RESTORATION OF PRESETTLEMENT AGE STRUCTURE OF AN ARIZONA PONDEROSA PINE FOREST

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Abstract. The age structure in 1876, the last year of the natural frequent-fire regime, of an unharvested ponderosa pine forest in northern Arizona was reconstructed from living and dead dendrochronological samples. Approximately 20% of the trees were >200 yr old in 1876 with ages ranging to 540 yr. If dead trees had not been included in the reconstruction, the distribution would have been biased toward younger trees and a 40% shorter age range. The presettlement age distribution was multimodal with broad peaks of establishment, consistent with the model of regeneration in ''safe sites'' where herbaceous competition and fire thinning are reduced. Although fire disturbance regimes and climatic conditions varied over the centuries before 1876, a clear relationship between these variations and tree establishment was not observed. Due to fire exclusion, reduced grass competition, and favorable climatic events, high levels of regeneration in the 20th century raised forest density from 60 trees/ha in 1876 to >3000 trees/ha in 1992. An ecological restoration experiment initiated in 1993 conserved all living presettlement trees and reduced the density of young trees to near-presettlement levels. Two important components for evaluating the restoration treatment effects are monitoring of old-tree persistence and patterns of future regeneration in the context of the presettlement reference age structure.

Key words: Arizona; climate; ecological restoration; fire regime; forest dynamics; natural conditions; old-growth; Pinus ponderosa; *regeneration.*

INTRODUCTION

Southwestern ponderosa pine (*Pinus ponderosa*) forests have undergone substantial changes in structure and function associated with livestock grazing, logging, and disruption of the natural frequent-fire regime following Euro-American settlement (Cooper 1960, Covington and Moore 1994*a*, Swetnam and Baisan 1996). Quantitative reconstructions of presettlement conditions, including age structure (the distribution and range of tree ages), serve as a basic point of reference central to restoration and management of these ecosystems (Covington et al. 1997, Fulé et al. 1997). Old trees have unique characteristics. They create habitat for various wildlife species through the persistence of dead tops and branches, which form ''living snags'' and provide structural diversity in tree height and patchy distribution. Old trees perpetuate genetic diversity over multicentury life-spans and they hold the tree-ring record of past climate and disturbance regimes (Swetnam and Brown 1992). The number of old trees in southwestern ponderosa pine forests has fallen markedly since settlement because of logging, increasing competition from dense young trees (Sutherland et al. 1991, Biondi et al. 1994), and increasing crown fires (Swetnam 1990).

Because they are usually the slowest organismic

variable in ecosystems, conservation of old-growth trees is a central management concern (Kaufmann et al. 1992). The dynamics of the presettlement ponderosa ecosystem, including regeneration (Cooper 1960, White 1985), responses to changing climate (Grissino-Mayer 1996; Swetnam and Betancourt, *unpublished manuscript*) and disturbance regimes (Covington and Moore 1994*a*), may be inferred to some extent from historic age structure, especially where both living and dead trees are sampled (Johnson et al. 1994). An understanding of these processes in the presettlement ecosystem, which reflected the selection pressures of the recent evolutionary environment, forms the basis for (1) management prescriptions (e.g., even- vs. uneven-aged management, rotation age [Smith 1986:8]); (2) determining desired future condition goals based on reference conditions (Kaufman et al. 1994); and (3) designing and evaluating ecological restoration treatments (Covington et al. 1997).

Climate is an important influence underlying episodic southwestern ponderosa pine seed production, germination, and seedling establishment (Pearson 1923, Schubert 1974, Savage and Swetnam 1990). Savage et al. (1996) used instrument weather records to examine the effect of climate on ponderosa pine regeneration at the Gustav A. Pearson Natural Area (GPNA), an unharvested research forest in northern Arizona that has been repeatedly measured since 1920 (Avery et al. 1976). They found that the criteria for

regeneration success, mainly warm and wet conditions several years before and ≤1 yr after regeneration events, occurred rarely. In the 20th century, only 1919 (a year of widespread ponderosa regeneration) and 1992 had highly favorable conditions.

Regional climatic events at multiyear scales, such as severe drought periods in the late 1500s and mid-1900s (D'Arrigo and Jacoby 1991, Grissino-Mayer 1996) also appear to have affected tree establishment, mortality, and fire disturbance regimes in many southwestern coniferous ecosystems (Swetnam and Betancourt 1990, Grissino-Mayer 1996, Swetnam and Betancourt, *unpublished manuscript*). In particular, evidence from dendrochronological sampling designed to measure extremely old ponderosa pines suggests that the late 1500s drought period may have led to a regional die-off, similar to that observed in pinyon pine (*Pinus edulis*) in central New Mexico during the 1950s drought (Swetnam and Betancourt, *unpublished manuscript*).

Frequent, low-intensity fire is the key disturbance process that regulated southwestern ponderosa pine ecosystems (Cooper 1960, Covington and Moore 1994*a, b,* Swetnam and Baisan 1996). White (1985) sampled living old-growth ponderosa pines at the GPNA in order to deduce regeneration patterns prior to 1876, the year in which fire exclusion was initiated (Dieterich 1980). He suggested that successful tree establishment depended on the creation of a ''safe site'' such as the ash bed of a consumed log, where seedlings could establish and grow above the lethal flaming zone. This model implies that seedling establishment and survival were low, but that the survival of saplings that passed through the competition–fire filter was high, leading to a relatively flat age distribution rather than the reverse-J age distribution expected in an uneven-aged forest with age-constant or age-increasing mortality (Silvertown 1987:101). In contrast, however, White (1985) found a high proportion of trees (74%) less than 100 yr old in 1876, producing a relatively large pulse of tree establishment resembling the reverse-J curve, preceded by a relatively continuous pattern of establishment back to 1572.

Ecological restoration treatments have been proposed to reverse the effects of extended fire exclusion, such as higher tree densities, reduced understory productivity and diversity, and the high threat of landscape-scale crown fires (Covington and Moore 1994*a*). Restoration treatments are designed to emulate the structure, function, and composition of indigenous ecosystems, restoring as far as possible the conditions characteristic of the evolutionary environment of native plants and animals (Covington et al. 1997). From 1993 to 1994, we initiated an ecological restoration experiment in a portion of the GPNA where managers recognized that increasing postsettlement tree density had come to pose an unacceptable fire hazard to the historic Fort Valley Experimental Forest headquarters buildings. The restoration treatments included thinning of most postsettlement trees, forest floor fuel reduction, recreation of grass fuelbeds, and prescribed burning. The experiments on the 4.7-ha study site comprised ~1.5 ha of full restoration treatment (thinning and burning), 1.5 ha with thinning but no burning, and 1.5 ha control, plus ~0.2 ha of excluded areas (Covington et al. 1997).

Determining reference conditions of forest structure was an initial step in the restoration experiment. Our first goal was to determine the historic presettlement age distribution of this portion of the Pearson forest in 1876, the last year of the presettlement frequent-fire regime (Dieterich 1980). We sampled dead as well as living trees to fully reconstruct age structure and draw the best-supported inferences possible about forest dynamics under past climatic and disturbance regimes. Our second goal was to contrast the historic reference age structure (1876) to that of the dense postsettlement forest (1992). Finally, we compared the reference condition (1876) to that of the restored forest (1994) in order to assess the initial restoration treatment and suggest criteria for future evaluation of forest age structure as a component of ecosystem restoration.

METHODS

Study area

The study area is a 4.7-ha virgin (never logged) ponderosa pine forest within the GPNA at the Fort Valley Experimental Forest, ~15 km NW of Flagstaff, Arizona. Trees >15.2 cm at breast height within the Natural Area have been measured at five- or ten-year intervals since 1920 (Avery et al. 1976 and *unpublished data*). The study area has gentle topography and a cool, subhumid climate. Mean annual precipitation is 57 cm, with approximately half occurring as snow. The remainder occurs as summer monsoonal rains following the spring/early summer drought. Soils are of volcanic origin, a fine montmorillonitic complex of frigid Typic Argiboroll and Mollic Eutroboralf (Covington et al. 1997). The ponderosa pine structure consists of groups of mature trees, characterized by larger size and yellowed bark, above dense thickets of smaller, dark-barked trees. Understory vegetation includes perennial grasses, primarily Arizona fescue (*Festuca arizonica*), mountain muhly (*Muhlenbergia montana*), and squirreltail (*Sitanion hystrix*), and forbs.

Field methods

The species, diameter at breast height (dbh), presettlement/postsettlement status, and condition were recorded for all living and dead trees in 1992. Field determination of presettlement or postsettlement status was based on size and appearance. All ponderosa pines >37.5 cm dbh and smaller pines with yellowed, platy bark were considered potentially presettlement, based on dendrochronological results from an adjacent area (White 1985). Condition classes were developed from

snag and log decomposition models applied in pon-
derosa pine forests in the Pacific Northwest (Maser et
al. 1979, Thomas et al. 1979), the Rocky Mountains
(Lundquist 1995), and Arizona (Covington and Moore
1994a, Fulé et al. 1997). The nine condition classes
were defined as: 1, living; 2, declining; 3, recent snag;
4, loose bark snag; 5, clean snag; 6, snag broken above
1.37 m; 7, snag broken below 1.37 m; 8, downed log;
and 9, cut stump. These classes were used to charac-
terize dead tree structure and to estimate the death dates
and sizes of presettlement-era trees.

Samples (cores, wedges, and disks) from all dead-
standing and downed ponderosa pines were obtained
with increment borers and chainsaws in 1993 to provide
ages and dates of death for the presettlement dead trees.
Most samples were taken at ~45 cm above ground level
(stump height). When the pattern of bark persistence
permitted, samples were taken from areas with bark
and without bark to allow examination of ring loss due
to weathering. Samples included some trees with rotten
centers for which only a minimum age could be de-
termined.

All the presettlement trees and a random subsample
of postsettlement trees were cored at 45 cm above
ground level (stump height) in 1992. Because several
cores from presettlement trees were damaged or distant
from the pith, increment cores were collected again
from all living presettlement trees in 1995. Increment
core collections were done to meet two research goals:
(1) determining tree age; and (2) reconstructing the size
of trees in 1876, the time fire exclusion began (Cov-
ington et al. 1997). The stump height coring is a com-
promise between the goal of determining total tree age,
which is most accurate when cores are taken as close
as possible to the ground (Telewski 1993, Savage et al.
1996), and the goal of determining past tree size by
calculating the radial growth increment from 1876 to
present. Diameter at stump height (dsh) is very highly
correlated with dbh, in contrast to the butt swell and
irregular stem form that would reduce the accuracy of
size reconstruction if trees were cored at ground level.
Trees were cored repeatedly wherever increment cores
were distant from the pith or where rot was encoun-
tered.

Laboratory methods

Samples were mounted and sanded with progres-
sively finer grit sandpaper. Samples from living and
dead trees were crossdated with the aid of skeleton
plots following the techniques of Stokes and Smiley
(1968). Ring widths of all presettlement samples were
measured to the nearest 0.01 mm with a computer-
compatible incremental measuring machine and dating
was checked with the COFECHA program (Grissino-
Mayer and Holmes 1993) against the master chronol-
ogy developed in this study and the chronology de-
veloped locally by Graybill (1987). Several samples
from dead presettlement trees could not be crossdated

initially so ring widths from these samples were mea-
sured and entered into COFECHA as floating series.
After the software identified periods of high correla-
tions with the master chronology, the dating was con-
firmed visually on the samples.

Center dates were determined as the pith dates at
sample height of 45 cm above ground level. Three to
ten years may be required for ponderosa pine seedlings
to reach this height in the Flagstaff area (Sackett 1984,
Cormier 1990). Some presettlement trees had to be
sampled higher to avoid areas of rot or damage. A
sample height of 1.37 m (breast height) was used for
38 living trees and heights between 0.7 and 2 m were
sampled for seven dead trees. Where the sample failed
to intercept the pith, or where the pith was rotten, the
number of years from the innermost ring to the pith
was estimated with a pith locator (concentric circles
matched to the approximate curvature and density of
the remaining inner rings). Only cores that reached the
pith were used in the subsample of postsettlement trees
($N = 115$ cores). Death dates of presettlement trees
that were dead in 1992 were identified by the final year
of growth below the bark or the location where the
inner bark was evidenced by bark beetle galleries.

A number of dead presettlement trees (59 trees, 21%
of the presettlement trees) could not be confirmed as
living or dead in 1876 because the year of death could
not be determined. Either the outermost ring dated as
<1876 or the sample could not be crossdated. For these
trees, a modeling approach based on tree diameter and
condition class was used to reconstruct past forest
structure. Rates of snag decomposition and snagfall
were taken from a locally calibrated model (Rogers et
al. 1984). Because these decomposition rates are im-
precise, a sensitivity analysis was carried out by com-
paring three different snag decomposition rate percen-
tiles (25, 50, and 75%) to examine the effect of slower
and faster decomposition. The method is described in
detail by Fulé et al. (1997).

Results

Two hundred and three trees were successfully dated
to center. The reconstructed 1876 age distribution (Fig.
1) shows several broad peaks of tree establishment,
especially in the late 1500s, around 1700, and in the
mid-1800s. The oldest tree, center date 1333, was >540
yr old in 1876. Only three trees have center dates before
the 1550s. Even after 1600, however, several decades
have few or no establishing trees and appear as dips
in the age distribution. The most pronounced dips occur
around 1615 and the mid-1700s. The youngest trees,
with center dates (at 45 cm) of 1871, 1872, and 1877,
were seedlings in 1876. Regeneration was fairly com-
mon in the presettlement GPNA forest (Fig. 1), with
tree establishment per decade fluctuating over approx-
imately an eight-fold range from 2 to 17 trees on the
4.7-ha study site (0.4–3.6 trees·ha^{-1}·decade^{-1}) from the
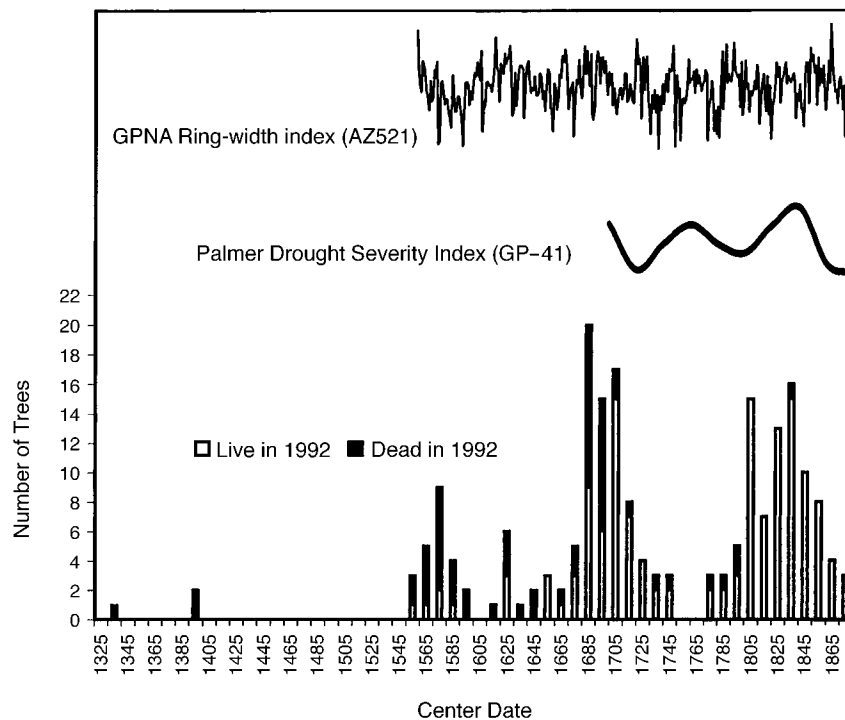1550s to 1870s. The maximum period without evidence

FIG. 1. Reconstructed 1876 age structure of the sampled 4.7-ha ponderosa pine stand at the Gus Pearson Natural Area (GPNA), Arizona. Dates are midpoints of 10-year age classes. Center dates of 203 trees are shown. The smoothed reconstructed Palmer Drought Stress Index GP-41 (Cook et al. 1996) and a standardized tree-ring width index for the GPNA (AZ521.CRN [Graybill 1987]) are shown for comparison with the presettlement tree establishment dates. All the indices are dimensionless.

of any tree establishment at this 4.7-ha site was two decades (1751–1770).

The tree-ring width index and climate features reconstructed from dendrochronological data are plotted in Fig. 1 above the age distribution. Nonoverlapping 20-yr mean values, emphasizing >20-yr trends, for the reconstructed summer (June–August) Palmer Drought Stress Index (PDSI) at the northern Arizona gridpoint nearest Flagstaff (Gridpoint 41 [Cook et al. 1996]) are compared with the longer ring-width index at the GPNA (Graybill 1987: AZ521.CRN). Trends in both indices are similar over the overlapping time period (~1700 to present).

Past research has emphasized the episodic nature of ponderosa regeneration, depending on annual to biennial climatic events (e.g., Schubert 1974, Savage et al. 1996). However, the multimodal peaks of presettlement tree establishment in Fig. 1 are relatively wide, ranging from 30 to 60 yr. We tested the possibility that wide establishment peaks were an artifact of imprecision in the center date estimation method by selecting the subset of samples, comprising 57% (117/203 trees) of the total number of dated trees, which either intersected the pith or were within an estimated 5 yr of center. This highly reliable subset had peaks of establishment as broad as the full data set (Fig. 2). In contrast, the postsettlement tree establishment pattern was relatively narrow with 77% of the center dates occur-

ring in the decade 1920–1929 and 92% in the two decades 1920–1939 (Fig. 3). Given the high probability that almost all of these trees actually germinated in 1919 (Savage et al. 1996), these results suggest that the imprecision in estimation of germination date due to sampling at stump height is contained within 20 yr. The broader peaks of presettlement tree establishment, in sum, appear to represent a true range of establishment dates, rather than being artifacts of the sampling or analysis methods. However, some of the highest presettlement establishment peaks, such as 1680–1699 or 1820–1839 may represent individual exceptionally good regeneration years.

The accuracy of field determination of presettlement status was high due to the combination of conservative identification of potentially presettlement living trees, ensuring that borderline trees are cored for age measurement, together with the high accuracy of identification of dead presettlement trees. Seventeen living trees, identified as potentially presettlement based on having dbh >37.5 cm but also having dark bark, were confirmed from their increment cores to be postsettlement trees. All dead material identified as presettlement in the field was confirmed to be of presettlement origin. Dead material of postsettlement origin was easily distinguished from presettlement dead material in the field by smaller size, darker bark, form (e.g., small, thin branches), and decay. Accurate field determination of
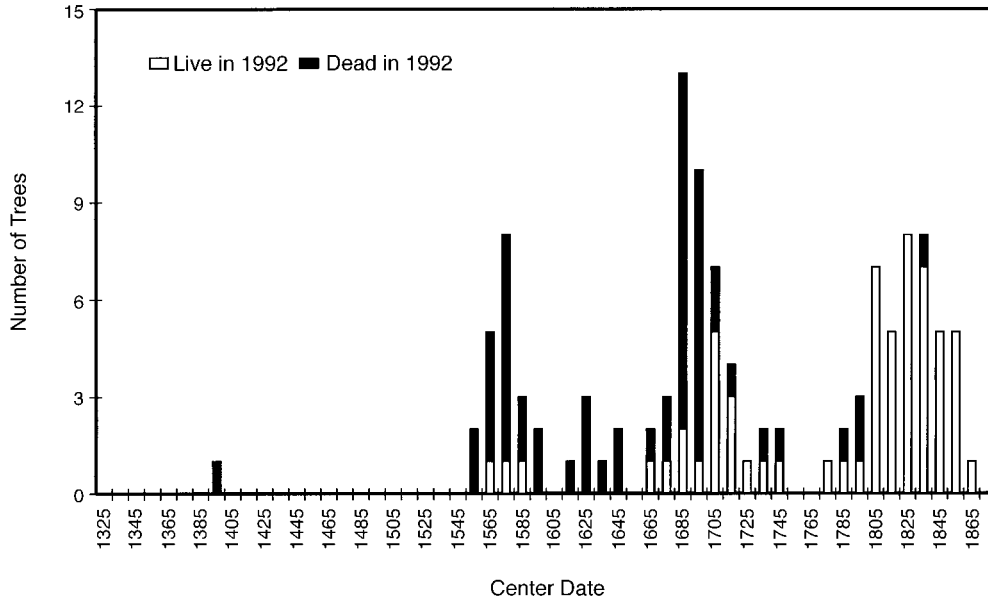
FIG. 2. Age structure of the subset of presettlement samples (117 of 203 trees) with samples within 5 yr of the tree pith.

living and dead presettlement trees is important not only for reconstruction research but also for ecological restoration treatments designed to emulate historic forest structure.

Center dates were determined for 71% (203/284) of the trees of presettlement origin. Inner ring dates ranging from 1492 to 1850 were determined for an additional 14% (41/284) of the presettlement trees (Fig. 4).

Because the inner ring dates vary over a broad range, the inability to determine center dates of these 41 trees does not appear to bias the age structure in Fig. 1, as would be the case if dates of a substantial cohort of trees of similar age were missing together. However, trees could be far older than the inner ring dates.

Determination of death dates was one of the objectives of dendrochronological analysis but decay of sap-
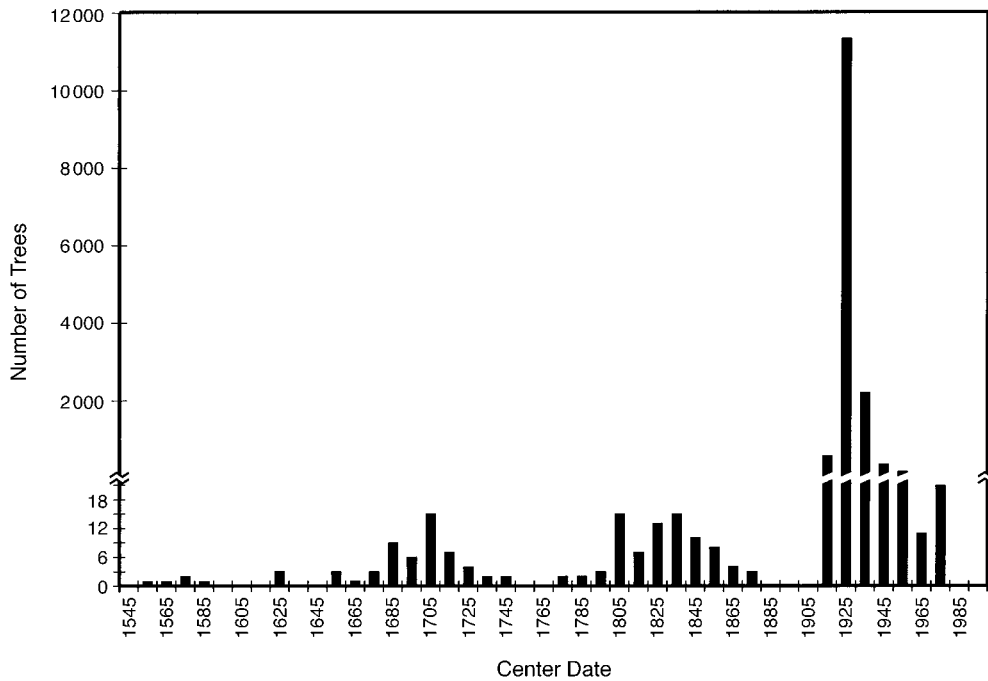

FIG. 3. Age structure in 1992 after 116 yr of fire exclusion. The graph is a composite of dated trees of presettlement origin and a subsample of dated trees of postsettlement origin.
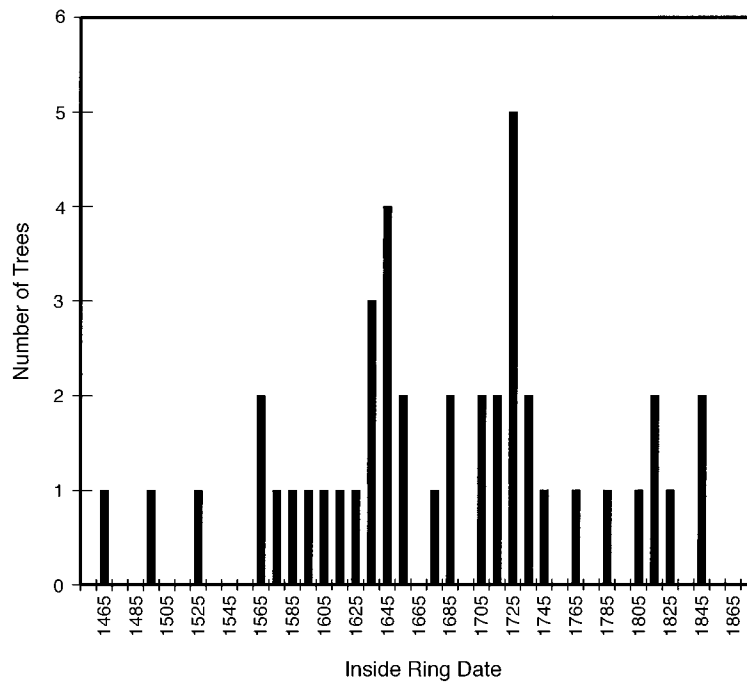
FIG. 4. Inner ring dates of sampled presettlement trees for which center date could not be determined.

wood rings prevented direct measurement of most death dates. In general, the majority of the sapwood was still present on these samples, but the rings closest to the cambium—critical for accurate death dating—appeared to be the most likely to decay. Death dates were determined on only 6 of the 86 dated dead trees (7%): five stumps (death years 1880, 1934, 1938, 1973, and 1975) and one downed log (1944). Stumps exist in the unharvested GPNA because of snag-felling to minimize fire hazard (a discontinued practice). No death dates before 1876 were found and many dead trees were alive in 1876 or later, as evidenced by post-1876 rings. However, the samples from 59 now-dead trees lacked direct evidence of post-1876 growth, i.e., post-1876 rings. All such trees were estimated to be alive in 1876 by applying the snag decomposition models with the fast (75%) and average (50%) decomposition rates (Fulé et al. 1997). Using the slow (25%) rate, two large trees were estimated to have pre-1876 death dates (both 1803) and three additional trees had estimated death dates shortly thereafter (1878 [two trees] and 1883).

Age structure of the forest was dominated by young trees in 1992 (Fig. 3). Dense thickets of trees, most originating in the highly favorable establishment year of 1919 (Savage et al. 1996), raised forest density from 60 trees/ha in 1876 to 3097 trees/ha in 1992. Residual age structure in 1994, following the restoration treatments on 3.2 ha, is shown in Fig. 5. The restoration thinning reduced forest density on the 3.2 ha treated area to 152 trees/ha. A margin of trees above the presettlement density was retained in part because the re-

placement trees for now-dead presettlement trees often had thin stems and sparse foliage due to the high density of the thickets in which they grew (Covington et al. 1997). The post-treatment forest is still numerically dominated by younger trees, primarily from the 1919 cohort, but the proportion of young trees relative to presettlement trees is reduced (Fig. 5). The relative age structures of the 1876, 1992, and post-treatment 1994 forests are compared in Fig. 6. In 1876, trees >200 yr old comprised ~20% of the forest, and trees >100 yr old made up 60%, leaving 40% of the age distribution in trees <100 yr old. By 1992, >99% of the age distribution was composed of the dense young trees below ~70 yr old. In the post-treatment (1994) forest, this younger cohort of trees still makes up ~80% of tree density.

DISCUSSION

Importance of including now-dead trees

Although the GPNA is an unlogged preserve, presettlement age structure would appear quite different if only living trees were sampled. Living trees, indicated with solid bars in Fig. 1, make up 71% (142/203 trees) of the center date samples, but the living-tree proportion of the presettlement age distribution declines toward the older age classes. The most recent peak of tree establishment, from 1760 to 1880, is represented in the sample by 82 living and 5 dead trees. The sample representing the previous broad establishment period, 1600 to 1759, includes 55 living and 35 dead trees. The earliest period, up to 1599, has only 5
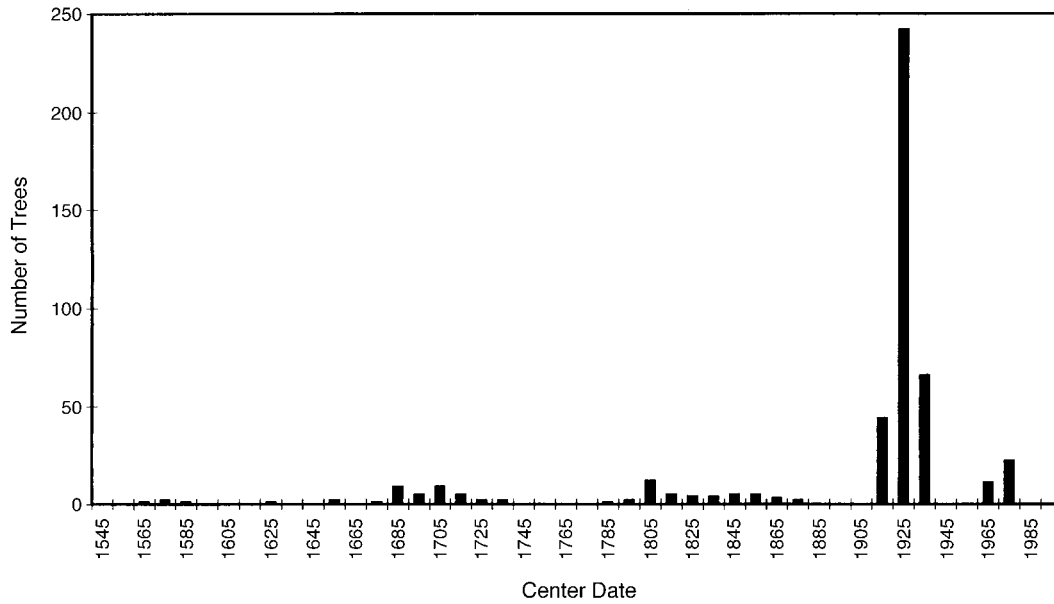
FIG. 5.   Age structure of the GPNA site following 1994 restoration treatment.

living and 21 dead trees in the sample. The oldest trees in 1876, three trees ranging from 482 to 543 yr old (at sampling height), are all dead today. If only living trees had been sampled, the apparently oldest tree in 1876 would have been only 322 yr old (center date 1554), shortening the age range by 221 yr (>40%).

The truncated presettlement age distribution created by excluding the now-dead component of age structure may be seen in the results of White (1985), who aged 236 living presettlement-era pines in the GPNA adjacent to our study site. The oldest trees he found were ~300 yr old in 1876 (but his largest-diameter trees were not aged and several sampled trees had rotten centers).

Even in unharvested forests increasing mortality of trees in the oldest age classes is a concern. Mortality of presettlement trees has risen substantially over the 20th century from 0.5 trees·ha^{-1}·decade^{-1} in the 1920s to as many as 5.9 trees·ha^{-1}·decade^{-1} in the 1970s at the 16-ha GPNA (Fig. 7). Increased competition from dense postsettlement trees leading to reduced vigor and defensive capabilities of the old trees, together with
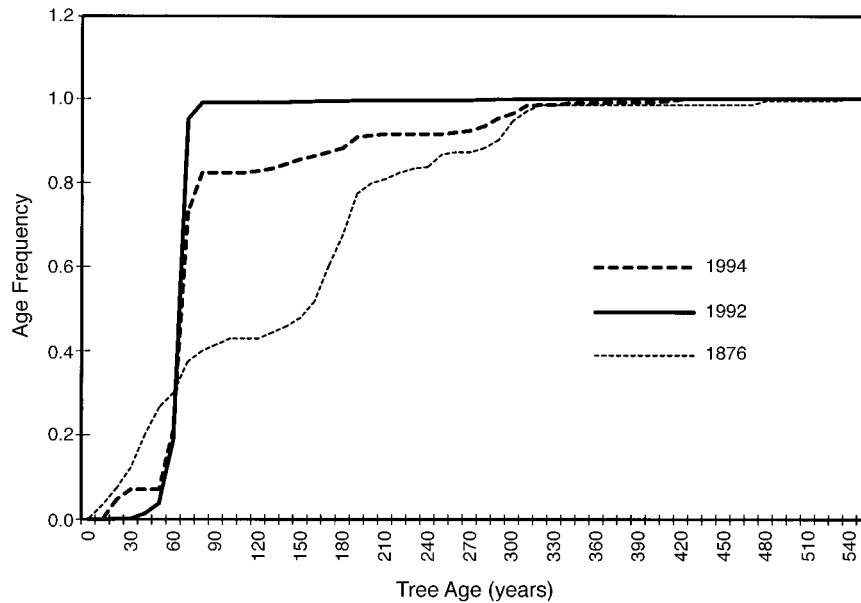

FIG. 6.   Cumulative frequency distributions of ponderosa pine age structure at the GPNA site in 1876 (presettlement forest), 1992 (after fire exclusion), and 1994 (after restoration treatment).
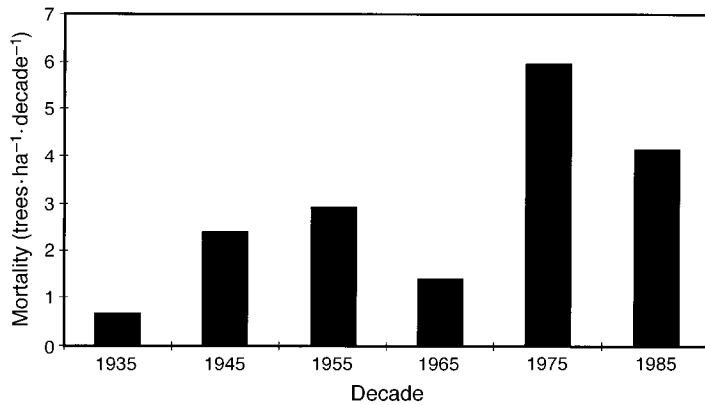
FIG. 7. Mortality of large ponderosa pine trees at the 16-ha GPNA has increased over the course of the 20th century. Data were collected at 5- or 10-yr intervals (Avery et al. 1976 and *unpublished data*).

stagnated nutrient cycling in the absence of fire, have been suggested as key causes for increased mortality (Sutherland et al. 1991, Biondi et al. 1994). In addition, the increased occurrence of crown fires due to high fuel loading and fuel continuity across the Southwest (Swetnam 1990) is killing old trees at a regional scale.

In harvested forests the absence of now-dead presettlement trees can obviously truncate the age structure. Fulé et al. (1997) sampled a 700-ha ponderosa pine forest that had been harvested beginning in the 1880s, located ~15 km SW of the GPNA. Based only on living tree samples, they found that the oldest tree in 1883, the date of fire regime disruption, was only 186 yr old (center date 1697), and the second-oldest tree was only 122 yr old. In contrast, numerous samples collected for fire history analysis at the same site from stumps (harvested between 1880 and 1933) and logs had center dates or inner rings before 1600; the three oldest samples established before 1450 (Fulé et al. 1997).

The high costs of dendrochronological sampling and analysis are likely to preclude extensive reconstructions of past age structure in most management situations. But managers should be aware that reference age structures based on data from living trees are probably biased toward younger trees even in unharvested forests. Where the oldest trees appear to have been missed, an approximate range of potential maximal ages could be developed based on data such as shown in Fig. 1 or in Swetnam and Brown (1992), who present maximal age information on a number of southwestern conifer species.

Forest dynamics, climate, and disturbance

By including dead trees in the age reconstruction, our results appear consistent with the seedling mortality–sapling survival model described by White (1985). Trees ≤100 yr old in 1876 made up only 42% (85/203 trees) of the overstory in our study (Fig. 1), producing a relatively flat age distribution in contrast to the large peak (74%) of trees <100 yr old found by White (1985). If dead trees had not been included in our study, the proportion of trees would be closer to White's re-

sults: the component <100 yr old would make up 58% of the sample (82/142 trees).

The use of static age structures to infer forest dynamics has been criticized by Johnson et al. (1994). By sampling living and dead trees to reconstruct a series of past stand conditions, they showed that the absence of trees in past age classes does not necessarily mean that no trees established in that period; the trees may have established and then died without ever growing into the canopy. Although this is a valuable caveat, southwestern ponderosa pine has a distinctly different forest structure, which can affect the interpretation of forest dynamics. The northern coniferous forests of lodgepole pine–Engelmann spruce (*Pinus contorta–Picea engelmannii*) studied by Johnson et al. (1994) were closed-canopy, dense stands (for dbh >3 cm, 1400–16 200 stems/ha), originating from high-intensity, stand-replacing fires. In contrast, presettlement southwestern ponderosa pine forests were open (7–116 stems/ha [Covington and Moore 1994*b*]) with a high proportion, up to 80%, of grassy openings (Covington and Sackett 1984, Covington et al. 1997). In such open conditions, ponderosa trees that survived the competition–fire filter would have been unlikely to die as suppressed subcanopy saplings, implying that the multimodal age distribution (Fig. 1) reflects actual long-term establishment patterns rather than the "missing cohorts" of regeneration detected by Johnson et al. (1994).

Climatic patterns do not appear to be easily related to presettlement tree establishment (Fig. 1; see also White 1985). The greatest fluctuation in the PDSI reconstruction was a drought period near 1890 followed by positive PDSI values in the early 20th century. The late-1500s drought (~1570 to 1600), described by Grissino-Mayer (1996) as the most severe short-term (<50 yr) southwestern drought in the past 2000 yr, is not covered by the PDSI reconstruction (Cook et al. 1996), but the GPNA tree-ring index shows a decline in the late 1500s. However, apart from the highly favorable moisture conditions in the early 20th century—the excellent period for seedling establishment de-

scribed by Savage et al. (1996)—other climate patterns do not appear to coincide consistently with the multimodal pattern of tree establishment. For example, the decline in pine establishment around 1870 (the end of the final presettlement regeneration pulse) does match a decline in PDSI values, but the mid-1700s regeneration gap occurred during a minor PDSI peak (Fig. 1). Relatively common regeneration, as well as the same mid-1700s absence of establishment, was also noted by White (1985) at the GPNA. Savage (1991) found similar steady presettlement regeneration patterns in the Chuska Mountains of Arizona and New Mexico (~180 km east of the study area), although the methodology of sampling above ground level did not give precise regeneration dates. These continuing patterns suggest that although presettlement trees did not establish densely, their establishment was not limited only to sporadic favorable years separated by long intervals, such as the 73-yr gap between the good conditions in 1919 and 1992 (Savage et al. 1996).

Combining the climate and disturbance histories may lead to a more complete picture of presettlement regeneration dynamics. Comparisons between the fire history developed by Dieterich (1980) and the GPNA age structure (Fig. 1) are limited by the small number of fire-scarred samples ($N = 7$ trees; $N = 1$ tree from 1540 to 1754). The small sample size means that fire intervals before the mid-1700s are probably overestimated, since the single sample tree is unlikely to have recorded every fire. In addition, the application of proportional filters to estimate fire size and/or intensity, based on fires scarring at least a single sample and then progressively 10%, 25%, etc. of the samples (Swetnam and Baisan 1996), is precluded with so few samples.

Dieterich (1980) did identify distinct periods of different fire return intervals since 1754. The overall composite fire interval (CFI) at Chimney Spring from 1754 to 1876, the year of the last fire, was 2.4 yr but the period from 1824 to 1869 recorded the highest frequency of fire recurrence (CFI = 1.7 yr) in the Southwest, covering most of the last presettlement regeneration peak at GPNA (Fig. 1). White (1985) suggested that these frequent fires could have prevented fuel accumulations that would support intense burning, perhaps allowing more seedlings to survive, in contrast to the less frequent, and possibly more intense, fires in the preceding 1754–1800 period (CFI = 3.8 yr). The mid-1800s (~1820–1860) were also a relatively wet period in the PDSI reconstruction (Cook et al. 1996). Favorable weather conditions, leading to good production of herbaceous and leaf litter fuels, could have supported more frequent fires. This interpretation is consistent with the high Southwest-scale presettlement fire occurrence following moist El Niño years, which facilitated fine-fuel production (Swetnam and Betancourt 1990, Swetnam and Baisan 1996). However, a relatively wet PDSI period also coincided with most of the longer interval fire period in the late 1700s (Fig. 1).

Additional fire history information with greater spatial and temporal depth would be needed to more fully explore the climate–fire disturbance–pine establishment relationship.

The clearest connection between climate, fire history, and forest structure is the tremendous regeneration pulse occurring under excellent climatic conditions in the early 20th century. As noted by Savage et al. (1996), although the climatic events themselves were probably not unprecedented, the establishment pulse may have been unique in the evolutionary history of ponderosa pine because of the extent of anthropogenic elimination of vegetative competition and the fire disturbance regime. The domination of resources by these dense young tree groups again changed the site. Even though a relatively large number of seedlings established in 1992 at our study area, the great majority have since died under the dense postsettlement canopy (P. Z. Fulé, *personal observation*). Without the changes caused by Euro-American settlement, the early 20th century could still have had a favorable regeneration pulse, with some seedlings surviving frequent but cooler fires supported by good fine-fuel production under moist conditions. However, the density of tree establishment would have remained orders of magnitude less.

Ecological restoration of forest age structure

The motivation for ecological restoration is generally based on the perception that an ecosystem has become degraded relative to its previous or reference state (Aronson et al. 1993, Jackson et al. 1995). The extent of reference knowledge required to make good restoration decisions is a matter of considerable debate, however, ranging from highly detailed reconstructions of historic ecosystem structure and process (e.g., Bonnicksen and Stone 1985, Aronson et al. 1995) to a broad understanding of past disturbance regimes and species composition (e.g., Hobbs and Norton 1996, Parsons and Van Wagtendonk 1996).

Reference conditions can be determined with great precision for many attributes of southwestern ponderosa pine ecosystems. The precise dendrochronological record, preserved in an arid climate and protected from fire for a century or more, permits reconstruction of past climate (e.g., a >2000-yr climate record in ponderosa pine forests [Grissino-Mayer 1996]), fire and other disturbance regimes (e.g., insect defoliation [Miller and Wagner 1989]), and tree structure for an extended period into the past. The natural range of variability (Morgan et al. 1994, Swanson et al. 1994) in reference conditions provides a perspective from which to evaluate contemporary conditions. For example, although presettlement GPNA tree establishment varied over an 8× range in the three centuries before fire exclusion, this variability is dwarfed by the increase of approximately two orders of magnitude in the early 20th century.

Restoration goals should be explicit and quantifiable (Aronson et al. 1995, Hobbs and Norton 1996) with objectives that can be attained within a reasonable time period (e.g., Jackson et al. 1995 suggested ~50 yr). How can these criteria be addressed in the context of age structure, when centuries may be required to regain the oldest trees?

In an integrated ecosystem restoration, we suggest that first, all living presettlement trees should be retained, conserving the slowest organismic variables. Second, the younger tree component will be maintained by selecting postsettlement trees to replace dead presettlement trees. An excess of these young trees should be retained, to account for potential increased mortality resulting from the restoration treatments themselves. Approximately three replacements were left for each dead presettlement tree in the present study (Covington et al. 1997). If too many trees are retained, however, the forest will remain far from reference conditions of tree density, spatial pattern, herbaceous production, crown fire hazard, etc. The cost and impacts of future removal of excess trees should also be considered.

Third, monitoring of age structure over time will serve as an ongoing standard of evaluation. Persistence of the oldest trees over successively longer periods is one indicator of restoration success; high mortality of these trees would indicate problems. For example, Sackett et al. (1996) found that mortality of presettlement trees in prescribed burned plots (39% over 20 yr) near the GPNA was over twice that of unburned plots (16% over 20 yr), leading to a re-evaluation of the treatment. Comparing mortality following treatments to that of ''untreated''—but nonetheless dense—adjacent stands can also present problems, because older trees in these stands are suffering a disproportionate growth reduction due to intense competition with younger trees (Sutherland et al. 1991, Biondi 1996). The reference age structure can help provide a benchmark. In the simplest demographic formulation, without making mortality or natality assumptions (Silvertown 1987), maintenance of 60 trees/23 ha ($\pm20\%$) in a distribution with a maximum age of 540 yr ($\pm20\%$) predicts a mortality rate range of 0.6–1.4 trees·ha^{-1}·decade,$^{-1}$ about 1–3% per decade. These figures are reasonably consistent with the 3.3% mortality per decade measured by Pearson (1950) on trees >30.5 cm dbh (many of which were probably presettlement trees) in a virgin ponderosa pine stand from 1925–1940, a period when competitive stress from postsettlement trees was probably still relatively low (Biondi 1996). The estimates are also consistent with the presettlement tree establishment rate of 0.4–3.6 trees·ha^{-1}·decade^{-1} at our study area.

Finally, the effect on tree establishment and mortality of ecological processes such as repeated fire disturbance in the restored system can be evaluated against the reference age distribution and other reference ecosystem structural parameters. These comparisons will contribute to an adaptive understanding of both past and present ecosystem dynamics, because our observations in a restored ecosystem will give insights into past mechanisms such as the safe site regeneration model. At the same time, our reference knowledge will help us evaluate whether restoration to within the range of natural variability succeeds.

Ecological restoration is neither a certain nor a static science. Novel and unpredicted anthropogenic impacts, such as the massive tree establishment early in the 20th century, may recur as CO_2 levels rise and exotic species are introduced. Management may have to substitute for missing parts of the indigenous ecosystem such as predation and supplemental fire ignitions. While the ability of restored native ecoystems to regain their self-regulating, sustainable character under these conditions is not clear, the risks of mortality on the scale of 10^6 ha, loss of biological diversity, and local extinctions through inaction are increasingly evident. Adaptive management experiments at scales relevant to ponderosa pine landscapes are needed to restore and conserve these threatened ecosystems.

Literature Cited

Aronson, J., S. Dhillion, and E. Le Floc'h. 1995. On the need to select an ecosystem of reference, however imperfect: a reply to Pickett and Parker. Restoration Ecology **3**(1):1–3.

Aronson, J., C. Floret, E. Le Floc'h, C. Ovalle, and R. Pontanier. 1993. Restoration and rehabilitation of degraded ecosystems in arid and semi-arid lands. I. A view from the South. Restoration Ecology **1**:8–17.

Avery, C. C., F. R. Larson, and G. H. Schubert. 1976. Fifty-year records of virgin stand development in southwestern ponderosa pine. U.S. Department of Agriculture Forest Service General Technical Report RM-22, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.

Biondi, F. 1996. Decadal-scale dynamics at the Gus Pearson Natural Area: evidence for inverse (a)symmetric competition? Canadian Journal of Forest Research **26**:1397–1406.

Biondi, F., D. E. Myers, and C. C. Avery. 1994. Geostatistically modeling stem size and increment in an old-growth forest. Canadian Journal of Forest Research **24**: 1354–1368.

Bonnicksen, T. M., and E. C. Stone. 1985. Restoring naturalness to National Parks. Environmental Management **9**(6):479–486.

Cook, E. R., D. M. Meko, D. W. Stahle, and M. K. Cleaveland. 1996. Tree-ring reconstructions of past drought across the conterminous United States: tests of a regression method and calibration/verification results. Pages 155–170 *in* J. S. Dean, D. M. Meko, and T. W. Swetnam, editors. Tree rings, environment, and humanity: proceedings of the international conference. Radiocarbon, Department of Geosciences, University of Arizona, Tucson, Arizona, USA.

Cooper, C. F. 1960. Changes in vegetation, structure, and growth of southwestern pine forests since white settlement. Ecology **42**:493–499.

Cormier, K. L. 1990. Modeling natural regeneration of even-aged ponderosa pine following shelterwood cutting in northern Arizona. Thesis. Northern Arizona University, Flagstaff, Arizona, USA.

Covington, W. W., P. Z. Fulé, M. M. Moore, S. C. Hart, T. E. Kolb, J. N. Mast, S. S. Sackett, and M. R. Wagner. 1997. Restoration of ecosystem health in southwestern ponderosa pine forests. Journal of Forestry **95**(4):23–29.

Covington, W. W., and M. M. Moore. 1994*a*. Southwestern ponderosa forest structure and resource conditions: changes since Euro-American settlement. Journal of Forestry **92**(1): 39–47.

Covington, W. W., and M. M. Moore. 1994*b*. Postsettlement changes in natural fire regimes: ecological restoration of old-growth ponderosa pine forests. Journal of Sustainable Forestry **2**:153–181.

Covington, W. W., and S. S. Sackett. 1984. The effect of a prescribed burn in southwestern ponderosa pine on organic matter and nutrients in woody debris and forest floor. Forest Science **30**:183–192.

D'Arrigo, R. D., and G. C. Jacoby. 1991. A 1000-year record of winter precipitation from northwestern New Mexico, USA: a reconstruction from tree-rings and its relation to El Niño and the Southern Oscillation. Holocene **1**(2):95–101.

Dieterich, J. H. 1980. Chimney Spring forest fire history. U.S. Forest Service Research Paper RM-220, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.

Fulé, P. Z., W. W. Covington, and M. M. Moore. 1997. Determining reference conditions for ecosystem management of southwestern ponderosa pine forests. Ecological Applications **7**:895–908.

Graybill, D. A. 1987. Unpublished tree-ring chronologies AZ521 and AZ547. Archived at the National Geophysical Data Center, World Data Center-A for Paleoclimatology, Boulder, Colorado, USA.

Grissino-Mayer, H. D. 1996. A 2129-year reconstruction of precipitation for northwestern New Mexico, USA. Pages 191–204 *in* J. S. Dean, D. M. Meko, and T. W. Swetnam, editors. Tree rings, environment, and humanity: proceedings of the international conference. Radiocarbon, Department of Geosciences, University of Arizona, Tucson, Arizona, USA.

Grissino-Mayer, H. D., and R. L. Holmes. 1993. International tree-ring data bank program library. Laboratory of Tree-Ring Research. University of Arizona, Tucson, Arizona, USA.

Hobbs, R. J., and D. A. Norton. 1996. Towards a conceptual framework for restoration ecology. Restoration Ecology **4**(2):93–110.

Jackson, L. L., N. Lopoukhine, and D. Hillyard. 1995. Ecological restoration: a definition and comments. Restoration Ecology **3**(2):71–75.

Johnson, E. A., K. Miyanishi, and H. Kleb. 1994. The hazards of interpretation of static age structures as shown by stand reconstructions in a *Pinus contorta–Picea engelmannii* forest. Journal of Ecology **82**:923–931.

Kaufmann, M. R., R. T. Graham, D. A. Boyce, Jr., W. H. Moir, L. Perry, R. T. Reynolds, R. L. Bassett, P. Melhop, C. B. Edminster, W. M. Block, and P. S. Corn. 1994. An ecological basis for ecosystem management. U.S. Forest Service General Technical Report RM-246, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.

Kaufmann, M. R., W. H. Moir, and W. W. Covington. 1992. Old-growth forests: what do we know about their ecology and management in the Southwest and Rocky Mountain regions? Pages 1–11 *in* M. R. Kaufmann, W. H. Moir, and R. L. Bassett (technical coordinators). Old-growth forests in the Southwest and Rocky Mountain regions. U.S. Forest Service General Technical Report RM-213, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.

Lundquist, J. E. 1995. Pest interactions and canopy gaps in ponderosa pine stands in the Black Hills, South Dakota, USA. Forest Ecology and Management **74**:37–48.

Maser, C., R. G. Anderson, K. Cromack, Jr., J. T. Williams, and R. E. Martin. 1979. Dead and down woody material. Pages 78–95 *in* Wildlife habitats in managed forests—the Blue Mountains of Oregon and Washington. U.S. Department of Agriculture Handbook 553, Washington, D.C., USA.

Miller, K. K., and M. R. Wagner. 1989. Effect of pandora moth (Lepidoptera: Saturniidae) defoliation on growth of ponderosa pine in Arizona. Journal of Economic Entomology **82**(6):1682–1686.

Morgan, P., G. H. Aplet, J. B. Haufler, H. C. Humphries, M. M. Moore, and W. D. Wilson. 1994. Historical range of variability: a useful tool for evaluating ecological change. Journal of Sustainable Forestry **2**:87–111.

Parsons, D. J., and J. W. van Wagtendonk. 1996. Fire research and management in the Sierra Nevada National Parks. Pages 25–48 *in* W. L. Halvorson and G. E. Davis, editors. Science and ecosystem management in the national parks. University of Arizona Press, Tucson, Arizona, USA.

Pearson, G. A. 1923. Natural reproduction of western yellow pine in the Southwest. U.S. Forest Service Bulletin 1105, Washington, D.C., USA.

———. 1950. Management of ponderosa pine in the Southwest. U.S. Agriculture Monograph 6, Washington, D.C., USA.

Rogers, J. J., J. M. Prosser, L. D. Garrett, and M. G. Ryan. 1984. ECOSIM: a system for projecting multiresource outputs under alternative forest management regimes. U.S. Forest Service Administrative Report, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.

Sackett, S. S. 1984. Observations on natural regeneration in ponderosa pine following a prescribed fire in Arizona. Forest Service Research Note RM-435, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.

Sackett, S. S., S. M. Haase, and M. G. Harrington. 1996. Lessons learned from fire use for restoring southwestern ponderosa pine ecosystems. Pages 53—60 *in* W. Covington and P. K. Wagner, technical coordinators. Conference on adaptive ecosystem restoration and management: restoration of cordilleran conifer landscapes of North America. U.S. Forest Service General Technical Report RM-GTR-278, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.

Savage, M. 1991. Structural dynamics of a southwestern pine forest under chronic human disturbance. Annals of the Association of American Geographers **81**(2):271–289.

Savage, M., P. M. Brown, and J. Feddema. 1996. The role of climate in a pine forest regeneration pulse in the southwestern United States. Ecoscience **3**(3):310–318.

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

Schubert, G. H. 1974. Silviculture of southwestern ponderosa pine: the status of our knowledge. U.S. Forest Service General Technical Report RM-123, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.

Silvertown, J. 1987. Introduction to plant population ecol-

ogy. Second edition. Longman Scientific and Technical, New York, New York, USA.

Smith, D. M. 1986. The practice of silviculture. Eighth edition. John Wiley and Sons, New York, New York, USA.

Stokes, M. A., and T. L. Smiley. 1968. An introduction to tree-ring dating. University of Chicago Press, Chicago, Illinois, USA.

Sutherland, E. K., W. W. Covington, and S. Andariese. 1991. A model of ponderosa pine growth response to precribed burning. Forest Ecology and Management **44**:161–173.

Swanson, F. J., J. A. Jones, D. A. Wallin, and J. H. Cissel. 1994. Natural variability—implications for ecosystem management. Pages 85–99 *in* M. E. Jensen and P. S. Bourgeron. Eastside Forest Ecosystem Health Assessment. Volume II. Ecosystem management: principles and applications. U.S. Forest Service, General Technical Report PNW-GTR-318, Pacific Northwest Research Station, Portland, Oregon, USA.

Swetnam, T. W. 1990. Fire history and climate in the southwestern United States. Pages 6–17 *in* Effects of fire management on southwestern natural resources. U.S. Forest Service General Technical Report RM-191, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.

Swetnam, T. W., and C. H. Baisan. 1996. Historical fire regime patterns in the southwestern United States since AD 1700. Pages 11–32 *in* C. D. Allen, editor. Proceedings of the 2nd La Mesa Fire Symposium. U.S. Forest Service General Technical Report RM-GTR-286, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.

Swetnam, T. W., and J. L. Betancourt. 1990. Fire–Southern Oscillation relations in the southwestern United States. Science **249**:1017–1020.

Swetnam, T. W., and P. M. Brown. 1992. Oldest known conifers in the southwestern United States: temporal and spatial patterns of maximum age. Pages 24–38 *in* M. R. Kaufmann, W. H. Moir, and R. L. Bassett, technical coordinators. Old-growth forests in the Southwest and Rocky Mountain regions. U.S. Forest Service General Technical Report RM-213, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.

Telewski, F. W. 1993. Determining the germination date of woody plants: a proposed method for locating the root/shoot interface. Tree-Ring Bulletin **53**:13–16.

Thomas, J. W., R. G. Anderson, C. Maser, and E. L. Bull. 1979. Snags. Pages 60–77 *in* Wildlife habitats in managed forests—the Blue Mountains of Oregon and Washington. U.S. Department of Agricultural Handbook 553, Washington, D.C., USA.

White, A. S. 1985. Presettlement regeneration patterns in a southwestern ponderosa pine stand. Ecology **66**:589–594.