

Long-term Dynamics of Giant Sequoia Populations: Implications for Managing a Pioneer Species¹

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Abstract: My colleagues and I have analyzed the age structure of four populations of giant sequoia (*Sequoiadendron giganteum* [Lindl.] Buchholz). We have found the following: (1) The amount of successful reproduction in a grove cannot be judged by the sizes of its trees. (2) Sequoia populations almost certainly were near equilibrium or increasing before the arrival of European settlers. (3) In this century, there has been a massive failure of sequoia reproduction in groves protected from fire but otherwise meant to be maintained in a natural state. (4) Before the arrival of European settlers, successful recruitment of mature sequoias depended on fires intense enough to kill the forest canopy in small areas. Thus, sequoia is a pioneer species, and this conclusion has specific management implications.

On walks I have taken through sequoia groves with members of conservation groups and the general public, our discussions raised several questions relevant to the preservation of sequoia groves. Here I will address four of these questions—four that I consider to be among the most important for understanding the dynamics and management of sequoia groves.

(1) *Can we determine whether a grove is successfully reproducing by the sizes of its sequoias?* Small sequoias, some less than 1 m (3.3 ft) tall, can be found in nearly any sequoia grove protected from logging and fire. Does this not contradict the popular and scientific literature, which abound with declarations that sequoias have not been reproducing successfully in otherwise undisturbed groves?

(2) *Were sequoia populations increasing, decreasing, or near equilibrium at the time of European settlement?* The answer to this question is critical as a backdrop for interpreting sequoia population trends during the post-settlement period.

(3) *Is reproduction sufficient to maintain sequoia populations in the absence of fire?* Even though sequoia seedling establishment declines precipitously in the absence of fire, might establishment on bare mineral soil exposed by treefalls be sufficient to maintain sequoia populations? After all, John Muir recognized that bare mineral soil was a necessary prerequisite for sequoia reproduction, and that fire created mineral soil seedbeds, but clearly stated that "[t]he fall of old trees ... furnishes fresh soil in sufficient quantities for the maintenance of the [sequoia] forests" (Muir 1878, in Jones 1977). Thus, is there really any reason for concern over sequoia reproduction, and is fire really necessary?

(4) *What were the key factors in the maintenance of sequoia populations before the arrival of Europeans?* This is the most all-encompassing question, and we must know

the answer if our goal is to maintain groves in as nearly a natural state as possible.

Methods

To answer these questions, my colleagues and I used increment cores to determine the ages of 659 mapped giant sequoias—nearly all of the living sequoias growing in four plots (6 to 18 ha in size) in Giant Forest and Atwell Grove (Sequoia National Park, California) and Mariposa Grove (Yosemite National Park, California). Two of the four study plots had recently been prescribed burned: Mariposa in the early 1970's, and central Giant Forest in 1982. Since we wished to collect data representative only of pre-burn conditions, we cored only those sequoias that were present before the two burns, ignoring seedlings that had become established as a result of the burns. Pre-burn sequoias were easily distinguished from post-burn seedlings, which had slender, flexible main stems. Reference to a pre-burn inventory of sequoias confirmed that only a few small pre-burn sequoias (usually 1 m [3.3 ft] tall or less) were killed in the central Giant Forest burn, meaning our estimates of the numbers of trees in different age classes were representative of pre-burn conditions.

Two-thirds of the living sequoias in our plots were less than 2 m (6.5 ft) in diameter. We were able to core these trees to the pith region, providing an accurate estimate of age from ring counts. Whenever possible, the cores were taken from ground level; when cores were taken from above ground level, the number of years missed to ground level was estimated using an approach modified from Agee and others (1986). If a core bypassed the pith, the number of years missed to the pith was estimated by first estimating the distance to the pith (Ghent 1955), then dividing by the average width of the innermost 10 rings. Analysis of error showed that even with these corrections, there was a tendency to underestimate the ages of trees, but usually by less than 10 years. Additionally, missing rings undoubtedly caused us to underestimate the ages of some very suppressed sequoias. However, underestimates from either of these sources are not large enough to affect the general conclusions of this paper.

Our increment borers were too short to reach the pith region of those sequoias greater than about 2 m diameter. Instead, we took two long cores from opposite sides of each tree, corrected tree diameter at core height for bark thickness (determined by probes), then applied an empirically-derived relationship (based on radial growth measurements from 451 stump tops; Huntington 1914) that sequoia age is a function of radial growth rate and radius to the 1.6 power. This approach has proved to be more accurate than that used

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by Hartesveldt and his colleagues (1975), though our age estimates on some large sequoias may have been off by one or more centuries. This error is of little importance for the purposes of this paper because it applies only to the largest trees and is unbiased.

Can We Determine Whether a Grove Is Successfully Reproducing by the Sizes of Its Sequoias?

A frequently quoted rule of thumb is that a giant sequoia adds one foot of diameter growth every 100 years. This generalization apparently originated with Harvey and his colleagues (1980, p. 48), who stated, "... for the first 800 years of growth the ratio of 1 ft in diameter growth equals 100 years is a reasonable estimate "By this rule, sequoias less than 30.4 cm (1 ft) diameter usually should be less than 100 years old; that is, they should be recent reproduction that became established during the era of fire suppression. The smallest sequoias we see in undisturbed groves—some of which are less than 1 m (3.3 ft) tall—should be particularly young. Since it is relatively easy to find small sequoias growing in groves protected from fire, it would appear that sequoias are successfully reproducing without fire or other disturbance.

However, our age determinations from increment cores show that the "one foot equals 100 years" rule of thumb usually underestimates the age of small sequoias, sometimes

drastically. For all four plots combined, 201 sequoias were less than 30.4 cm (1 ft) diameter, but only 54 of these (about one in four) were less than 100 years old. Even this is probably an overestimate, given that our age estimates tended to be conservative. Of these 54 sequoias less than 100 years old, only 10 were less than 70 years old. At the opposite extreme, one 30-cm diameter sequoia was nearly 300 years old, and at least eight sequoias that had not yet reached breast height (i.e., were less than 1.4 m tall) were more than 100 years old; we have even found 100-year-old sequoias less than 1 m (3.3 ft) tall. Thus, most of the small sequoias we see in protected groves are not recent reproduction, but are quite old—usually over 100 years.

If the old rule—one foot diameter equals 100 years—is flawed, can we come up with a new age versus size rule that will tell us which sequoias are recent reproduction? We cannot, for two reasons. First, the relationship between age and size is poor. To illustrate this point, I have plotted age versus size for central Giant Forest and Atwell, the two plots with the largest number of sampled trees. For sequoias of a given diameter at a particular site, age often will vary by as much as a factor of four (*fig. 1*). Second, the rules change from place to place. The best-fit lines (by least-squares regression) show that in the larger size classes, the ages of sequoias at central Giant Forest are nearly twice those at Atwell (*fig. 1*); therefore a rule relating age to size in one location will not necessarily hold in another location. In the particular case of central Giant Forest and Atwell, this is

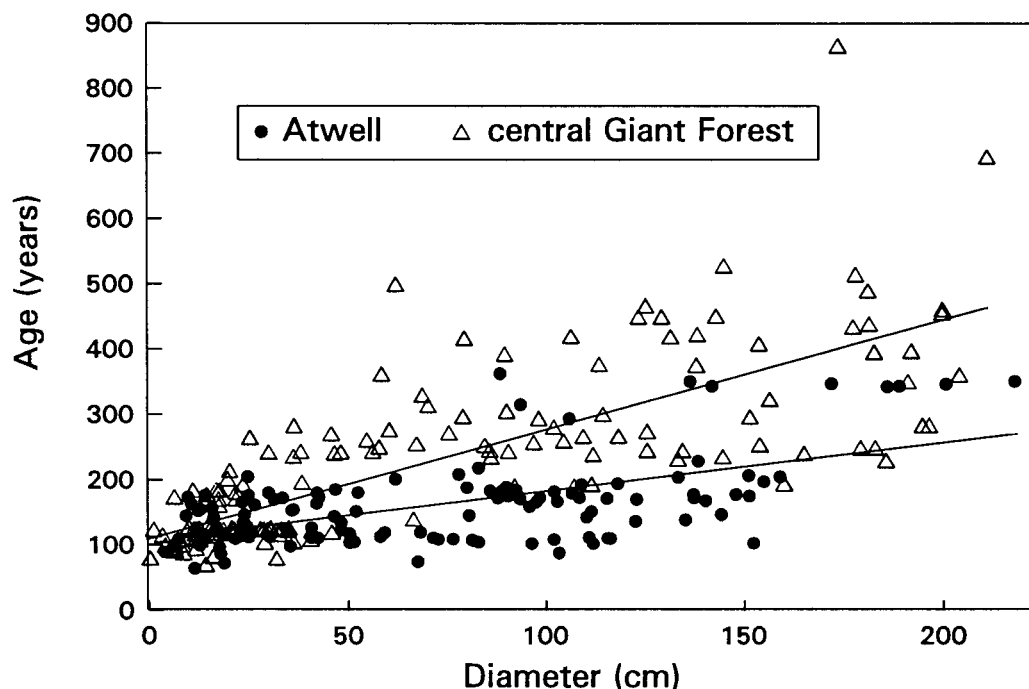


Figure 1—Age versus diameter for giant sequoias in the Atwell and Giant Forest groves. Only data from those sequoias whose ages were determined by increment cores that reached the pith region are included. The relationship between age and size is poor and changes from site to site. (Atwell: $y = 0.72x + 108$, $r^2 = 0.31$. Central Giant Forest: $y = 1.66x + 107$, $r^2 = 0.60$)

of little importance in the smaller size classes; at other locations, age differences in the smaller size classes might be important.

Clearly, we cannot use the sizes of sequoias to judge whether a grove is successfully reproducing. Very small sequoias can be quite old, and the relationship between age and size is poor.

Were Sequoia Populations Increasing, Decreasing, or Near Equilibrium at the Time of European Settlement?

To interpret recent sequoia population trends, we need to understand past trends. We can get clues to presettlement population trends by looking at the present overall age structure of sequoia populations, averaging across the four study sites and lumping sequoia ages by century to get a broad picture, smoothing out site-to-site and decade-to-decade variation in sequoia establishment.

Today, young sequoias (those less than a few hundred years old) far outnumber old sequoias (*fig. 2*). Ignoring, for the moment, sequoias that became established in the post-settlement period (the 1900's), we see that the youngest age class has the most individuals; nearly half of all sequoias alive today became established in the 1800's. Does this indicate that before European settlement there was a rapidly accelerating population boom in sequoias? Not necessarily. Forests with many more young trees than old trees are

typical the world over (Harper 1977). This is because death rates typically are very high in young trees, which are more vulnerable than old trees to drought, shading, fire, pathogens, browsing, and crushing by falling neighbors. Therefore very few young trees survive to be old trees, meaning there will always be many more young trees than old in an equilibrium population. (An equilibrium population is one in which the number of trees in each age class, and therefore the number of trees in the whole population, stays constant through time. Such populations are also called "stationary.") Thus, the pre-1900 age-structure of sequoias (*fig. 2*) has the general shape expected for a forest near equilibrium.

However, the pre-1900 age structure might also be consistent with an increasing population or even a decreasing population, depending on the probability of a sequoia surviving from one century to the next. To help distinguish among the possibilities, I used sequoia survival probabilities in both the presence and absence of fire (Lambert and Stohlgren 1988) to develop a hypothetical equilibrium age structure for sequoia populations; this hypothetical age structure closely matched the actual age structure shown in *figure 2*. Thus, independent survivorship data suggest that the age structure of the sequoias we sampled resembles that of a population near equilibrium, not a population in significant increase or decline.

But how can we explain data suggesting that sequoia populations were near equilibrium when we know that both climate and fire regimes have varied substantially in sequoia

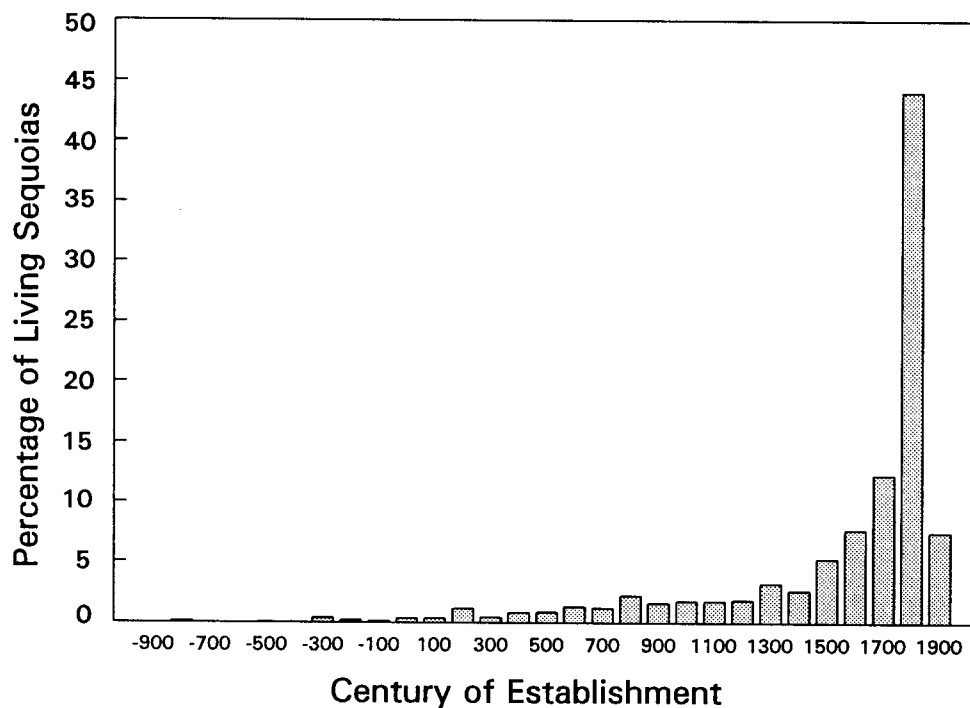


Figure 2—Percentage of living giant sequoias by century of their establishment. The data are from increment cores taken in four plots in the Atwell, Giant Forest, and Mariposa groves. This century—the 1900's—is at far right.

groves over the last few millennia (Graumlich 1993, Hughes and Brown 1992, Swetnam 1993, 1994)? I believe the answer lies in the scale and precision of our data. Changes in climate and fire regimes have been most pronounced at the scale of decades to a few centuries; consequently, century-scale drifts in sequoia population dynamics undoubtedly occurred and may show up in *figure 2* as deviations from the overall trend of continuously decreasing numbers with age. At the millennial scale, however, century-scale deviations appear to be small relative to the overall trend. However, we must also keep in mind that our age estimates for larger sequoias may be off by a century or more (as described earlier), potentially decreasing the apparent magnitude of some of the deviations from the overall trend of decreasing numbers with age. Fortunately, the latter problem will not change our qualitative conclusions about the overall status of sequoia populations, which depend on the overall shape of the curve, not the magnitude of individual deviations.

A compelling set of independent data suggests that, at roughly the time of European settlement, sequoia populations may have been increasing rather than staying near equilibrium. Anderson (1994) has found that relative concentrations of sequoia pollen in meadow sediment have been increasing almost continuously over the last four millennia, implying an increasing population, or at least a maturing population (assuming mature sequoias shed more pollen than young). A possible way to resolve the apparent contradiction between the age structure and pollen data is to assume that sequoia populations were indeed increasing or maturing over the last few millennia, but quite recently (within the last few centuries) finally approached an age structure near equilibrium. However, since we presently have no way to test this possibility, it is safest to remain skeptical.

With a good bit of confidence, then, we can state that sequoia populations were not significantly declining at the time of European settlement, but were either near equilibrium or were increasing. We presently cannot distinguish between the latter two possibilities.

Is Reproduction Sufficient to Maintain Sequoia Populations in the Absence of Fire?

Given that sequoia populations were almost certainly near equilibrium or increasing before European settlement, how much sequoia reproduction would we expect to find this century, assuming no radical departure from past conditions? The answer is simple: we would find more living sequoias with establishment dates in this century than in the preceding century, because this is the only way to maintain an equilibrium or growing population. (Though this century is not quite over, the conclusions of the following arguments will remain unchanged.) In fact, given the extremely low survival of sequoia seedlings in their first few years of life (Harvey and Shellhammer 1991), we would expect to find

many times more living sequoias (by orders of magnitude) that date to this century than to the preceding century.

Such is clearly not the case. In groves protected from fire but otherwise managed for natural conditions, far fewer living sequoias have establishment dates in this century than in the preceding century (*fig. 2*). There is not nearly enough reproduction to maintain sequoia populations in these groves. John Muir was wrong; establishment of seedlings on mineral soil exposed by treefalls is not nearly sufficient to maintain sequoia populations.

What Were the Key Factors in the Maintenance of Sequoia Populations Before the Arrival of Europeans?

We have seen that sequoia reproduction presently is far too low to maintain current sequoia populations. A large body of research links fire with successful sequoia seedling establishment (see especially Harvey and others 1980), and evidence is abundant that in the millennia before the arrival of Europeans, fires burned through sequoia groves every few years (Swetnam 1993, 1994). Was fire by itself sufficient to ensure sequoia regeneration?

Regeneration can be viewed as occurring in two steps: establishment and recruitment. Establishment refers to successful seed germination, rooting of the seedling, and survival for the first few summers; recruitment refers to the growth of the seedling into a mature, seed-producing tree. I argue that nearly any fire, by itself, is sufficient to promote at least some sequoia seedling establishment. Successful recruitment of mature sequoias, however, usually requires a narrower set of conditions: a fire intense enough to kill the forest canopy locally, and perhaps one or more wet summers following the fire. I will present three types of evidence to make the case for the importance of locally intense fire: (1) fires intense enough to kill the forest canopy locally did indeed occur in sequoia groves before forest structure and fuel loads were significantly altered by Europeans; (2) post-fire sequoia seed dispersal, seedling establishment, growth, and survival are highest where fires have burned most intensely; and (3) most living sequoias today occur in even-aged clumps that likely correspond to "hot spots" that killed the forest canopy in past fires.

Evidence of the first type comes from John Muir's vivid description of a fire he watched burn through a sequoia grove--probably Atwell Grove--in the fall of 1875 (Muir 1901). This was the last extensive fire to occur in the Atwell region (Swetnam 1992), and it likely took place before the newly-arrived European settlers had significantly influenced grove structure, composition, or fuel loads. In other words, the conditions under which the fire burned probably were representative of conditions before the arrival of Europeans. Muir watched the fire "... creeping and spreading beneath the trees ..., slowly nibbling the cake of compressed needles and scales with flames an inch high, rising here and there to

a foot or two on dry twigs and clumps of small bushes and brome grass." In other places, however, Muir saw "... big bonfires blazing in perfect storms of energy where heavy branches mixed with small ones lay smashed together in hundred cord piles ..., huge fire-mantled trunks on the hill slopes glowing like bars of hot iron ... [and] young trees vanishing in one flame two or three hundred feet high." Modern fires of this intensity kill the forest canopy locally. It appears, then, that within the matrix of a gentle surface fire, local patches burned intensely enough to open holes in the forest canopy (see also Stephenson and others 1991).

Modern observations provide the second type of evidence--that sequoia seed dispersal, seedling establishment, growth, and survival are highest where fires have burned most intensely. Seed dispersal depends on the drying of sequoia cones. By drying cones high in the canopy of mature sequoias, intense fires cause the release of much more seed than light fires; consequently, seedling densities can be more than five times greater where fires have burned most intensely (Harvey and others 1980, Kilgore and Biswell 1971). Since sequoia seedlings are intolerant of shade (Harvey and others 1980, Stark 1968), they grow fastest where the forest canopy has been opened, meaning that those seedlings germinating where fires have burned most intensely are most likely to outcompete other species and to survive subsequent fires (Harvey and others 1980, Harvey and Shellhammer 1991). Indeed, seedling survival is more than 10 times greater where fires have burned most intensely (Harvey and others 1980, Harvey and Shellhammer 1991).

A particularly vivid example of differences in seedling establishment, growth, and survival can be found in Redwood Canyon of Kings Canyon National Park, where a prescribed fire in 1977 accidentally killed all trees except large sequoias in an area of a few hectares. Fifteen years after the fire, the area supported the densest growth of sequoia seedlings found in the national parks of the Sierra Nevada (*fig. 3*). At the center of the hot spot, where the fire burned most intensely, about 0.16 ha (0.4 acres) of sequoia seedlings formed a nearly continuous cover, interrupted by only a few scattered deerbrush (*Ceanothus integrissimus*). The many other dense patches of seedlings within the hot spot were not as large, yet still formed overlapping groups that each included tens to hundreds of seedlings 3 to 8 m (10 to 26 ft) tall. I found one seedling that, 15 years after the fire, had reached a height of 8.7 m (nearly 30 ft), implying an average height growth of nearly 0.6 m (2 ft) per year. This sequoia had already begun to put on cones.

In stark contrast, to the west, south, and east of the hot spot I was unable to find a single sequoia seedling growing in those areas where the fire had burned, but the upper forest canopy had remained intact. I found sequoia seedlings under intact upper canopy only to the north of the hot spot, where the angle of the sun's rays allowed some sunlight to reach the soil surface. Even then, these seedlings occurred in only two main groups of a few square meters each, and most seedlings were only 0.1 to 0.5 m (0.3 to 1.6 ft) tall, the tallest



Figure 3—Vigorous sequoia reproduction where a locally intense fire created an opening in the forest canopy. The fire burned in Redwood Mountain Grove, Kings Canyon National Park, in 1977. The firs and cedars in the background were killed by the fire, whereas the large sequoia at right was not. In some areas of the burn, sequoia seedlings already had reached more than 8 m (26 ft) tall 15 years after the fire.

reaching 0.8 m (2.6 ft). In intermediate areas of the burn, where the upper forest canopy was partially killed, the abundance and height of sequoia seedlings was intermediate between those found under the intact canopy to the north of the hot spot and those found in the main body of the hot spot.

Our tour of the regeneration cycle is completed by the third type of evidence—that "hot spots" not only were the site of vigorous seedling establishment and growth, but also were the sites of recruitment of most mature sequoias. By mapping the sequoias of known age in the four study plots, we found that most sequoias occur in even-aged clumps corresponding to known fire dates in the tree-ring record (*fig. 4*; see also Stephenson and others 1991). In two of these sequoia clumps (dating to the 1860's at central Giant Forest and the 1870's at Atwell), we further determined the ages of all non-sequoia trees (mostly white fir). The vast majority of the non-sequoia trees were the same age as the sequoias, or younger. Since only a scattered few non-sequoia trees dated to before the last known fire, the implication is that this fire killed virtually all trees that had been growing where

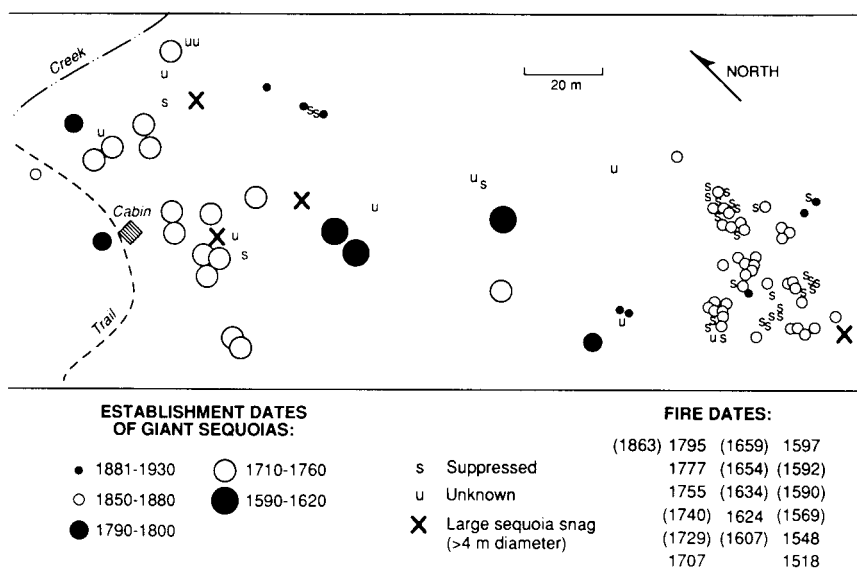


Figure 4—Even-aged clumps of sequoias in a portion of the central Giant Forest plot, Sequoia National Park. The clump at right corresponds to a "hot spot" where all but two established trees (white fir, not shown) were killed in a presettlement fire, almost certainly the fire of 1863. Most of the sequoias in the clump became established soon after the 1863 fire; the relatively wide range of dates given for their symbol (1850-1880) is meant to include temporal outliers, probably resulting from error in our ability to exactly determine ages. The clump at left presumably resulted from a hot spot during one or more of the fires of the early 1700's. Fire dates without parentheses indicate that distinct fire scars for that date were found on opposite sides of the plot; parentheses indicate that fire scars were found only on one side of the plot, hence it is somewhat less certain the fire actually burned through the plot. (Figure reprinted from Stephenson and others 1991, with permission of the Tall Timbers Research Station.)

the even-aged sequoias now stand. Collectively, the data presented in this section imply that most sequoia recruitment was limited to areas where fire killed all or most of the forest canopy.

Work by Harvey and his colleagues (1980) and my own observations suggest that summertime desiccation is the main cause of sequoia seedling death, and that seedling survival is greatest when the first few summers after a fire are wet, allowing the seedlings to develop a large enough root system to endure future droughts. This suggests the following scenario (*table 1*). After a locally high-intensity fire, seedling establishment is high and will yield high recruitment of mature trees if the next few summers are wet, or low recruitment if they are dry. After a low-intensity fire, seedling establishment is low and will yield insignificant recruitment regardless of the weather in the following summers. Intermediate levels of fire intensity and summertime moisture would yield intermediate levels of establishment and recruitment. This scenario should be viewed as probable but tentative, subject to more detailed investigation.

Implications: Managing a Pioneer Species

A large body of research points directly at fire suppression as the cause of this century's massive failure in sequoia

reproduction (see especially Harvey and others 1980). Therefore, if we wish to maintain sequoia groves in as nearly a natural state as possible (which is the National Park Service's goal), we must reintroduce fire. But not just any fire will do.

Giant sequoia is what is known as a "pioneer species," requiring canopy-destroying disturbance to complete its life cycle. Ecologists now recognize disturbance as a major shaper of plant communities the world over, opening new ground for colonization--especially by pioneer species--and creating a dynamic, shifting mosaic of patches of different ages. Sequoia forests are not unique; "patch dynamics" driven by canopy-destroying disturbance are the rule in forest communities, not the exception (Oliver and Larson 1990, Pickett and White 1985, Platt and Strong 1989).

We need to know the natural spatial scale of canopy-destroying disturbance in sequoia groves if we are to understand the management implications of patch dynamics. Gaps created by natural disturbance can range from a few tens of square meters, such as those created by treefalls in the deciduous forests of eastern North America, to thousands of hectares, such as the enormous areas burned in lodgepole pine forests of the Yellowstone region. Natural gaps in the sequoia/mixed-conifer forest were on the low end of this continuum in gap sizes. The even-aged patches of sequoias we have sampled so far have ranged from less than 0.03 ha

Table 1--Probable scenario of sequoia establishment and recruitment¹ resulting from different combinations of fire intensity and summertime weather following the fire.²

Summer	High fire intensity	Low fire intensity
Wet summer(s) following fire	Abundant establishment Abundant recruitment	Low establishment No or insignificant recruitment
Dry summer(s) following fire	Abundant establishment Low recruitment	Low establishment No or insignificant recruitment

¹Establishment is successful seed germination, rooting of the seedling, and survival for the first few summers; recruitment is the growth of the seedling into a mature, reproducing tree.

²Intermediate levels of fire intensity and summertime moisture would result in intermediate levels of establishment and recruitment.

(0.08 acre) to more than 0.4 ha (1 acre), suggesting that the minimum size of forest gaps leading to significant sequoia recruitment was 0.1 ha (to the nearest order of magnitude). This estimate of gap size almost certainly is low for two reasons: (1) successful sequoia recruitment often is limited to only a portion of a given gap, leading to an even-aged patch of sequoias that was smaller than the gap itself, and (2) subsequent fires and windthrows of sequoias undoubtedly reduced the area occupied by sequoias in a given patch. Much larger gaps surely were formed from time to time, such as during the AD 1297 fire in Mountain Home Grove (Stephenson and others 1991).

A bird's-eye view of a sequoia grove following a typical presettlement surface fire probably would have revealed a relatively open, green, mostly intact forest canopy with a scattering of small holes resulting from local hot spots. The canopy holes were the sites of most successful sequoia recruitment, leading to the stately groups of sequoias we admire today. The management implication is clear: if we wish to maintain sequoia groves in as nearly a natural state as possible, we must accept not only fire, but fire intense enough to open occasional holes in the forest canopy. Current management fires rarely meet this criterion, and then only by accident.

If we are willing to accept management practices that less closely mimic natural processes, we could physically cut openings in the forest, following with a light surface fire to prepare a mineral soil seed bed. We would usually then need to sow sequoia seeds or plant sequoia seedlings, since a light surface fire will induce little seed release from sequoia cones, leading to low seedling establishment. Although this approach may be successful on a small scale, I believe it has some serious drawbacks. First, it is impractical on a large scale. Sequoia and Kings Canyon National Parks, for example, have 35 sequoia groves totalling more than 3350 ha (8300 acres), and many of these groves lie in remote areas inaccessible by road or trail. Sending chainsaw crews through the groves at a frequency mimicking the natural fire interval, followed by burning and planting, would be a massive, prohibitively expensive undertaking. More important, intense fires probably do much more for sequoia seedlings than just open the canopy. To name two possibilities, intense

fire may kill pathogens and alter soil properties (such as friability and wettability) to favor seedling growth and survival (Harvey and others 1980, Harvey and Shellhammer 1991). Using patchy intense fire is conservative; it is the approach most likely to continue the processes that have maintained sequoia populations for millennia, whether we fully understand those processes or not.

Regardless of the management approach we may favor, I believe one message overrides all. For we who revel in the beauty of sequoia groves, this century's failure of sequoia reproduction is nearly invisible against a backdrop of seeming timelessness. We strain our necks to see the old trees, not noticing the lack of young trees. Given the great age attained by sequoias, this century's relatively short gap in reproduction will not endanger the long-term survival of the species in nature, assuming we take measures to reverse it. We must take seriously our role as stewards passing on the forest unimpaired to future generations and restore sequoia reproduction, soon.

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