Ecological Applications, 9(4), 1999, pp. 1253–1265 © 1999 by the Ecological Society of America

# REFERENCE CONDITIONS FOR GIANT SEQUOIA FOREST RESTORATION: STRUCTURE, PROCESS, AND PRECISION

### NATHAN L. STEPHENSON<sup>1</sup>

U.S. Geological Survey, Western Ecological Research Center, Sequoia and Kings Canyon Field Station, Three Rivers, California 93271-9651 USA

Abstract. National Park Service policy directs that more natural conditions be restored to giant sequoia groves, which have been altered by a century of fire exclusion. Efforts to find a reasonable and practical definition of "natural" have helped drive scientists and land managers to use past grove conditions as reference conditions for restoration. Extensive research aimed at determining reference conditions has demonstrated that past fire regimes can be characterized with greater precision than past grove structures. Difficulty and imprecision in determining past grove structure has helped fuel a debate between "structural restorationists," who believe that forest structure should be restored mechanically before fire is reintroduced, and "process restorationists," who believe that simple reintroduction of fire is appropriate. I evaluate old and new studies from sequoia groves to show that some of the arguments of both groups have been flawed. Importantly, it appears that restoration of fire without a preceding mechanical restoration may restore the pre-Euro-American structure of sequoia groves, at least within the bounds of our imprecise knowledge of past grove structure. However, the same may not be true for all forest types that have experienced lengthy fire exclusion. Our ability to draw robust generalizations about fire's role in forest restoration will depend heavily on a thorough understanding of past and present interactions among climate, fire, and forest structure. Use of reference conditions will be central to developing this understanding.

Key words: conifer forest; fire ecology; process restoration; reference conditions; Sequoiadendron giganteum; Sierra Nevada, California; structural restoration.

### Introduction

National Park Service (NPS) policy directs NPS land managers to maintain "... natural environments evolving through natural processes minimally influenced by human actions" (National Park Service 1988). Where human activities have significantly altered the structure, composition, or function of protected ecosystems, those ecosystems "... may be manipulated where necessary to restore natural conditions." These seemingly simple policy directions present scientists and land managers with an extraordinarily difficult set of problems. What is "natural?" Is it possible to describe natural conditions with reasonable confidence? Is it possible to restore such conditions? If so, how? The use of past ecosystem conditions as reference conditions is central to addressing these and related questions.

For the purposes of this paper, I define reference conditions as the spectrum of ecosystem conditions (i.e., structure, composition, and function) found within a defined area over a specified time period preceding

Manuscript received 18 May 1998; revised 11 February 1999; accepted 11 February 1999; final version received 8 March 1999. For reprints of this Invited Feature, see footnote 1, p. 1177.

<sup>1</sup> E-mail: Nathan\_L.\_Stephenson@usgs.gov

Euro-American settlement (cf. Kaufmann et al. 1994, 1998, Fulé et al. 1997, Moore et al. 1999). The term is closely related, or identical, to frequently-used terms such as natural variability, natural range of variability, historical variation, and historical range of variability (Landres et al. 1999).

Here I present a case study illustrating some of the challenges in using past ecosystem conditions as reference conditions for forest restoration. For the giant sequoia ecosystems of California's Sierra Nevada, one of the primary limitations to the usefulness of reference conditions is that, even with relatively low precision, it is only possible to determine reference conditions for a very few ecosystem elements. Of necessity, then, this paper focuses on the narrow subset of ecosystem elements for which we have the best information on past conditions: fire regimes and forest structure. (For simplicity, I will use the term structure to refer to both species composition and the physical arrangement of trees, including the sizes, ages, and spatial arrangement of forest gaps and patches, and the diameters, heights, densities, spatial arrangement, and species of trees within the patches.) Fortunately, fire and trees are two of the most important keystone elements (sensu Holling 1992) of sequoia ecosystems. That is, fire and trees are members of a handful of ecosystem elements that play a dominant role in structuring ecosystems and entraining most other ecosystem elements.

A second challenge is that there is an inherent difference in the precision with which ecosystem elements can be characterized, with characterization of past fire regimes being more precise than characterization of past forest structure. Difficulty and imprecision in determining structural reference conditions has helped lead to a debate between "structural restorationists," who argue that forest structure should be restored mechanically before fire is reintroduced, and "process restorationists," who argue that simple reintroduction of fire is appropriate (Vale 1987, Stephenson 1996). I use our best current knowledge on the past structure of sequoia groves in an attempt to bring the debate closer to resolution.

Decades of research into past and present structure and function of sequoia ecosystems (e.g., Harvey et al. 1980, Weatherspoon et al. 1986, Aune 1994, Stephenson 1996) have provided a knowledge base that is surpassed in few ecosystems. Thus, the challenges encountered in using reference conditions in sequoia grove restoration cannot be blamed entirely on lack of basic research; instead, they may reflect limitations that are likely to be faced by scientists and land managers working in other forest ecosystems.

### NEED FOR RESTORATION

Giant sequoias (Sequoiadendron giganteum; nomenclature follows Burns and Honkala 1990) are the largest trees on the planet and are among the oldest, sometimes living for ≥3000 yr. Sequoias almost never occur in pure stands; numerically, most sequoia groves are overwhelmingly dominated by Abies concolor (white fir), with Pinus lambertiana (sugar pine) commonly being the next most abundant species, followed by giant sequoia and several other tree species (Rundel 1971). The 75 naturally-occurring sequoia groves are mostly found in the southern Sierra Nevada (Rundel 1972), collectively occupying about 14 600 ha. Roughly 90% of grove area is under public jurisdiction (Stephenson 1996).

For at least the two millennia preceding Euro-American settlement, predominantly low- to moderate-intensity surface fires burned in portions of individual sequoia groves with a mean frequency of ~3–8 yr (Swetnam et al. 1992, Swetnam 1993). With the loss of Native American ignitions and suppression of lightning fires that followed Euro-American settlement, most grove areas today have experienced a 100–130-yr period without fire—a fire-free period that is unprecedented over at least the last two millennia, and probably much more (Swetnam et al. 1992, Anderson and Smith 1997). This lack of fire has resulted in important changes in grove conditions. Giant sequoia reproduction, which in the past depended on frequent

fires to expose mineral soil and open gaps in the forest canopy, has effectively ceased in groves protected from fire (and other disturbances, such as logging), and reproduction of other shade-intolerant species has been reduced (Harvey et al. 1980, Stephenson 1994; Stephenson, unpublished data). Today more area is dominated by dense intermediate-aged forest patches, and less by young patches, than in the past (Bonnicksen and Stone 1978, 1982a, Stephenson 1987). Groves have become denser in many areas, with increased dominance of shade-tolerant species (Fig. 1). Shrubs and herbaceous plants are probably less abundant than in the past (Kilgore and Biswell 1971, Harvey et al. 1980). Perhaps most importantly, dead material has accumulated, causing an unprecedented buildup of surface fuels (Agee et al. 1978, van Wagtendonk 1985). Additionally, "ladder fuels" capable of conducting fire into the crowns of mature trees have increased (Kilgore and Sando 1975, Parsons and DeBenedetti 1979; see Fig. 1). One of the most immediate consequences of these changes is an increased hazard of wildfires sweeping through groves with a severity that was rarely encountered in pre-Euro-American times (Kilgore and Sando 1975, Stephens 1995, 1998).

Given that these changes in grove conditions were caused by recent human activity, National Park Service (NPS) policy directs that, to the extent possible, natural conditions be restored. It can be argued that this policy is impractical, especially in the face of new ecosystem stressors such as air pollution, introduced pathogens, and potentially rapid, human-induced climatic change. However, NPS policy ultimately is a reflection of public values and desires, to which land managers must respond to the best of their abilities. While "natural" conditions may never be achieved, they might be approached more closely, at least until such time that the effects of new stressors might become overwhelming.

### WHAT ARE NATURAL CONDITIONS?

Given this need to restore natural conditions in sequoia groves, what is a reasonable interpretation of "natural?" Is it the condition that would exist if the dominant Euro-American culture had never arrived, and therefore only Native American cultures influenced ecosystems? Or is it the condition that would exist in the absence of all human influences? Although a literal reading of NPS policy suggests the latter (National Park Service 1988), the policy does not explicitly address the role of Native American cultures and therefore remains ambiguous. Reasonable arguments have been made for both interpretations (e.g., Graber 1983, 1995, Dennis and Wauer 1985, Kilgore 1985, Parsons et al. 1986, Hunter 1996, Landres et al. 1998).

While it has not always been the case, for the purpose of restoring giant sequoia ecosystems, NPS managers presently tend to use the former definition of natural: the (dynamic) conditions that would exist if the dom-





Fig. 1. (Top) The Confederate Group of giant sequoias in Mariposa Grove, Yosemite National Park, was nearly free of understory trees circa AD 1890. (Bottom) By 1970, in the absence of frequent surface fires, a dense thicket of white firs grew at the base of the sequoias. Not all areas in sequoia groves have experienced such dramatic changes. (Photos courtesy of B. M. Kilgore, National Park Service.)

inant Euro-American culture had never arrived, but Native Americans had continued to use the landscape (Kilgore 1985, Parsons 1995). This choice is largely driven by practicality, since it is easier to estimate the conditions that would exist today if Euro-Americans had never arrived (using pre-Euro-American conditions as our best, though imperfect, model) than to estimate conditions that would exist in the absence of all human influences (for which we presently have no good models, including forest dynamics models of sufficient accuracy). It is also possible that the distinction is irrelevant. Although the most effective means by which Native Americans influenced Sierran forests was through their use of fire (Anderson and Moratto 1996), 20th-century records of lightning ignitions suggest that at a landscape scale there may be little difference between Native American and lightning-only fire regimes in sequoia groves. That is, fire frequency at broad scales may have been limited mostly by weather, fuel continuity, and fuel quality, rather than by availability of ignitions (Swetnam et al. 1992, Stephenson 1996, Vale 1998). Thus, there is a reasonable possibility that regardless of Native American use of fire, conditions in sequoia groves in the presence of Native American cultures would be similar to those in the absence of all human influences.

Given the de facto choice of most sequoia managers to use pre-Euro-American forest conditions as our best model of natural conditions (that is, what would exist today if Euro-Americans had never arrived), we must define a point in time, or time period, of reference. As discussed in Capabilities and limitations, physical constraints limit our ability to quantitatively describe past forest conditions at a specific point in time. Additionally, the natural tendency for vegetational change to lag behind climatic change suggests that forest conditions at any given moment are, to a large degree, a legacy of preceding decadal- and centennial-scale shifts in climate and fire regimes (e.g., Sprugel 1991, Millar 1997, Millar and Woolfenden 1999). It therefore seems reasonable to conclude that the link between past sequoia grove conditions and the climate at a particular moment was somewhat weak. Reasonable reference conditions for restoration, then, should bracket a range of possible outcomes, such as would be found over a relatively long time period (Sprugel 1991).

Paleoecological records help set limits on reasonable pre-Euro-American reference periods. Pollen records from meadow sediments demonstrate that, within present sequoia grove boundaries, sequoias (and to a lesser degree firs) began to increase dramatically in importance relative to pines ~4500 yr BP, coincident with a slight global cooling (Anderson 1994, Anderson and Smith 1994). Though the pollen records suggest that changes in the relative proportions of tree species in groves have continued up to the present, the most dramatic changes were completed by about 1000 yr before

Euro-American settlement. During that 1000-yr period, both climate and fire regimes continued to vary within groves (Hughes and Brown 1992, Graumlich 1993, Scuderi 1993, Swetnam 1993). Warmth during ~AD 1100–1375 corresponds to the Medieval Warm Period identified in proxy records elsewhere in the world (Fig. 2). Fires in sequoia groves during the Medieval Warm Period were relatively frequent and of limited spatial extent (Swetnam 1993). Cooler temperatures dominated during ~AD 1450–1850, corresponding to the Little Ice Age; fires during this period were less frequent and of greater spatial extent. Precipitation changes were such that wet and dry periods occurred during both the Medieval Warm Period and Little Ice Age (Fig. 2). Importantly (and in contrast to the population dynamics of Pinus balfouriana at treeline in the Sierra; Lloyd and Graumlich 1997), the combined effects of these changing climate and fire regimes on giant sequoia demographics and age structure were small to moderate, at least at centennial time scales and regional spatial scales (Stephenson 1994; Stephenson, unpublished data).

Over the last few decades, climate in sequoia groves has fallen within the range of the millennium preceding Euro-American settlement, though toward the warm, wet extreme (Fig. 2). This fact, coupled with the long-term compositional shifts and lagged vegetation response to climatic change, lead me to suggest that the millennium preceding Euro-American settlement is a reasonable reference period for giant sequoia ecosystems (Stephenson 1996; but see Millar and Woolfenden [1999] for a contrasting viewpoint).

## CAPABILITIES AND LIMITATIONS OF TOOLS FOR DESCRIBING REFERENCE CONDITIONS

Having chosen forest conditions in the millennium preceding Euro-American settlement as reference conditions, how well are we able to determine those conditions? Nearly all efforts to determine past fire regimes in sequoia groves have been based on fire scars in tree rings (e.g., Kilgore and Taylor 1979, Swetnam et al. 1992, Swetnam 1993). In general, the accuracy and precision of fire scar studies might be reduced in at least three ways. First, injuries and resulting scars caused by mammals, insects, pathogens, or tree falls might sometimes be mistaken for fire scars (Agee 1993). In giant sequoia tree rings, however, nearly all scars are likely to be caused by fire; compared to other conifers, giant sequoias are relatively resistant to insects and pathogens (Weatherspoon 1990), and have thick bark that resists damage by animals and tree falls. More importantly, there is an excellent correspondence between scar dates and the dates of known historic fires (Swetnam et al. 1992, Swetnam 1993). A second potential problem of fire scar studies is that, if sample sizes are too small, many past fires might go undetected (Agee 1993). This problem has been minimized in se-

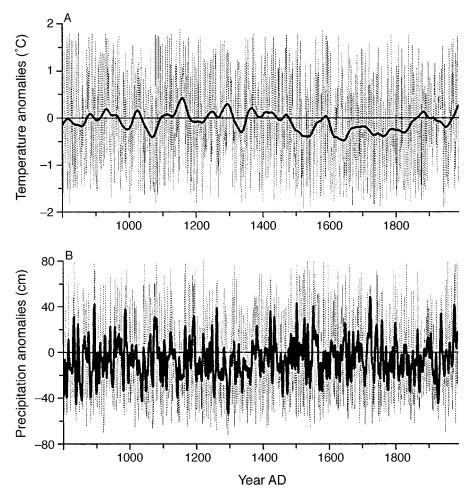


Fig. 2. Tree ring reconstructions of (A) summer temperature and (B) winter precipitation in the southern Sierra Nevada since AD 800 (......), expressed as departures from the mean of the observational record (1928–1988). The smoothed series (\_\_\_\_\_) emphasize the frequency of variation shown to be most important in spectral analyses of the reconstructed climatic record (>100 yr for temperature; >14.5 yr for precipitation). (Redrawn from Graumlich [1993], courtesy of L. Graumlich.)

quoia groves by large sample sizes; fire-scar records have come from 16–29 dead sequoias arrayed in small clusters within each of five widely scattered groves, for a total sample of >500 partial tree sections and several thousand individual scars (Swetnam et al. 1992, Swetnam 1993). Graphs of the number of fires recorded in a given sampling cluster, relative to number of trees sampled, indicates that this sampling intensity has probably captured most fires (Swetnam et al. 1992). Finally, imprecision can result if individual scars are not cross dated (Madany et al. 1982). All of the several thousand scars used by Swetnam (1993) to reconstruct fire regimes in sequoia groves were cross dated to the precise year.

Thus, given the great length and high quality of tree ring records found in sequoia groves, it has been a relatively straightforward task to quantify several past characteristics of perhaps the most important keystone process (sensu Holling 1992) shaping sequoia ecosystems: fire. Fire scar studies have allowed temporal as-

pects of fire regimes, such as climatically induced changes in fire frequency, to be determined with annual resolution over periods of millennia (Swetnam 1993). With less precision, positions of scars within individual rings have allowed the season of individual fires to be inferred; most were late-season fires (Swetnam et al. 1992). Spatial aspects of fire regimes, such as fire size and patterns of fire severity, have also been determined or inferred, but with generally lower accuracy and precision than temporal aspects (Swetnam 1993, Caprio et al. 1994, Caprio and Swetnam 1995, Mutch and Swetnam 1995).

Compared to the characterization of past fire regimes, however, characterization of past sequoia grove structure is, by nature, generally more imprecise and qualitative. Here, I briefly review the capabilities and limitations of the various tools and approaches that have been used to describe past grove structure.

Analysis of old plot data (e.g., Stephens 1995, Stephens and Elliott-Fisk 1998).—The earliest available

plot data from sequoia groves (Sudworth 1900) are probably biased. Sudworth's size structure data for every tree species are modal in the middle size classes, not the smallest size classes. This strongly suggests that his sampling was biased toward older forest patches, that he ignored small trees, or both. However, his data might help us understand conditions specifically in old-growth patches, 30–40 yr after Euro-American settlement.

Analysis of old written accounts (e.g., Bonnicksen 1975, Bonnicksen and Stone 1978).—A handful of old written accounts supply qualitative descriptions of conditions surrounding, and sometimes within, sequoia groves in the late 1800s and early 1900s. There is some contradiction among the written accounts and their interpretations. For example, Otter (1963) believed grove conditions of the late 1800s were artifacts of shepherds' fires, although this conclusion is contradicted by the fire scar record (Swetnam et al. 1992, Stephenson 1996). Many written accounts were probably biased toward scenes that were particularly memorable to the chroniclers.

Repeat photography (e.g., Vankat 1970, Kilgore 1972, Vankat and Major 1978).—Photographs are vivid windows on past grove conditions, sometimes showing dramatic changes (Fig. 1). However, only limited aspects of past grove structure can be quantified from photographs, which are two-dimensional projections of small portions of three-dimensional forests. Most photographs may have been biased toward attractive or dramatic, but not necessarily representative, scenes. Most early photographs from sequoia groves date from the late 1800s, usually one or more decades following Euro-American arrival.

Analysis of forest age structure (e.g., Vankat and Major 1978, Kilgore and Taylor 1979, Parsons and DeBenedetti 1979, Stephenson 1994).—Forest age structure alone is difficult to interpret. For example, without detailed demographic information (which are usually lacking), one cannot determine whether finding many more young trees than old trees indicates an increasing, steady-state, or declining tree population. Additionally, accurate tree age estimates can be remarkably difficult to obtain (Veblen 1992), especially for very large trees (Stephenson and Demetry 1995). However, obviously multimodal age distributions can reveal periods of high and low success in tree recruitment, allowing us to qualitatively infer conditions in centuries past. Additionally, spatial clumping of age classes can sometimes be used, with caution, to infer minimum forest gap sizes in the past.

Analysis of the physical legacies of past forest conditions (e.g., Bonnicksen and Stone 1982a, b).—Related to the preceding approach, analysis of logs, snags, and the sizes or ages of living trees can sometimes be used to estimate past forest conditions by backward projection from present conditions. Unfortunately, logs

of the overwhelmingly most abundant tree species in sequoia groves, white fir, rot quite rapidly in the Sierra Nevada, having a half-life of only 14 yr (Harmon et al. 1987). Thus, the most accurate reconstructions may be limited to the postsettlement era (Stephenson 1987). With consideration given to this caveat, this approach can still be used to set broad limits on possible past grove conditions.

Inferring forest composition from pollen and macrofossils (e.g., Anderson 1994, Anderson and Smith 1994).—Pollen and macrofossils from meadow sediment have revealed changes in the relative abundances of different tree species in sequoia groves over periods of ≥10 000 yr. General forest aspect (open or closed) can be inferred from the relative abundances of pollen from shade-intolerant trees and understory plants. However, pollen cannot reveal other aspects of forest structure, such as gap and patch sizes, proportions of trees in different age classes, and so on.

Biological inference and contemporary analogs (e.g., Harvey et al. 1980).—Present-day studies of the shade tolerance, seed dispersal, and seedling germination and establishment traits of the various Sierran conifers, coupled with studies of fire effects and our knowledge that fires burned frequently through pre-Euro-American sequoia groves, allow us to qualitatively infer general grove conditions of the past. By themselves, these studies do not allow us to define precise forest structures for specific locations or times in the past. Additionally, because fire exclusion has altered forest structure, contemporary forest response to fires cannot automatically be assumed to be a perfect analogue of past response.

Forest dynamics models (e.g., Kercher and Axelrod 1984, Miller and Urban 1999, 2000).—Computer models can quantify and formalize biological inference. No computer-based, gap-phase forest dynamics model has yet been explicitly applied to estimate grove conditions at a specific time or time period in the past. Forest dynamics models depend heavily on the assumptions and empirical data that drive them, which in many cases are untested or unreliable. However, modeling of past conditions deserves more serious attention.

In summary, descriptions of past grove structure usually are limited in three ways: (1) most descriptions should be considered qualitative, not quantitative; (2) the best available information is strongly biased toward describing grove conditions in the late 1800s or early 1900s (after Euro-American settlement); and (3) results are often specific to only a few locations. A broader discussion of the limitations of tools for describing forest reference conditions can be found in Swetnam et al. (1999).

Thus, though I have argued that the entire millennium preceding Euro-American settlement is a potentially logical period for determining reference conditions, we can do so with relatively high precision only

for fire regimes, not grove structure. As imprecise as our knowledge of past grove structure is, it is, however, still useful (as discussed in the following sections). Elsewhere I have summarized our best current estimate of past grove structure (Stephenson 1996).

# STRUCTURAL RESTORATION, PROCESS RESTORATION, AND REFERENCE CONDITIONS

The relatively substantial difference in the accuracy and precision with which reference conditions for fire regimes vs. forest structure can be determined has helped fuel a debate between "structural restorationists" and "process restorationists" (Vale 1987). Much of the debate can be distilled to a simple question: is the mechanical removal of trees a necessary step in forest restoration, or can process (fire) alone restore forest structure? Structural restorationists have argued that extensive, selective tree cutting, aimed at recreating relatively precisely defined pre-Euro-American forest conditions, was a necessary step in forest restoration (Bonnicksen and Stone 1978, 1982b, 1985). They concluded, based on comparisons of present forest structure to reference conditions, that fire suppression had led to more uniform fuel and vegetation conditions within sequoia groves, thus blurring the boundaries between formerly distinct forest patches of different ages and structures (Bonnicksen and Stone 1978, 1982b). This increased uniformity in forest conditions, they argued, would be perpetuated even after fire was reintroduced, thereby erasing the original character of the forest mosaic. They implied that, although knowledge of pre-Euro-American grove structure was imperfect, it would be better to apply that imperfect knowledge than to do nothing, or to perpetuate unnatural conditions by reintroducing fire without an initial mechanical restoration. It should be emphasized that most structural restorationists, including Bonnicksen and Stone, have included reintroduction of natural processes (especially fire) in their goals; however, natural processes were only to be restored following an initial mechanical restoration of forest structure.

In contrast, process restorationists, led by National Park Service scientists and land managers in the Sierra Nevada, have argued that mechanical removal of trees is not a necessary step in restoration. They contended that initial forest structure is of little importance; the goal of restoration is to restore the major processes (particularly fire) that shaped sequoia ecosystems in pre-Euro-American times in such a way that "... the interaction of those processes with other ecosystem elements . . . [is] . . . similar to that which would have occurred had modern humans not intervened" (Bancroft et al. 1985, Parsons et al. 1986, Parsons 1990). Among the arguments presented in support of process restoration, three were influenced by limited knowledge of past forest structure. First, process restorationists argued that past climate and fire regimes were so variable that, by chance, during some pre-Euro-American periods sequoia grove structure was probably similar to that of today's supposedly unnatural groves (Bancroft et al. 1985, Graber 1985, Parsons et al. 1986). Thus, there was probably no need for structural restoration, since, in the aggregate, modern groves probably already fell within the bounds of natural variation. Second, process restorationists argued that it is difficult to justify the expense and disturbance of mechanical restoration when structural reference conditions are ill defined or possibly inaccurate (Parsons et al. 1986). Third, some scientists and managers thought it possible (and even likely) that the restoration of fire regimes alone, without a preceding mechanical restoration of structure by selective cutting, would restore a forest structure similar to that of pre-Euro-American times (Harvey et al. 1980, Bancroft et al. 1985). Broader summaries of structural and process restorationist viewpoints can be found elsewhere (Vale 1987, Stephenson 1996).

The structural and process restorationist arguments that I have summarized fall near the extremes of a continuum. A "hybrid" approach to forest restoration, incorporating both structural and process restorationist elements, has been suggested by Agee and Huff (1986). Like process restorationists, Agee and Huff viewed mechanical restoration of a precisely defined pre-Euro-American forest structure as impractical and perhaps even undesirable. They suggested the use of prescribed fire, rather than extensive tree cutting, as an agent of restoring structure to broadly defined natural conditions. However, like structural restorationists, they recognized that unnaturally heavy fuel accumulations might result in unnatural fire effects, such as unusually high death rates of old-growth pines. They therefore suggested that limited mechanical intervention might be needed before fire is reintroduced, such as mechanical removal of fuels from the bases of selected oldgrowth trees.

Here, I reassess the structural and process restorationist viewpoints by sequentially reexamining arguments presented by both groups, in light of both new and old research. A decade of renewed research on reference conditions and fire effects in sequoia groves has provided a rich background to support such a reassessment.

### Reassessing structural restorationist arguments

In support of their contention that reintroduction of fire without a preceding mechanical restoration of forest structure would perpetuate unnatural grove changes, Bonnicksen and Stone (1981) cited spatial data from a single  $80\times80$  m plot established in a recently burned portion of a sequoia grove. Bonnicksen and Stone found that white firs 41–60-yr-old (that is, a cohort that became established since fire exclusion became effective) within the recently burned plot were clumped in

a hierarchical pattern. Since two separate unburned plots in the same grove showed similar hierarchical clumping of firs in the same age class, they concluded that "... the prescribed burn did not significantly alter the pattern for this age class." They additionally concluded that "[s]ince this [hierarchical] pattern was not characteristic of most older age classes [of white firs in the same three plots] it was probably not characteristic of the presettlement giant sequoia-mixed conifer forest community." By Bonnicksen and Stone's reasoning, these findings demonstrated that fire perpetuated a Euro-American-induced change in the forest mosaic. They implied that similar changes probably existed, and would be perpetuated, in other sequoia groves where prescribed fire is reintroduced without a preceding mechanical restoration (Bonnicksen and Stone 1978, 1981, 1982b, 1985).

For several reasons, Bonnicksen and Stone's arguments are unpersuasive. First, their analysis was based on only a single burned plot. Second, they did not actually measure changes in forest pattern resulting from a fire; they inferred changes by comparison with two different unburned plots. Third, though they concluded that the present clumping of 41-60-yr-old firs was unnatural, because it differed from that of older firs, it has long been known that tree spatial pattern changes fundamentally with age (e.g., Laessle 1965); that is, the present spatial pattern of old trees is not an adequate reference condition for the past spatial pattern of young trees. Finally, and most importantly, direct evidence from the studies that I will now discuss demonstrates that high spatial heterogeneity in present-day fuels, prescribed fire behavior and effects, and consequent forest response result in a forest mosaic that is, within the precision of our reference conditions, similar to that of pre-Euro-American times.

After a century of fire exclusion, surface fuel loads within sequoia groves are high, but are also highly variable. Kilgore (1973a) found extreme fuel variability at scales of a few meters. Variability is also high over larger areas; average fuel loads within each of 26 ~0.1 ha plots within several sequoia groves (stratified random sampling) ranged 42-301 Mg/ha, a seven-fold difference (M. Keifer, unpublished data). Such variability in fuels results in spatial variability in prescribed fire residence time and energy release. For example, Kilgore (1973a) found that total energy released during a prescribed fire varied by several orders of magnitude over a distance of a few meters. Changes in daily and seasonal weather and fuel moisture, accentuated by differences in local topography and fuels, lead to high variability in fire intensity (Kilgore 1973b, Harvey et al. 1980). During two prescribed fires, flame length (a measure related to fire intensity) at predesignated monitoring points varied from 0 m (smoldering combustion) to >1 m (M. Keifer, unpublished data). In a pocket of extremely heavy fuels during another prescribed fire, flame lengths were >12 m.

Such variability in fire behavior and intensity, in turn, contributes to variability in fire effects and forest response. For example, Gebauer (1992) showed that spatial heterogeneity in four of seven soil characteristics in a sequoia grove was significantly greater in recently burned areas than in areas that had not burned for more than a century (there was no significant trend in the remaining three soil characteristics). Kilgore (1973a) showed that nonuniform fuels and fire behavior broke a relatively uniform thicket of young white fir into a distinct gap (>0.05 ha) and two smaller remaining thickets. Demetry (1995) found that 18 forest gaps, created by a number of prescribed fires that burned under different conditions, were of variable size (the author's nonrandom sample included gaps of 0.067-1.17 ha). In a more extensive survey using remote imagery, the approximate modal gap size (to the nearest order of magnitude) was 0.1 ha for a large portion of a sequoia grove subjected to a number of prescribed fires (A. Demetry, unpublished data). These gap sizes correspond to pre-Euro-American gap sizes inferred from sequoia age structure analysis (Stephenson et al. 1991, Stephenson 1994). They also roughly correspond to the modern-day 0.0135-0.16-ha forest patch sizes found in a sequoia grove by Bonnicksen and Stone (1981, 1982a), especially if we keep in mind that patch size usually is smaller than gap size, since regeneration is nonuniform within gaps (Demetry

In addition to creating gaps similar to those of pre-Euro-American times, prescribed fire restores other aspects of grove structure, at least within the limits of our knowledge of past grove structure (Stephenson 1996). The fire-induced death of small understory trees and the lower branches of larger trees reduces "ladder fuels" that have resulted from a century of fire exclusion (Kilgore and Sando 1975, Keifer 1998). Live tree density is reduced, on average, by 47-81% following prescribed fires (Kilgore 1973a, Keifer 1998). Most of the reduction is in firs <30 cm diameter, and especially in firs <10 cm diameter (those trees that occur in abnormally dense thickets resulting from fire exclusion). The relative density of sequoias >1.4 m tall has more than tripled in 10 yr following prescribed fire, mostly at the expense of white fir (Keifer 1998), thus pushing grove structure toward pre-Euro-American reference conditions (Stephenson 1996). Additionally, a recent computer model of Sierran mixed-conifer forest dynamics (excluding giant sequoias) suggests that, following a century of fire exclusion, reintroduction of fire alone will immediately begin to restore forest basal area, spatial structure, and species composition (Miller 1998, Miller and Urban 2000). According to the model, restoration continues with subsequent fires until it is estimated to be complete, within about two centuries. Collectively, these data suggest that, within the limits of our knowledge of pre-Euro-American forest conditions, process restoration alone can restore or sustain several aspects of sequoia grove structure. We can not yet state with certainty, however, whether other aspects of grove structure ultimately will be restored, such as the proportions of forest patches in different age classes or with particular species compositions.

## Reassessing process restorationist arguments

I now turn to the process restorationists' arguments. In light of recent research, the first argument (which contends that grove structure similar to today's probably occurred naturally at some point in pre-Euro-American times) is almost certainly false, at least at broad spatial scales. The fossil pollen record (Anderson 1994, Anderson and Smith 1994) shows that large compositional changes (and presumably structural changes) occurred in sequoia groves over the last 10000 yr, sometimes including species combinations that no longer exist. However, grove composition similar to today's is a relatively recent phenomenon, spanning only the last few millennia. Within these last few millennia, mean fire-free intervals for groves before Euro-American settlement generally ranged 3-8 yr; maximum firefree intervals generally ranged 15-30 yr, with an absolute maximum of 40–60 yr in small portions of some groves (Swetnam et al. 1992, Swetnam 1993). However, no fire-free interval has been as long as that experienced by groves during the last 100-130 yr of Euro-American fire exclusion (Swetnam et al. 1992, Swetnam 1993). As a result of this unprecedented fire-free period, there has been a nearly complete failure of sequoia regeneration, which is also apparently without precedent over the last few millennia (Stephenson 1994; Stephenson, unpublished data). Inference would suggest that shade-tolerant trees such as white fir are more abundant than ever, mostly in the smaller size classes (Kilgore 1972, 1973b). These combined lines of evidence suggest that, at least at broad spatial scales, present grove conditions are without precedent.

The foundation of the second process restorationist argument, that targets for structural restoration are ill-defined or possibly inaccurate, remains firm; our estimates of structural reference conditions for sequoia groves are, by nature, relatively inaccurate and imprecise. However, they are still useful. Whether they are so imprecise as to argue against the expense and disturbance of a mechanical restoration is a separate question, which I will not address.

It appears that the third process restorationist argument also remains valid. That is, within the bounds of our imprecise knowledge of past grove structure, it appears that the reintroduction of fire alone, without a preceding mechanical treatment, may restore a grove structure similar to that of pre-Euro-American times

(see Reassessing structural restorationist arguments; Stephenson 1996).

### DISCUSSION AND CONCLUSIONS

A central finding of this case study is that we can determine the past characteristics of perhaps the most important keystone ecosystem process in sequoia groves—fire—with greater precision than we can determine past ecosystem structure. Consequently, sequoia managers presently are forced to set rather broad or qualitative targets for structural restoration. Managers must be content knowing that they are moving grove structure in the right direction, but within bounds that are relatively broad.

This imprecision is not unique to sequoia groves; other researchers working in forests shaped by frequent fires have found that they can characterize past fire regimes with greater precision than past structure (e.g., Millar 1997). Even when there is negligible loss of the legacies of past forest structure (snags and logs) to decomposition, such as in southwestern ponderosa pine forests (Fulé et al. 1997), past fires will have consumed most of the legacies of trees that died before Euro-American settlement (Mast et al. 1999). Precise characterization of past forest structure therefore usually will be limited to a snapshot in time following the last fire, and therefore may reflect recent (and perhaps unique) environmental contingencies more than variability over ecologically meaningful time periods (Millar 1997, Millar and Woolfenden 1999, Moore et al. 1999). These difficulties are encountered even though forest structure is one of the few elements of ecosystem structure whose past characteristics have some chance of being determined, however imprecisely. Determining reference conditions for other ecosystem elements, such as abundance and distribution of herbaceous vegetation and wildlife populations, is likely to be even more difficult and imprecise (Millar 1997, Moore et al. 1999). Still, in most cases scientists and managers may be better off having qualitative or imprecise reference conditions than none at all (e.g., Millar 1997, Landres et al. 1999).

I have summarized evidence suggesting that, for giant sequoia groves in the Sierra Nevada, restoration of a keystone process might lead to restoration of forest structure. However, three caveats must be attached. First, in some areas within sequoia groves, fuel accumulations are now so great that prescribed fires might kill more old-growth pines than would have died if fire had never been excluded; such a phenomenon has been observed in some other western mixed-conifer ecosystems (e.g., Swezy and Agee 1991). Mitigation may require mechanical removal of fuels from the bases of selected old-growth trees before fire is reintroduced (Agee and Huff 1986), which is a form of mechanical structural restoration that falls well short of attempting to mechanically recreate a precise forest structure that

existed at a specific point in time. Second, some aspects of forest structure may be restored more slowly through prescribed fire alone than through tree cutting followed by fire. Specifically, many white firs in the large cohort that became established during fire exclusion have now reached sizes that are relatively resistant to being killed by prescribed fire. Cutting can rapidly thin this cohort. However, fire alone also thins the cohort, and judicious use of different ignition techniques and seasonal timing of fire can hasten the thinning. Third, there is no hope of restoring some aspects of forest structure in less than a few centuries, regardless of whether one takes a structural restorationist or a process restorationist approach. For example, a century of fire exclusion has led to an unprecedented and nearly complete failure of sequoia regeneration. This missing cohort of sequoias can never be replaced. However, the consequences of this missing cohort on forest structure and function are probably relatively small and are likely to diminish with time; the growth rates of individual sequoias are so variable (Stephenson 1994, Stephenson and Demetry 1995) that the present hole in the size structure of sequoia populations will probably become effectively invisible within a few centuries.

What determines whether ecosystem structure can be restored by reintroduction of a keystone process? Hobbs and Norton (1996) have presented a simple conceptual model in which ecosystems can exist in several alternative stable states. Transitions to some states involve crossing thresholds that preclude easy restoration, such as by simple reintroduction of a keystone process. It seems reasonable to conclude that in a fireprone ecosystem, the longer that fire has been excluded (relative to its longest pre-Euro-American return intervals), the more likely it will be that the ecosystem has crossed such a threshold. The threshold may be determined by the nature of the process once it is restored, by the nature of the ecosystem's structure, or both. For example, has forest structure changed to the point that prescribed fire cannot be introduced without a high probability of unnaturally severe effects? Has a species that perpetuates an altered fire regime become firmly entrenched? Has an important species been extirpated?

Reference conditions can begin to give us clues as to where that threshold might be for western coniferous forests. Sequoia groves, which have now experienced fire exclusion for two to four times longer than the longest pre-Euro-American fire-free period (Swetnam et al. 1992), generally may not have crossed such a threshold. In contrast, some southwestern ponderosa pine forests have experienced fire exclusion for up to 10× longer than the longest pre-Euro-American fire-free period (Swetnam and Baisan 1996, Fulé et al. 1997). Some of these forest stands are now so dense that a threshold may have been crossed; fire cannot be reintroduced without a high potential for unnaturally

severe effects, suggesting that a preceding mechanical treatment may sometimes be necessary and appropriate (Fulé et al. 1997, Moore et al. 1999).

Regardless of forest type, spatial variability in forest structure usually is so great that site-specific decisions often must be made as to whether fire alone can restore forest structure, or whether a preceding mechanical treatment is needed. If a mechanical treatment is needed, decisions must also be made as to whether restoration of forest structure will be accomplished entirely by mechanical means before fire is reintroduced, or partly by mechanical means followed by prescribed fire. In the latter case, the goal of mechanical forest thinning is limited to reducing the probability of unnaturally severe fire, thereby creating a forest structure that can safely support the reintroduction of fire as the primary tool of forest restoration (Agee and Huff 1986). In practice, the decision as to which restoration approaches will be applied to a specific piece of land (fire, mechanical, or both) will also be heavily influenced by social concerns such as economics, land management goals, legal status of the land (such as designated wilderness), accessibility for treatment, and so on (Stephenson 1996).

Our ability to draw more robust generalizations about fire's role in forest restoration will depend heavily on a more thorough understanding of past and present interactions between fire and forest structure. Use of reference conditions will be central to developing this understanding.

# ACKNOWLEDGMENTS

I thank J. Keeley, M. Keifer, P. Landres, J. Manley, K. Menning, C. Millar, D. Parsons, P. Stine, T. Swetnam, and two anonymous reviewers for their insightful and helpful comments. This work is a contribution to the U.S. Global Change Research Program of the U.S. Geological Survey, Biological Resources Division.

# LITERATURE CITED

Agee, J. K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, D.C., USA.

Agee, J. K., and M. H. Huff. 1986. Structure and process goals for vegetation in wilderness areas. Pages 17–25 *in* R. C. Lucas, compiler. Proceedings—National wilderness research conference: current research, 23–26 July 1985, Fort Collins, Colorado, USA. U.S. Forest Service General Technical Report **INT-212**.

Agee, J. K., R. H. Wakimoto, and H. H. Biswell. 1978. Fire and fuel dynamics of Sierra Nevada conifers. Forest Ecology and Management 1:255–265.

Anderson, M. K., and M. J. Moratto. 1996. Native American land use practices and ecological impacts. Pages 187–206 in Sierra Nevada Ecosystem Project: final report to Congress, volume II, assessments and scientific basis for management options. Wildlands Resources Center Report No. 37, Centers for Water and Wildlands Resources, University of California, Davis, California, USA.

Anderson, R. S. 1994. Paleohistory of a giant sequoia grove: the record from Log Meadow, Sequoia National Park. Pages 49–55 *in* P. S. Aune, technical coordinator. Proceedings of the Symposium on Giant Sequoias: their place in the ecosystem and society, 23–25 June 1992, Visalia, California,

- USA. U.S. Forest Service General Technical Report **PSW-151**
- Anderson, R. S., and S. J. Smith. 1994. Paleoclimatic interpretations of meadow sediment and pollen stratigraphies from California. Geology 22:723–726.
- Anderson, R. S., and S. J. Smith. 1997. The sedimentary record of fire in montane meadows, Sierra Nevada, California, USA: a preliminary assessment. Pages 313–327 in J. S. Clark, H. Cachier, J. G. Goldammer, and B. Stocks, editors. Sediment records of biomass burning and global change. North Atlantic Treaty Organization Advanced Science Institute Series, Volume I 51. Springer-Verlag, Berlin, Germany.
- Aune, P. S., technical coordinator. 1994. Proceedings of the symposium on giant sequoias: their place in the ecosystem and society, 23–25 June 1992, Visalia, California, USA. U.S. Forest Service General Technical Report PSW-151.
- Bancroft, L., T. Nichols, D. Parsons, D. Graber, B. Evison, and J. van Wagtendonk. 1985. Evolution of the natural fire management program at Sequoia and Kings Canyon National Parks. Pages 174–180 in J. E. Lotan, B. M. Kilgore, W. C. Fischer, and R. W. Mutch, editors. Proceedings—symposium and workshop on wilderness fire, 15–18 November 1983, Missoula, Montana, USA. U.S. Forest Service General Technical Report INT-182.
- Bonnicksen, T. M. 1975. Spatial pattern and succession within a mixed conifer–giant sequoia forest ecosystem. Thesis. University of California, Berkeley, California, USA.
- Bonnicksen, T. M., and E. C. Stone. 1978. An analysis of vegetation management to restore the structure and function of presettlement giant sequoia—mixed conifer forest mosaics. Contract report to the U.S. National Park Service, Sequoia and Kings Canyon National Parks, California, USA
- Bonnicksen, T. M., and E. C. Stone. 1981. The giant sequoia—mixed conifer forest community characterized through pattern analysis as a mosaic of aggregations. Forest Ecology and Management 3:307–328.
- Bonnicksen, T. M., and E. C. Stone. 1982a. Reconstruction of a presettlement giant sequoia—mixed conifer forest community using the aggregation approach. Ecology **63**:1134–1148
- Bonnicksen, T. M., and E. C. Stone. 1982b. Managing vegetation within U.S. National Parks: a policy analysis. Environmental Management 6:101–102,109–122.
- Bonnicksen, T. M., and E. C. Stone. 1985. Restoring naturalness to national parks. Environmental Management 9: 479–486.
- Burns, R. M., and B. H. Honkala, technical coordinators. 1990. Silvics of North America: 1. Conifers. U.S. Forest Service Agriculture Handbook 654, Washington D.C., USA.
- Caprio, A. C., L. S. Mutch, T. W. Swetnam, and C. H. Baisan. 1994. Temporal and spatial patterns of giant sequoia radial growth response to a high severity fire in AD 1297. Contract report to the California Department of Forestry and Fire Protection. Mountain Home State Forest, California, USA.
- Caprio, A. C., and T. W. Swetnam. 1995. Historic fire regimes along an elevational gradient on the west slope of the Sierra Nevada, California. Pages 173–179 in J. K. Brown, R. W. Mutch, C. W. Spoon, and R. H. Wakimoto, technical coordinators. Proceedings: symposium on fire in wilderness and park management, 30 March–1 April 1993, Missoula, Montana, USA. U.S. Forest Service General Technical Report INT-GTR-320.
- Demetry, A. 1995. Regeneration patterns within canopy gaps in a giant sequoia—mixed conifer forest: implications for forest restoration. Thesis. Northern Arizona University, Flagstaff, Arizona, USA.

- Dennis, J. G., and R. H. Wauer. 1985. Role of Indian burning in wilderness fire planning. Pages 296–298 in J. E. Lotan, B. M. Kilgore, W. C. Fischer, and R. W. Mutch, editors. Proceedings—symposium and workshop on wilderness fire, 15–18 November 1983, Missoula, Montana, USA. U.S. Forest Service General Technical Report INT-182.
- 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.
- Gebauer, S. B. 1992. Changes in soil properties along a postfire chronosequence in a sequoia–mixed conifer forest in Sequoia National Park, California. Thesis. Duke University, Durham, North Carolina, USA.
- Graber, D. M. 1983. Rationalizing management of natural areas in national parks. Bulletin of the George Wright Society 4:48–56.
- icy and the role of national parks. Pages 345–349 in J. E. Lotan, B. M. Kilgore, W. C. Fischer, and R. W. Mutch, editors. Proceedings—symposium and workshop on wilderness fire, 15–18 November 1983, Missoula, Montana, USA. U.S. Forest Service General Technical Report INT-182.
- —. 1995. Resolute biocentrism: the dilemma of wilderness in national parks. Pages 123–135 in M. E. Soulé and G. Lease, editors. Reinventing nature? Responses to postmodern deconstruction. Island Press, Washington, D.C., USA.
- Graumlich, L. J. 1993. A 1000-year record of temperature and precipitation in the Sierra Nevada. Quaternary Research 39:249–255.
- Harmon, M. E., K. Cromack, Jr., and B. G. Smith. 1987. Coarse woody debris in mixed-conifer forests, Sequoia National Park, California. Canadian Journal of Forest Research 17:1265–1272.
- Harvey, H. T., H. S. Shellhammer, and R. E. Stecker. 1980. Giant sequoia ecology. U.S. Department of the Interior National Park Service, Washington, D.C., USA.
- Hobbs, R. J., and D. A. Norton. 1996. Towards a conceptual framework for restoration ecology. Restoration Ecology 4: 93–110.
- Holling, C. S. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. Ecological Monographs 62:447– 502.
- Hughes, M. K., and P. M. Brown. 1992. Drought frequency in central California since 101 BC recorded in giant sequoia tree rings. Climate Dynamics 6:161–167.
- Hunter, M. 1996. Benchmarks for managing ecosystems: are human activities natural? Conservation Biology 10:695– 697
- Kaufmann, M. R., R. T. Graham, D. A. Boyce, W. H. Moir, L. Perry, R. T. Reynolds, R. L. Bassett, P. Mehlhop, 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.
- Kaufmann, M. R., L. S. Huckaby, C. M. Regan, and J. Popp. 1998. Forest reference conditions for ecosystem management in the Sacramento Mountains, New Mexico, USA. U.S. Forest Service General Technical Report RMRS-GTR-19.
- Keifer, M. 1998. Fuel load and tree density changes following prescribed fire in the giant sequoia–mixed conifer forest: the first 14 years of fire effects monitoring. Pages 306–309 *in* T. L. Pruden and L. A. Brennan, editors. Fire in ecosystem management: shifting the paradigm from suppression to prescription. Tall Timbers Fire Ecology Conference Proceedings, No. 20. Tall Timbers Research Station, Tallahassee, Florida, USA.
- Kercher, J. R., and M. C. Axelrod. 1984. A process model

- of fire ecology and succession in a mixed-conifer forest. Ecology **65**:1725–1742.
- Kilgore, B. M. 1972. Fire's role in a sequoia forest. Naturalist **23**:26–35.
- . 1973a. Impact of prescribed burning on a sequoia—mixed conifer forest. Proceedings of the Tall Timbers Fire Ecology Conference 12:345–375.
- ——. 1985. What is "natural" in wilderness fire management? Pages 57–67 in J. E. Lotan, B. M. Kilgore, W. C. Fischer, and R. W. Mutch, editors. Proceedings—symposium and workshop on wilderness fire, 15–18 November 1983, Missoula, Montana, USA. U.S. Forest Service General Technical Report INT-182.
- Kilgore, B. M., and H. H. Biswell. 1971. Seedling germination following fire in a giant sequoia forest. California Agriculture 25:8–10.
- Kilgore, B. M., and R. W. Sando. 1975. Crown-fire potential in a sequoia forest after prescribed burning. Forest Science 21:83–87.
- Kilgore, B. M., and D. Taylor. 1979. Fire history of a sequoia-mixed conifer forest. Ecology 60:129–142.
- Laessle, A. M. 1965. Spacing and competition in natural stands of sand pine. Ecology 46:65-72.
- Landres, P. B., P. Morgan, and F. J. Swanson. 1999. Overview of the use of natural variability concepts in managing ecological systems. Ecological Applications 9:1179–1188.
- Landres, P. B., P. S. White, G. Aplet, and A. Zimmermann. 1998. Naturalness and natural variability: definitions, concepts, and strategies for wilderness management. Pages 41–50 in D. L. Kulhavy and M. H. Legg, editors. Wilderness and natural areas in eastern North America: research, management, and planning. Center for Applied Studies, Stephen F. Austin State University, Nacogdoches, Texas, USA.
- Lloyd, A. H., and L. J. Graumlich. 1997. Holocene dynamics of tree line forests in the Sierra Nevada. Ecology 78:1199– 1210
- Madany, M. H., T. W. Swetnam, and N. E. West. 1982. Comparison of two approaches for determining fire dates from tree scars. Forest Science 28:856–861.
- Mast, J. N., P. Z. Fulé, M. M. Moore, W. W. Covington, and A. E. M. Waltz. 1999. Restoration of presettlement age structure of an Arizona ponderosa pine forest. Ecological Applications 9:228–239.
- Millar, C. I. 1997. Comments on historical variation and desired condition as tools for terrestrial landscape analysis. Pages 105–131 in S. Sommarstrom, editor. What is watershed stability? Proceedings of the sixth biennial watershed management conference. Water Resources Center Report No. 92, University of California, Davis, California, USA.
- Millar, C. I., and W. B. Woolfenden. 1999. The role of climate change in interpreting historic variability. Ecological Applications 9:1207–1216.
- Miller, C. 1998. Forest pattern, surface fire regimes, and climatic change in the Sierra Nevada, California. Dissertation. Colorado State University, Fort Collins, Colorado, USA.
- Miller, C., and D. L. Urban. 1999. A model of surface fire, climate, and forest pattern in the Sierra Nevada, California. Ecological Modelling 114:113–135.
- Miller, C., and D. L. Urban. 2000. Modeling the effects of fire management alternatives on Sierra Nevada mixed-conifer forests. Ecological Applications, *in press*.
- Moore, M. M., W. W. Covington, and P. Z. Fulé. 1999. Reference conditions and ecological restoration: a southwestern ponderosa pine perspective. Ecological Applications 9: 1266–1277.
- Mutch, L. S., and T. W. Swetnam. 1995. Effects of fire severity and climate on ring-width growth of giant sequoia

- after burning. Pages 241–246 in J. K. Brown, R. W. Mutch, C. W. Spoon, and R. H. Wakimoto, technical coordinators. Proceedings: symposium on fire in wilderness and park management, 30 March–1 April 1993, Missoula, Montana, USA. U.S. Forest Service General Technical Report INT-GTR-320.
- National Park Service. 1988. Management policies: U.S. Department of the Interior, National Park Service. U.S. Government Printing Office, Washington, D.C., USA.
- Otter, F. L. 1963. The men of Mammoth Forest. Edwards Brothers, Ann Arbor, Michigan, USA.
- Parsons, D. J. 1990. Restoring fire to the Sierra Nevada mixed conifer forest: reconciling science, policy, and practicality. Pages 271–279 in H. G. Hughes and T. M. Bonnicksen, editors. Proceedings of the first annual meeting of the Society for Ecological Restoration. University of Wisconsin, Madison, USA.
- have we learned in 25 years? Pages 256–258 in J. K. Brown, R. W. Mutch, C. W. Spoon, and R. H. Wakimoto, technical coordinators. Proceedings: symposium on fire in wilderness and park management, 30 March–1 April 1993, Missoula, Montana, USA. U.S. Forest Service General Technical Report INT–GTR–320.
- Parsons, D. J., and S. H. DeBenedetti. 1979. Impact of fire suppression on a mixed-conifer forest. Forest Ecology and Management 2:21–33.
- Parsons, D. J., D. M. Graber, J. K. Agee, and J. W. van Wagtendonk. 1986. Natural fire management in national parks. Environmental Management 10:21–24.
- Rundel, P. W. 1971. Community structure and stability in the giant sequoia groves of the Sierra Nevada, California. American Midland Naturalist 85:478–492.
- 1972. An annotated check list of the groves of Sequoiadendron giganteum in the Sierra Nevada, California. Madroño 21:319–328.
- Scuderi, L. A. 1993. A 2000-year tree ring record of annual temperatures in the Sierra Nevada mountains. Science **259**: 1433–1436.
- Sprugel, D. G. 1991. Disturbance, equilibrium, and environmental variability: what is "natural" vegetation in a changing environment? Biological Conservation 58:1–18.
- Stephens, S. L. 1995. Effects of prescribed and simulated fire and forest history of giant sequoia (Sequoiadendron giganteum [Lindley] Buchholz)—mixed conifer ecosystems of the Sierra Nevada, California. Dissertion. University of California, Berkeley, California, USA.
- . 1998. Evaluation of the effects of silvicultural and fuels treatments on potential fire behaviour in Sierra Nevada mixed-conifer forests. Forest Ecology and Management 105:21–35.
- Stephens, S. L., and D. L. Elliott-Fisk. 1998. Sequoiadendron giganteum—mixed conifer forest structure in 1900–1901 from the southern Sierra Nevada, CA. Madroño 45:221–230
- Stephenson, N. L. 1987. Use of tree aggregations in forest ecology and management. Environmental Management 11:
- . 1994. Long-term dynamics of giant sequoia populations: implications for managing a pioneer species. Pages 56–63 *in* P. S. Aune, technical coordinator. Proceedings of the Symposium on giant sequoias: their place in the ecosystem and society, 23–25 June 1992, Visalia, California, USA. U.S. Forest Service General Technical Report **PSW-151**.
- . 1996. Ecology and management of giant sequoia groves. Pages 1431–1467 in Sierra Nevada Ecosystem Project: final report to Congress, volume II. Assessments and scientific basis for management options. Wildlands Resources Center Report No. 37, Centers for Water and Wild-

- lands Resources, University of California, Davis, California, USA.
- Stephenson, N. L., and A. Demetry. 1995. Estimating ages of giant sequoias. Canadian Journal of Forest Research 25: 223–233.
- Stephenson, N. L., D. J. Parsons, and T. W. Swetnam. 1991. Restoring natural fire to the sequoia–mixed conifer forest: should intense fire play a role? Proceedings of the Tall Timbers Fire Ecology Conference 17:321–337.
- Sudworth, G. 1900. Notes on big tree groves: excerpts on fire, lumbering, range, and soil and water conditions. Compiled by A. M. Avakian, December 1939. California Forest and Range Experiment Station, Berkeley, California, USA.
- Swetnam, T. W. 1993. Fire history and climate change in giant sequoia groves. Science **262**:885–889.
- Swetnam, T. W., C. D. Allen, and J. L. Betancourt. 1999. Applied historical ecology: using the past to manage the future. Ecological Applications 9:1189–1206.
- 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, technical editor. Fire effects in southwestern forests. Proceedings of the Second La Mesa Fire Symposium, 29–31 March 1994, Los Alamos, New Mexico, USA. U.S. Forest Service General Technical Report RM-GTR-286.
- Swetnam, T. W., C. H. Baisan, A. C. Caprio, R. Touchan, and P. M. Brown. 1992. Tree-ring reconstruction of giant sequoia fire regimes. Final report on Cooperative Agreement No. DOI 8018-1-0002 to U.S. Department of the Interior National Park Service, Sequoia and Kings Canyon National Parks, California, USA.
- Swezy, D. M., and J. K. Agee. 1991. Prescribed-fire effects on fine-root and tree mortality in old-growth ponderosa pine. Canadian Journal of Forest Research 21:626–634.

- Vale, T. R. 1987. Vegetation change and park purposes in the high elevations of Yosemite National Park, California. Annals of the Association of American Geographers 77:1– 18.
- —. 1998. The myth of the humanized landscape: an example from Yosemite National Park. Natural Areas Journal 18:231–236.
- Vankat, J. L. 1970. Vegetation change in Sequoia National Park, California. Dissertation. University of California, Davis, California, USA.
- Vankat, J. L., and J. Major. 1978. Vegetation changes in Sequoia National Park, California. Journal of Biogeography 5:377–402.
- van Wagtendonk, J. W. 1985. Fire suppression effects on fuels and succession in short-fire-interval wilderness ecosystems. Pages 119–126 *in* J. E. Lotan, B. M. Kilgore, W. C. Fischer, and R. W. Mutch, editors. Proceedings—symposium and workshop on wilderness fire, 15–18 November 1983, Missoula, Montana, USA. U.S. Forest Service General Technical Report INT-182.
- Veblen, T. T. 1992. Regeneration dynamics. Pages 152–187
  in D. C. Glenn-Lewin, R. K. Peet, and T. T. Veblen, editors.
  Plant succession: theory and prediction. Chapman and Hall,
  London, UK.
- Weatherspoon, C. P. 1990. Sequoiadendron giganteum (Lindl.) Buchholz. Pages 552–562 in R. M. Burns and B. H. Honkala, technical coordinators. Silvics of North America: 1. Conifers. U.S. Forest Service Agriculture Handbook 654, Washington, D.C., USA.
- Weatherspoon, C. P., Y. R. Iwamoto, and D. D. Piirto, technical coordinators. 1986. Proceedings of the workshop on management of giant sequoia, 24–25 May 1985, Reedley, California, USA. U.S. Forest Service General Technical Report PSW-95.