

Heterogeneity in ponderosa pine/Douglas-fir forests: age and size structure in unlogged and logged landscapes of central Colorado

Merrill R. Kaufmann, Claudia M. Regan, and Peter M. Brown

Abstract: Tree age and size structures were compared within and among topographic categories in portions of a 35-km² unlogged landscape and a comparable adjacent logged landscape. Tree density was generally higher in the logged landscape. One fifth of plots in the unlogged landscape had trees older than 400 years, but no trees older than 400 years remained in the logged landscape plots. Ten recruitment pulses were identified for the unlogged study area, accounting for 49% of all trees measured during 26% of the 421-year survival record. Recruitment pulses in the logged area accounted for fewer trees during a larger amount of time. Most recruitment periods in the unlogged landscape coincided with known past major fires. The mixed-severity historical fire regime created openings that persisted for as long as 148 years. The following components exist in the unlogged landscape: (i) forest patches having a distinct age cap reflecting regeneration following an earlier stand-replacing fire, (ii) uneven-aged forest patches having no evidence of an age cap, (iii) openings created by fire, and (iv) riparian areas. Results suggest that the logged landscape is poised to regain an old-growth age distribution, and tree removal in the logged landscape could restore the size distribution found in the unlogged landscape. However, the unlogged landscape has openings not found in the logged landscape that should be considered in restoration efforts at a landscape scale.

Résumé : Les structures de dimension et d'âge des arbres ont été comparées à l'intérieur et entre des unités topographiques dans des portions d'un paysage de 35 km² où il n'y a pas eu de coupe et d'un paysage adjacent et comparable où il y a eu des coupes. La densité des arbres était généralement plus élevée dans le paysage avec des coupes. Dans le paysage sans coupe, une parcelle sur cinq contenait des arbres plus vieux que 400 ans alors qu'il ne restait aucun arbre de 400 ans dans les parcelles du paysage avec des coupes. Dix vagues de recrutement ont été identifiées dans l'aire d'étude non coupée représentant 49% de tous les arbres mesurés pour 26% des 421 années de données de survie. Les vagues de recrutement dans la zone coupée représentaient moins d'arbres pendant une période plus longue. La plupart des périodes de recrutement dans le paysage sans coupe coïncidaient avec d'importants feux survenus dans le passé et dont on connaît l'existence. Le régime passé des feux dont la sévérité était variable a créé des ouvertures qui ont persisté pour aussi longtemps que 148 ans. On trouve les composantes suivantes dans le paysage sans coupe : (i) des îlots de forêt dont la limite d'âge indique clairement qu'une période de régénération survenue suite à un feu a entraîné le remplacement du peuplement, (ii) des îlots de forêt inéquienne où la limite d'âge n'est pas évidente, (iii) des ouvertures créées par le feu et (iv) des zones ripariennes. Les résultats suggèrent que le paysage avec des coupes est en voie de retrouver une distribution d'âges typique d'une vieille forêt et que la coupe des arbres dans le paysage avec des coupes pourrait rétablir la distribution des dimensions qu'on retrouve dans le paysage sans coupe. Cependant, le paysage intact a des ouvertures qu'on ne retrouve pas dans le paysage avec des coupes, ce qui devrait être considéré dans les efforts de restauration à l'échelle du paysage.

[Traduit par la Rédaction]

Introduction

Most forests in the southern Rocky Mountains and southwestern United States have been altered significantly from

their condition before European settlement. While change is normal in all ecosystems, logging, grazing, and fire suppression since the late 1800s increased the rate of change and resulted in conditions outside the natural or historical range of variability (Landres et al. 1999; Swanson et al. 1994). In the southern Rocky Mountains and Southwest, logging occurred in all forest types and was particularly heavy in more accessible and productive sites. Heavy unregulated grazing began in most areas by the late 1800s and extended into the mid-1900s before grazing pressures were brought under control. Fire cessation occurred initially with the introduction of livestock, which reduced surface fuels, and continued through the 20th century by active fire suppression activities (Fulé et al. 1997; Swetnam and Baisan 1996).

Important structural features and regulating processes of forests occur at multiple scales, including patches, stands, and

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landscapes. In this paper, we refer to patches as the smallest grouping of trees readily distinguished from neighboring groups in 1:6000 color infrared photographs. Patches may be as small as 0.1 ha. Stands refer to groups of contiguous and relatively similar patches, generally in uniform topographic settings (e.g., north slopes). Landscapes refer to areas large enough to assess the size of major disturbances, in our case fires that were larger than 10 km². Ideally, studies of extensive forest reserves impacted only minimally by logging, fire suppression, and grazing would provide insight into historical patch and stand structure in landscapes (Baker 1992; Moore et al. 1999; Turner and Romme 1994). Current forests, especially those accessible to logging and grazing, have at best only isolated and often non-representative areas protected from human activities, and these remnants of earlier landscapes almost never are extensive enough for study of the components, patterns, and processes that comprised and regulated historical forests at a landscape scale. Hadley and Veblen (1993) suggested that through human disturbances such as logging, grazing, burning, and fire suppression, many Colorado Front Range montane forests are now more homogeneous at stand and landscape scales than when they were regulated solely by natural processes.

Most data on the historical structure of ponderosa pine forests comes from the southwestern United States. However, important differences exist between ponderosa pine forests found in the Southwest and those in the southern and central Rocky Mountains and elsewhere. In many portions of the Southwest, fires in ponderosa pine forests historically occurred at average intervals of 2–10 years (Covington and Moore 1994; Fulé et al. 1997; Laven et al. 1980; Swetnam 1990; Swetnam and Baisan 1996), and stand-replacing fires were presumed to be very rare (Cooper 1960; Moore et al. 1999; Woolsey 1911). Ponderosa pine stands historically were uneven aged, low in density, locally patchy, and often had extensive bunch-grass understories. In contrast, fires in many portions of the southern and central Rocky Mountains were not as frequent, even at the forest–grassland ecotone (Brown et al. 1999; Goldblum and Veblen 1992). Less frequent fires may have included areas of non-lethal surface fire and areas where fire burned intensely and created openings, resulting in landscape patterns that may have been considerably different from those in the Southwest (Brown et al. 1999; Peet 1981; Turner and Romme 1994). This mixed-severity fire pattern is similar to the “mixed and variable fire regime” described by Brown (1995) and “moderate-severity fire regime” described by Agee (1998).

Several sites in the Colorado Front Range have been studied to characterize vegetation patterns in relation to disturbance (Hadley and Veblen 1993; Veblen and Lorenz 1986, 1991). These studies differ from ours in that many of their sites had been influenced by human activities. Only a few of their sites were dominated by ponderosa pine, and in all cases the tree age data excluded trees less than 4 cm diameter at breast height. This favors an interpretation of recruitment peaks after disturbance somewhat different from what complete tree age data might show. Nonetheless, these papers emphasize spatial heterogeneity at the large-landscape scale, especially among forest types, and the effects of human disturbances on the age structure within forest types.

One of the greatest limitations in ecosystem assessments

is the lack of suitable information describing pre-settlement reference landscapes. While various literature and other sources provide useful information (Kaufmann et al. 1994; Kaufmann et al. 1998; Landres et al. 1999; Moore et al. 1999; Swetnam et al. 1999; Veblen and Lorenz 1991; White and Walker 1997), usually historical data are fragmentary and not very quantitative. Data quantifying reference landscape characteristics for ponderosa pine in the Southwest and especially the Rocky Mountains are limited. For example, Arno et al. (1995) conducted a study on the age structure of ponderosa pine/Douglas-fir stands in western Montana, but after extensive searching, a number of their plots had to be located on steep topography because more representative sites had been altered. This lack of representation of historical landscape components severely limits our understanding of historical landscape characteristics. Several authors have discussed tree recruitment processes, sometimes reaching somewhat inconsistent views that may be related to the scale of measurement and effects of key processes that differ among geographic locations (Arno et al. 1995; Cooper 1960; Covington and Moore 1994; Mast 1993; Mast et al. 1999; Savage et al. 1996; White 1985). In the Colorado Front Range, studies on historical insect activity have been reported for Douglas-fir dominated forests generally above 2400 m elevation (Hadley and Veblen 1993; Swetnam and Lynch 1989), but these forests provide limited insight into the processes affecting ponderosa pine dominated forests below 2500 m.

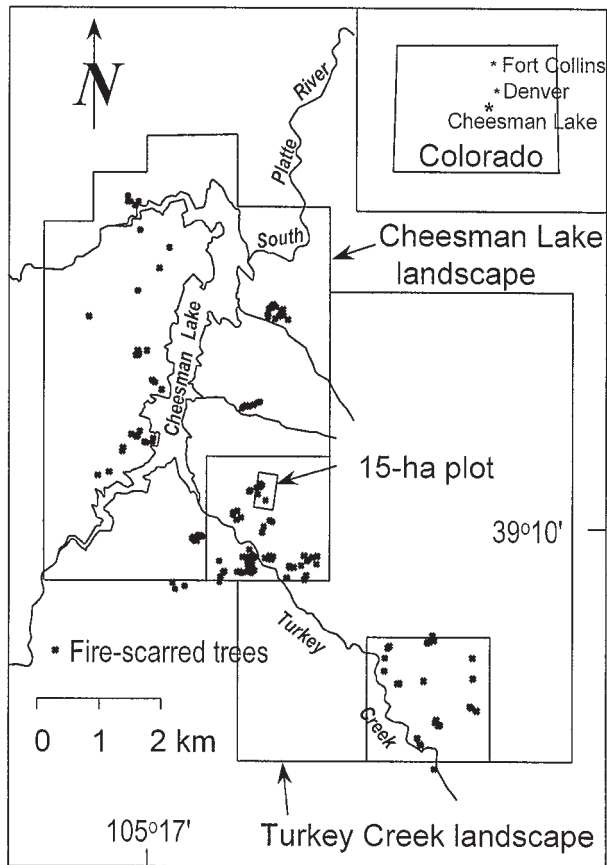
In this paper we document forest age and structural characteristics in a 35-km² ponderosa pine/Douglas-fir forest in the Colorado Front Range Mountains that has never been logged and has been protected from livestock grazing for over 90 years. This landscape surrounds Cheesman Lake, a reservoir on the South Platte River owned by the Denver Water Department. The Cheesman Lake landscape offers an exceptional opportunity to study spatial and temporal patterns in an unlogged forest landscape and to compare these patterns with those of logged areas nearby. Tree age and size structure and the species composition of portions of these unlogged and logged landscapes were compared across five topographic categories. Data presented here and fire-history data presented by Brown et al. (1999) are used to examine the factors that appear to have governed the observed age structure and composition of individual tree patches in the landscapes, including the creation of openings by fire and their reforestation. These data provide a basis for ongoing studies at larger spatial scales that address the role of fire and other natural disturbances, tree recruitment, climate, and topography as factors regulating natural landscape patterns over time. Collectively, these studies are being used to assess current forest conditions and potential restoration treatments (including wildfire mitigation in areas of urban encroachment) in the context of ecological sustainability at a landscape scale (Kaufmann et al. 2000).

Methods

Study sites

The Cheesman Lake landscape is in the montane forest zone about 60 km southwest of Denver, Colo. Elevations range from 2100 (water level of the reservoir) to 2400 m. Six tree species

Fig. 1. Map of area showing the unlogged Cheesman Lake and logged Turkey Creek landscapes. The 15-ha plot and two 4-km² areas below center are described in the text. ✖, fire scar sampling sites discussed in Brown et al. (1999).



occur in the study area: ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.), Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco), blue spruce (*Picea pungens* Engelm.), trembling aspen (*Populus tremuloides* Michx.), narrow-leaf cottonwood (*Populus angustifolia* James), and Rocky Mountain juniper (*Juniperus scopulorum* Sarg.). The studies reported here were conducted in two 4-km² study areas (Fig. 1). The study area in the unlogged Cheesman Lake landscape is southeast of the reservoir. It is characterized by irregular topography that includes the lower portion of Turkey Creek (a perennial stream) and several intermittent streams, forested slopes of all aspects, and flatter upland areas and ridgetops. Early reports indicate that the Cheesman Lake landscape was unlogged at the end of the 19th century, although logging in nearby areas of the South Platte basin was in progress (Jack 1900; General Land Office field notes 1879 and 1882). Cattle grazing occurred late in the 19th century throughout the South Platte basin including the Cheesman Lake landscape, but it apparently was not excessive and was largely confined to riparian areas (Jack 1900). Cattle grazing was excluded from the Cheesman Lake landscape by fencing after dam completion in 1905. The Turkey Creek study area is upstream in the same drainage. The Turkey Creek management history includes multiple periods of logging since the late 1800s, grazing from the 1880s to the 1940s, fire suppression, and prescribed burning over the southwest portion of the 4 km² (Jack 1900; General Land Office field notes 1879 and 1882; records of the Pike National Forest).

Because these two study areas are not replicated, it is important to address potential factors that may complicate comparisons of data

between the areas. Two types of differences could invalidate comparisons. There are potential environmental differences involving topography, soils, and climate and biological differences in forest development stemming from dissimilar timing of natural disturbances and patterns of tree recruitment and survival. Environmental differences were minimized by selecting two study areas physically close together that have very similar topographic and soil conditions. The two areas are separated by a distance of only 1 km. Topographic maps were used to identify boundaries for 2 × 2 km areas in the Turkey Creek drainage that contained slopes and aspects in roughly equal proportions in the unlogged and logged landscapes. This allowed plot selection with similar slopes and aspects for the two areas. The Turkey Creek 4-km² area averages about 150 m higher in elevation than the Cheesman Lake area, but both are well within the elevational range of the ponderosa pine/Douglas-fir forest type. Soils are gravelly coarse sandy loams derived from weathered Pikes Peak granite and classified as sandy-skeletal, mixed, frigid, shallow typic Ustorthents or sandy-skeletal, mixed, shallow typic Cryorthents (USDA Forest Service 1992). Isohietal maps of rainfall distribution suggest minimal difference in annual rainfall between the two areas. Maximum tree heights were similar within topographic categories between areas, and a comparison of understory plant diversity between the areas indicated considerable species overlap (Jaccard's coefficient 0.61; M.R. Kaufmann and T.J. Stohlgren, unpublished data).

It is less evident, and harder to demonstrate, that patch and stand characteristics were similar for the two areas prior to European settlement. However, there is considerable evidence that fire, the dominant factor affecting landscape patterns in this forest system, was similar for the two study areas prior to settlement. Our fire history covers a period of eight centuries and an area of about 40 km² (Brown et al. 1999). While logging appears to have destroyed most of the oldest fire-scarred trees in the Turkey Creek study area (and relatively few stumps persist), our fire history appears to be complete from the 1631 fire to the present. These data indicate that major fires in 1631, 1723, and 1851 prior to logging and grazing activities affected both areas (i.e., neither area provided evidence of a large fire affecting only one area). Evidence also exists of several smaller fires that burned in only one or the other area. Remnant old-growth patches on south aspects appeared similar, although we did not specifically collect paired plot data to confirm this. While we have too little evidence to conclude that the age and size structure and species composition provided similar original patch and stand structures in the two landscapes, we are convinced that fire, the primary natural disturbance factor, had a similar effect on both areas. Thus, while lack of replication creates risks in data interpretation, we believe that cautious use of data comparing the two study areas is valid for this and other ongoing studies.

Sampling (4 km²)

Complete tree inventories were obtained in twenty-five 0.1-ha forested plots distributed randomly within topographic strata across each 4-km² study area at Cheesman Lake and Turkey Creek (Fig. 1). Plots were selected to have a minimum of 15 trees per plot (minimum tree height of 1.37 m), although several south-facing plots selected early in the study had fewer trees. At the time of plot selection and sampling, a map describing patch locations and forest overstory condition of patches was not available, and plots were stratified based on topography and the minimum tree density. Five plots each were distributed on north-facing, south-facing, east- and west-facing, flat-high, or low-riparian areas. Plot locations were selected using a random grid coordinate table and a grid overlay on each 4-km² area. The first five grid cells falling in each topographic category and meeting the minimum tree density and qualification rules were selected. These rules specified that, for north, south, and east or west aspects, plot azimuth was within 20°

of the cardinal direction, and plot slope was between 15 and 35%. For the flat-high plots (typically on or near ridges), plot azimuth could be any value, but plot slope was under 10%. For the low-riparian areas, plots were located where most trees could be influenced by increased water availability in the stream channel; plots were kept above the bank of permanent streams but could cross intermittent streams. Plot aspect for low-riparian plots varied, but plot slope was generally under 15%. A digital elevation model was used later to assess landscape areas by aspect and slope (Cheesman Lake only; Turkey Creek data were not available to us at the time of analysis). For the entire Cheesman Lake landscape, north aspects ($0 \pm 45^\circ$, slopes $> 10\%$) accounted for 22% of the land area; south, 21%; east, 25%; and west, 26%. The remaining 6% (land having up to 10% slope) included both upper flat and low-riparian areas, which occurred in roughly equal proportions but were not distinguished in this analysis.

Each 0.1-ha plot was 20×50 m (slope distance), with the long axis aligned down the fall line for the north, south, east, and west plots. These plots also were used for modified Whittaker understory sampling (Stohlgren et al. 1995) in another portion of our studies. Within each 0.1-ha plot, diameter at breast height, total height, species, live or dead status, and stem location were measured for every tree at least 1.37 m tall. PROC MULTTEST in SAS was used to run permutation *t* tests to compare tree densities and basal areas between species and among aspects, and between the Cheesman Lake and Turkey Creek landscapes (SAS Institute Inc. 1996). This procedure in SAS automatically maintained the type I error rate ($p = 0.05$) by adjusting the *p* values from a family of hypothesis tests. The permutation option specifies that the *p* values be adjusted by resampling the data without replacement.

Age determinations

Ages were determined on 20 trees per plot, except where fewer trees occurred on some of the earlier plots sampled or where heartrot occasionally prevented age determination. Increment cores were obtained with a borer at 30–40 cm above the point where the pith was projected to meet the ground. To obtain a random sample of tree ages, the nearest tree (breast height or taller) to each of a series of five points (corners and center of a 4×10 m grid) in each corner of the 20×50 m plot were sampled regardless of species or size. In addition, other trees in plots appearing to be 200 years old or older were sampled for a complete inventory of old trees. Earlier studies indicated that ponderosa pine old-growth characteristics (flattened crown tops, proliferated branches at the top, large and often drooping branches, smooth yellowish bark, and more open crown structure) generally appear at an age of about 200 years (Kaufmann 1996). This additional sampling identified six trees pre-dating 1800. The ages of these trees are reported below, but they were not used in statistical analyses. The total number of cores used in analyses was 419 for Cheesman Lake and 452 for Turkey Creek. Of the 871 tree ages determined, 61.5% were ponderosa pine, 34.2% were Douglas-fir, 1.8% were aspen, 1.6% were blue spruce, 0.5% were juniper, and 0.3% were narrow-leaf cottonwood. Note, however, that only trees 1.37 m (breast height) or taller were sampled. This resulted in underestimates of trees dating to the last several decades of the 20th century.

Increment cores were cross-dated using standard dendrochronological methods (Stokes and Smiley 1968; Swetnam et al. 1985). We developed a tree-ring chronology for the area that extended from 991 to 1997 (the earlier years from fire scar samples). The number of rings to the pith on cores where pith was not present was estimated using templates of concentric circles (Appelquist 1958). We estimate that more than half of the cores reached within two rings of the pith, and more than 90% were within 10 rings.

We were especially interested in relating age structure and tree establishment to ecologically significant factors and events that characterize the forest history; thus, we wanted an estimate of ger-

mination (recruitment) year rather than pith year measured at a height of 30–40 cm. Arno et al. (1995) applied two correction factors to estimate germination years (for obtaining total tree age). They used the growth rate of the innermost ring of off-center cores and the estimated distance to the pith to estimate the number of rings missed. They also used tree regeneration studies to estimate the number of years required for trees to reach coring height (30 cm). Their studies relied on ring counts, which were verified on a subsample of their data to agree within 10 years of cross-dated estimates of tree age. In our studies, we cross-dated every sample.

We used a three-step process to estimate recruitment year. First, we destructively sampled small trees from both north and south slopes (10 ponderosa pine and 10 Douglas-fir trees for each slope) to determine the age difference between the ground and 35 cm heights. These trees ranged in age at the ground line from 16 to 87 years. The number of annual rings per 5 mm for the innermost rings at the 35-cm height was measured, and a linear regression line was fitted using the number of rings per 5 mm as the independent variable and age difference between the ground and 35 cm as the dependent variable. A weak but significant positive relationship was found for each species (for pine, $p = 0.003$, $R^2 = 0.39$; for Douglas-fir, $p = 0.04$, $R^2 = 0.20$), indicating that radial growth rate at 35 cm improved the estimate of the number of years required for the tree to reach that height compared with using a single value for all trees. The average width of the 95% confidence interval for individual tree predictions was 12 years for ponderosa pine and 10 years for Douglas-fir.

Next, tree cores from study plots were placed into three growth rate categories (high, medium, and low). For a subsample of cores, these mean growth rates and 95% confidence intervals were 2.35 ± 0.31 , 4.41 ± 0.77 , and 9.70 ± 1.97 rings/5 mm for ponderosa pine and 3.5 ± 1.24 , 5.88 ± 0.72 , and 11.09 ± 1.83 rings/5 mm for Douglas-fir, respectively (based on 3–17 trees per group). Where the pith was missed by more than a few years, the medium growth rate was assumed. Finally, the correction factor for each species and growth category was determined using the regression equations from destructively sampled trees applied to the mean growth rate for the category, and this value was subtracted from the pith year determined for each core to estimate the germination or recruitment year (pith year at the ground). Correction factors ranged from 5 to 13 years for ponderosa pine and from 13 to 18 years for Douglas-fir. These factors are similar to those observed by Veblen and Lorenz (1986) who reported fewer years for reaching a coring height of 15 cm. For the 4% of the cored trees that were not ponderosa pine or Douglas-fir, we applied ponderosa pine corrections to juniper and Douglas-fir corrections to aspen, blue spruce, and narrow-leaf cottonwood (reflecting their common associations in the field). While the procedures we followed involved uncertainty in determinations of the recruitment year, we chose this uncertainty over that associated with trying to connect temporal ecological significance to pith years measured at a height of 30–40 cm. Furthermore, aggregated estimates of tree recruitment peaks based on many trees were probably less variable than individual tree recruitment year estimates because the distribution of the age difference – radial growth rate relationship (for the 40 destructively sampled trees) appeared to be normal.

Temporal recruitment patterns

Estimated recruitment years for the trees randomly selected in each plot and for the randomly selected plots in each topographic category were used to examine variability in temporal patterns of recruitment among plots within each topographic category and between 4-km² areas (Cheesman Lake and Turkey Creek). We chose 5-year running means as a useful expression of annual recruitment for individual plots and areas. Graphically, a single tree appears as 0.2 trees recruited per year for 5 years, thereby reflecting the uncertainty associated with estimating the exact recruitment year for

Table 1. Tree density and basal area for each aspect calculated using five plots per aspect.

Aspect	Ponderosa pine	Douglas-fir	Other	Total
Tree density (trees/ha)				
Cheesman Lake				
North	390 (136, 920) ^{a†}	756 (224, 1158) ^{b†}	7 (0, 12)	1153 (955, 1459) ^d
South	187 (96, 359) ^{a†}	32 (0, 138) ^{c†}	0 (0, 0)	219 (96, 379) ^e
East–west	258 (135, 421) ^{a†}	92 (22, 185) ^{c†*}	0 (0, 0)	350 (157, 475) ^{e*}
Flat–high	131 (82, 257) ^{a*}	83 (10, 135) ^c	0 (0, 0)	214 (154, 267) ^{e*}
Low–riparian	291 (149, 482) ^{a†}	65 (32, 143) ^{c†}	23 (0, 31)	379 (240, 570) ^e
Turkey Creek				
North	234 (213, 287) ^{fg†}	870 (436, 1905) ^{h†}	125 (0, 426)	1229 (649, 2288) ^j
South	351 (138, 490) ^{fg†}	45 (0, 85) ^{i†}	6 (0, 21)	402 (191, 575) ^j
East–west	441 (223, 692) ^{f†}	283 (149, 447) ^{hi†*}	4 (0, 11)	728 (501, 948) ^{j*}
Flat–high	272 (210, 360) ^{fg†*}	152 (110, 200) ^{hi†}	8 (0, 40)	432 (340, 500) ^{j*}
Low–riparian	184 (130, 230) ^g	470 (30, 1400) ^{hi}	494 (140, 790)	1148 (510, 2330) ^j
Basal area (m²/ha)				
Cheesman Lake				
North	15.5 (9.0, 26.4) ^a	15.7 (4.8, 22.6) ^b	0.0 (0.0, 0.1)	31.3 (26.1, 34.8) ^{c*}
South	14.4 (7.8, 22.0) ^{a†}	0.4 (0.0, 1.2) ^{c†}	0.0 (0.0, 0.0)	14.8 (8.9, 22.0) ^{de}
East–west	15.9 (12.3, 23.6) ^{a†}	1.7 (0.1, 5.2) ^{c†*}	0.0 (0.0, 0.0)	17.6 (13.0, 23.9) ^{de}
Flat–high	9.4 (3.7, 15.4) ^{a†}	1.5 (0.0, 2.6) ^{c†*}	0.0 (0.0, 0.0)	10.8 (6.3, 15.4) ^{e*}
Low–riparian	20.7 (15.5, 28.7) ^{a†*}	0.6 (0.0, 2.3) ^{c†*}	0.0 (0.0, 0.1)	21.3 (15.7, 31.1) ^d
Turkey Creek				
North	8.7 (4.2, 11.4) ^{f†}	15.0 (11.7, 18.9) ^{h†}	0.2 (0.0, 0.6)	23.9 (20.4, 30.3) ^{i*}
South	14.1 (10.7, 17.4) ^{f†}	1.3 (0.0, 2.8) ^{g†}	0.3 (0.0, 0.7)	15.7 (13.1, 18.1) ^j
East–west	12.3 (7.0, 21.7) ^{f†}	8.1 (2.4, 11.5) ^{gh†*}	0.0 (0.0, 0.1)	20.4 (12.6, 24.1) ^{ij}
Flat–high	13.9 (10.1, 16.9) ^{f†}	4.8 (4.0, 5.7) ^{g†*}	0.1 (0.0, 0.3)	18.8 (14.2, 22.4) ^{ij*}
Low–riparian	8.6 (5.7, 11.0) ^{f*}	9.0 (0.8, 18.4) ^{gh*}	4.6 (0.5, 16.0)	22.2 (16.6, 25.7) ^{ij}

Note: Values are means, with minimum and maximum values given in parentheses. The column labeled “Other” includes Rocky Mountain juniper, blue spruce, aspen, and narrow-leaf cottonwood. Results of permutation *t* tests on families of comparisons are shown as follows. Values with different letters are significantly ($p < 0.05$) different among aspects within species and areas (Cheesman Lake or Turkey Creek).

[†]Significant differences between ponderosa pine and Douglas-fir within aspects.

*Significant difference within aspect between the Cheesman Lake and Turkey Creek areas.

any single tree. Composite recruitment patterns (using 5-year running means) were constructed for the Cheesman Lake and Turkey Creek areas by combining 25 plots for each area. These results are not area weighted for each topographic category.

Tests for recruitment peaks were conducted using either the number of trees recruited per year for each area or the number of plots per 4 km² having recruitment in given years. In both cases, estimated recruitment years were used, not 5-year running means. Peaks were identified using Silverman’s kernel density estimates of multimodality (Silverman 1981). Silverman’s test involves the identification of peaks (inflection points) in segments of a distribution that have been averaged within critical window widths. As the critical window width is decreased in successive analyses, peaks in the density distribution emerge. The *p* values identify the proportion of bootstrap samples in a simulation that are likely to have more than the tested number of modes, and we rejected additional modes when the *p* value exceeded 0.2. Results presented later indicate that the closest recruitment peaks identified were 11 years apart. Most were 16 or more years apart, well exceeding the ~10–12 year confidence intervals on estimates of individual tree recruitment year.

Sampling (15 ha)

A 15-ha plot within the Cheesman Lake 4-km² study area (Fig. 1) was sampled for another study. For this paper, we report on the age and spatial location of trees in that plot that predate 1800. Trees in the 15-ha plot were stem-mapped with a laser sur-

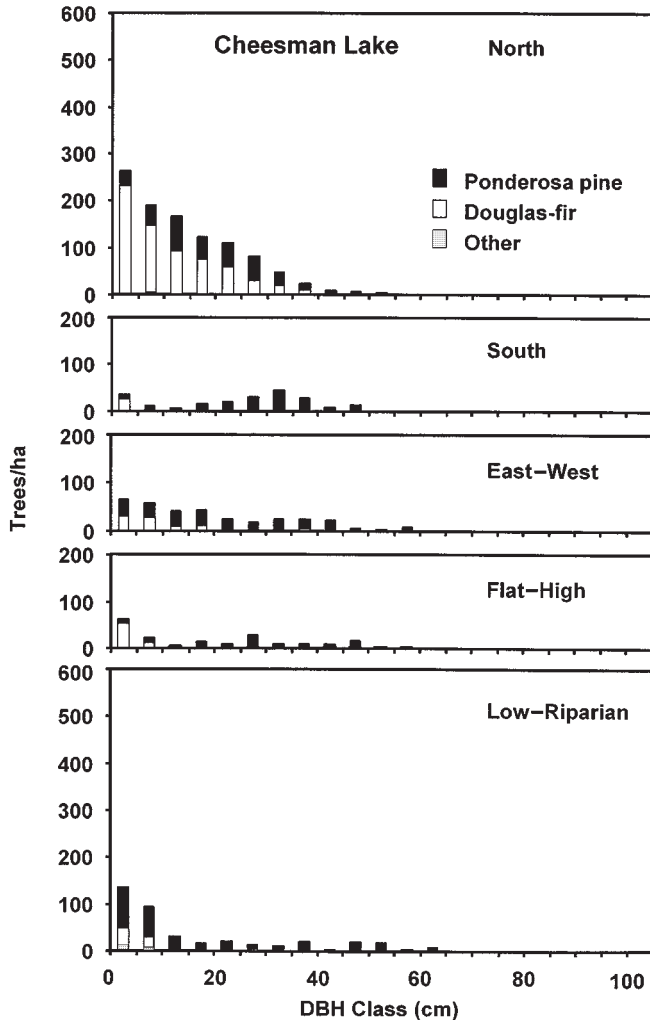
vey instrument that provided *x*, *y*, and *z* coordinates for each tree. The 15-ha area was divided into 25 × 25 m subplots. Using diameters to subsample trees for age determination, we cored one tree per species randomly selected from each 10-cm diameter class from each subplot. Because larger trees were less common and did not occur in many subplots, we sampled all trees above 40 cm (generally not more than one or two additional trees in some of the subplots). This sampling scheme also captured a large portion of the trees larger than 30 cm and a significant portion between 20 and 30 cm; thus, it is likely to be a complete or nearly complete sample of trees pre-dating 1800. Dating of cores followed procedures described above.

Results

Structure of 0.1-ha plots in 4-km² study areas

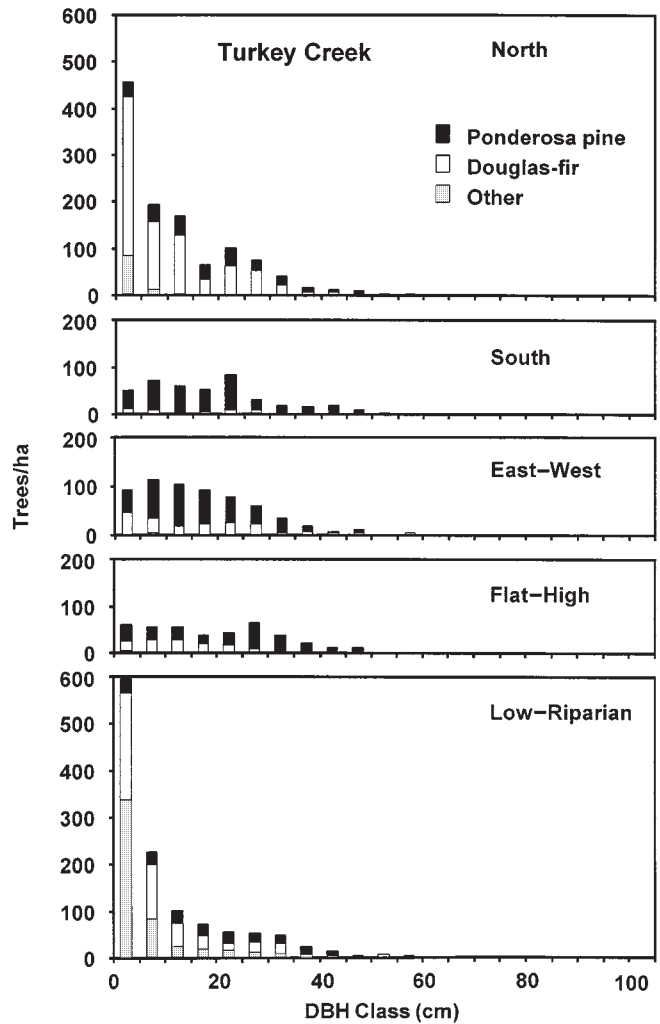
Tree densities and basal areas in Table 1 summarize results from five 0.1-ha plots per topographic category in forested portions of the Cheesman Lake and Turkey Creek 4-km² study areas. The total density of trees on 25 0.1-ha plots in the unlogged Cheesman Lake 4-km² study area varied from 96 to 1459 trees/ha, and basal areas ranged from 6.3 to 34.8 m²/ha (Table 1). Tree density in the logged Turkey Creek plots varied from 191 to 2330 trees/ha, and total tree densities were significantly higher in the Turkey Creek area than in Cheesman Lake for the east–west and flat–high

Fig. 2. Diameter class distribution of all live trees, combined for five 0.1-ha plots in each topographic category (25 plots total) in the Cheesman Lake 4-km² study area. Scales were selected to match those used in Fig. 3. These data may not represent landscape patterns, because the areas occupied by each topographic stratum are not taken into account.



topographic categories. The range of total basal area was less in the Turkey Creek area (12.6–30.3 m²/ha; Table 1). Total basal areas were higher in the north topographic category in Cheesman Lake and higher in the flat-high category in Turkey Creek. Overall area means are not given, because results cannot be area weighted until mapping data for the study areas are available. Several differences in tree density and basal area were observed among topographic categories within species (Table 1). In Cheesman Lake, ponderosa pine and Douglas-fir were far more numerous than other species for all topographic categories except low-riparian, where small numbers of juniper, blue spruce, aspen, and cottonwood (“other” column in Table 1) made them the most species-rich plots in the unlogged study area. North-facing plots in Cheesman Lake averaged almost twice as many Douglas-fir as ponderosa pine trees (only one plot had more ponderosa pine than Douglas-fir), with a small number of junipers. Ponderosa pine was more prevalent than Douglas-fir in the

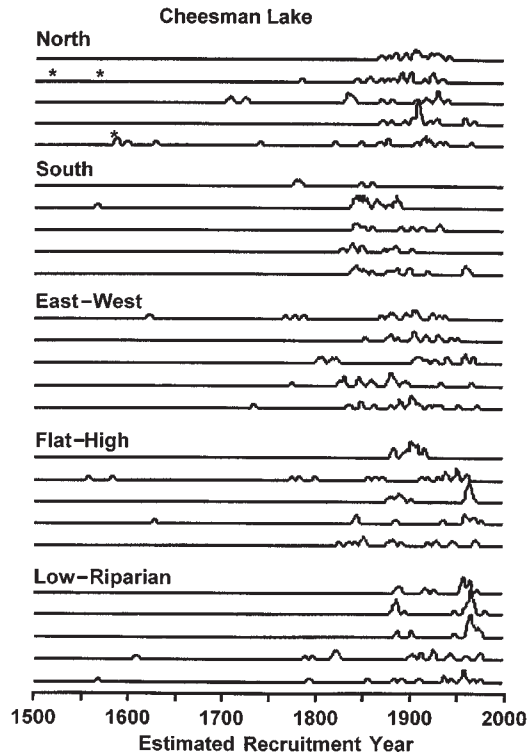
Fig. 3. Diameter class distribution of all live trees, combined for five 0.1-ha plots in each topographic category (25 plots total) in the Turkey Creek 4-km² study area. These data may not represent landscape patterns, because the areas occupied by each topographic stratum are not taken into account.



south, east, or west, and low-riparian topographic categories. In Turkey Creek, Douglas-fir densities were higher than ponderosa pine densities in both north and low-riparian categories, and more blue spruce and aspen were found in low-riparian areas, with very high blue spruce or aspen densities in certain individual plots. In addition, juniper and aspen were more widely distributed among topographic categories in Turkey Creek than in Cheesman Lake.

Diameter-class distributions illustrate considerably different overstory structures across topographic categories in the two areas (Figs. 2 and 3). Ponderosa pine trees were larger in diameter than Douglas-fir trees at the Cheesman Lake area. Mean diameters of ponderosa pine by topographic category ranged from 21.6 to 31.2 cm for Cheesman Lake and from 16.7 to 22.3 cm for Turkey Creek (data not shown). Mean diameters of Douglas-fir trees by topographic category ranged from 5.5 to 14.6 cm for Cheesman Lake and from 12.2 to 16.8 cm for Turkey Creek. Similar species differences were observed with height (data not shown). While

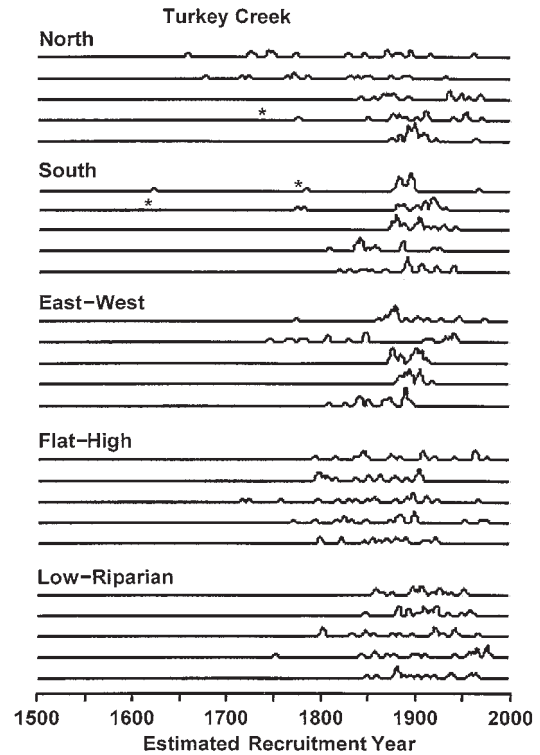
Fig. 4. Recruitment patterns for individual plots (one plot per line) in the Cheesman Lake 4-km² study area. Values are estimated recruitment years for cored trees that were randomly selected, expressed as a 5-year running average to reflect uncertainty in estimating exact year of recruitment. For the vertical scale, one tree (see smallest peaks in figure) is represented as 0.2 tree/year for 5 years. Asterisks show the ages of additional trees not included in the random sample but cored because they appeared to be older than 200 years.



Douglas-fir was rarely evenly distributed among diameter classes, in several cases ponderosa pine was equally represented over a fairly broad diameter range (north, east-west, flat-high in Cheesman Lake, Fig. 2; low-riparian in Turkey Creek, Fig. 3); in south-facing Cheesman Lake plots, the most frequent diameter class was 30–35 cm. The north topographic category was dominated by smaller-diameter Douglas-fir trees in both areas. The low-riparian plots in both areas had a large percentage of trees in the diameter classes smaller than 10 cm. Most were ponderosa pine in Cheesman Lake, but in Turkey Creek, Douglas-fir, blue spruce, and aspen outnumbered ponderosa pine, juniper, and narrowleaf cottonwood.

The age-class distribution of randomly selected trees for five 0.1-ha plots in each topographic category is shown for Cheesman Lake and Turkey Creek in Figs. 4 and 5. Each line shows the age distribution (based on 5-year running mean) for estimated tree recruitment years. Tree recruitment varied widely among plots within topographic categories, among categories, and between areas. Differences existed in the number of old trees per plot and per area for the Cheesman Lake and Turkey Creek sample areas. Data for numbers of old trees shown in Figs. 4 and 5 are summarized in Table 2. Both the Cheesman Lake and Turkey Creek areas

Fig. 5. Recruitment patterns for individual plots (one plot per line) in the Turkey Creek 4-km² study area. Values are estimated recruitment years for cored trees that were randomly selected, expressed as a 5-year running average to reflect uncertainty in estimating exact year of recruitment. For the vertical scale, one tree (see smallest peaks in figure) is represented as 0.2 tree/year for 5 years. Asterisks indicate the ages of additional trees not included in the random sample but cored because they appeared to be older than 200 years.



have 34–38 trees older than 200 years. These trees were found on about half of the plots (12 of 25 in each case), with the remaining plots having only younger trees. Trees older than 200 years occurred in all topographic categories. The numbers of trees older than 300 and 400 years were much higher for the unlogged Cheesman Lake area than for the logged Turkey Creek area. Trees more than 300 years old occurred on about one third of the Cheesman Lake plots (in all topographic categories), and trees older than 400 years occurred on one fifth of the plots (all but one topographic category), compared with less than one fifth and none of the plots for Turkey Creek. Old trees were predominately ponderosa pine at both areas, but nearly one third (11 of 38) of the trees older than 200 years at Turkey Creek were Douglas-fir. Differences also existed in the age of the oldest trees within each plot. These are examined later in this section.

Data for all individual plots shown in Figs. 4 and 5 were aggregated for the Cheesman Lake and Turkey Creek areas (Fig. 6). The plots were not weighted for area represented by each topographic category, therefore the data may not reflect the age structure for each area as a whole. While these are survival data for all past tree recruitment and do not represent actual germination and establishment, the distinct peaks

Table 2. Number of old trees for the Cheesman Lake and Turkey Creek areas, and number of plots having old trees (out of 25 plots total in each area).

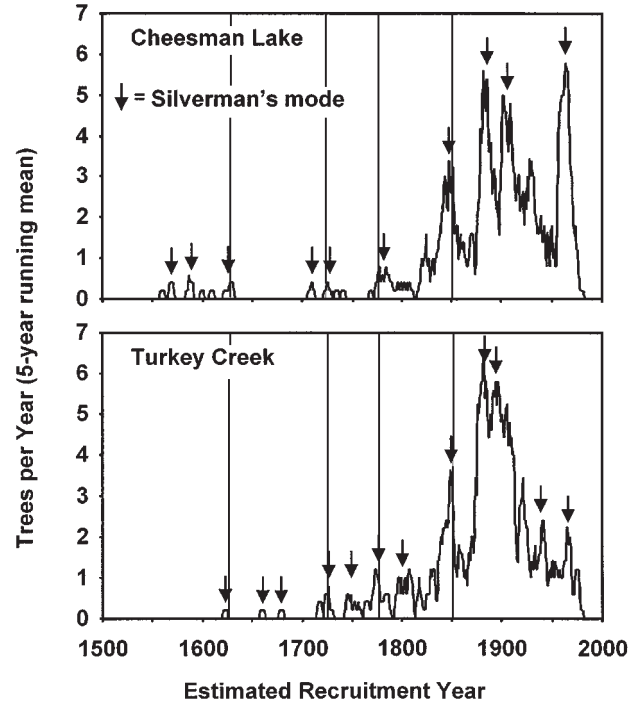
Age exceeds	Species			No. of plots
	PP	DF	Total	
Cheesman Lake				
200 years	31	3	34	12
300 years	14	1	15	8
400 years	10	0	10	5
Turkey Creek				
200 years	27	11	38	12
300 years	4	0	4	4
400 years	0	0	0	0

Note: Trees older than 200, 300, or 400 years are those for which the germination year predates 1798, 1698, or 1598. The total sample size was 432 trees for Cheesman Lake and 456 trees for Turkey Creek. PP, ponderosa pine; DF, Douglas-fir.

in tree numbers over time suggest that tree recruitment varied considerably. Results of the Silverman multimodality test for recruitment peaks are presented in Table 3. The Silverman multimodality test identified 10 modes or pulses of tree recruitment at Cheesman Lake and 12 modes at Turkey Creek (first and fourth columns in Table 3, arrows in Fig. 6). The test identified seven plot recruitment modes at Cheesman Lake and 11 plot modes at Turkey Creek (second and fifth columns in Table 3), all of which coincided closely with tree recruitment modes for each area. Six modes coincided relatively well between the two areas: 1620s, 1720s, 1770s – 1780s, 1840s, 1880s, and 1960s. The fire data in Table 3 are discussed in the next section.

To assess how important tree recruitment pulses were in accounting for live trees at the time of sampling, data in Fig. 6 (aggregated from Figs. 4 and 5) were analyzed to determine the percentage of surviving trees that were recruited during these specific recruitment periods (Table 4). Trees having estimated recruitment years within ± 5 years of each mode identified with the Silverman test were counted and compared with total recruitment for the appropriate century. Using these 11-year windows, 26% of all years were considered recruitment years at Cheesman Lake compared with 37% at Turkey Creek. At Cheesman Lake, 49% of all tree recruitment occurred during 26% of the entire sampling period, whereas 35% of all recruitment occurred during 37% of the time at Turkey Creek. A one-sample proportions test with continuity correction (MathSoft 1999) indicated that tree recruitment at Cheesman Lake was higher during the identified recruitment peaks ($p < 0.001$) than expected if recruitment was uniformly distributed over time. No difference was observed at Turkey Creek. Furthermore, the percentage of all trees recruited per century that were recruited during these periods (last column in Table 4) declined somewhat at Cheesman Lake (above 70 to below 50%) but declined dramatically at Turkey Creek (100–23%). The disproportionately higher pulsed recruitment at Cheesman Lake may be associated with cycles of favorable recruitment conditions affecting seed production, germination, and seedling establishment. We suspect that the same patterns of tree recruitment occurred at Turkey Creek prior to logging; however, trees removed by logging removed evi-

Fig. 6. Tree recruitment patterns for twenty-five 0.1-ha plots combined in the Cheesman Lake and Turkey Creek study areas. Values for each year are the sums of running average estimates of tree recruitment per year shown in Figs. 4 and 5. Arrows indicate peak recruitment years identified with the Silverman kernel density multimodality analysis using specific (not running average) estimated recruitment year for individual cored trees (see Table 3). Vertical lines indicate years (1631, 1723, 1775, and 1851) when fire burned across both study areas.



dence of the pulses, and recruitment after about 1880 or 1890 was affected by logging, grazing, and fire suppression.

Plot age structure and disturbance

A number of modes in tree recruitment identified by the Silverman test differ between the Cheesman Lake and Turkey Creek areas (see arrows in recruitment peaks in Fig. 6). The earliest modes at Turkey Creek represent trees left after logging, and several modes reflect only single trees; thus, differences between the two areas before 1800 are hard to interpret. The most notable differences between the areas occurred at the end of the 19th century and into the 20th century. The 1894 recruitment mode in Turkey Creek (Fig. 6, Table 3) may have resulted from logging and grazing very late in the 19th century. The Cheesman Lake mode at 1906 may exist in the Turkey Creek data but is masked by the 1894 mode. Only one mode in the 20th century (1960s) was common to both areas; other modes, including those too small to be identified in the Silverman test, appeared to occur at different times for the two areas. These 20th century differences also probably reflect the different logging and grazing histories of the two areas. We do not have specific logging dates for the Turkey Creek study area.

Large differences among plots were found in the age of the oldest tree (Figs 4 and 5). Some Cheesman Lake plots did not have old trees, suggesting that a major natural disturbance killed all trees (significant human disturbance did not

Table 3. Tree and plot recruitment modes identified with Silverman's multimodality test, and fire history data.

Cheesman Lake 4 km ²			Turkey Creek 4 km ²			Other fire years	Comments
Tree modes	Plot modes	Fire years	Tree modes	Plot modes	Fire years		
						1197	Earliest fire scars sampled
						1496	Scars in Cheesman 4-km ² area and elsewhere in Cheesman
						1534	>5 km ² in area, but only small portion of Cheesman 4 km ²
1568	1570						
1588		1587					>50% of sampled trees scarred, fire >10 km²
1627	1626	1631	1623*	1623*	1631		>50% of sampled trees scarred, fire >10 km²
			1660*	1660*			
			1678*	1678*			
						1696	>10 km ² in area, mostly north of Cheesman 4 km ²
1709							
1727	1728	1723	1724	1724	1723		>50% of sampled trees scarred, fire >10 km²
			1748	1748			
1782	1784	1775	1774	1774	1775		Small number of fire scars over >10-km ² area
			1801	1800			
		1841					Fire scars in half of Cheesman 4 km ²
1847	1847	1851	1848	1849	1851		>50% of sampled trees scarred, fire >10 km²
1885	1889		1883	1883		1880	Fire scars in north half of Cheesman landscape, north of Cheesman 4 km ²
			1894				
1906							
			1940	1940			
1963	1962	1963	1965	1965			Fire suppressed at 10–20 ha

Note: Tree recruitment modes were identified on the aggregate tree age data set for each area using individual estimated tree recruitment years (summarized on a 5-year running mean basis in Fig. 6). Plot recruitment modes were identified based on tree recruitment by plot rather than by tree count, thereby reflecting a spatial component of tree recruitment rather than a proportion of the total tree population. Fire years and related comments are summarized from Brown et al. (1999). Bold indicates fire years and associated recruitment modes for large fires that scarred a large portion of fire scar samples in both 4-km² study areas. Asterisks indicate only one tree or plot per mode.

begin until the late 1800s and did not include logging), and the present age structure reflects tree recruitment and survival patterns following the disturbance. Reduced numbers of old trees in the logged Turkey Creek study area confound the interpretation of the age of the oldest tree per plot for this area. We examined the fire history of the two 4-km² study areas reported by Brown et al. (1999), and we examined the patterns of insect activity in recent decades (see discussion below) for explanations of the age structure, especially the ages of the oldest trees in each plot. Key fire events are summarized in Table 3, based on fire scar samples collected in these landscapes (Fig. 1; data from Brown et al. (1999)). Four major fire years affected both the Cheesman Lake and Turkey Creek 4-km² study areas. These were 1587, 1631, 1723, and 1851. These fires apparently followed a mixed-severity or mixed and variable burning pattern (Agee 1998; Brown 1995), with portions of the fires burning intensely and killing all trees in patches, and portions burning as nonlethal surface fires. In addition, an extensive but apparently very light surface fire occurred in 1775.

Evidence suggests that openings were created by the 1851 and 1723 fires. The ages of the oldest trees in some plots clearly postdated these major fire years, while in other plots older trees survived although fires apparently burned

through the plots (Brown et al. 1999). At Cheesman Lake, all trees in several flat-high and low-riparian plots postdated the 1851 fire (Fig. 4). These data are consistent with complete tree mortality from fire in these stands. We also found that the death year for remnant logs in openings just north of the Cheesman Lake 4-km² area coincided with the 1851 fire (Brown et al. 1999). Coarse woody debris similar to tree remnants from 1851 was observed in 48 of 49 openings in the area known to have burned in 1851 (M. Tobler, Colorado State University, Fort Collins, Colo, personal communication). These openings persist on south-facing slopes nearly 150 years after the fire. Furthermore, an examination of General Land Office field notes for the Cheesman Lake and surrounding townships indicated that a large number of openings existed in the 1870s and 1880s, many of them having a large number of dead trees and often large amounts of charcoal and charring.

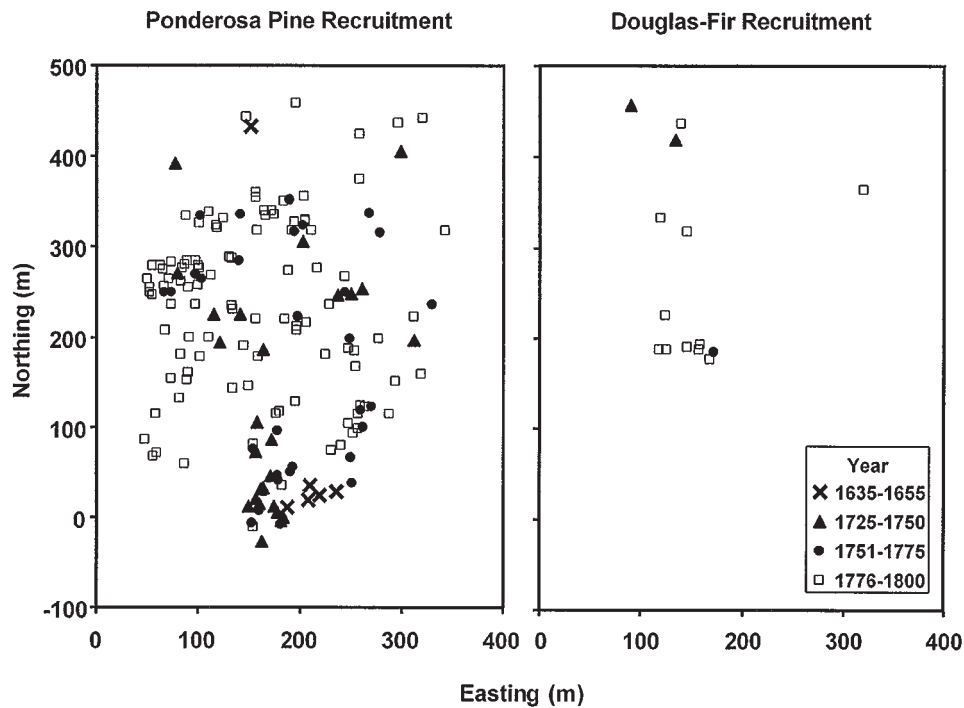
Four of five south-facing plots in the Cheesman Lake 4-km² study area had no trees pre-dating the fire in 1723 (Fig. 4). The oldest trees in these plots dated to after 1800, suggesting that the plots may have been unforested for 75 years. The location and ages of trees pre-dating 1800 in the 15-ha plot (see Fig. 1) provide further evidence that fire may have killed trees in patches while leaving behind enclaves of trees pre-dating the fire (Fig. 7). While many ponderosa pine

Table 4. Surviving trees in 11-year recruitment periods for Cheesman Lake and Turkey Creek 0.1-ha plots.

Interval (years)	Years in recruitment periods	Total no. of trees recruited by century	No. of trees in recruitment periods	Percent in recruitment periods
Cheesman Lake (421-year survival record)				
1560–1600	22	7	5	71
1601–1700	11	4	3	75
1701–1800	33	19	10	53
1801–1900	22	172	79	46
1901–1980	22	217	107	49
Total	110	419	204	
% of total	26		49	
Turkey Creek (357-year survival record)				
1623–1700	33	3	3	100
1701–1800	33	34	17	50
1801–1900	44	248	101	41
1901–1979	22	167	39	23
Total	132	452	160	
% of total	37		35	

Note: One to four recruitment periods occurred during each 100-year period (Table 3, Fig. 6). For Cheesman Lake, 49% of surviving trees were recruited in 26% of the total survival period. For Turkey Creek, only 35% of surviving trees were recruited in 37% of the total survival period.

Fig. 7. Spatial and temporal pattern of tree recruitment of ponderosa pine and Douglas-fir trees in a 15-ha plot within the Cheesman Lake 4-km² study area. Easting and Northing are distances in metres from the southwest corner of the plot. All trees over 40 cm were cored and aged, and when combined with aging of a subsample of smaller diameter classes, the sample is likely to have included all trees pre-dating 1800.



trees and a small number of Douglas-fir trees recruited between 1725 and 1800 occurred throughout the 15-ha area, only a very small number of surviving ponderosa pine trees predate the 1723 fire. These are a small group at the south end of the plot and a single tree near the north edge of the plot. These data suggest that a patchy fire burned intensely

enough to kill all trees through the center portion of the plot area. The small group of surviving trees at the south end of the plot was on a south-facing slope where tree density may have been too low to support a crown fire. All trees shown in Fig. 7 survived the 1851 fire. Fire scars and scorched rings in increment cores indicate the fire burned in the 15-ha

plot; however, many trees survived, while less than 1 km north a large number of openings noted above were created by the same fire.

Discussion

Landscape heterogeneity

Heterogeneity in forest age structure, size structure, and species composition is a natural characteristic of unlogged forested landscapes, and measurements of heterogeneity provide insight into the ecological integrity of forests (Frelich and Reich 1995). In the Colorado Front Range, improved understanding of patch and stand patterns and characteristics in historical landscapes is useful for identifying general management goals that sustain or restore ecosystems at a landscape scale. Knowledge of such patterns is also useful for identifying historical landscape features that might guide the selection of silvicultural treatments to mitigate wildfire risks at the urban-wildland interface.

The Cheesman Lake landscape offers an opportunity to characterize the spatial and temporal heterogeneity and species composition of a historical landscape generally uninfluenced by anthropogenic effects. We believe that many features of the Cheesman Lake landscape reflect historical processes even though fire suppression has occurred during the 20th century. We also believe that environmental differences between Cheesman Lake and the adjacent Turkey Creek landscape are slight and contributed very little to observed differences in forest characteristics, so that comparisons of the areas will provide indications of how management has altered the spatial structure of patches and stands in the landscape (Mladenoff et al. 1993).

Natural factors contributed to historical montane forest heterogeneity at multiple spatial scales (Brown et al. 1999; Peet 1981; Hadley and Veblen 1993; Swetnam and Lynch 1989). These include fire patterns across the landscape, climate effects on seed production and seedling establishment, insect and disease activity, soils, and topographic effects on microclimate. We believe that patchiness in the ponderosa pine dominated Cheesman Lake landscape stems from two primary processes. First, major fires created openings of various sizes but left in place unburned or lightly burned areas that retained former patches or portions of former patches. Second, tree recruitment in openings created by fire occurred largely during specific recruitment periods, but it was influenced by local topographic conditions (with exposed areas becoming reforested only slowly) and most likely by long-term climatic variability. Thus multiple patches of regeneration of different ages could have developed within a single crown fire area, related in part to differential lags in seedling establishment. These primary process effects on patch structure are augmented over time by secondary processes affecting survivorship of trees.

The Cheesman Lake landscape appears to include four major vegetation structures. Two of these are forests that differ in a specific age structure characteristic. First, a portion of the landscape is covered with forest patches that appear to have an age cap, with all trees post-dating certain years (probably past stand-replacing fires as discussed below). The proportion of the landscape in this condition will be determined after mapping and additional age sampling are com-

pleted, but field observations suggest that three fourths or more of the landscape has an age cap. Another portion of the landscape is comprised of patches that do not appear to have a specific age cap; rather, these patches appear to result from a long history of microscale disturbances with no evidence of a past major stand-replacing event. The third landscape structure is the riparian system. Though limited in spatial extent in the Cheesman Lake landscape, this component provides a high percentage of the biological diversity (data not shown).

The fourth landscape structure includes openings and areas of very low forest density (Kaufmann et al. 2000). Coarse woody debris with intact bark was collected in several of these openings and dated to a death year of 1851, the year of a large fire in the Cheesman Lake landscape (Brown et al. 1999). Some openings having no trees or only several trees per hectare still exist following the 1851 fire. These are on mostly south-facing slopes and range in size from less than 1 ha up to about 20 ha as measured on 1:6000 aerial photographs. Openings are found on both sides of the reservoir, especially just north of the Cheesman Lake 4-km² study area (Fig. 1), but others exist directly south of the Cheesman Lake landscape outside the study area. In a number of presently forested 0.1-ha plots, recruitment may not have occurred for decades following the 1851 or 1723 fires (Fig. 4). We believe that such openings were more common before modern fire suppression efforts. General Land Office Survey field notes from the 19th century frequently referred to openings and areas of complete tree mortality from fire in surrounding townships. Descriptions of the Plum Creek Timber Land Reserve (Jack 1900) include several references to persistent openings and areas of low forest density, particularly on south slopes. It appears that the majority of openings in the landscape are transient rather than permanent, because every opening we have examined throughout the landscape except one has remnants of trees. This suggests that openings are not due to soil conditions or hydrologic or climatic factors.

The spatial extent of old-growth patches and stands in unlogged montane forest landscapes is elusive information (Kaufmann et al. 1992). In the Cheesman Lake landscape, 12 of 25 plots in the 4-km² study area had trees older than 200 years. Ongoing sampling of tree age across the entire Cheesman Lake landscape in conjunction with mapping of patch and stand areas will help determine not only the percent of the landscape that is populated with an old-growth component, but also the distribution pattern of old-growth trees in patches and stands in the landscape. Nonetheless, data presented here suggest that old trees are found in a large portion in the landscape. Regan (1997) examined the old-growth component in mixed conifer forests of the Sacramento Mountains of southern New Mexico. While she concluded that spatially explicit reconstructions at patch scales are often difficult because of the limited resolution of available data, her data suggested that old growth was far more extensive in the late 19th century landscape prior to logging, fire exclusion, and the resulting changes in fire regimes. Her research was on a very different forest system than found at Cheesman Lake, but it illustrates a useful approach for assessing historical old-growth forests where historical forests have been nearly completely destroyed.

Natural disturbance regimes

The fire history of the Cheesman Lake area is complex, and the historical fire regime is best described as mixed-severity or mixed and variable (Agee 1998; Brown 1995). Widespread fires occurred a number of times across the Cheesman Lake and Turkey Creek landscapes, and apparently most fires included both a surface and stand-replacing fire component (Brown et al. 1999; Kaufmann et al. 2000). There is no evidence of frequent surface fires in any one location (e.g., multiple fire scars a few years apart on single trees) as is typical in the ponderosa pine/bunch grass system in the southwestern United States (Covington and Moore 1994; Fulé et al. 1997, Swetnam 1990; Swetnam and Baisan 1996). Consequently, many old fire scars persist even in remnant materials, preserving a long-term record of fires in the landscape (one down log has been dated to an estimated germination year of 991 AD and at least four others to the 1000s, and two log remnants have fire scars dated to 1197). Based on historical fire frequency, we suspect that fire suppression during the 20th century has probably prevented at least two major fires. Historically, fires exceeding 10 km² in area occurred somewhere in the Cheesman Lake landscape about every 50–60 years (Brown et al. 1999). Because most of the major fires in the Cheesman Lake landscape coincided with tree recruitment peaks (see discussion below), it is possible and perhaps even probable that a major fire would have occurred somewhere in the landscape during the recruitment peaks of the 20th century (around 1906, 1963, or perhaps 1930). The only fire recorded at several locations for the 20th century occurred in 1963 (Brown et al. 1999). This fire was actively suppressed after reaching a size of 20–40 ha. While the true historical landscape would probably reflect these additional large fires, we believe that many features of the Cheesman Lake landscape still reflect the effects of the historical fire regime.

Evidence suggests that the lack of old trees in many plots is related to the effects of past fires rather than to insects or pathogens. Insect epidemics during recent decades have caused extensive mortality in previously logged forests in the Colorado Front Range (Schmid and Mata 1996; USDA Forest Service Rocky Mountain Region Forest Health Management Group reports). A severe mountain pine beetle outbreak in the 1970s killed large numbers of ponderosa pine trees everywhere in the Front Range (McCambridge et al. 1982). A tussock moth outbreak in the early 1990s in the lower portion in the South Platte basin killed a high percentage of Douglas-fir trees (and a number of ponderosa pine trees where the epidemic was most intense). Western spruce budworms killed many Douglas-fir trees in the 1980s through much of the Colorado Front Range, a synchronized outbreak that may have resulted from the homogeneous forest structures that have developed during the last century (Swetnam and Lynch 1989).

None of these outbreaks reached epidemic proportions in the unlogged Cheesman Lake landscape. A small percentage of ponderosa pine trees were killed by mountain pine beetles during the 1970s outbreak (evidenced by slowly decomposing trees that still have attached bark with beetle holes). The tussock moth epidemic that killed thousands of Douglas-fir trees in the early 1990s reached the edge of the Cheesman Lake landscape but killed only a few trees in the landscape.

At one point, we speculated that a mountain pine beetle outbreak preceded the 1847 recruitment peak and may have increased the intensity of the 1851 fire, but we found no tree ring evidence to support this. In the unlogged landscape, the most severe mortality in Douglas-fir that we observed was caused by the Douglas-fir beetle, which typically kills small groups of no more than a few trees. In ponderosa pine, patches of dwarf mistletoe infestations are relatively common and kill a portion of trees in infected areas. General Land Office field notes indicate similar infestations more than a century ago. The apparent lack of insect epidemics in the unlogged landscape may stem from the lower overall forest density in this landscape compared with that of previously logged forests (Table 1). Complete mortality from insect outbreaks is rare even in logged areas, and the lack of significant mortality in the unlogged landscape during epidemic years nearby suggests that complete tree mortality is far more likely to have resulted from lethal fire than from insect or pathogen outbreaks.

Temporal patterns of fire and tree recruitment

The coincidence of fire years and tree recruitment periods in the Cheesman Lake landscape is striking (Table 3), although it is difficult to ascribe a cause–effect relationship between the two. Fires in 1587, 1631, 1723, 1775, 1851, and 1880 (the latter in the north part of the Cheesman landscape outside the 4-km² study area; Brown et al. 1999) coincided with many recruitment periods in 0.1-ha plots (Fig. 6) and were within a few years of recruitment modes (Table 3). Tree recruitment and fire may be related to the same low-frequency climatic cycles. Climatic conditions favoring tree recruitment (Pearson 1933; Savage et al. 1996) also favor the accumulation of fine surface fuels (grasses and forbs) that contribute to fire spread. However, evidence suggests that tree recruitment may peak before fires occur (1631 and 1851 in Table 3) or may lag behind fires by as much as a century or more. The coincident timing of fires and periods of tree recruitment probably stems from a similar cause for the two but with a spatial disassociation, such that mortality from a fire may have occurred in one location while tree recruitment was occurring elsewhere during the same period. For this reason, tree age alone is inadequate to establish dates of major disturbance for a specific site in this forest system (Lorimer 1985).

It follows that there is a similar periodicity for fire and tree recruitment. The mean fire return interval for large-scale fires in the Cheesman Lake landscape was about 60 years (or 50 years counting the 1775 fire that left only a few fire scars over a large area) (Brown et al. 1999). Recruitment peaks of appreciable size from the 0.1-ha plots and common to both areas occurred in the 1770s–1780s, 1840s, 1880s, and 1960s (Fig. 6, Table 3). However, Mast et al. (1999) found little association between ponderosa pine recruitment and the Palmer drought severity index (PDSI). We cannot entirely discount the possibility that mountain pine beetle or other insect epidemics or other non-climatic factors synchronized recruitment peaks or fire behavior across the landscape, though we have no evidence to suggest that they did.

Results presented here appear to be consistent with other studies indicating that ponderosa pine forests are generally

uneven-aged but feature even-aged or nearly even-aged cohorts at some scale (Arno et al. 1995; Cooper 1960; Mast et al. 1998, 1999; Pearson 1933; Savage et al. 1996; White 1985). However, the peak periods for recruitment and major fires at Cheesman Lake do not coincide well with other reported patterns elsewhere. While we have not completed a climate reconstruction for the Cheesman Lake area, PDSIs for southeastern and east-central Colorado (grid cells 59 and 60; Cook et al. 1998) provide little indication that peaks at Cheesman Lake coincide with low drought index (wet) periods. Similarly, the Cheesman Lake recruitment peaks in the 1770s–1780s, 1840s, 1880s, and 1960s correlate more with dry July PDSI values rather than wet values for the southern Rocky Mountains in New Mexico (Swetnam and Betancourt 1998, Fig. 3). Nor did tree recruitment periods coincide consistently with observed cycles in other ponderosa pine studies, including tree ring chronologies in Rocky Mountain National Park (Mast 1993; Mast et al. 1998), and tree recruitment periods in western Montana (Arno et al. 1995) and the Gus Pearson Natural Area in northern Arizona (Mast et al. 1999; White 1985). The Cheesman Lake area is near the transition zone between the southwestern summer monsoon climate pattern and areas farther north generally not dominated by monsoonal moisture flows. Causes of periodicities in fire and tree recruitment regimes in the Cheesman Lake area clearly require more study.

Anthropogenic effects on forest structure

Logging in the late 1800s most likely removed most of the larger (and probably older) trees from the Turkey Creek study area, and remaining trees grew rapidly with reduced competition for resources. By themselves, data from the Turkey Creek plots only weakly support the widely held view that logged forests are more dense, younger, and have smaller diameter trees than unlogged forests. However, the design of this study was not intended to address the comparison of entire landscapes. The study intentionally focused on portions of the unlogged and logged landscapes that were relatively well forested, and no attempt was made to assess landscape characteristics such as openings or sparsely forested areas at the landscape scale. While the Turkey Creek area has few trees older than 300 years (Table 2), the number of trees older than 200 years and the number of large trees are not very different for the two areas (Figs. 2 and 3). The age and size structure of the Turkey Creek plots suggest that the logged forest could be placed on a restoration trajectory using silvicultural treatments that reduce tree densities in certain diameter classes while retaining desirable components such as trees older than 200 years.

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References

- Agee, J.K. 1998. The landscape ecology of western forest fire regimes. *Northwest Sci.* **72**: 24–34.
- Applequist, M.B. 1958. A simple pith locator for use with off-center increment cores. *J. For.* **56**: 141.
- Arno, S.F., Scott, J.H., and Hartwell, M.G. 1995. Age-class structure of old growth ponderosa pine/Douglas-fir stands and its relationship to fire history. USDA For. Serv. Res. Pap. No. INT-RP-481.
- Baker, W.L. 1992. Effects of settlement and fire suppression on landscape structure. *Ecology*, **73**: 1879–1887.
- Brown, J.K. 1995. Fire regimes and their relevance to ecosystem management. *Proc. Soc. Am. For.* 1994: 171–178.
- Brown, P.M., Kaufmann, M.R. and Shepperd, W.D. 1999. Long-term, landscape patterns of past fire events in a ponderosa pine forest of central Colorado. *Landscape Ecol.* **14**: 513–532.
- Cook, E., Meko, D., Stahle, D., and Cleaveland, M. 1998. Reconstruction of past drought across the conterminous United States from a network of climatically sensitive tree-ring data. NOAA Paleoclimatology Program website at <http://www.ngdc.noaa.gov/paleo/usclient2.html>.
- Cooper, C.F. 1960. Changes in vegetation, structure, and growth of southwestern pine forest since white settlement. *Ecol. Monogr.* **30**: 129–164.
- Covington, W.W., and Moore, M.M. 1994. Southwestern ponderosa forest structure—changes since Euro-American settlement. *J. For.* **92**: 39–47.
- Frellich, L.E., and Reich, P.B. 1995. Spatial patterns and succession in a Minnesota southern-boreal forest. *Ecol. Monogr.* **65**: 325–346.
- Fulé, P.Z., Covington, W.W., and Moore, M.M. 1997. Determining reference conditions for ecosystem management of southwestern ponderosa pine forests. *Ecol. Appl.* **7**: 895–908.
- Goldblum, D., and Veblen, T.T. 1992. Fire history of a ponderosa pine/Douglas-fir forest in the Colorado Front Range. *Phys. Geogr.* **13**: 133–148.
- Hadley, K.S., and Veblen, T.T. 1993. Stand response to western spruce budworm and Douglas-fir bark beetle outbreaks, Colorado Front Range. *Can. J. For. Res.* **23**: 279–491.
- Jack, J.G. 1900. Pikes Peak, Plum Creek, and South Platte Reserves. *In* Forest reserves, 20th Annual Report. U.S. Geological Survey, 1898–99, Part V. U.S. Government Printing Office, Washington, DC. pp. 39–115.
- Kaufmann, M.R. 1996. To live fast or not: growth, vigor, and longevity of old-growth ponderosa and lodgepole pine trees. *Tree Physiol.* **16**: 139–144.
- Kaufmann, M.R., Moir, W.H., and Covington, W.W. 1992. Old-growth forests: what do we know about their ecology and management in the Southwest and Rocky Mountain Regions? USDA For. Serv. Gen. Tech. Rep. No. RM-213.
- Kaufmann, M.R., Graham, R.T., Boyce, D.A., Jr., Moir, W.H., Perry, L., Reynolds, R.T., Bassett, R.L., Mehlhop, P., Edminster, C.B., Block, W.M., and Corn, P.S. 1994. An ecological basis for

- ecosystem management. USDA For. Serv. Gen. Tech. Rep. No. RM-246.
- Kaufmann, M.R., Huckaby, L.S., Regan, C.M., and Popp, J. 1998. Forest reference conditions for ecosystem management in the Sacramento Mountains, New Mexico. USDA For. Serv. Gen. Tech. Rep. No. GTR-RMRS-19.
- Kaufmann, M.R., Huckaby, L.S., and Gleason, P. 2000. Ponderosa pine in the Colorado Front Range: long historical fire and tree recruitment intervals and a case for landscape heterogeneity. *In* Proceedings of the Joint Fire Science Conference and Workshop: Crossing the Millennium: Integrating Spatial Technologies and Ecological Principles for a New Age in Fire Management, 15–17 June 1999, Boise, Idaho. *Edited by* L.F. Neuenschwander, K.C. Ryan, G.E. Gollberg, and J.D. Greer. University of Idaho and International Association of Wildland Fire, Moscow, Idaho. pp. 153–160.
- Landres, P.B., Morgan, P., and Swanson, F.J. 1999. Overview of the use of natural variability concepts in managing ecological systems. *Ecol. Appl.* **9**: 1179–1188.
- Laven, R.D., Omi, P.N., Wyant, J.G., and Pinkerton, A.S. 1980. Interpretation of fire scar data from a ponderosa pine ecosystem in the central Rocky Mountains, Colorado. *In* Proceedings of the Fire History Workshop, Tucson, Arizona. USDA For. Serv. Gen. Tech. Rep. No. RM-81. pp. 46–49.
- Lorimer, C.G. 1985. Methodological considerations in the analysis of forest disturbance history. *Can. J. For. Res.* **15**: 200–213.
- Mast, J.N. 1993. Climatic and disturbance factors influencing *Pinus ponderosa* stand structure near the forest/grassland ecotone in the Colorado Front Range. Ph.D. dissertation, University of Colorado, Boulder.
- Mast, J.N., Veblen, T.T. and Linhart, Y.B. 1998. Disturbance and climatic influences on age structure of ponderosa pine at the pine/grassland ecotone, Colorado Front Range. *J. Biogeogr.* **25**: 743–755.
- Mast, J.N., Fulé, P.Z., Moore, M.M., Covington, W.W., and Waltz, A.E.M. 1999. Restoration of presettlement age structure of an Arizona ponderosa pine forest. *Ecol. Appl.* **9**: 228–239.
- MathSoft. 1999. S-PLUS 2000 guide to statistics. Vol. 1. Data Analysis Products Division, MathSoft, Seattle, Wash.
- McCambridge, W.F., Hawksworth, F.G., Edminster, C.B., and Laut, J.G. 1982. Ponderosa pine mortality resulting from a mountain pine beetle outbreak. USDA For. Serv. Res. Pap. No. RM-235.
- Mladenoff, D.J., White, M.A. and Pastor, J. 1993. Comparing spatial pattern in unaltered old-growth and disturbed forest landscapes. *Ecol. Appl.* **3**: 294–306.
- Moore, M.M., Covington, W.W., and Fulé, P.Z. 1999. Reference conditions and ecological restoration: a southwestern ponderosa pine perspective. *Ecol. Appl.* **9**: 1266–1277.
- Pearson, G.A. 1933. A twenty-year record of changes in an Arizona pine forest. *Ecology*, **17**: 270–276.
- Peet, R.K. 1981. Forest vegetation of the Colorado Front Range. *Vegetatio*, **45**: 3–75.
- Regan, C.M. 1997. Old-growth forests in the Sacramento Mountains, New Mexico: characteristics, stand dynamics, and historical distributions. Ph.D. thesis, Colorado State University, Fort Collins.
- SAS Institute Inc. 1996. SAS/STAT software: changes and enhancements for release 6.12. SAS Institute Inc, Cary, N.C.
- Savage, M., Brown, P.M., and Feddema, J. 1996. The role of climate in a pine forest regeneration pulse in the southwestern United States. *Ecoscience*, **3**: 310–318.
- Schmid, J.M., and Mata, S.A. 1996. Natural variability of specific forest insect populations and their associated effects in Colorado. USDA Forest Service Gen. Tech. Rep. No. RM-GTR-275.
- Silverman, B.W. 1981. Using kernel density estimates to investigate multimodality. *J. R. Stat. Soc. B*, **43**: 97–99.
- Stohlgren, T.J., Falkner, M.B., and Schell, L.D. 1995. A modified-Whittaker nested vegetation sampling design. *Vegetatio*, **177**: 113–121.
- Stokes, M.A., and Smiley, T.L. 1968. An introduction to tree-ring dating. University of Chicago Press, Chicago, Ill.
- Swanson, F.J., Jones, J.A. Wallin, D.O. and Cissel, J.H. 1994. Natural variability—implications for ecosystem management. *In* Ecosystem management: principles and applications. Vol. II. Eastside forest ecosystem health assessment. *Technical editors*: M.E. Jensen and P.S. Bourgeron USDA For. Serv. Gen. Tech. Rep. No. PNW-GTR-318. pp. 80–94.
- Swetnam, T., Thompson, M.A., and Sutherland, E.K. 1985. Using dendrochronology to measure radial growth of defoliated trees. U.S. Dep. Agric. Agric. Handb. No. 639.
- Swetnam, T., Allen, C.D., and Betancourt, J.L. 1999. Applied historical ecology: using the past to manage for the future. *Ecol. Appl.* **9**: 1189–1206.
- Swetnam, T.W. 1990. Fire history and climate in the southwestern United States. *In* Proceedings of the Symposium on Effects of Fire Management of Southwestern U.S. Natural Resources, 14–18 Nov. 1988, Tucson, Ariz. *Technical coordinator*: J.S. Krammes. USDA For. Serv. Gen. Tech. Rep. No. GTR-RM-191. pp. 6–17.
- Swetnam, T.W., and Baisan, C.H. 1996. Historical fire regime patterns in the southwestern United States since AD 1700. *In* Proceedings of the 2nd La Mesa Fire Symposium, 29–31 Mar. 1994, Los Alamos, N. Mex. *Edited by* C.D. Allen. USDA For. Serv. Gen. Tech. Rep. GTR-RM-286. pp. 11–32.
- Swetnam, T.W., and Betancourt, J.L. 1998. Mesoscale disturbance and ecological response to decadal climatic variability in the American Southwest. *J. Clim.* **11**: 3128–3147.
- Swetnam, T.W., and Lynch, A.M. 1989. A tree-ring reconstruction of western spruce budworm history in the southern Rocky Mountains. *For. Sci.* **35**: 962–986.
- Turner, M.G., and Romme, W.H. 1994. Landscape dynamics in crown fire ecosystems. *Landscape Ecol.* **9**: 59–77.
- USDA Forest Service. 1992. Soil survey of Pike National Forest, eastern part, Colorado. USDA Forest Service Rocky Mountain Region and Soil Conservation Service, Lakewood, Colo.
- Veblen, T., and Lorenz, D.C. 1986. Anthropogenic disturbance and recovery patterns in montane forests, Colorado Front Range. *Phys. Geogr.* **7**: 1–24.
- Veblen, T., and Lorenz, D.C. 1991. The Colorado Front Range: a century of ecological change. University of Utah Press, Salt Lake City.
- White, A.S. 1985. Presettlement regeneration patterns in a southwestern ponderosa pine stand. *Ecology*, **66**: 589–594.
- White, P.S., and Walker, J.L. 1997. Approximating nature's variation: selecting and using reference information in restoration ecology. *Restoration Ecol.* **5**: 338–249.
- Woolsey, T.S., Jr. 1911. Western yellow pine in Arizona and New Mexico. U.S. Dep. Agric. Agric. Bull. No. 101.