The Fire Ecology of Sequoia Regeneration

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In all likelihood, the giant sequoia (*Sequoiadendron giganteum*) is today an extant species of tree because of the role fire plays in its regeneration. Fire, *per se*, is not an absolute requisite for its reseeding, but, of the several disturbance factors known to promote its regeneration, fire has been the most extensive and the most often repeated within its native range. The idea is not a recent one; John Muir (Muir, 1878) recognized the role of fire in sequoia groves as early as 1878 when he wrote, "... *fire, the great destroyer of Sequoia, also furnishes bare, virgin ground, one of the conditions essential for its growth from the seed.*"

This concept was apparently not widespread or at least not accepted and despite the strengthening statements of George Sudworth, Willis Jepson, and later, Woody Metcalf and Harold Biswell, the role of fire has been effectively subverted by the growing public aversion to fire in the forest. Fires, which burned through Sierran plant communities with a degree of regularity before the advent of Western Civilization (Biswell, 1961, and Hartesveldt, 1964) were effectively prevented or suppressed before becoming widespread. During this period, conditions developed in sequoia groves which were contrary to the goals established for their management. Feeling that full protection against fire and a "hands off" attitude were the best management criteria, sequoia management agencies inadvertently permitted the development of two problems, each in need of study for possible solutions:

1. Regeneration of sequoias is greatly reduced or prevented in groves approaching the climax stage of plant succession in the absence of disturbance factors.
2. Fire hazards have become extreme where the reduction of fires has permitted long-time accumulations of fuel.

The latter problem is receiving attention by a group from the University of California under the direction of Dr. Harold Biswell.

The former problem, that of sequoia regeneration, is the basis of a series of field studies which began in 1964 and which are both encouraged and financed by the National Park Service. The hypotheses which are the foundation of these studies center around two major factors which result from physical disturbances to the existing sequoia communities. The most highly regarded of these, historically speaking, is the exposure of bare mineral soil to the sequoia's tiny seeds. This idea, fostered by Muir, has been repeated in slightly varying context by several later authors. A second factor which only recently has been emphasized is the role of opening the crown canopy for seedling survival. Beetham (1962) suggests that sequoias are highly shade intolerant and that even though germination of the seeds occurs, seedling survival is problematical in shaded situations.

The earlier of these two factors has been grossly oversimplified and neither has been well enough understood to serve adequately as a criterion for the achievement of management goals. A third objective of this study is to determine the most practical methods of achieving the requisite conditions for sequoia regeneration.

The area chosen for study is located in the Redwood Mountain Grove, Kings Canyon National Park,

Fig. 1. Long-term fire prevention permits fuel accumulations as seen here in Trail Area, Kings canyon National Park. In such areas, broadcast burning is precluded because of the risk involved. Photo by R. Hartesveldt.

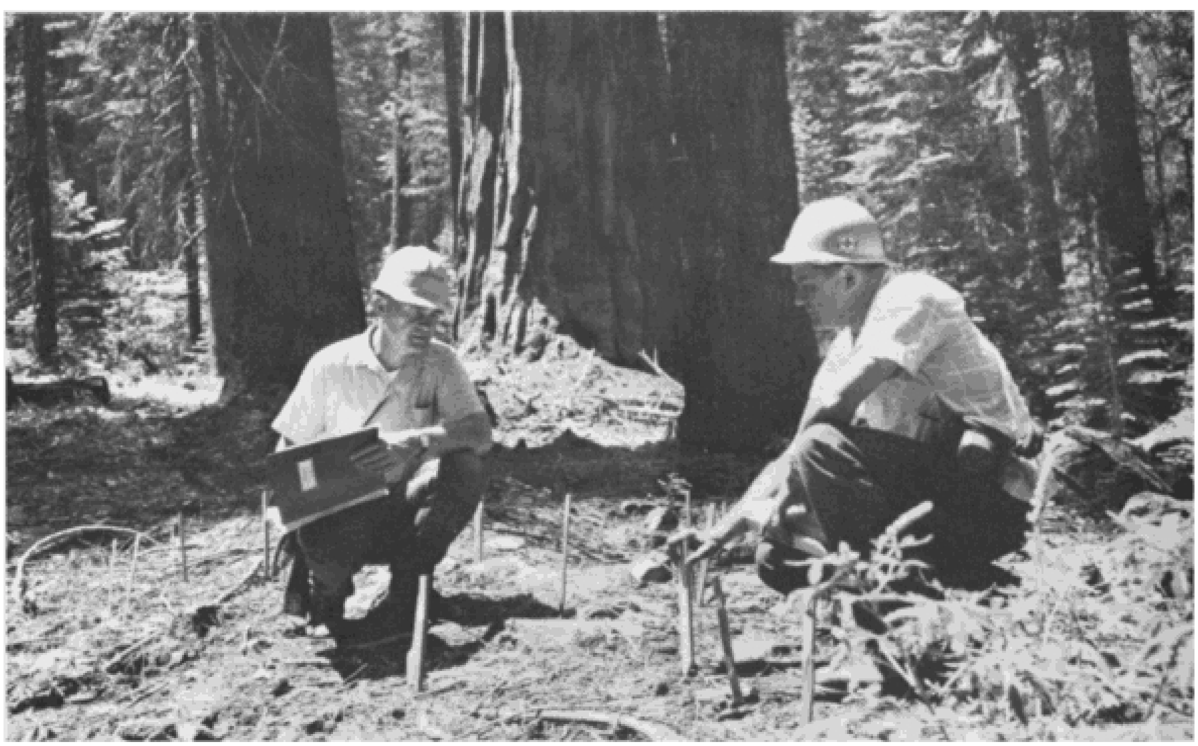

Fig. 2. Hartesveldt and H.T. Harvey staking new crop of sequoia seedlings in burned area, July, 1967. Photo by James Howell.

along the fire access road which drops down from Redwood Saddle and parallels Redwood Creek. On the assumption that fire would be used as one manipulative tool, it seemed desirable to locate and utilize an area which was but little used by the public and one which presented no undue fire hazards. The four study units chosen were well supplied with water nearby and the road was adequate for the transportation of both men and heavy equipment. It is closed to public vehicular traffic and, although used as a trail, it serves few people during the summer months. Another major criterion in selecting these sites for experimentation was the advanced status of plant succession and the lack of sequoia reproduction. For example, in North Area, there is only one sequoia less than 5 feet in diameter and one in the 5- to 10- foot class and the others all exceed 10 feet.

Four study sites were selected and named as follows: North Area, 4 acres; Trail Area, 8 acres; Ridge Area, 4 acres; and South Area, 8 acres. One-half of each area was manipulated, the remainder serving as controls. The vegetation of the first three areas was sampled by means of regularized rectangular plots. Woody vegetation taller than one meter was sampled by 72 5- by 20-meter plots, while all other vegetation was sampled by 159 1- by 2-meter plots. South Area

Fig. 3. Park Forester Ray Murphy and R. Hartesveldt lighting off Ridge Area with drip tourches on Labor Day, 1965. Photo by Ron Taylor.

was sampled by the line intercept method for small vegetation while the random pairs method was used for tree species.

Three of the four areas contained so many dead snags and downed logs as to preclude broadcast burning. After felling the snags, a cleat-tread bulldozer was employed to move and pile the logs for burning in North Area. To minimize the physical disturbance to the soil, a rubber-tired Hough Payloader was employed for the same purpose in Trail Area, while a bulldozer with a brush blade was used to move logs in South Area into windrows for burning. The physical soil disturbance by the cleat-tread equipment was the great- est here of the three areas. Ridge Area, which was largely free of dead trees and logs, was broadcast burned after the construction of a mineral fire line. Although Trail Area was principally a pile burn operation, a large percentage of the remaining ground debris was consumed by fire that burned slowly outward from the piles. From these operations, land was both burned and physically disturbed and the crown canopy was partially opened during the manipulations.

RESULTS

The manipulations have introduced some rather significant changes in the abiotic environment of each study area which have, in turn, influenced changes in both abundance and distribution of plants. Both fire and physical disturbances have either reduced or eliminated the leaf litter and duff. As a result of the manipulations, five new categories of substrate conditions were recognized:

1. Surface burns – resulting from low intensity fires in the leaf litter and duff.
2. Mechanically disturbed soils – resulting from machinery which either caused soil scarification or soil and litter compaction.
3. A combination of mechanical disturbances and surface burns.
4. Fire trail – mechanical disturbance by bulldozer.
5. Burn pile areas – where fire was both intense and prolonged.

In many places, plant succession was so far advanced that dense clusters of young white firs precluded the use of prescribed fire to open the forest floor to light. The removal of this vegetation by axe and saw and the felling of snags increased the ground level light intensity by about two-fold except in Ridge Area where there was less dangerously combustible material to be removed. Soil surfaces were now exposed to greater amounts of direct sunlight which raised the average air temperature by about 10° F. Maximum surface temperatures of the soil were in some cases more than doubled. After- noon temperatures of the soil surface rose commonly to 120° F, and a high of 157° F was recorded in one area having a southwest exposure and soil darkened by char from the burn. Temperatures were monitored by means of a tiny thermistor.

Plant successional changes began to manifest themselves in the growing season following manipulation. During the summer of 1966, a total of 2,013 sequoia seedlings were discovered in the manipulated portions of Trail, North and Ridge Areas. Xone was found in the controls. Each seedling was assigned a number and was marked with a narrow stake bearing its number, and was then catalogued along with such information as the nature of the substrate, stage of development, position of the seedling with respect to proximity to rocks, fallen limbs, etc., height of survivors at the end of the first summer, and date of death. Survivorship counts were begun on a weekly basis in an attempt to ascertain the rate of death and the factors involved in seedling survival. When more than 5,000 sequoia seed- lings appeared in 1967 of which 10 were in the controls, a similar procedure was followed and the data are now being transferred to data processing cards to facilitate analyses.

An equally significant change was in the populations and distribu- tion patterns of small-seeded annual plants which invaded the disturbed areas irregularly, but sometimes densely. These included a small borage, *Cryptantha affinis, Gilia gilioides* and *Guyophytum nuttallii* whose populations were virtually non-existent in the study areas prior to manipulation. Similarly, a biennial, *Phacelia mutabilis,* and two shrubs, *Ribes roezlii* and *Ceanothus parvifolius* appeared abundantly but with varying frequency. Whereas *Ribes* began to show a rather even and widespread distribution, the *Ceanothus* was much more abundant on soils whose litter layers had been burned off. Specimens first appeared in North Area only on the perimeters of burn piles, indicating possibly a delicate germination relationship with fire.

Sweet cicely, *Osmorhizu chilensis,* maintained a rather static population following the manipulations, while forest floor perennials such as hawkweed, *Heiracium albunz,* and trail plant, *Adenocaulon bicolor,* have both declined in abundance during the same time. Both species

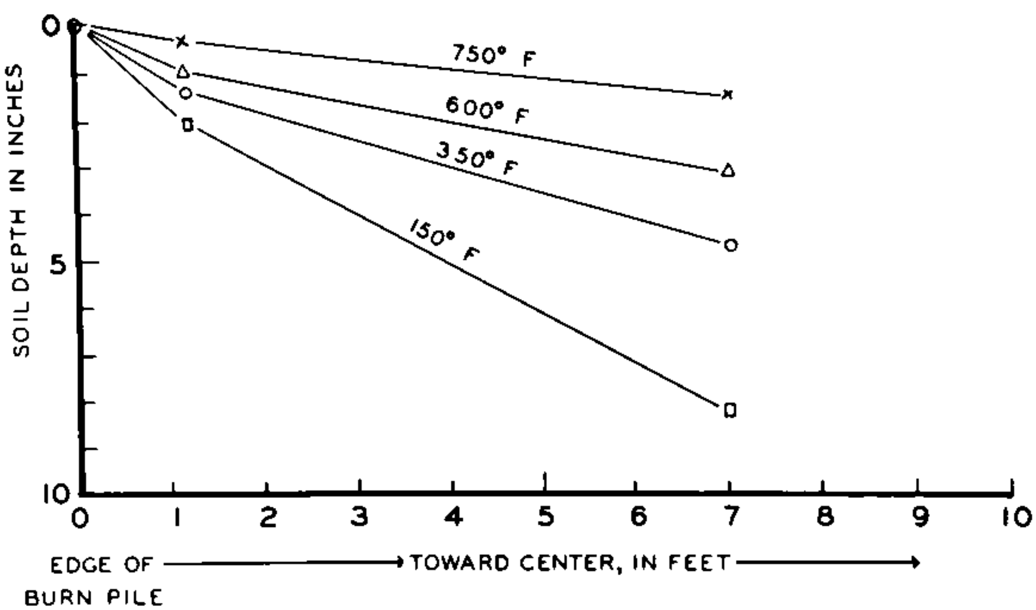

Fig. 4. Heat penetration of soil under burn piles.

show optimum growth in terms of numbers at about 4% of total sunlight. Following manipulation, the sample plots where these species had been the most abundant showed an average light value of 23.5% of full sunlight. Light determinations were derived by the anthracene method of Waring and Major (1962).

The soil beneath the burn piles is being revegetated more slowly than beneath the broadcast burns. After two growing seasons, the centers of some are still nearly bare. Oddly enough, the sequoias which have seeded into these soils have shown a significantly greater survival than on any other substrate. This is also amply demonstrated by the clusters of young sequoias found in Yosemite's Mariposa Grove. They occupy the sites of burn piles of debris removed in operations dating back to about 1910 (Hartesveldt, 1962). Several hypotheses may help to explain the higher survival of sequoias in the burn pile soils. The available data suggests that prolonged high temperatures were responsible. Temperatures exceeded 750° F, and the temperature of 150° F, which is lethal to most organisms, penetrated to an average depth of 8 inches (Fig. 4).

The hypotheses which we would advance are:

1. Alteration of physical soil conditions so as to create a more friable soil into which seeds may penetrate and water and roots gain easy access.
2. The destruction of adverse biotic agents such as pathogens and inhibitory substances from adjacent plants.
3. The elimination of other plants, both seeds and rootstocks, which might preempt the area from the sequoia seedlings if they repopulated it rapidly.

Increased moisture retention is not necessarily implicit in this observation, but the apparent commonest cause of sequoia seedling death on all substrates in both 1966 and 1967 was root desiccation.

SEQUOIA REGENERATION AND SURVIVAL

The regeneration of the giant sequoia is predicated upon an exacting set of factors which must occur in the proper sequence. Some of these are genetic in nature, others are dependent upon the disturbance of normal plant successional stages, while others are climatic. The sequoia, which has a low shade tolerance, is an early stage tree whose survival is dependent upon its capacity to obtain adequate soil moisture and to overtop the general crown canopy level to maintain its foliage in a well-lit stratum of the forest. Regeneration is scanty to absent in shaded areas. If seeds germinate, they generally die aborning, or shortly thereafter. There are presently five factors upon which we will elaborate that exert a significant influence upon regeneration and the subsequent distribution pattern and age structure of maturing sequoia communities:

1. The physical attributes of the substrate on which seeds fall.
2. The age and number of cones which are dispersing seeds and the time of their release.
3. The mode, pattern and distance of seed dispersal from parent trees.

4. The length of time seeds retain their viability after dispersal.
5. The amount of soil moisture and light available for seedling survival.

For each of these factors, fire plays a role.

The means by which substrate conditions are disturbed for seedbed preparation appears immaterial. Any situation which permits the seed roots to come into contact with moist mineral soil is of great importance. Sequoias have seeded into burned areas, on Rood plains scoured free of litter and duff, in avalanche chutes, in root pits of fallen trees, along roadsides and in logged over areas. Of these means, fire has probably been the most widespread and most often repeated. Prior to protection under park status in 1864, the Mariposa Grove sustained fires every 20-25 years in a given locality, a fact ascertained by increment borings (Hartesveldt, 1964) . In a more recent study in Sequoia National Park, the basal area curves of younger sequoias often regress closely to dates of fires indicated in the growth patterns of older sequoias found growing more toward the interior of the groves.

The provision of a soft, friable soil surface in which the light- weight sequoia seeds (1/5,700 oz. each) may be buried is perhaps a major role which fires play in increasing the number of seeds germinating. It has been demonstrated in laboratory experiments that sequoia seeds germinate in the greatest numbers when covered with a few millimeters of soil. Surface germination, even with a continuously wetted substrate, was poor. The soil surface friability is probably short-lived because of rainfall and snow which compacts the soil. Widely spaced age groups of sequoia trees may, indeed, be the result of this short-term germinating situation. It was noticed, also, that seedlings appeared in numbers coming up along side partially buried rocks, limbs, etc. It is thought that soil surface drying caused some shrinkage along the object and thus provided an avenue for seed burial.

Physical litter disturbance produced a situation in which seeds were covered with soft friable soil and the actual germination conditions were very much the same as in burned areas.

The age and number of cones dispersing seeds is only indirectly a function of fire. Sequoia cones and seeds attain maturity at the end of the second year, but may remain on the trees in a green photo- synthetic condition for as long as 20 years more. Studies have shown that seed viability percentages increase from the second year through the fifth year of cone retention and then decrease (Hartesveldt, Harvey and Shellhammer, 1967). The role which fire may play here involves the Sierra chickaree *(Tamiasciurus douglasii)*, a small squirrel which harvests the cones of several trees for food. Unlike the cones of firs and pines in which the seed is the quarry, the succulent flesh of the sequoia cone scales is the food sought. The seeds are only partially consumed and many are usually spilled on the ground. Observations by Dr. Howard Shellhammer indicate that sequoia cones are used by chickarees minimally in years when cone crops of other species are abundant. Although the role of the chick- aree as an agent of seed dispersal is not well understood, it has been observed that the cone-loading (number of cones per tree) may be considerably altered when the squirrels cut great numbers of green cones from individual trees in a short period of time. Studies in Ridge, North and Trail Areas show a remarkably good correlation between numbers of seedlings and cone-loading of parent trees. One further consideration which may prove significant is that following fires which kill many of the firs and pines but leave relict sequoias, chickarees may intensify their use of sequoia cones and thus possibly aid in the dispersal of seeds at a time when substrate conditions are optimal. Despite seed densities up to 7,500 per square meter, re- generation is virtually non-existent if the substrate conditions are inadequate.

Fires which open the crown canopy influence both the wind distribution of seeds and the length of time seeds retain their viability after dispersal. The latter is perhaps the more significant of the two. The light, which is so necessary for seedling survival also proves lethal to sequoia seeds which have fallen on the surface of the soil and are subject to direct radiation from the sun. Field studies have shown that from 10 to 20 days of partial exposure to the sun's rays is sufficient to kill the embryos. The temporal correlation of seed dispersal and proper substrate conditions is, then paramount, to the first step of giant sequoia regeneration.

The next step in seedling survival is the first few years of life when soil desiccation in the shallow rooting zone of the seedling becomes a critical factor. Here, the influences of fire may be either beneficial or detrimental to the seedling. The amount of light necessary for photosynthesis in small seedlings also increases the evaporative and transpirational losses of soil moisture. While the seedling is glaucous and tends to reflect light, it is still often overcome by soil desiccation. Thus, survival becomes dependent upon the weather or upon sub- strate conditions which provide an imbalance in favor of soil moisture during the growing season. Drainageways

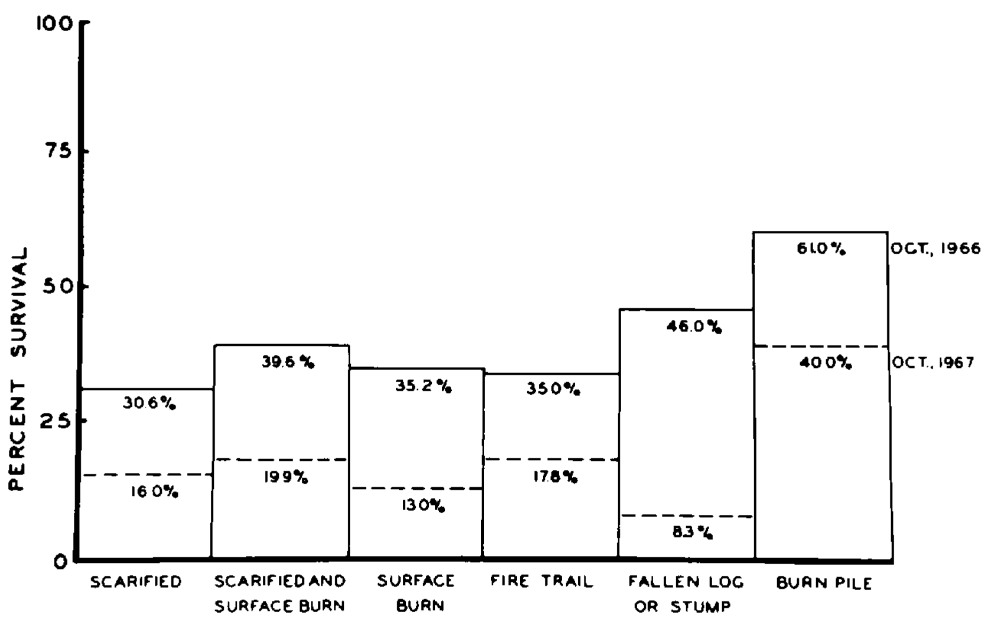

Fig. 5. Comparison of substrate conditions and survival of sequoia seedlings.

become likely situations for the establishment of the species even in years when soil moisture elsewhere is poor.

Early in the summer of 1966, new seedling sequoias began to die, apparently because of the drouth. A weekly mortality count was commenced in which the seedling was exhumed and the cause of death was sought. By September 1, 45% of the 2,013 seedlings remained alive. The figure dropped to 30% by October 21st and to 10% by the following July. Dry soil which stranded the roots was the most commonly determined cause of death. Other apparent causes were insect damage (Stecker, 1967), disturbance by birds and mammals, sunscald and winterkill. By October 21, 1967, only 286, or 1.4% of the 1966 population of sequoia seedlings remained alive.

Three survival factors were identified: the stage of seedling development at time of discovery, the nature of the substrate, and the proximity of the seedlings to solid objects partially buried in the soil.

At the time of discovery, each seedling was categorized on the basis of its stage of development. Some plants bore only the cotyledons, some had both cotyledons and secondary leaves, some had only secondary leaves while others had already developed one or more branches. By October 21, 1966, only 20% of those discovered in the cotyledon stage remained alive whereas 75% of those with branches already developed survived the dry summer. This is interpreted to mean that those genetic and environmental conditions which have enabled seedlings to develop to the branching stage have also enabled them to survive the rigors of early life. Although all the permutations and combinations of growth characteristics of these seedlings have not yet been analyzed, there is a likelihood that those with the largest crown size and the greatest number of branches also have the greatest root development. The greater the root development, the better the survival value, particularly in a year of drouth.

In Fig. 5, the comparison of survival of more than 1,600 seedlings growing on the substrates enumerated earlier is presented. One other type of substrate, logs or stumps, is included. Although surprisingly high initial survival percentage in this category, the total number of seedlings involved is only 12. The most significant phenomenon of survival is that 40% of the seedlings in the burn pile soils were still surviving in October, 1967, or triple the survival percentage for surface burn seedlings. The hypotheses for this survival have al- ready been presented.

Lastly, the proximity of seedlings to rocks, pieces of limb, bark and other materials on the ground appears to have been favorable from both the standpoint of growth and survival. The

Table 1. Seedling survival September 1, 1966 to October 21, 1966

Characteristics of Seedlings	Seedlings Next to Rocks, Limbs, etc	Seedlings Not Next to Rocks, Limbs, etc.
Average Height	37.9 mm	33.7 mm
Possess Branches	48.0 %	44.0 %
Survival	86.0 %	77.0 %

percentages shown in Table 1 are based upon the survival during the period from September 1, 1966 to October 21, 1966. Four hundred and seventy-five seedlings were involved.

The higher survival rate for seedlings in close proximity to objects may be due to several factors. The objects reduce direct insolation at the soil surface and thus reduces desiccation of the soil and pro- longs the time at which permanent wilting is reached. Objects may also deflect winds from the seedlings which would reduce transpirational water losses. The soil interfaces with those objects partially buried in the ground serve further as channelways for rapid infiltration

of water which could improve the immediate soil moisture regime for plant growth and survival. This, in turn, would influence more rapid and deeper root penetration.

In summary, sequoia seed germination and seedling establishment are related strongly to manipulation disturbances to the substrate, the opening of the forest floor to light and to the proximity of suitable substrate with trees of heavy cone loading. Seedling survival appears to be related to physical factors which were altered through the manipulation disturbances, other facets of the substrate and to the time of germination with respect to root development in the later stages of soil moisture depletion. It is felt that fires have a qualitative as well as a quantitative relationship to sequoia regeneration. At least the hotter fires seemed to have produced conditions more ideal for seedling survival than light fires or other conditioning of the substrate.

These studies are scheduled to be completed in 1974 when the hypotheses presented in this paper will be substantiated or otherwise modified according to the final survival pattern of young sequoias. But even though fire, as a manipulative tool, has proven effective on an experimental basis in fostering sequoia regeneration, its prac- tical use in groves of advanced plant succession awaits the resolution of the other problem of how to accomplish this goal in the face of all-time high fire hazard conditions.

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