have been used for this purpose in the past (e.g. Shinneman & Baker, 1997). These reports provide direct estimates of the density of small trees near or before AD 1900 in some areas. Precise determination of the proportion of the landscape with a particular tree density usually is not feasible. Nevertheless, the tree density estimates in the 16 forest reserve reports and related documents from the Rocky Mountains used here (Fig. 1) are adequate for evaluating some of the questions posed in the Introduction.

Another source of reliable information on historical fire regimes and forest structure in Rocky Mountain forests consists of tree-ring reconstructions of past fire regimes and forest conditions (Arno *et al.*, 1995b, 1997; Kaufmann *et al.*, 2000; Veblen *et al.*, 2000; Ehle & Baker, 2003; Sherriff, 2004). Relevant aspects of fire history methods are discussed in further detail later, but the critical parameter for the current discussion is the severity of past fires. This requires dating the year of a fire using fire scars, combined with age data from nearby trees (Bekker & Taylor, 2001; Ehle & Baker, 2003; Sherriff, 2004). High-severity fire is identified by evidence that a contiguous area of trees died about the time of a fire and/or regenerated in a pulse after a fire. A precise date for the fire usually comes from a surviving tree inside the high-severity fire or on its margin. Low-severity fires, in contrast, are identified by fire scars from more than one location along with intervening trees that mostly pre-date and thus survived the fire. A single fire event is identified as mixed severity if it has substantial fractions of burn area with evidence of both high- and low-severity fire. We use all available tree-ring studies with both fire scars and age structure (Fig. 3a). Note that we specifically omit fire-history studies that rely only upon dating fire scars (Fig. 3a), as these studies lack data on age structure and thus do not provide evidence about fire severity. Tree-ring reconstructions of tree density near or before AD 1900 also are used (some of the points in Fig. 3b), although these estimates often are only approximations, due to mortality of some of the trees present at that time.

THE APPLICABILITY OF THE TWO MODELS

Was the historical fire regime dominated by low-severity surface fires?

In Rocky Mountain ponderosa pine–Douglas fir forests, data from the few places with the necessary tree age and fire-history evidence suggest that the pre-20th century fire regime varied in severity, and displayed more mixed- and high-severity fires than expected under the low-severity model. In Colorado, ponderosa pine–Douglas fir forests at Cheesman Lake, southwest of Denver (Brown *et al.*, 1999; Huckaby *et al.*, 2001), pure ponderosa pine forests in Rocky Mountain National Park (Ehle & Baker, 2003), and ponderosa pine–Douglas fir forests in many other locations in northern Colorado's Front Range (Sherriff, 2004) had variable-severity fire, based on tree-ring evidence, as summarized in a recent review (Romme *et al.*, 2003). In Montana, tree-ring studies show that some ponderosa pine–Douglas fir forests had infrequent high-severity fires as well as more frequent low-severity fires (Barrett, 1988; Arno *et al.*, 1995b, 1997). The area of these forests from eastern Montana to northeastern Wyoming, including the Black Hills, appears to have had variable fire severity, based on historical and tree-ring evidence (Shinneman & Baker, 1997; Arno & Allison-Bunnell, 2002). Forest-reserve reports also indicate that mixed- and high-severity fire (Fig. 4) occurred in pure ponderosa pine forests from Idaho to Colorado (see Table S1, Items 1, 6, 8, 14, 17, 18, 28, 32–38, 40, 42) and in mixed

Figure 4 High-severity fire in a ponderosa-pine forest in the Black Hills in the late 1800s (reproduced from Graves, 1899, plate XXXV).

ponderosa pine–Douglas fir forests (see Table S1, Items 1, 12, 15, 26, 43). Where Douglas fir was more common or dominated, the reports suggest that high-severity fire was also more common (see Table S1, Items 2, 10, 11, 13, 15, 24, 25). Indeed, in Douglas fir forests in ponderosa pine landscapes, surface fires are seldom mentioned – the predominant fire type was reported to be high severity. High-severity fires were reported during early forest examinations in Douglas fir and ponderosa pine–Douglas fir forests on several national forests in Idaho in AD 1900–1915 (Ogle & DuMond, 1997). Reported high-severity fires in ponderosa pine–Douglas fir forests often covered thousands of hectares (see Table S1, Items 15, 37), and exceptional fires of 24,000 to 52,000 ha (60,000 to 128,000 acres) are also reported (see Table S1, Items 38, 42, 43). Only the smallest of these large fires was in a logged area (see Table S1, Item 42).

Low-severity surface fires are mentioned in forest reserve reports for Idaho (see Table S1, Items 3, 7, 9, 42), Montana (see Table S1, Items 16, 19, 20, 21, 42), Wyoming and South Dakota (see Table S1, Items 28–30, 42), and Colorado (see Table S1, Items 30, 41, 42). The reports recognize that low-severity surface fires are promoted by low-density forest with a grassy understorey and by the ability of mature ponderosa pine to resist damage by fire (see Table S1, Items 3, 6, 10, 19, 23, 42). However, low-severity surface fires alone do not imply that mixed- or high-severity fire was lacking, because low-severity fire was also part of the variable-severity model.

Although variable fire-severity appears to have characterized most of the range of ponderosa pine–Douglas fir forests in the Rocky Mountains, in limited areas high-severity fire was absent over the last few centuries. Some stands in Montana (Barrett, 1988; Arno *et al.*, 1995b, 1997), south-western Colorado (Wu, 1999) and the Colorado Front Range (Huckaby *et al.*, 2001; Ehle & Baker, 2003; Sherriff, 2004) were uneven-aged, based on tree-ring reconstructions, suggesting an absence of high-severity fire and dominance by low-severity fire. These stands were more common on lower-elevation or drier sites (Barrett, 1988; Wu, 1999; Veblen *et al.*, 2000; Arno & Allison-Bunnell, 2002; Ehle & Baker, 2003; Sherriff & Veblen, in press). In the only studies to date spanning the elevational range of ponderosa pine, about 20% of the ponderosa pine zone on public and private land in northern Colorado was found to have been dominated by low-severity fires (Platt, 2004; Sherriff, 2004; Platt *et al.*, 2006), suggesting a more low-severity than variable-severity model.

We stress that fire-history data and forest age structures document substantial variation in the fire regime along elevation and moisture gradients within the broad vegetation zone characterized by ponderosa pine–Douglas fir forests, reflecting local variations in moisture availability and other factors that determine fuels productivity and other vegetation attributes (Peet, 1981). For example, in the northern Colorado Front Range, in a *c.* 61,000 ha area of ponderosa pine–Douglas fir forests extending from 1800 m to 3000 m elevation, the area of more abundant low-severity fire was successfully predicted from elevation and topographic variables (Sherriff, 2004). Although the zone of more low-severity fire is broadly associated with lower elevations, at a finer scale abiotic factors also account for smaller areas of predominantly low-severity fire at mid- to upper elevations in the ponderosa pine zone (Sherriff, 2004).

Why is the natural fire regime in most Rocky Mountain ponderosa pine–Douglas fir forests variable in severity? Extended droughts and high winds can lead to exceptional fire spread across a broad spectrum of fuel loads and forest structures. For example, almost 25,000 ha of ponderosa pine–Douglas fir forest burned on a single day (9 June 2002), driven by strong winds (Finney *et al.*, 2003). Yet, brief episodes when the winds declined and fuel moisture rose, led to low-severity fire in the same landscape (Finney *et al.*, 2003), suggesting that extreme weather, not fuels, was the chief cause of high-severity fire under those conditions. Even during summer, ponderosa pine–Douglas fir landscapes in the Rocky Mountains are subject to rapid increases in wind speed and changes in direction from jet streams or cold fronts (Baker, 2003). During spring and fall, more frequent cold fronts, along with strong down-sloping winds (foehn or chinook winds), can lead to rapidly spreading, high-severity fires if ignitions occur. Furthermore, variation in topography and time since fire lead to considerable variation in tree density and fuel loads over short distances, as reviewed later. A major fire, burning for days or weeks, may incur substantial variation in wind speed and direction, fuel loads and fuel moisture. During the Hayman fire in Colorado in 2002, strong southwesterly prefrontal winds drove a major fire run through both young and old forests. After the front, winds blew the fire back south, followed by southeasterly winds, before another major fire run, driven again by southwesterly winds (Finney *et al.*, 2003). A map shows a patchy mosaic of varying severity, reflecting this variation in fuels, wind and topography (Fig. 5).

Was tree density generally low and comparable to tree density under the low-severity model?

Both tree-ring reconstructions and forest reserve reports document that tree density was highly variable in Rocky Mountain ponderosa pine–Douglas fir forests near or before AD 1900, suggesting that the low-severity model is inappropriate in most cases. Pre-fire-exclusion tree densities in ponderosa pine forests under the low-severity model were estimated to fall between about 7 and 60 trees ha^{-1} (Covington & Moore, 1994), ranging up to 140 trees ha^{-1} in some areas (Fulé *et al.*, 2002). In contrast, two studies in the northern Colorado Front Range report that current densities of trees that were alive in AD 1900 (an underestimate of AD 1900 tree density) vary from 68 to 3052 trees ha^{-1} (Ehle & Baker, 2003) and 39 to 3,410 trees ha^{-1} (Sherriff, 2004). This compares with modern tree density in the unlogged and ungrazed (for a century) Cheesman Lake area, south-west of Denver, of 96–1459 trees ha^{-1} (Kaufmann *et al.*, 2000). In Montana, reconstructions found tree densities in mature ponderosa pine were between 116–249 trees ha^{-1} near AD 1900, but data are lacking for forests of other ages (Arno *et al.*, 1995a,b). In Black Hills ponderosa pine forests, tree densities reconstructed for AD 1874 varied from 25 to 1600 trees ha^{-1} (McAdams, 1995). Forest reserve reports support this large variability, documenting tree densities from 17 to 19,760 trees ha^{-1} in ponderosa pine and 39 to 7410 trees ha^{-1} in Douglas fir forests in the Rocky Mountains near or before AD 1900

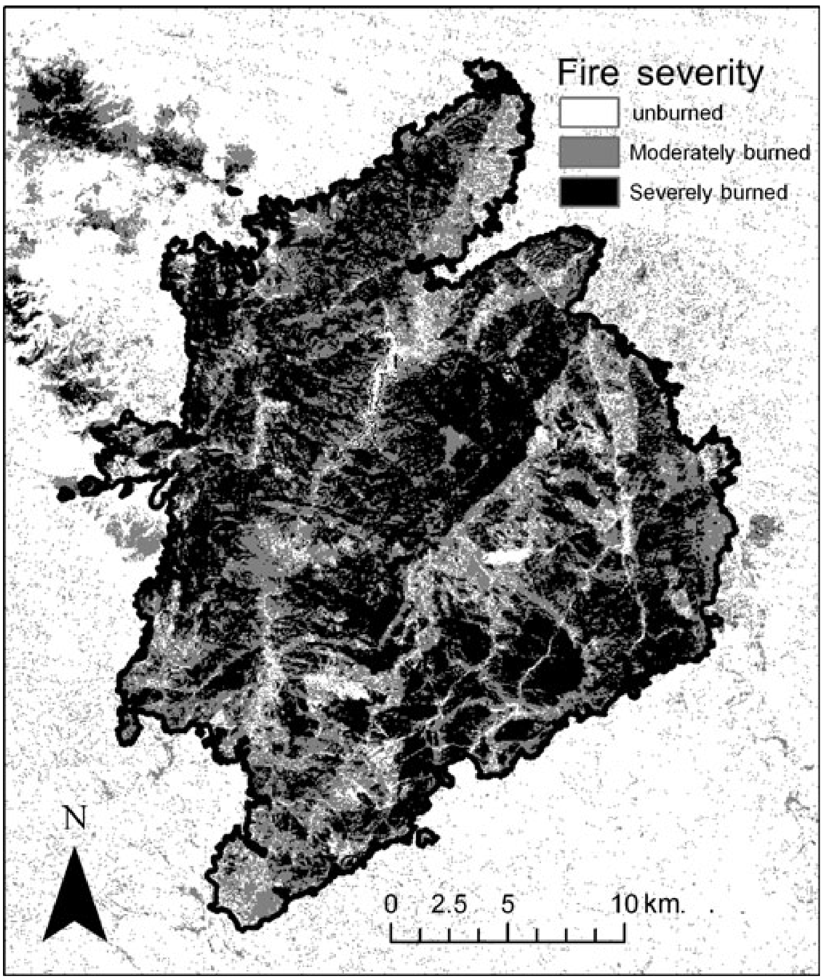

Figure 5 Variation in fire severity, Hayman Fire, Colorado, 2002. Derived from US Geological Survey composite image of differenced normalized burn ratio from Landsat TM (http://edc2.usgs.gov/fsp/severity).

Table 2 Estimates of tree density in Rocky Mountain ponderosa pine (PIPO)–Douglas fir (PSME) forests near or before AD 1900. These estimates are either (1) direct reports from near AD 1900 by scientists or (2) reconstructions, based on current trees that were alive near AD 1900

Fig. 3b number	Range (trees acre^{-1})	Range (trees ha^{-1})	Notes	Forest type	Age of forest	Reference/source
1	7–288	17–710	Large trees only (e.g. > 30 cm)	PIPO	Variable	Brown & Cook (2005)*
2	10–294	25–725	Mean = 344 trees ha^{-1}	PIPO	Unknown	McAdams (1995) (< 2000 bf/acre forests)†
3	16–1380	39–3410	Trees > 4 cm	PIPO & PSME	100–250 years	Sherriff (2004)‡
4	20–30	49–74	Trees > 70 cm	PIPO & PSME	Unknown	Table S4 Item 6 (in Supplementary Material)
5	28–116	68–286	Trees > 5 cm	PIPO	100–200 years	Ehle & Baker (2003)§
6	47–101	116–249	Pre-1900 trees only	PIPO & PSME	205–445 years	Arno *et al.* (1995b)¶
7	81	200	Trees > 1.37 m tall	PIPO	*c.* 90 years	Boyden *et al.* (2005)
8	88	217	Trees > 12.7 cm	PIPO	Likely > 200 years	Pinchot (1908), Table 1
9	93	230	Trees > 12.7 cm	PIPO & PSME	Likely > 300 years	Pinchot (1908), Table 3
10	100–120	247–296		PSME	Unknown	Table S4 Item 12 (in Supplementary Material)
11	107–143	264–353	From ratios in description	PIPO	'Orig. forest' (old growth)	Table S4 Item 10 (in Supplementary Material)
12	111–648	275–1600	Mean = 633 trees ha^{-1}	PIPO	Unknown	McAdams (1995) (2–5000 bf/acre forests)†
13	150–200	370–494		PIPO	100 years	Table S4 Item 10 (in Supplementary Material)
14	200–300	494–741	Trees > 10 cm in 'second growth'	PIPO	Likely < 100 years	Table S4 Item 7 (in Supplementary Material)
15	200–300	494–741		PSME	100–150 years	Table S4 Item 4 (in Supplementary Material)
16	402–1236	992–3052	Trees > 5 cm	PIPO	20–40 years	Ehle & Baker (2003)§
17	800–1500	1976–3705	'In some localities'	PIPO & PSME	Unknown	Table S4 Item 1 (in Supplementary Material)
18	800–1500	1976–3705	Trees > 10 cm in 'second growth'	PSME	Likely < 100 years	Table S4 Item 7 (in Supplementary Material)
19	1000–3000	2470–7410		PSME	Young	Table S4 Item 4 (in Supplementary Material)
20	7000–8000	17,290–19,760		PIPO	Young	Table S4 Item 11 (in Supplementary Material)

*This estimate excludes goshawk plots because some of them were not forested in AD 1900. Tree density in 1900 is likely to be an underestimated due to loss of small trees present in 1900 (Brown & Cook, 2005).

†This estimate is tree density in AD 1874, not 1900. Tree density in 1874 is likely to be an underestimated due to loss of small trees present in 1874. bf/acre, board-feet per acre.

‡This estimate is tree density in AD 2003, not AD 1900, but stand age was estimated for AD 1900. These trees were all alive in AD 1900, but others are likely to have died and disappeared, so this is an underestimate of AD 1900 density.

§This estimate is tree density in AD 1999, not AD 1900, but stand age was estimated for AD 1900. These trees were all alive in AD 1900, but others are likely to have died and disappeared, so this is an underestimate of AD 1900 density.

¶The estimate was derived by adding 'number of overstorey trees per acre in 1991–93' and 'estimated number of overstorey trees per acre that died after 1900' from their Table 2, excluding Flathead stands, which have a mixture of tree species.

(Table 2). Qualitative remarks mirror this large quantitative range (see Table S4, Items 2, 3, 6). Leiberg (1897) says 'The number of trees to the acre varies so greatly that it is almost impossible to give, even approximately, an estimate' (see Table S4, Item 6).

Three factors, that explain this great variation in tree density, are identified in the forest reserve reports: tree species composition, environment and stand development. Where forests included more Douglas fir or other trees, density was higher than in pure ponderosa pine forests (see Table S4, Items 2, 6, 7, 12, 14, 17). Tree density was low in lower-elevation stands and on drier sites and was higher in more mesic stands, found on more northerly facing slopes or at higher elevations (see Table S4, Items 2, 4, 5, 6, 17). Mesic stands often also contained Douglas fir and other trees, so composition and environment were correlated, but density varied with environment even within forests consistent in composition (see Table S4, Item 5). Pure Douglas fir forests usually had

> 250 trees ha^{-1}, while pure ponderosa pine forests could be, but were not always, lower in density (Table 2).

Stand development appears to have strongly affected tree density (see Table S4, Items 1, 3, 6, 8, 10, 11). Young stands (< 100 years old) were naturally dense, having about 1000–20,000 trees ha^{-1} (Figs 2b & 6a), while older stands typically had < 750 trees ha^{-1} (Table 2). High initial tree density, followed by thinning, is a natural mode of regeneration and stand development in Rocky Mountain ponderosa pine–Douglas fir forests (Peet, 1981; Lundquist & Negron, 2000; Ehle & Baker, 2003; Sherriff, 2004; see Table S4, Items 8, 11; Fig. 6a), unlike under the low-severity model. However, some young stands were not dense (Fig. 7). Nonetheless, even park-like Rocky Mountain stands were denser than under the low-severity model (see Table S4, Items 3, 6, 14–16, 18; Table 2), and nearly all Rocky Mountain ponderosa pine–Douglas fir forests, for which there are data, were much denser, often by a factor of 5–10 times (Table 2).

Figure 7 Young, open, low-density ponderosa-pine forest in the Lewis and Clarke forest reserve in the late-1800s (reproduced from Ayres, 1900a, plate IX, part B).

Figure 6 (a) Dense, young ponderosa pine trees regenerating naturally after high-severity fire in the late 1800s (reproduced from Graves, 1899, plate XXI A), and (b) a surface fire and a small, dense group of regenerating ponderosa pine trees in the Black Hills in the late 1800s (reproduced from Graves, 1899, plate XXI B).

How do fires of different severity affect spatial and temporal variation in tree density?

Given that stand development strongly influences tree density, how is the fire regime linked to stand development processes? Contemporary observations document that low-severity surface fires kill small ponderosa pine and Douglas fir trees (Baker & Ehle, 2001). Similar fires killed small trees in the pre-fire exclusion era, based on forest reserve reports from Idaho to Colorado (see Table S2). One report, on the western Bitterroot reserve, says 'a certain percentage of saplings usually pass through a fire unharmed, the amount depending on their age and the quantity of litter on the ground' (Leiberg, 1900a, p. 350), which is also evident in an early photograph (Fig. 6b) and is consistent with observations of contemporary fires (Baker & Ehle, 2001).

Although low-severity surface fires kill small trees in ponderosa pine–Douglas fir forests, tree establishment increases after these fires (Sackett, 1984; Boyce, 1985) because of reduced competition with bunchgrasses for moisture and nutrients, shown experimentally in the Southwest (Pearson, 1942). Seed germination and seedling survival are also favoured by bare mineral soils (Sackett, 1984; Boyce, 1985) or scorched needles on top of mineral soil (Bonnet *et al.*, 2005). In Rocky Mountain National Park, regeneration of ponderosa pine in the pre-EuroAmerican era was elevated within the first 10 years after low-severity fires and did not continue during longer intervals after fire (Fig. 8). In south-western Colorado, regeneration of ponderosa pine occurred almost entirely within 20 years after fires (Wu, 1999). Forest reserve reports also indicate that low-severity surface fires favour tree regeneration (see Table S3). Reports from Idaho, Montana and Wyoming–South Dakota suggest that, after surface fires, small trees are often found, sometimes in dense thickets (see Table S3). Small trees of Douglas fir, white fir (*Abies concolor* (Gord. & Glend.) Lindl. E Hildbr.), or other

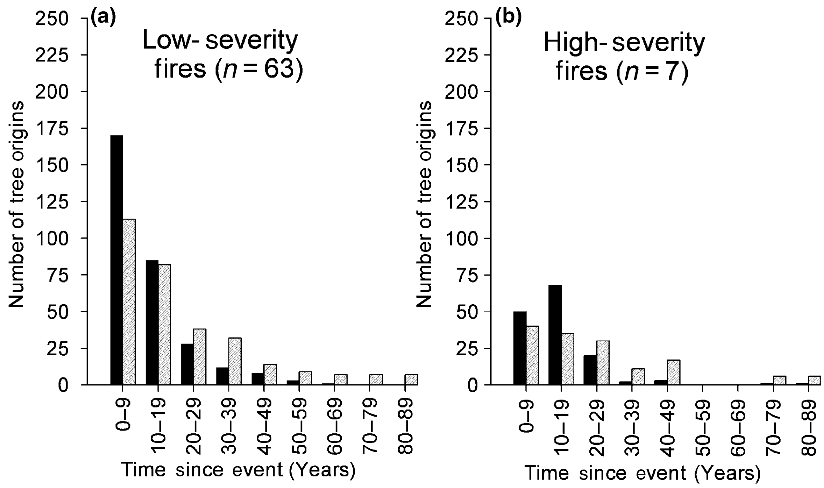

Figure 8 Observed (solid bars) and expected (shaded bars) density of tree regeneration vs. interval since fire for (a) low-severity surface fires and (b) high-severity fires in ponderosa pine forests in Rocky Mountain National Park, Colorado. Expected density is the same total density assigned proportion to the actual frequency of fire intervals. Reproduced from Ehle & Baker (2003) with permission of the Ecological Society of America.

shade-tolerant species were present as thickets in the understorey of some mature ponderosa pine–Douglas fir forests and often appear to increase after fire (see Table S3). Short fire-free intervals or episodes of fire were found in other studies to lead to periodic cohorts of shade-tolerant trees in western ponderosa pine–Douglas fir forests prior to EuroAmerican settlement (Wu, 1999; Agee, 2003). Regeneration may be concentrated within 1–2 decades after fire, because lower competition, bare mineral soil and other conditions disappear as the understorey recovers. Small trees regenerating after fire can be killed by the next surface fire; long-term survival of ponderosa pine after surface fire requires a fire-free period of several decades or more (Baker & Ehle, 2001).

Ponderosa pine and Douglas fir also regenerate after high-severity fires, often at high density, although density may vary with site conditions (Peet, 1981). In the Colorado Front Range, regeneration after high-severity fires was abundant and naturally dense (Veblen & Lorenz, 1986; Hadley & Veblen, 1993; Kaufmann *et al.*, 2000; Ehle & Baker, 2003; Sherriff & Veblen, in press). Tree-ring dating suggests that tree regeneration also followed high-severity fires in the pre-fire exclusion era in Montana ponderosa pine–Douglas fir forests (Arno *et al.*, 1995b, 1997) and in south-western Colorado (Wu, 1999). Early forest examinations (AD 1900–1915) documented dense reproduction of both Douglas fir and ponderosa pine in places after high-severity fire on several national forests in Idaho (Ogle & DuMond, 1997). Trees generally regenerate even after very large high-severity fires. The Hayman fire in Colorado in 2002, for example, burned in part in dense, young forests that regenerated after large high-severity fires in the late 1800s (Jack, 1900). However, regeneration can sometimes be delayed (Graves, 1899; Leiberg, 1904b), creating openings that may slowly fill in over a century or more (Kaufmann *et al.*, 2000). More typically, forest reserve reports indicate that dense thickets of small trees naturally followed high-severity fires in both ponderosa pine (e.g. see Table S4, Items 8, 11) and Douglas fir (Leiberg, 1899a) forests, and this high density often persisted for decades (Table 2), suggesting that the low-severity model is inappropriate.

At the landscape scale (i.e., a few hundred ha or more) in Rocky Mountain ponderosa pine–Douglas fir forests, variable fire severity and variation in environment led to a mosaic of patches naturally varying in age and tree density. Some patches were large. Extensive areas of old forest (e.g. > 200 year-old) covered the Black Hills (Graves, 1899; Shinneman & Baker, 1997), the west side of the Bitterroot (Leiberg, 1900a) and parts of other reserves. Some reserves also had large stands of mature (e.g. > 100-year-old), but not old forest, as in Montana's Little Belt Mountains (Leiberg, 1904b). Expanses of recently burned or young ponderosa pine–Douglas fir forest also occurred, as in the Black Hills (Graves, 1899) and southern Colorado (Jack, 1900). Some of these were in logged forests, but most were not. Other landscapes had finer-scale mosaics of burned and unburned forest of various ages (Graves, 1899). Some early photos show this finer scale spatial variability in tree density and patch age (Fig. 9). Landscape-scale fire histories with age-structure analysis (Huckaby *et al.*, 2001; Ehle & Baker, 2003) have found similar patchy patterns. Landscape-scale evidence is scanty, but suggests that the uniform, low density, old-growth landscape, expected under the low-severity model, was not the predominant pattern in most areas of Rocky Mountain ponderosa pine–Douglas fir forest.

Dense patches of tree establishment can often be clearly linked to documented severe fires, but climatic variability may also influence tree establishment and survival. For example, short intervals (i.e. 1–3 years) of abundant ponderosa pine establishment have been linked to short intervals of favourable climate in northern Arizona (Savage *et al.*, 1996). Similarly, in the northern Colorado Front Range, recent (i.e. post-1970) annual episodes of ponderosa pine establishment in grassland ecotones have been linked to 1–2 year periods of wet climate (League, 2004; League & Veblen, 2006). Some retrospective studies of pre-20th century forest conditions have suggested that multi-decadal wet periods are responsible for 30–40 year pulses of tree regeneration evident in age structures in the Rockies (Boyden *et al.*, 2005; Brown & Cook, 2005; Brown & Wu, 2005). However, some of the pulses during wet periods were immediately preceded by fires (e.g. AD 1684 and 1818 in

Figure 9 A ponderosa pine landscape in AD 1903 along Hermosa Creek about 25 km north of Durango, Colorado. Photo by E. Howe (No. 204) courtesy of the US Geological Survey Photographic Library, Denver, Colorado.

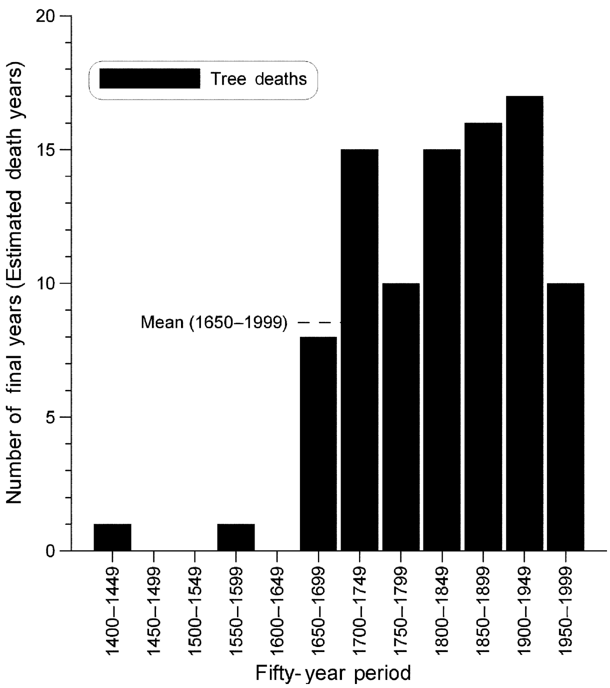

Figure 10 Estimated 50-year period when dead wood died in nine plots in ponderosa pine forests in Rocky Mountain National Park, Colorado. The null hypothesis, that tree deaths are independent of 50-year period since 1650, cannot be rejected ($\chi^2 = 3.102$, $P = 0.796$).

Brown & Wu, 2005), and the effects of fire and climate are thus confounded. Furthermore, some wet periods are not associated with above average numbers of tree establishment dates in these studies. Other age-structure studies in the Front Range have not shown a clear association between episodes of establishment of ponderosa pine and climatic variability, independent of fire (Mast *et al.*, 1998; Kaufmann *et al.*, 2001; Ehle & Baker, 2003). However, these retrospective age-structure studies all have limited ability to resolve potential confounding of fire and climate effects over the long-term or of grazing and, in some cases, logging effects during the past *c.* 150 years. Future studies need to overcome the confounding and potential complexity of interactions that have limited the ability to retrospectively identify and quantify a climatic effect on tree regeneration.

In summary, under the variable-severity model, which appears to better fit the available evidence for ponderosa pine–Douglas fir forests in the Rocky Mountains, the landscape mosaic naturally varies over time and space as a result of variable-severity fire and other processes that kill trees and facilitate regeneration. After high-severity fire or other disturbance, a pulse of dense tree regeneration may occur and, as these trees mature, tree density increases relative to the pre-disturbance forest (Veblen & Lorenz, 1986; Ehle & Baker, 2003; Sherriff, 2004). Ongoing low-severity fires, as well as insects, disease and other small disturbances, may kill a tree or small groups, lowering density, but also encouraging new regeneration, resulting in a fine age mosaic (Lundquist & Negron, 2000). However, the next moderate or high-severity event may kill larger groups of these trees, reducing tree density again, although trees remain denser than expected under the low-severity model. Because fires and other events are spatially variable, at any one time adjacent or nearby stands may differ significantly in tree density, age and fuel loads (Hadley & Veblen, 1993; Ehle & Baker, 2003; Sherriff, 2004).

How did historical fire regimes affect fuels?

Ideas about how fuel loads fluctuated during the pre-fire exclusion era must be inferred from contemporary observations of trends in fuel with time since fire and inferences about changes in the processes that produce and consume fuels, because there are no direct data on fuel loads in the pre-fire exclusion era. Under the low-severity model, large, dead wood should be maintained at relatively low levels by low-severity surface fires. Because fire is a principal fuel-load regulator, fuel accumulation would be relatively more homogeneous than where fire severity is highly variable. Under a variable fire-severity model, fuel beds would tend to be strongly spatially heterogeneous, and not accumulate consistently after fires. Moreover, other processes (e.g. disease and windstorms) may so affect fuel production rates and patterns that a consistent response to fire or fire exclusion is clouded or not at all evident.

In the Rocky Mountains, large data sets from the northern Rockies ($n = 6706$ plots; Brown & See, 1981) and Colorado ($n = 328$ plots; Robertson & Bowser, 1999) indicate that the particulars of a stand's history (e.g. timing of fires or windstorms) determine fuel loads, and these loads are spatially heterogeneous. Specifically, the multiple processes that produce dead fuels, such as disease and disturbances (e.g. root disease, beetles, lightning, wind, fire and frosts), damage and kill trees of all ages. Spatio-temporal variability in these processes prevents consistent trends in fuel buildup (Knight, 1987; Robertson & Bowser, 1999; Lundquist & Negron, 2000; Harmon, 2002). The available evidence appears more consistent with the variable-severity model, which emphasizes variability in the landscape fuel mosaic and the multiple fuel-producing processes.

THE EFFECTS OF LAND USES ON FOREST CONDITIONS

The effects of land uses on forest structure are comparatively well known for the low-severity model (e.g. Friederici, 2003), and are likely similar in the Rocky Mountains where this model is appropriate. However, in most of the region, where the variable-severity model is more appropriate, tree density, age and fuels were highly variable, making responses to land use difficult to detect or attribute to a land use. Re-photography shows that tree cover has increased in some Rocky Mountain ponderosa pine–Douglas fir forests over the last century (e.g. Veblen & Lorenz, 1991), and there is also evidence of density increase from tree-ring reconstructions (e.g. McAdams, 1995). There are many plausible explanations of these changes, including natural processes (e.g. recovery after disturbance), reviewed earlier, as well as land-use effects (fire exclusion, logging, and livestock grazing), which are now discussed in turn.

Effects of fire exclusion on tree density and fuels

Researchers have commonly assumed that long intervals between fires will lead to increased survival of tree regeneration, so excluding fires is thought to increase tree density (e.g. Arno *et al.*, 1997). This may be true under the low-severity model, but, in the variable-severity model, the effects of fire exclusion are more complex. After severe fires, both ponderosa pine and Douglas fir typically establish abundantly. Less fire in the 20th century (Brown *et al.*, 1999; Veblen *et al.*, 2000) has resulted in comparatively fewer opportunities for tree establishment. This is reflected in tree population age structures indicating abundant establishment for several decades following severe fires in the 19th century and relatively little establishment during the 20th century (Veblen & Lorenz, 1986; Ehle & Baker, 2003; Sherriff, 2004). Some ponderosa pine–Douglas fir fires in the late 1800s and early 1900s burned severely during regional drought years (e.g. 1851, 1872, 1879, 1880, 1889, 1910 and 1919) that affected large parts of the Rocky Mountain region (Barrett *et al.*, 1997; Brown *et al.*, 1999; Veblen *et al.*, 2000; Sherriff, 2004). Thus, the high stand densities, that are interpreted as effects of fire exclusion in the low-severity model, in the variable-severity model may reflect recovery after these widespread, severe fires and also logging (see below) in the late-19th century.

Exclusion of low-severity fire, under the variable-severity model, can reduce, not increase ponderosa pine regeneration (Ehle & Baker, 2003), but can also enhance seedling survival under certain circumstances. Elsewhere in the western USA, relict mesas that were never grazed by livestock, but that had long intervals without fire, show that tree regeneration may be low where surface fires are rare or are excluded and disturbances from human activities do not occur (Rummell, 1951; Madany & West, 1983). Fire exclusion in undisturbed forests may reduce ponderosa pine regeneration (Ehle & Baker, 2003), but in the post-settlement era, where soil disturbance associated with mining or road construction promotes ponderosa pine establishment (Sherriff, 2004), the survival of these juveniles would be enhanced by subsequent fire exclusion. At low elevation sites in the Front Range, where the low-severity model more likely applies, climatic variation in ecotonal areas also promoted seedling establishment (League, 2004) and ponderosa pine generally survived abundantly in the 20th century following the exclusion of low-severity fires which otherwise could have killed the seedlings (Mast *et al.*, 1998; Sherriff, 2004). However, the relative importance of livestock grazing and other disturbances in triggering this tree establishment is not known. Overall, available evidence suggests that, where the variable-severity model applies, observed post-settlement tree density increases are most typically recovery from past mixed- or high-severity fires or logging. Exclusion of low-severity fires may only have facilitated tree regeneration on otherwise disturbed sites, or where the low-severity model applies on low elevation xeric sites (Sherriff, 2004).

Has fire exclusion resulted in unnatural fuel buildups that have shifted the fire regime towards significantly more severe fires? The complexity of this question is illustrated here for the example of large, dead wood, which is only one of several types of fuel. Fire exclusion affects not only the rate of consumption of fuels, but the rate of processes that produce fuels (e.g. tree mortality). Excluding fires lowers consumption of wood on the forest floor, but also shuts down the damage and mortality process, potentially decreasing the production of dead fuels from live trees (Harmon, 2002). Excluding fires reduces the input of snags and dead wood that are the largest dead fuels in these forests (Brown & See, 1981), leaving this wood in live trees that are less flammable. Large, dead wood and associated smaller branchwood and twigs can increase fire intensity and severity (Agee, 1993; Brown *et al.*, 2003), so the contribution of dead wood to fire severity could be reduced, not increased by fire exclusion. Is there empirical evidence that dead wood has or has not built up? In Rocky Mountain National Park, the deaths of 110 down or standing dead trees dated in nine plots in ponderosa pine forests did not support the hypothesis that dead wood had built up since fire exclusion in 1915 (Fig. 10; Ehle & Baker, 2003). Furthermore, substantial amounts of large, dead wood on the floor in Colorado ponderosa pine–Douglas fir forests are not recent inputs, but have been there for hundreds of years (Fig. 10; Brown *et al.*, 1999).

Present loadings of large, dead wood [generally > 3″ (7.5 cm) diameter] in Rocky Mountain ponderosa pine–Douglas fir forests range widely. The mass of large, dead wood in mature Colorado ponderosa pine–Douglas fir forests is low (mean = 3.4 Mg ha^{-1} for 328 plots; Robertson & Bowser, 1999) relative to similar forests in the northern Rockies (9–23 Mg ha^{-1}; Brown & See, 1981), Black Hills (mean = 12.7 Mg ha^{-1} for 151 plots in a variety of forests; Reich *et al.*, 2004), and Southwest (18 Mg ha^{-1}; Sackett, 1979). At one site in south-western Colorado, large wood averaged 17.7 Mg ha^{-1} (Romme *et al.*, 1992).

Because there are no direct data on fuel loads in the pre-fire exclusion era, present fuel loads can only be evaluated in a relative sense. For example, in the northern Rockies, Brown & See (1981) estimated the wood needed for wildlife habitat and mycorrhizal activity, indicators of ecosystem health, and said '…ponderosa pine and Douglas fir cover types are deficient in downed woody material or contain only slight excesses…' (p. 9), as 22–34 Mg ha^{-1} was considered by these authors to be necessary, fuel levels that are above most existing levels in these forests. Brown *et al.* (2003) recommended 11–45 Mg ha^{-1} in warm, dry ponderosa pine and Douglas fir, and up to 67 Mg ha^{-1} in cool Douglas fir forests, as an optimum to maintain soil health, while keeping fire hazard low. They also suggest that high fire hazard occurs if large dead fuels exceed about 55 Mg ha^{-1}, well above present fuel loads in most Rocky Mountain ponderosa pine–Douglas fir forests.

The notion, under the low-severity model, that fire exclusion leads to fuel buildup to hazardous levels is not supported in the case of large, dead wood in most Rocky Mountain ponderosa pine–Douglas fir forests. Nor does tree density, often considered a fuel, necessarily increase with only fire exclusion in these forests, as reviewed earlier. Available evidence suggests that, in most Rocky Mountain ponderosa pine–Douglas fir forests where the variable-severity model applies, there is no need to decrease large, dead wood [> 3″ (7.5 cm) in diameter], if the goal is to offset effects of fire exclusion in ecological restoration. Retaining or increasing large, dead wood may be a more common restoration need in forests affected by fire exclusion or by logging, reviewed next.

Effects of logging and livestock grazing on tree density and fuels

It has long been known that logging of large overstorey trees in ponderosa pine forests can lead to a pulse of tree regeneration, often concentrated within one to a few decades after logging, and this pulse, if it occurs, can later become a dense, young understorey in the forest (Curtis & Wilson, 1958; Smith & Arno, 1999). For example, the Lick Creek study in Montana documented that an original stand of about 125 trees ha^{-1} before logging in 1907–1911 had over 1500 trees ha^{-1} by 1948 (Smith & Arno, 1999). Logging is favourable to the establishment of the relatively shade-intolerant ponderosa pine by opening up the stand and exposing bare mineral soil suitable for tree seedling establishment, but the density of establishment after logging is highly variable (Schubert, 1974; Veblen & Lorenz, 1986; Heidmann, 1988). Kaufmann *et al.* (2000), for example, found total tree densities were significantly higher on only about half of a logged landscape relative to the comparable, unlogged Cheesman Lake landscape of Colorado. Many ponderosa pine–Douglas fir forests had been high-grade logged by about AD 1900 (e.g. Graves, 1899; Romme *et al.*, 2000), leading to potential tree-density increases during recovery, a process that continues today. In the northern Colorado Front Range, most sites of ponderosa pine–Douglas fir forests logged in the late 19th or early 20th centuries now support dense populations of young trees, although many of these sites were also burned and grazed (Veblen & Lorenz, 1986, 1991).

Logging may increase or decrease fuels, depending on whether stumps and residual material (slash) are burned or removed, but large, dead wood is clearly reduced because tree boles are removed. In the early days, slash was routinely left, greatly increasing the loadings of small and fine fuels that most directly affect fire severity (Dodge, 1972; Harmon, 2002). As wood became more valuable, less was left, and sanitation–salvage operations also removed snags and dead wood, so that wood fell below historical levels, leading eventually to minimum standards for retention after harvest (Harmon, 2002). Where logging removes larger, more fire-resistant trees, the smaller fuels (including small, live trees) that contribute to fire severity may still be increased (Weatherspoon & Skinner, 1995). Logged forests today may often be deficient in large, dead wood, because tree boles were removed, and this wood may often need to be increased when restoring logged stands.

Livestock grazing may have complex effects, but generally increases tree density in formerly open stands and thereby increases the fine fuels that contribute most to fire intensity and severity. Removal of grass reduces competition, allowing more trees to successfully regenerate, shown experimentally in the Southwest (Pearson, 1942), and also by paired comparisons in other parts of the West, in which mesas subject to livestock grazing have much higher tree density than do comparable nearby ungrazed mesas (Rummell, 1951; Madany & West, 1983). Grazing can also initially reduce the quantity of fine grass fuels needed for surface fires, and the onset of heavy grazing in south-western ponderosa pine landscapes is temporally associated with a marked reduction in surface fires (e.g. Savage & Swetnam, 1990). However, fine fuels are likely not to have remained low for long. Higher tree density increases fine fuels that lead to faster fire spread and increases ladder fuels that lead fire into the canopy (Zimmerman & Neuenschwander, 1984), together increasing the potential for more fires and more severe fires. However, this potential effect is most important in mature and old-growth forests, which are rare today, and in younger forests evidence of tree density increase is difficult to detect or is minor, as explained later.

In Rocky Mountain ponderosa pine–Douglas fir forests, most of the apparent increase in tree density over the last century is not in undisturbed mature forests, but in the younger forests that predominate today that may not be overly dense for their age, as explained below. These young forests regenerated after burning and/or logging, accompanied in some places by overgrazing, since EuroAmerican settlement, and are now recovering from these disturbances, as is well documented in the Black Hills and southern Rockies (Gary & Currie, 1977; Veblen & Lorenz, 1986; Shinneman & Baker, 1997; Romme *et al.*, 2000). Extreme droughts in these areas during the second half of the 19th century promoted widespread fires, ignited either by humans or by lightning, which today are reflected in extensive areas of dense, post-fire stands (Veblen *et al.*, 2000; Schoennagel *et al.*, 2004). However, every forest-reserve report (Fig. 1) documents wasteful logging as well as large fires, that were thought to have been set by early settlers, so this pattern occurs throughout the Rockies.

Ponderosa pine–Douglas fir landscapes in the Rocky Mountains today have increased tree density and tree size due in part to normal recovery from these past natural (fire) and human disturbances. Tree regeneration may continue for 30–50 years after these major disturbances (Veblen & Lorenz, 1986), and density may appear to increase for some time after that, as trees grow taller and crowns expand, filling in the canopy. Early historical photographs reveal many burned and/or logged ponderosa pine–Douglas fir forests that were already dense at the time of their disturbance in the 19th century (e.g. Veblen & Lorenz, 1991). Tree density increase, due to recovery from past disturbance, does not necessarily require restoration, as explained further in the next section.

RESTORATION

Identifying the restoration model for a particular landscape

The goal of ecological restoration is to enhance the resilience and sustainability of ecosystems through management decisions that return them to a state considered to be within the historical range of conditions prior to significant impacts from EuroAmerican land uses (Landres *et al.*, 1999). To achieve ecological restoration, as well as ecosystem-based management in general, managers need to understand how past disturbances shaped landscapes prior to permanent EuroAmerican settlement (Veblen, 2003).

It is impossible to determine the correct restoration model for a particular place without some collection of information on the site to be restored (White & Walker, 1997; Veblen, 2003). In ponderosa pine–Douglas fir ecosystems of the Rocky Mountains, over short distances, such as on slopes of opposite aspect, either the low-severity or the variable-severity model may apply (Ehle & Baker, 2003; Sherriff, 2004). How is the model to be determined? The key criterion to distinguish these two models is the presence or absence of high-severity or variable-severity fires prior to logging and fire exclusion. Abundant fire scars of different dates are required to document the low-severity model, but it is necessary to sample sufficient age structure, along with fire scars, to determine whether trees regenerated in a pulse, suggesting high-severity fire occurred (Kaufmann *et al.*, 2000; Ehle & Baker, 2003; Sherriff, 2004). Dating down wood to identify episodes of synchronous tree death (Ehle & Baker, 2003) and dating growth releases on surviving trees (Goldblum & Veblen, 1992) can help date past high-severity fires. It is also essential to cross-date fires, so individual fires can be traced, as well as to have multiple, unbiased sampling locations across a landscape (e.g. Bekker & Taylor, 2001). Once a set of sites has been classified by fire regime, it is possible to produce a predictive map of fire regimes (Sherriff, 2004). Of course, site-specific and local fire-history data may lead to new models, or allow more definition of these two models. For example, more data are needed to be able to specify the relative importance of high-severity or mixed-severity fire where the variable-severity model is appropriate.

Identifying land-use effects, followed by reversal and modification

Under the variable-severity model, to determine if tree density in a particular stand is outside the range of historical variability requires comparison with historical data from stands at the same stage of development (Table 2), not with more mature or old-growth forests. Forests logged around AD 1900, that are roughly a century old today, are compared to 100-year-old stands around AD 1900, which had up to about 750 trees ha^{-1} (Table 2), a density not likely to be exceeded today in many cases. For example, an 80-year-old ponderosa pine stand in Montana had 593 trees ha^{-1} in the 1990s (Arno *et al.*, 1995a,b), a density not exceptional in forests of this age in the northern Rockies near to AD 1900 (Table 2). Similarly, present densities of trees in relatively undisturbed mature forests in Colorado average 241 trees ha^{-1}, ranging from 40 to 810 trees ha^{-1} ($n = 328$ plots; Robertson & Bowser, 1999), comparable to the range of variability in tree densities for similar mature stands near to or before AD 1900 (Table 2). Local tree-density estimates must be used, but thinning today's forests, whether young or old, to dramatically lower tree densities is not likely to be warranted at the stand level in most Rocky Mountain ponderosa pine–Douglas fir forests where the variable-severity model applies.

Although livestock grazing and logging or physical disturbances (e.g. roads and mining) are expected to have increased tree density, the pattern and magnitude of this increase is difficult to quantify at the stand level, given high natural variability in density. To determine this requires detailed analysis of age-structure for comparison of nearby logged and unlogged forests (e.g. Kaufmann *et al.*, 2000), and analysis of livestock grazing records or records of other disturbance. Relatively undisturbed mature forests are likely to be not far outside historical variability for tree density and fuels, as suggested above. Thus, this type of research may not be cost effective for these forests, particularly because as these stands age, natural thinning processes and passive restoration of low-severity fire may accomplish some reduction in density. The most effective restoration strategy for undisturbed mature and old-growth forests is likely a passive approach, in which fire is restored, but natural processes (from fire and other sources of mortality) accomplish gradual restoration of tree density and fuels.

A complex restoration problem that does require research is the matter of shade-tolerant trees (e.g. white fir and Douglas fir), which are often thought to have increased in ponderosa pine forests because of fire exclusion or logging (e.g. Arno *et al.*, 1995b; Wu, 1999; Kaufmann *et al.*, 2001; Keane *et al.*, 2002a). Livestock grazing has also been shown, in an exclosure study, to favour Douglas fir regeneration in mixed forests (Zimmerman & Neuenschwander, 1984). The hypothesis for increased Douglas fir, based on the low-severity model, is that cessation of frequent surface fires is allowing Douglas fir to invade ponderosa pine stands. However, fire scar and tree age data do not support that hypothesis, at least for the northern Colorado Front Range (Sherriff, 2004). Evidence was also presented earlier that these trees were present in other Rocky Mountain forests near to or before AD 1900 as a component of the canopy of some mature forests, as thickets in the understorey of some forests, and often appear to increase after fire (see Table S3). Moreover, past episodes of high-severity fires associated with droughts also would have resulted in patchy stand ages across landscapes (Veblen *et al.*, 2000), and therefore varying relative abundances of ponderosa pine and Douglas fir (Agee, 2003). Because multiple explanations exist for the presence and abundance of young, shade-tolerant trees, these trees need to be dated and linked definitively to a particular land use (e.g. livestock grazing, logging, fire exclusion) before their removal is ecologically appropriate in restoration, and so that the correct land use, as discussed later, can be modified.

Where the low-severity model applies, restoration at the stand level is appropriate. At low elevations in the northern Colorado Front Range, near the ecotone with the Plains grassland, thinning to restore more open conditions is consistent with evidence of past fire and landscape structure (Sherriff, 2004). We caution, however, that the extent of the landscape in this area that fits this more low-severity model for ponderosa pine is only about 20% of the ponderosa pine zone. Relatively little of the area suitable for restoration through thinning is on Forest Service land, which is the main source of funding for both restoration and fire hazard reduction (Platt, 2004).

Under the variable-severity model, the proportions of the historical landscape that contained patches of different age and tree density would have varied substantially over time due to relatively long periods with minimal fire occurrence followed by episodes of widespread and severe burning at landscape scales (Brown *et al.*, 1999; Veblen *et al.*, 2000). This is an important contrast with the low-severity model in which low-severity fires are believed to have occurred often enough to maintain a relatively uniform uneven-aged, old-growth landscape (Covington & Moore, 1994). For the variable-severity fire regime, more research is needed to characterize historical spatial variability in the proportions and configurations of particular categories of forest age, fuel loads and tree density across landscapes. However, any fixed restoration target (e.g. crown closure in AD 1900; Kaufmann *et al.*, 2001) under the variable-severity model is inappropriate, as it may just be an instant when crown closure happened to be low due to preceding fires that were particularly high in severity. Instead a multi-century, landscape-scale restoration framework is needed. Although the variable-severity restoration model is incomplete at the landscape scale, it can still guide management response to severe fires. For example, the modern occurrence of extensive and severe fires in the Rocky Mountains should not be perceived as outside the historical range of variability for ponderosa pine–Douglas fir forest forests, and should not trigger efforts to create forest structures that would exclusively support low-severity fires.

Current knowledge is sufficient for guiding efforts to restore old-growth structures today which are scarce due to widespread logging and anthropogenic burning in the late 19th to early 20th centuries (Veblen & Lorenz, 1986; Schoennagel *et al.*, 2004). Slight thinning and prescribed fire could be used to encourage development of structures (e.g. large trees and down wood) typical of later stages of stand development in some of these young stands as a step in the direction of restoration at the landscape scale (Kaufmann *et al.*, 2001). The resulting increase in sizes of ponderosa pine will result in larger seed crops favourable to wildlife and also in nesting sites for cavity-nesting birds (Krannitz & Duralia, 2004). However, in management aimed at accelerating the recovery of old-growth structures, protection of all pre-EuroAmerican trees is needed to ensure that this restoration truly leads to old forests, and the wood from thinning is generally needed to replenish wood lost to logging or burning.

If even the modest landscape restoration warranted now is begun without identification of land-use effects at the stand level and modification of those land uses, restoration may be futile. Identification of which land uses affected a stand proposed for restoration is essential. Fire exclusion, logging and livestock grazing do not have the same effects on these forests, their effects vary with environment, and they require different restoration actions. Before restoration begins, it makes sense to modify or minimize the particular land uses that led to the need for restoration, to avoid repeating degradation and ongoing, periodic subsidies that merely maintain land uses at non-sustainable levels (Hobbs & Norton, 1996). For example, thinning an overgrazed forest, without restoring native bunchgrasses lost to grazing, may simply lead to a new pulse of tree regeneration that will have to be thinned again. Moreover, if bunchgrasses are restored, new grazing methods that will sustain restored native bunchgrasses are needed. These bunchgrasses have been shown in Southwestern forests to be a key ecosystem component that discourages or prevents tree regeneration (Pearson, 1942).

CONCLUSIONS

The data available to address the applicability of the variable-severity and low-severity models include about 80 observations from 16 forest reserve reports (Fig. 1), supplementary historical analyses (e.g. Shinneman & Baker, 1997), 10 fire scar/age structure studies (Fig. 3a), and 20 direct measurements or reconstructions of tree density near AD 1900 (Fig. 3b, Table 2). Based on these data together, the variable-severity model, which emphasizes an important role for severe fires in the historical fire regime, appears to apply to a larger portion of the ponderosa pine–Douglas fir zone in the Rocky Mountains than does the low-severity model. In most Rocky Mountain ponderosa pine–Douglas fir forests, the variable-severity model, in which forest structures were shaped mainly by infrequent severe fires, is consistent with the evidence of fire history and tree age structures in these forests. Only limited areas of ponderosa pine–Douglas fir forests in the Rocky Mountains, primarily at low elevations and on xeric sites, appear to have been shaped primarily by low-severity fires. To assess which model may best fit a potential management area, site-specific information on fire history and forest conditions is required.

For the purpose of ecological restoration in Rocky Mountain ponderosa pine–Douglas fir landscapes, the most appropriate action at the present time is a mixture of modest passive and active approaches. Undisturbed mature forests require little or no restoration – a passive approach is best. Active approaches may include a little thinning of young stands to enhance structures typical of later stages of development, combined with protection of old trees, reversal of adverse effects of logging and livestock grazing, and changes in land uses so they do not continue to cause degradation. Reintroduction of both low-severity surface fires and high-severity fires may be feasible under some circumstances of land use. However, reintroduction of fire should not be based on converting dense mature stands into sparse open woodlands based on the false premise that surface fires previously maintained tree populations at low densities. Thinning these forests is likely to lead to renewed tree regeneration, hence a need for renewed thinning, in a potentially endless, costly and futile cycle that does not restore the forest. Large, dead wood in most of these forests does not need reduction; certainly, raking, piling and burning large, dead wood is misdirected as these fuels may be ancient and are more likely to be in deficit than in surplus. A modest suite of reversal–reform approaches will provide benefits for both people and the ecosystem, and can begin today, even without needed research at the landscape scale. Ponderosa pine–Douglas fir forests in the Rocky Mountains, where the variable-severity model applies, are not in seriously degraded condition, compared to forests in which the low-severity model applies, and do not require much costly thinning and other active restoration actions. The variable-severity model, which applies to most of these forests, suggests that Rocky Mountain ponderosa pine–Douglas fir landscapes historically were dense, have long been naturally fire-prone, are dangerous places to live, and will remain so after restoration.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article online from http://www.Blackwell-Synergy.com:

Table S1 Observations in forest reserve reports on fire severity in ponderosa pine–Douglas fir forests

Table S2 Observations in forest reserve reports on killing of small trees by surface fires

Table S3 Observations in forest reserve reports on tree regeneration after surface fires

Table S4 Observations in forest reserve reports on the density of trees in ponderosa pine–Douglas fir forests

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