BIOLOGICAL AND MANAGEMENT IMPLICATIONS OF FIRE-PATHOGEN INTERACTIONS IN THE GIANT SEQUOIA ECOSYSTEM

Douglas D. Piirto
Natural Resources Management Department, California Polytechnic State University, San Luis Obispo, Ca 93407

John R. Parmeter, Jr and Fields W. Cobb Jr.
Department of Plant Pathology, University of California, Berkeley, Ca 94720

Kevin L. Piper
Natural Resources Management Department, California Polytechnic State University, San Luis Obispo, Ca 93407

Amy C. Workinger
Department of Plant Pathology, University of California, Berkeley, Ca 94720

William J. Otrosina
U.S. Department of Agriculture, Forest Service, Southern Research Station, forestry Sciences Laboratory, 320 Green Street, Athens , GA 30602-2044

Abstract

An overriding management goal for national parks is the maintenance or, where necessary, the restoration of natural ecological processes. In Sequoia-Kings Canyon and Yosemite National Parks, there is concern about the effects of fire suppression on the giant sequoia-mixed conifer forest ecosystem. The National Park Service is currently using prescribed fire management and prescribed burning as tools to reintroduce fire as a natural process. However, there are questions about the positive and negative effects of reintroducing fire in the giant sequoia-mixed conifer ecosystem. Reintroducing fire in the Sierra Nevada forests needs critical evaluation with respect to the pathogens that affect giant sequoias. We designed a 3-year study, funded by the U.S. Department of the Interior, National Park Service, to: (1) determine the effects of fire scars and their re-burning on the incidence, extent, and survival of fungi in giant sequoia; (2) identify pathogens, insects, location of decay, and other characteristics present in standing old-growth giant sequoia fire scars; (3) evaluate host specialization and cross infectivity of isolates of Heterobasidion annosum from white fir (Abies concolor), red fir (Abies magnipca), and giant sequoia (Sequoia gigantea); and (4) develop criteria and recommendations for monitoring the effects of fire on pathogens in giant sequoia stands. The total circumference of giant sequoia trees affected by fire scars ranged from 3.3% to 69.5%. Cross-sectional area affected by fire scars ranged from 3.2% to 53.7%. The season of year in which prescribed burning takes place could influence the effect fire has on giant sequoia. A survey of 90 fire scars for the presence of resin, MycocaIicium, carpenter ants, other insects, Arachnids, decay above and below groundline, and bird activity (i.e., cavities) yielded a high presence of each factor when all burn groups were combined. Statistically significant differences in bird cavity activity, decay above groundline, and carpenter ant activity were noted among the unburned group, 1-year burn group, and 5-year burn group. The Pilodyn wood tester was effective in determining the presence of decay above and below groundline. A variety of microfungi were found associated with giant sequoia fire scars. The fungi most frequently isolated were: *Byssochlamys fulva* from 34 out of 90 fire scars (38%), *Acrodontium intermissum* from 22 out of 90 fire scars (24%), and *Tritirachium* sp. from 14 out of 90 fire scars (16%). Several other microfungi and Basidiomycetes were also identified. H. annosum acts as both a saprophyte and a pathogen in the giant sequoia-mixed conifer ecosystem. The results of these experiments have demonstrated H. annosum can spread from true fir to giant sequoia and vice versa, given that they are of the same ”S” intersterility group.

INTRODUCTION

The giant sequoia (Sequoia gigantea, refer to Davidson 1972, Piirto 1977) was once extensively distributed in western North America. It is now limited in range to approximately 75 groves (Rundel 1972). These scattered groves are located on the western slope of the Sierra Nevada within a narrow belt 260 miles long from Placer County to Tulare County, California between 3,000 feet and 8,000 feet (1,000 – 2,700 meters) elevation. Optimum elevations vary from 4,500 feet to 5,000 feet (1,500 – 1,700 meters) in the north to 6,000 feet to 7,000 feet (2,000 – 2,300 meters) in the south (Meyer 1952). Nearly all giant sequoias are found on nonglacial soils where preglacial stands were possibly left undisturbed (Muir 1877).

Approximately 90% of all giant sequoia acreage is now in public ownership (Leisz 1994). Of this public ownership, approximately 30% is under jurisdiction of the U.S. Department of the Interior, National Park Service (NPS), 50% is administered by the U.S. Department of Agriculture, Forest Service (FS), and 10% is managed by other organizations, such as the State of California and the U.S. Department of the Interior, Bureau of Land Management, and private individuals, account for the remaining grove areas (Rogers 1997). These agencies, organizations, and private individuals have employed a variety of management strategies for giant sequoia. For example, the California Department of Forestry and Fire Protection (CDF) employs uneven-aged forest management practices (e.g., selective cutting) and prescribed burning to meet management objectives for the Mountain Home grove of giant sequoias (Dulitz 1994). The FS has used, until recently, both even-aged and uneven-aged forest management incorporating a variety of fuel reduction or site preparation treatments (McDonald 1994, Stewart et al. 1994). The NPS employs prescribed burning, focusing primarily on fuel reduction, in Sequoia-Kings Canyon and Yosemite National Parks (Parsons 1994).

The overriding management goal for National Parks is maintenance or, where necessary, the reintroduction of natural ecological processes. In Sequoia-Kings Canyon, and Yosemite National Parks, concern has been expressed over the effects of nearly a century of fire suppression. The NPS is currently using prescribed burning to reintroduce fire as a natural process (Christensen et al. 1987, Piirto and Parmeter 1988, Parsons 1990, Parsons 1994).

Prior to the current fire program, attempts to suppress all natural and human-caused fires in the giant sequoia-mixed conifer forest during the past half century have resulted in accumulation of extreme quantities of dead and living fuels. The accumulation resulted in what has been termed the highest degree of fire hazard ever observed in giant sequoia communities (Hartesveldt 1962, 1964, 1965). Parsons (1994) stated, “Impacts from fire suppression, air pollution, visitor use and associated facilities, and other human induced changes must be mitigated through active management action.”

Fire must be carefully and sensitively restored to the giant sequoia forest. Dr. A. Starker Leopold, Chairman of the Leopold Committee commissioned by Secretary of the Interior Steward L. Udall to investigate resource management policies in Yellowstone National Park, stated (Leopold et al. 1963): “... forest and chaparral areas that have been completely protected from fire for long periods may require careful advance treatment before even the first experimental blaze is set. Trees and mature brush may have to be cut, piled and burned before a creeping fire can be risked.” At the same time, research must determine the ecological role of fire so that management techniques can be guided by the best knowledge available (Kilgore 1972).

Today, prescribed burning is being widely implemented as a fire management tool on NPS lands. For example, the overall goal of the Sequoia-Kings Canyon National Park (SEKI) fire management program in the giant sequoia-mixed conifer forest is to restore or maintain the natural range of fire behavior and effects (i.e., fire regime), to the maximum extent possible so ecosystems can operate essentially unimpaired by human interference (Sequoia and Kings Canyon National Parks 1992).

The implementation of the NPS fire management program resulted in significant public concern. The visual impacts and the direct burning of living old-growth trees (i.e., fire scar enlargement, pathogen-insect activity, and/or mortality) are examples of some of the concerns associated with prescribed burning. It was recognized that more research was needed on fire effects (Christensen et al. 1987, Parsons 1990, Parsons 1994). One significant research area

involved the interactions between fire and pathogens in the giant sequoia ecosystem (Christensen et al. 1987). Therefore, the objectives of our research were to: (1) determine the effects of fire scars and their re-burning on the incidence, extent, and survival of fungi in giant sequoia; (2) identify pathogens, insects, location of decay, and other fire scar characteristics present in standing old-growth giant sequoia fire scars; (3) evaluate host specialization and cross infectivity of isolates of *Heterobasidion annosum* from fir and giant sequoia; and (4) develop recommendations for monitoring the effects of fire on pathogens in giant sequoia stands.

LITERATURE REVIEW

Fire affects pathogens in a variety of ways. While none of these effects have been adequately evaluated for giant sequoia ecosystems, some possible fire effects with important management implications have been described (Parmeter 1977, Piirto 1977). Fire or its absence can: (1) directly affect pathogens (i.e., reduce inoculum levels); (2) directly affect pathogens through inhibiting or encouraging the growth of organisms that influence pathogen development and activity, e.g., the stimulation of *Trichoderma* spp. by fire which in turn inhibits Armillaria spp., or by the effects of smoke on microorganism development (Reaves et al. 1990, Parmeter and Uhrenholdt 1975, Parmeter and Uhrenholdt 1976, Zagory et al. 1983, Zagory and Parmeter 1984); (3) bring about dramatic changes in stand composition which in turn can influence pathogen epidemiology; (4) affect individual host plants through the creation of infection courts, especially for heart rot fungi (Hepting 1935, Boyce 1961, Nelson et al. 1933, Nordin 1958, Harvey et al. 1976, Piirto 1994); (5) increase and/or decrease plant vigor; (6) affect physical and microbial environments; and (7) be influenced by the activities of pathogens; i.e., with fuel accumulation in *H. annosum* centers (Parmeter 1977, Piirto 1977, Piirto 1994, Piirto et al. 1984a, Piirto et al. 1992 a,b).

H. annosum may accumulate on white fir (Abies concolor) and then attack nearby giant sequoias (Piirto 1977). Fires may cauterize giant sequoia fire scars and thus reduce decay (Christensen et al. 1987). While these aspects are recognized and in need of study, it is likely that other effects occur. Research that monitors fire effects on disease will be required to understand these interactions (Piirto and Parmeter 1988, 1990).

The management implications of how a disease impacts stands of giant sequoia are not well understood (Parmeter 1986). A review of earlier published lists of pathogens (Boyce 1948, Anon 1960, Peace 1962, Hepting 1971, Bega 1978) of forest trees indicates that few pathogens of giant sequoia have been described. Giant sequoia is not mentioned in Boyce's (1948) classic text on forest pathology. However, pathogens and fungi on sequoia have been described (e.g., Bega 1964, Piirto et al. 1974, Piirto et al.l977, Piirto 1984a,b, Piirto 1994).

Knowledge of giant sequoia diseases is increasing, but specific effects on regeneration, stand development, and old-growth trees remain relatively unknown. Additionally, laboratory soil block decay resistance trials by Piirto (1977) revealed that charring of giant sequoia sapwood and heartwood and of white fir sapwood had little effect on decay resistance. Because many previous workers have reported fire scars as entrance courts for decay fungi, it was expected that this charred tissue would be more susceptible to decay. The specific role that fire scars play in decay development may be: (1) removal of outer protective layers (i.e., bark and or callus tissue); and (2) development of cracks (i.e., checking) which facilitate entrance of water, insects, decay, and various other organisms.

MATERIALS AND METHODS

Fire Scar-Pathogen Studies

Study Areas and Fire Scar Selections

Fire scars on living old-growth giant sequoia trees in Giant Forest (SEKI) were sampled from three prescribed burn categories (Figure 1). They were 1-year-old burns, 5-year-old burns, and an unburned group (trees had not been exposed to fire for at least 50 years). Giant sequoia trees were randomly selected from three unburned and six prescribed burned areas. These random selections were made from the 1964 Sequoia Tree Inventory for Giant Forest (Hammon, Jensen, and Wallen Mapping and Forestry Service Inc. 1964, 1970, 1975, 1976; Western Timber Service 1970).

Thirty fire scars were sampled within each of the three burn groups. The 1-year and 5-year burn

Figure 1. Giant Sequoia fire scar on a tree in the Prometheus prescribed burn area in Giant Forest, Sequoia-Kings canyon National Park. This fire scar was evaluated as part of a 5-year burn group. Note the fuel loading that has developed during the 5-year period since the prescribed burn.

groups were further subdivided into early- and late-season burns. Ninety fire scars were surveyed using the procedures discussed below. This sample size met parameters for the evaluation of significant differences by chi-squared analysis. In addition, all visible fire cars, including the randomly selected survey scar on each tree, were measured to determine percent circumference and percent cross-sectional area affected by fire.

Fire Scar Measurements

Giant sequoia fire scar measurements were taken to determine the percent circumference and percent of cross-sectional area of trees affected by fire scars at groundline. This information was collected to quantitatively evaluate fire scar damage (Piper 1992). Giant sequoia fire scars were measured at groundline to obtain circumference affected. Stakes were placed around the base of each tree to represent the estimated circumference of an undamaged tree. Each fire scar was measured to evaluate height, width, and depth from this estimated groundline. The percent circumference at groundline affected by fire scars for a given tree was determined as follows:

1. Measure the circumference of a tree at groundline.
2. Measure the widths of all fire scars present on the tree at groundline.
3. Take the sum of all fire scar widths and divide by the measured circumference value. Example:
   a. Total fire scar width(s) = 21.3 feet (7 meters)
   b. Measured circumference of tree = 71.6 feet (24 meters)
   c. Percent of circumference with fire scars = (21.3 feet/71.6 feet)100 = 29.7%

The percent of cross-sectional area affected by fire scars for a given tree at groundline was calculated as follows:

1. Measure the circumference of the tree at groundline.
2. Calculate the diameter of the tree at groundline, using the circumference measurement: diameter = (circumference/m)
3. Calculate the radius of the tree: radius = (diameter/2)
4. Calculate the cross-sectional area of the tree at groundline: Area = πr^2
5. Determine the area of all fire scars at groundline:
   a. Draw, to scale, the circumference of the tree.
   b. Using the same scale, and utilizing the depth and width measurements taken in the field for each scar, draw them in place on the scale drawing of the tree's circumference (or cross-sectional area).
   c. When all fire scars had been drawn to scale within the circumference of a given tree's cross-sectional area, a planimeter was used to measure each fire scar's given area.
   d. Sum all scar areas at groundline and divide this number by the cross-sectional area of the tree. This value equals the percent of cross-sectional area of a tree affected by fire scars.

Fire Scar Survey

Field procedures were developed to evaluate fire-pathogen interrelationships in old-growth giant sequoia based on a survey to assess individual fire scar characteristics. In the event a tree had more than one fire scar, a single scar was randomly chosen to survey. Part of the evaluation consisted of an ocular inspection to detect the presence or absence of the following:

1. Resin on scar
2. *Mycocalicium* (a fungus typically associated with redwood (Sequoia sempervirens) and giant sequoia fire scars [Bonar 1971])
3. Carpenter ants
4. Other insect activity
5. Decay above ground
6. Decay below ground
7. Animal signs (e.g., cavities constructed by birds)
8. Change in fire scar characteristics due to prescribed burning:
    a. Enlargement (width)
    b. Recession (depth)
    c. Callus tissue damage Photographs were taken of each fire scar and of any outstanding characteristics noted during the evaluation.

Decay Detection

In conjunction with the fire scar survey, a Pilodyn (Proceq SA, Riesbachstrasse 57, CH-8034 Zurich, Switzerland) wood tester was utilized to facilitate decay detection above and below ground. The Pilodyn was selected for decay detection in standing old-growth giant sequoia fire scars because other methods were outdated, inappropriate, or inconvenient for field use (Piirto and Wilcox 1978, Wilcox 1983, 1988, 1991). The Pilodyn is relatively easy to use and offers a non-destructive method for testing wood. The wood tester works on the premise that delivering a calibrated amount of force to a probe will drive the probe deeper as wood soundness decreases. On a scale of l – 40, a measurement of 15 or less is considered sound wood. Test readings were taken across the face of the scar above and below groundline. The number of readings varied with the size of the scar surface.

Isolation and Identification of Fungi

Wood cores for isolation of decay fungi were taken from various suspected decay areas across the base of the fire scar. Three hundred ninety-nine core samples were taken with a wood increment borer from above and below groundline in areas of the fire scar where the highest unsound Pilodyn ratings were recorded. Aseptic techniques were followed (i.e., rinsing increment borer with alcohol and storing cores in sealed straws) to reduce the chance of contaminating the cores as they were collected and transported. The cores were transported to a mycology laboratory at California Polytechnic State University, San Luis Obispo, where isolations were made.

Chips of the wood cores were placed on a selective medium for the isolation of wood-rotting fungi. The selective medium was formulated after Hunt and Cobb (1971) and contained benomyl, dichloran, and phenol added to potato dextrose agar (PDA) after autoclaving. The isolation procedure, using aseptic methods, involved cutting of wood cores in 0.25 inch (0.63 centimeter) segments starting from the outer end of the core and working inward. Once the core had been segmented, each segment was flamed and placed in a Petri dish containing the selective media which then was sealed with parafilm.

When fungi appeared on wood core segments, Petri dishes were reopened, also under aseptic conditions, and fungi were transferred into slant tubes containing PDA. An initial grouping of the slant tubes was made according to a fungus' physical appearance and hyphal structure. After grouping all fungi in this manner, the sample groups were shipped to Dr. June Wang (Professor and Mycologist at College of Environmental Science and Forestry, State University of New York [SUNY], Syracuse) for identification of isolated fungi.

These procedures were followed for the field seasons of 1989 and 1990. One difference in isolation procedures for the cores collected during 1990 involved using the remainder of a core after it was segmented. The portion remaining was dipped into a solution of 1 milliliter (benomyl, dichloran, and phenol) per 200 milliliters of deionized water and then placed in a Petri dish on PDA medium and sealed with parafilm. This procedure was performed to utilize all of the core material and to determine if dipping the wood samples in the solution would yield additional isolations.

Insect Identification

As part of the fire scar survey, insects were collected to document species associated with giant sequoia fire scars. Individual insects were collected (when they were observed on specific fire scars) and placed in vials. Dr. David Wood, Forest Entomologist, University of California, Berkeley, assisted with insect identification. Two duplicate insect collection sets were made.

Prescribed Burning Probe Trials

Evaluating fire scar characteristics to ascertain differences resulting from prescribed burning can be done in a number of ways. One method involves ocular evaluation of fire characteristics after prescribed burning has taken place and comparison with fire scars on living giant sequoia trees in unburned (no history of prescribed burning) areas. This is largely the method that has been previously explained and used for this study. However, an associated study was undertaken to determine if changes in fire scar dimensions and characteristics could be determined by placing probes across the face of selected fire scars on several old-growth giant sequoia trees prior to prescribed burning.

Three prescribed burn areas in Giant Forest (SEKI) were selected for this probe trial: (1) Tharps Burn, (2) McKinley Burn, and (3) Huckleberry Burn. All areas were prescribed burned during the 1988 field season. Ceramic probes and stainless steel probes cut to 12 inches (0.3 meters) in length were placed across the face of ten fire scars on nine different old-growth giant sequoia trees. Three fire scars in each of the Tharps and Huckleberry Burn areas, and four fire scars in the McKinley burn area had probes placed in them prior to prescribed burning. The probes were placed into the fire scar so that only one inch (2.54 centimeters) was visible above the surface of the fire scar. Probes were randomly placed across the face of the fire scar both at or just above ground line and across the fire scar face at approximately 4.5 feet (1.5 meters) above the ground.

The majority of the probes were stainless steel. However, a few ceramic probes were also intermixed with the stainless steel probes to determine whether or not probe material was a factor in heat concentration. Probes were evaluated to determine if combustion of wood material occurred. The difference in the amount of exposed probe length from the prefire condition was used to judge whether or not a change of the fire scar surface had occurred as a result of the prescribed burning operation.

*Pathogenicity and Genetics of **Heterobasidion annosum***

Heterobasidion annosum is the casual agent of annosus root disease and a major pathogen in giant sequoia-mixed conifer forests. *H. annosum* has been identified and collected from fallen giant sequoias (Piirto et al. 1974). The root systems of these fallen giant sequoia trees show characteristic signs of *H. annosum* decay. The significance of its contribution to giant sequoia tree failure is unquantified. To assess the relationship of fire to the activities of *H. annosum* in the giant sequoia ecosystem, it is necessary to first understand the genetic and biological characteristics of the fungus. We pursued this objective through a combination of field sampling, host specificity trials (e.g., seedling greenhouse experiments), and genetic analysis.

Field Sampling

Field sampling focused on:

1. Collecting *H. annosum* sporophores from fallen giant sequoia trees;
2. Collecting sporophores as they may occur from the base of the tree to the top of the tree (i.e., in streaks) on fallen giant sequoia trees to determine whether (a) a single genetic individual fruits in a streak as it colonizes the stem of the tree and (b) multiple individuals colonize and fruit along the same path;
3. Collecting from as many associated true fir trees (*Abies concolor* and *Abies magnifica*) as possible to determine genetic similarity between giant sequoia and true fir isolates and assess the possibility of cross-infection between host species.

Over the course of three field seasons (1988 – 1990), 28 basidiocarps were successfully collected from Sequoia and Kings Canyon and Yosemite National Parks and Nelder Grove. Eighteen specimens came from giant sequoia and 10 from true fir. From these collections, 42 fungal isolates were obtained in the laboratory (28 single spore and 14 tissue).

Table 1. Early season versus late season prescribed burn fire scar analysis of giant sequoia trees in Sequoia-Kings Canyon and Yosemite National Parks.

Season of burn	Burned during previous year: Percentage of groundline circumference	Burned during previous year: Percentage of cross-sectioned area	Burned 5 years previously: Percentage of groundline circumference	Burned 5 years previously: Percentage of cross-sectioned area
Late season	29	17	33	19
Early season	25	14	20	14

Host Specificity Trials

Four host species: giant sequoia, white fir, ponderosa pine (*Pinus ponderosa*), and the universal suscept, Sitka spruce (*Picea sitchensis*) were inoculated with isolates of *H. annosum* collected from true fir (3 isolates) and giant sequoia (3 isolates). All isolates used in the experiments were collected from Sequoia and Kings Canyon National Parks in the summer of 1988. The greenhouse experiments, located on the University of California at Berkeley campus, were a controlled randomized block design. Fifteen trees per species per isolate comprised a treatment. The 28 treatments (6 isolates + 1 control X 4 hosts) were replicated 3 times for a total of 1,260 seedlings.

As seedling mortality occurred, dead trees were pulled from the experiments, dissected in the laboratory and analyzed for the presence of H. annosum. Experiment 4D. 1 which began in October 1989 was terminated in September 1990 after mortality declined drastically.

A second experiment 4D.2 was undertaken in spring 1991 and terminated in October 1991. This second experiment was initiated because of lower than expected mortality in Experiment 4D.1. In order to reduce between block variance, the number of experimental blocks was increased to four in the second experiment. Two additional isolates were also included for comparison purposes.

Genetic Analysis

Isozyme, sexual compatibility trials, and vegetative compatibility trials were undertaken to determine the genetic similarity of isolates taken from giant sequoia, white and red fir. A detailed description of the procedures and results obtained from these genetic analysis trials can be found in Otrosina et al. (1992) and Piirto et al. (1992b).

Isozyme analysis, which serves as a precise means to determine the intersterility group of an isolate, was made on all 42 isolates of H. annosum.

The 28 single spore isolates were used for the sexual compatibility tests to determine clonal identity. All single spore isolates were paired with each other and themselves (392 total pairings). Cultures were examined for the presence of clamp connections, the sign of sexual compatibility. The 14 tissue isolates were paired with each other and themselves to test the clonal identity of diploid or tissue derived isolates.

RESULTS

Fire Scar-Pathogen Studies

The major results of this NPS fire-pathogen study are summarized below. Refer to Piirto et al. (1992 a, b), Otrosina et al. (1992), and Piper (1992) for additional information.

Fire Scar Measurements

Seasonal differences in prescribed burning could be influencing the circumference or cross-sectional area at groundline affected by fire scars. However, only in the 5-year burn group was a significant difference seen in percent of circumference affected by fire scars between late and early season burns (Table 1).

As much as 70% of the circumference (values ranged from 3.3Vo to 69.5% with an average of 27.3%) and as much as 54% of the cross-sectional area (values ranged from 3.2% to 53.7% with an average of 15.6%) of the giant sequoia trees in our sample were affected by fire scars at groundline. No significant differences, however, were noted among the three burn groups in terms of percent circumference and percent cross-sectional area affected by fire scars (Table 2).

Table 2. Groundline circumference (%) and cross-sectional area (%) of giant sequoia affected by fire in the three burn groups.[1]

Burn group	Percent circumference			Percent cross-sectional area		
	Mean	SD[2]	Range	Mean	SD[2]	Range
1-year	26.9	17.2	3.7 to 67.8	15.4	8.6	3.2 to 43.3
5-year	26.9	15.4	3.3 to 69.5	16.6	11.1	3.3 to 53.7
Unburned	28.2	11.7	9.6 to 55.2	14.9	6.5	4.3 to 29.1

[1] Least Significant Difference (5%) = 7.64.
[2] SD = Standard Deviation.

Upon closer examination of the fire scars in the 1- and 5-year burn groups, we observed damage to callus tissue around existing fire scars 52% of the time, with recessional and enlargement damage noted 57% and 35% of the time, respectively (Piirto et al. 1992 a, b, Piper 1992).

Fire Scar Survey

The survey of 90 fire scars for the presence of resin, Mycocalicium, carpenter ants, other insects, Arachnids (i.e., spiders), decay above and below groundline, and bird activity (i.e., cavities) indicated a high incidence of each factor when all burn groups were combined. For example, resin was present 86% of the time on all fire scars surveyed, Mycocalicium was present on 78% of the fire scars surveyed, decay below ground was present on 63% of all fire scars surveyed. Arachnids were associated with 88% of all fire scars surveyed. Statistically significant differences in bird activity, decay above groundline, and carpenter ant activity were noted between the unburned group, 1-year burn group, and 5-year burn groups. This apparently indicates an association between these observed characteristics and the occurrence of fire (Table 3).

Decay Detection

A significance test was performed for all Pilodyn readings taken from the 90 fire scars surveyed (Piirto et al. 1992 a, b. Piper 1992). A t-test indicated a statistically significant difference between the above ground versus below groundline readings. This could be the result of the presence or absence of decay and variations in wood moisture content above versus below groundline. However, more decay is detectable below ground compared to above ground. Micro-environmental conditions and direct exposure of fire-damaged tissue to microorganisms in the soil facilitate disease an decay development.

Isolation and Identification of Fungi

The Pilodyn wood tester was useful in identifying areas potentially inhabited with fungi. Two hundred-five fungal isolates were obtained from 69 of 90 fire scars sampled. After grouping the fungal isolates, 17 were identified (Table 4). The fungi most frequently isolated were *Byssochlamys fulva* (a heat-resistant fungus), which was isolated from 34 of 90 (38%) fire scars sampled, *Acrodontium intermissum* (a preservative detoxifier), which was isolated from 22 of 90 (24%) fire scars, and *Tritirachium* sp. (entomogenous fungi), which was isolated from 14 of 90 (16%) fire scars. Other isolated fungi include: *Neosartorya pscheri* (a heat-resistant fungus), *Epicoccum nigrum* (a soft rot fungus), *Leptographium* sp. (a staining fungus), *Hyalorhinocladiella* sp. (tolerates pentachlorophenol; see Wang et al. 1989), *Mariannaea elegans* (found to have formed soft rot cavities in European white birch (Betula pendula) and Scotch pine (*Pinus sylvestris*); Levy 1969), and Basidiomycetes (fungi which cause white or brown rots). A positive identification of *Phlebia subserialis* was made of one of the four confirmed Basidiomycete cultures isolated from giant sequoia fire scars. This organism is known to affect both hardwoods and softwoods as a white rotter which may have potential in biological pulping processes (Dorworth 1992, personal communication; Burdsall 1992, personal communication).

Fungal association with fire scars was greatest in the 5-year burn group and lowest in the 1-year burn group (Table 4). Prescribed burning appears to have its greatest effect on the incidence of fungi immediately following the burn. This effect appears to diminish over time. Some stimulation of fungal growth (i.e., specific organisms) by prescribed burning may occur; however, the full effect is not

Table 3. Presence of various giant sequoia fire scar attributes.

Survey items	Presence (%)				Chi-square[1,2]
	Un-burned	1-year	5-year	All	
Resin	93%	77%	87%	86%	3.42
Mycocalicium	83%	67%	83%	78%	3.21
Carpenter ants	87%	37%	60%	61%	15.80*
Other insects	50%	60%	73%	61%	3.46
Arachnids	97%	77%	90%	88%	5.80
Decay above	70%	23%	33%	42%	14.85*
Decay below	73%	60%	57%	63%	2.01
Bird activity	83%	30%	60%	58%	17.58*

[1] Degrees of freedom = 2, significance level (0.05) = 5.99.
[2] * = significant ($P < 0.05$).

Table 4. Fungi isolated from giant sequoia fire scars in Giant Forest, Sequoia-Kings Canyon National Park.[1]

Fungal taxa	Unburned	1-year	5-year	Total
Byssochlamys fulva	10 (29%)	2 (6%)	22 (65%)	34
Acrodontium intermissum	12 (55%)	4 (18%)	6 (27%)	22
Tritirachium sp. W.	2 (20%)	4 (40%)	4 (40%)	10
Tritirachium sp. Y.	2	0	2	4
Penicillium thomii	1 (11%)	0	8 (89%)	9
Mariannaea elegans	0	0	3	3
Neosartorya fischeri	0	0	2	2
Paecilomyces sp. W.	0	0	1	1
Paecilomyces fulvus	0	0	2	2
Rhinocladiella sp.	0	0	2	2
Epicoccum nigrum	0	1	0	1
Hyalorhinocladiella sp.	1	0	0	1
Leptographium sp. A.	0	1	0	1
Leptographium sp. B.	1	0	0	1
Exserohilum sp.	0	0	1	1
Wardomyces sp.	0	1	0	1
Phlebia subserialis	1	0	0	1
Unknown Basidiomycetes	0	0	3	3
Unknowns (F99, F120)	0	2	0	2
Total	30 (30%)	15 (15%)	56 (55%)	101[2]

[1] The numerical value represents the number of fire scars from which a fungal organism was isolated. Thirty fire scars for each burn group with a total of ninety fire scars for all groups combined were examined.
[2] A fire scar could have more than one fungus isolated from it thus causing this number to exceed 90 fire scars.

evident for several years following the burn. There are, however. differences between individual fungi in terms of their response to prescribed burning. For example, the heat-resistant fungus *Byssochlamys filva* was most commonly observed in the 5-year burn group and the preservative detoxifier fungus *Acrodontium iritermissiim* was most commonly seen in the unburned group.

The majority of the fungi identified were micro-fungi which are ubiquitous and cosmopolitan (Wang and Zabel 1990). Some are plant pathogens and some are human pathogens, but most are saprobes that derive nourishment from decaying organic matter. These microfungi have been found associated with utility poles made of Douglas-fir (*Pseudotsuga menziesii*), southern pine (*Pinus* spp.), and western red cedar (*Thuja plicata)*. Some have been shown to cause soft rot and degradation of wood structure. Recent research suggests some of the microfungi can also reduce the fungitoxicity of wood preservative chemicals (Duncan and Deverall 1964, Dence et al. 1979, Wang and Zabel 1990). Based on previous research, it is possible that the microfungi isolated from giant sequoia may play a role in the decay process. An organism that has been found on exudate of exposed heartwood of redwood and giant sequoia fire scars is *Mycocalicium sequoiae* (Bonar 1971, Piirto 1977, and Piirto et al. 1992a).

Table 5. Insects collected from giant sequoia fire scars in Giant Forest (SEKI).

Insects collected	Frequency of observation
Hymenoptera	
Ichneumonidae (Ichneumons)	11
Formicidae, Camponotus sp. (Carpenter ants)	55
Sphecidae sp. (Thread-waisted wasp)	1
Pompilidae sp. (Spider wasps)	1
Coleoptera	
Cerambycidae, *Dorcasina grossa* (Long-horned beetle)	1
Tenebrionidae, *Eleodes* subgen, *Blapylis alticolus* and *Blapylis productus* (Darkling beetles)	6
Cantharidae (Soldier beetle)	1
Curculionidae (Snout beetle)	21
Diptera	
Anthomyiidae (Anthomyid fly)	1
Neuroptera	
Raphidiidae (Snakeflies)	2
Orthoptera	
Gryllacrididae, *Ceuthophilus* (Cave cricket)	20
Hemiptera	
Coreidae (Leaf-footed bug)	1

Insect Identification

Insects found in association with giant sequoia fire scars include reports for six different insect orders. Thirteen individual insects were identified (Table 5). Insects identified most frequently were *Ichneumonidae* (Ichneumons), *Camponotus* sp. (carpenter ants), *Curculionidae* (snout beetle), *Ceuthophilus* sp. (cave cricket), and *Blapylis alticohis* and *B. productiis* (darkling beetles). Seven insects less commoniy associated with giant sequoia fire scars include: *Sphecidae* (thread-waisted wasp). *Pompilidae* (spider wasps), *Dorcasina grossa* (long-horned beetle), *Cantharidae* (soldier beetle). *Anthomyiidae* (Anthomyid fly), Raphidiidae (snakeflies), and *Coreidae* (Leaf-footed bug). A collection of insects from this study is located at the museum maintained by the U.S. Department of the Interior, National Park Service at Sequoia and Kings Canyon National Park in Three Rivers, CA.

Prescribed Burning Probe Trials

The tabulated results of the probe trials are shown in Table 6. A change in fire scar surface characteristics was observed in 35% of the near groundline probes and 24% of the above groundline probes (4.5 feet). Overall, 24 out of 77 probes, or 31% of the probes, revealed a change in fire scar surface characteristics resulting from prescribed burning operations. The magnitude of the change varied from less than 0.5 inch (1.3 centimeters) to over 6 inches (15.2 centimeters) of combustion

Table 6. Results from probe trials to test effects of fire on existing giant sequoia fire scars.

Burn area and tree number	Probe condition after burning					
	Groundline		Above groundline (4.5± feet)		Total	
	Change	No change	Change	No change	Change	No change
Tharps Burn						
944	1	6	1	4	2	10
945	2	3	2	3	4	6
946	4	3	0	3	4	6
Subtotal/Percent	7 (37%)	12 (63%)	3 (23%)	10 (77%)	10 (31%)	22 (69%)
McKinley Burn						
950	4	3	0	2	4	5
951	1	2	1	0	2	2
952	2	1	1	1	3	2
953	2	4	1	1	3	5
Subtotal/Percent	9 (47%)	10 (53%)	3 (43%)	4 (57%)	12 (46%)	14 (54%)
Huckleberry Bum						
954	0	6	0	2	0	8
955	1	3	0	2	1	5
956	1	3	0	1	1	4
Subtotal/Percent	2 (14%)	12 (86%)	0 (0%)	5 (100%)	2 (11%)	17 (89%)
Totals	18 (35%)	34 (65%)	6 (24%)	19 (76%)	24 (31%)	53 (69%)

occurring on the fire scar face. In one case, the probe could not be found because of the significant amount of combustion that occurred in the fire scar.

One drawback of this particular method of evaluating fire scar changes due to prescribed burning involves initial placement of the probes. Considerable combustion on most of the ten fire scars that we sampled occurred where the probes were not located. However, despite the drawbacks of this method, it is clear that changes (i.e., enlargement) occur to fire scars from prescribed burning operations. The amount of change that occurs seems to be a function of several fire behavior parameters (e.g., fuel moisture content, amount of both fine and heavy fuel accumulation at or near the base of old-growth giant sequoia trees, relative humidity, temperature, and other factors).

Pathogenicity and Genetics of ***Heterobasidion annosum***

As with the fire scar-pathogen studies, only a brief summary of the *H. annosum* pathogenicity and genetic results is provided here. Reference should be made to Piirto et al. (1992 a, b) and Otrosina et al. (1992) for a more detailed discussion.

Pathogenicity Trials

In Experiment 4D.1, (Table 7) annosum root disease mortality was limited to 258 seedlings (24% of the total). Although this number is substantially lower than expected and mortality for Sitka spruce is the only statistically significant value, several trends should be noted. Mortality in giant sequoia was extremely low, with only 2% of the seedlings succumbing to *H. annosum*. Sitka spruce maintains its position as the universal suscept, with 63% (170 trees) positive for H. annosum. These values, although statistically significant, are lower than expected. The Sitka spruce data attest to the pathogenicity of both the true fir and giant sequoia derived isolates. There is no statistical difference between isolates collected from true fir and those collected from giant sequoia.

The second experiment (4D.2 (Table 8)) was conducted because of the lower than expected mortality observed in Experiment 4D.1. Despite relatively low Sitka spruce mortality in this experiment, overall mortality of both giant sequoia and white fir was greater than in Experiment 4D.1. When the isolate data are grouped by host source, the sequoia isolates appear less virulent. It is important to note that while mortality is low, isolates collected from fir are capable of causing disease in giant sequoia and vice versa in greenhouse trials. The fact that giant sequoia mortality is low may attest to the hardiness of the species.

Genetic Analysis

A brief discussion of the genetic analysis results is presented here because of their importance to the overall findings of the study. More detailed information on the genetic analysis procedures and results obtained can be found in Otrosina et al. (1992) and Piirto et al. (1992b).

All 42 Heterobasidion annosum isolates included in the isozyme analysis trials were found to belong to the "S" intersterility group. This characteristic may allow giant sequoia and true fir derived isolates to cross-infect hosts (Piirto 1977).

The presence of clamp connections, the sign of sexual compatibility, was found on all but one isolate pairing and no selfs in the sexual compatibility trials. The two incompatible isolates, or clones, were found on opposite ends of a fallen giant sequoia tree near Crescent Meadow in Sequoia National Park. The fact that clones (same individuals) occur more that 100 feet apart on the same tree may indicate that the fungus is operating both as a pathogen (while the tree was alive) and as a saprophyte. No tissue clones were evident in the vegetation compatibility trials.

SUMMARY, CONCLUSIONS AND MANAGEMENT IMPLICATIONS

There is no doubt that fire plays an important ecological role in the giant sequoia-mixed conifer ecosystem. Research has clearly documented fire regimes in relation to several interacting variables (i.e., regional climate phenomena, local site variables). Fire frequency has dropped considerably since 1860 (Swetnam 1993).

Fire managers are faced with the task of reintroducing fire into giant sequoia groves in a careful and responsible manner. Defining what "careful and responsible manner" means was part of the impetus for the fire-pathogen research described here. There were concerns that fire scars could increase in size during prescribed burning. Fire scars are known entrance courts for pathogen and insect attack (Piirto 1994). Several questions formed the basis for this study: (1) What percentage of circumference and cross-sectional area do fire scars occupy on large old-growth giant sequoia trees? (2) What amount of change occurs to fire scars on giant sequoia trees from prescribed burning operations? (3) What microorganisms and insects are associated with giant sequoia fire scars? (4) Are the populations of *H. annosum* in giant sequoia and white fir trees genetically similar? (5) Are isolates of *H. annosum* from giant sequoia and white fir pathogenic?

Circumference of giant sequoia trees affected by fire scars ranged from 3.3% to 69.5%. Cross-sectional area affected by fire scars ranged from 3.2% to 53.7%. Reliance upon averages based on groundline circumference and cross-sectional area data could be useful as a gauge of the extent of the structural support base affected by fire scars on individual trees. These average values could provide useful information for managers of giant sequoia groves when making decisions regarding protective measures to take prior to (e.g., pretreating fuels around old-growth trees) and during (e.g., hose lays used to put out burning fire scars that are substantially increasing in size over an extended period of time) prescribed burning operations.

No statistically significant differences exist among the three burn group categories for amount of circumference and cross-sectional area affected

Table 7. Incidence of seedlings infected and killed from inoculation with *Heterobasidion annosum*. experiment 4D.1[1]

Iso-late	Source	Giant sequoia #	Giant sequoia %	White fir #	White fir %	Sitka spruce #	Sitka spruce %	Ponderosa pine #	Ponderosa pine %	Isolate total #	Isolate total %
T241	Abies	0	0	3	7	32	71	18	40	53	30
T243	Abies	1	2	5	11	23	51	12	27	41	23
T247	Abies	1	2	7	16	34	76	8	18	50	28
T505	Sequoia	0	0	4	9	33	73	3	7	40	22
T507	Sequoia	3	7	4	9	25	56	2	4	34	19
T508	Sequoia	1	2	8	18	23	51	8	18	40	22
Species total & ave.[2]		6	2	31	12	170*	63*	51	19	258	24

Number and percent of seedlings infected and killed.

[1] 45 trees inoculated/treatment.
[2] ave = average for the percent columns; * = statistically significant value ($p<0.01$).

Table 8. Incidence of seedlings infected and killed from inoculation by *Heterobasidion annosum*, experiment 4D.2[1].

		Number and percent of seedlings infected and killed									
		Giant sequoia		White fir		Sitka spruce		Ponderosa pine[2]		Isolate total	
Isolate	Source	#	%	#	%	#	%	#	%	#	%
ORE 102	Abies	3	5	29	48	19	32	—	—	51	28
T241	Abies	0	0	20	30	12	20	3	5	35	15
T243	Abies	5	8	26	43	5	8	—	—	36	20
T247	Abies	5	8	29	48	10	17	—	—	44	24
T505	Sequoia	0	0	17	28	9	15	—	—	26	14
T507	Sequoia	1	2	3	5	0	0	—	—	4	2
T508	Sequoia	3	5	3	5	2	3	—	—	8	4
170-2	Australia	3	5	2	5	1	1	—	—	6	3
Species total & averages[3]		20	4	129*	27*	58	12	3	5	210	14

[1] 60 trees inoculated/treatment.
[2] Only inoculated with isolate T241.
[3] = average for the percent columns: * = statistically significant values (Chi-square $p < 0.01$).

by fire scars at groundline (Tables 1 and 2). However, upon closer examination of the fire scars in the 1-year and 5-year prescribed burn groups, substantial damage to the callus tissue, recession, and obvious damage directly associated with the prescribed burning operation were observed. Use of statistically non-significance results between burn groups to justify prescribed burning programs based on the premise that no damage to old-growth trees is occurring is inappropriate and not supported under closer scrutiny. The season of the year in which prescribed burning takes place could influence the effect fire has on giant sequoia trees, based on data from the 5-year burn group which showed a significant difference between early-season and late-season prescribed burns and their effect on giant sequoia fire scars. Though this finding was limited to the 5-year burn group and not found to be significant in the 1-year burn group, this finding warrants further investigation into other factors, such as fuel loading, fuel moisture, and other fire behavior parameters. It must be recognized that the possibility exists that season of burn is having an effect on fire scar development and enlargement in giant sequoia trees.

It was noted that: (1) resin was present on 86% of the fire scars examined; (2) carpenter ants were commonly observed on 61% of the fire scars examined; (3) a variety of insects and arachnids were commonly found on fire scars; (4) decay is frequently observed behind the fire scar above and more frequently below ground; (5) bird cavity activity was commonly seen on 58% of the fire scars examined (Table 3). Statistically significant differences in bird cavity activity, decay above groundline, and carpenter ant activity were noted between the unburned group, 1-year burn group, and 5-year burn group.

The Pilodyn readings showed a significant difference between the above and below groundline readings, with the area below groundline exhibiting a much higher presence of decay. This could be a result of two independent or interacting factors: presence or absence of decay, and variations in wood moisture content above and below groundline. Even though decay does exist above groundline, there is a notable difference in the presence of decay between the two areas.

There are common associations of a variety of microfungi with giant sequoia fire scars. The fungi most frequently isolated were: *Byssochlamys fulva* from 34 of 90 (38%) fire scars, *Acrodontium intermissum* from 22 of 90 (24%) fire scars, and *Tritirachium* sp. from 14 of 90 (16%) fire scars. Other identified fungi associated with giant sequoia fire scars were: *Neosartorya fischeri*, *Epicoccum nigrum*, *Leptographium* sp., *Hyalorhinocladiella* sp., *Marianriaea elegans.* Four confirmed Basidiomycete cultures were isolated from giant sequoia fire scars with one culture being identified as Phlebia subserialis (Bourd. et Galzin) Donk. Prescribed burning affects the incidence (i.e., extent) and type of organisms that occur in the fire scar area. This effect appears to be time-related. Populations of some fungal species are diminished and others appear to be stimulated by prescribed burning activities in giant sequoia groves.

H. annosum acts as both a saprophyte and a pathogen in the giant sequoia-mixed conifer ecosystem. The results of these experiments demonstrated *H. annosum* can spread from true fir to giant sequoia and vice versa given they are from the same "S" intersterility group. *H. annosum* isolates from true fir and giant sequoia are pathogenic. These findings add credence to the hypothesis that changing stand structure and ecosystem interactions resulting from the absence of fire could also be affecting pathogen interactions between true fir and giant sequoia. The increase of *Abies* sp. in the understory as a result of fire exclusion and its common role as a host for H. annosum are clearly suggestive.

The management implications of these research findings focus primarily on the need to include additional provisions for protecting old-growth giant sequoia and important associated trees during prescribed burning operations, particularly when fuel accumulation and/or stand density is high in and around the base of these trees and when existing fire scars already occupy a significant amount of the circumference and cross-sectional area of the tree. This recommendation is consistent with recommendations made by several previous researchers (e.g., Leopold 1963).

Monitoring the effects of prescribed burning on decay and insect populations should be part of a fire monitoring program. Attention should be focused on the amount of mortality that occurs directly or indirectly from insect and disease attack following prescribed burning operations. A system to measure and survey fire scar characteristics and changes that occur from prescribed burning operations should be included as part of the fire monitoring program. Recommendations for monitoring fire-pathogen interactions are included in a report by Piirto and Parmeter (1990).

ACKNOWLEDGMENTS

This research work would not have been possible without the financial and logistical support from the U.S. Department of the Interior, National Park Service and the McIntire Stennis program. This support is very much appreciated.

Special acknowledgment and appreciation are expressed to: (1) Dr. David Parsons, Dr. Jan van-Wagtendonk, Mr. Larry Bancroft, Mr. Tom Nichols, Ms. Patti Haggerty, Ms. Anne Esperanza, and other personnel from the National Park Service; (2) Dr. David Wood, Ms. Tina Bailey, and other personnel from the University of California at Berkeley; (3) Dr. Tom Chase formerly with the Pacific Southwest Forest and Range Experiment Station, U.S. Department of Agriculture, Forest Service; (4) Dr. June Wang of State University of New York at Syracuse (SUNY) and Ms. E. Dorworth of the Center for Forest Mycology research at Madison, Wisconsin for assistance in identifying fungal isolates; and (5) Dr. Tim Plumb, Dr. V. L. Holland, Ms. Carol Osgood, Ms. Margaret Cardoza, and Ms. Joyce McAlexander from California Polytechnic University for secretarial and administrative support of this project.

LITERATURE CITED

Anonymous. 1960. Index of plant diseases in the United States. Agriculture Handbook 165. U.S. Department of Agriculture, Washington, DC.

Bega, R.V. 1964. Diseases of sequoia. Pages 131 – 139 in Diseases of widely planted forest trees. FAO/IUFRO symposium on internationally dangerous forest diseases and insects. U.S. Department of Agriculture, Washington, DC.

Bega, R.V. 1978. Diseases of Pacific coast conifers. Agriculture Handbook 521. U.S. Department of Agriculture, Washington, DC.

Bonar, L. 1971. A new Mycocalicium on scarred sequoia in California. Madrono 21:62 – 69.

Boyce, J.S. 1948. Forest pathology. McGraw-Hill, New York.

Boyce, J.S. 1961. Forest pathology. Third Edition. McGraw-Hill Book Co., New York.

Burdsall, H. 1992. Personal communication.

Christensen, N.L., L. Cotton, T. Harvey, R. Martin, J. McBride, P. Rundel, and R. Wakimoto. 1987. Final report – review of fire management program for sequoia-mixed conifer forests of Yosemite, Sequoia and Kings Canyon National Parks. Unpublished report on file at Sequoia-Kings Canyon National Parks, Three Rivers, CA.

Davidson, J.G.N. 1972. Pathological problems in redwood regeneration from seed. Dissertation. University of California, Berkeley.

Dence, C.W., D.J.K. Wang, and P.R. Durkin. 1979. Toxicity reduction through chemical and biological modification of spent pulp bleaching liquors. Environmental Protection Agency, Washington, D.C.

Dorworth. E. 1992. Personal communication.

Dulitz, D. 1994. Management of giant sequoia on Mountain Home Demonstration State Forest.

Pages 118 – 119 in P.S. Aune (technical coordinator). Proceedings of the symposium on giant sequoias: their place in the ecosystem and society. General Technical Report PSW-GTR-151, U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, CA.

Duncan, C.G., and F.J. Deverall. 1964. Degradation of wood preservatives by fungi. Applied Microbiology 12:57 – 62.

Hammon, Jensen, and Wallen Mapping and Forestry Service, Inc. 1964, 1970, 1975, 1976. Unpublished reports on file at Sequoia and Kings Canyon National Parks, Three Rivers, CA.

Hartesveldt, R.J. 1962. The effects of human impact upon Sequoia gigantea and its environment in the Mariposa Grove, Yosemite National Park, California. Dissertation. University of Michigan at Ann Arbor.

Hartesveldt, R.J. 1964. Fire ecology of giant sequoia: controlled fires may be one solution to survival of the species. Naturai History Magazine 73:12 – 19.

Hartesveldt, R.J. 1965. An investigation of the effect of direct human impact and of advanced plant succession on Sequoia gigantea in Sequoia and Kings Canyon National Parks. Unpublished report on file with the U.S. Department of the Interior, National Park Service, San Francisco, California.

Harvey, A.E., M.F. Juergensen, and M.J. Larsen. 1976. Intensive fiber utilization and prescribed fire: effects on the microbial ecology of forests. General Technical Report INT-28, U.S. Department of Agriculture, Forest Service.

Hepting, G.H. 1935. Decay following fire in young Mississippi Delta hardwoods. Technical Bulletin 474, U.S. Department of Agriculture.

Hepting, G.H. 1971. Diseases of forest and shade trees of the United States. Agriculture Handbook 386. U.S. Department of Agriculture. Washington, DC.

Hunt, R.S., and F.W. Cobb, Jr. 1971. Selective medium for the isolation of wood-rotting basidiomycetes. Canadian Journal of Botany 49:2064-2065.

Kilgore, B.M. 1972. Impact of prescribed burning program for sequoia-mixed conifer forest. Tall Timbers Fire Ecology Conference Proceedings 12:345 – 376.

Leisz, D. 1994. Remarks for the giant sequoia symposium. Pages 1 – 4 in P.S. Aune (technical coordinator). Proceedings of the symposium on giant sequoias: their place in the ecosystem and society. General Technical Report PSW-GTR-151, U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, CA.

Leopold, A.S., S.A. Cain, C.M. Cottam, I.N. Gabrielson, and T.L. Kimball. 1963. Wildlife management in national parks. American Forests 69:32 – 35, 61 – 63.

Levy, J.F. 1969. Studies on the ecology of fungi in wood fence posts. Pages 1:424-428 in A.H. Walters and J.J. Elphick (eds.). Biodeterioration of materials. Elsevier Publishing Company, New York.

McDonald, J.E. 1994. The Sequoia Forest Plan settlement agreement as it affects Sequoiadendron giganteum: a giant step in the right direction. Pages 126 – 128 in P.S. Aune (technical coordinator). Proceedings of the symposium on giant sequoias: their place in the ecosystem and society. General Technical Report PSW-GTR-151, U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, CA.

Meyer, F.A. 1952. The status of Sequoia gigantea in the Sierra Nevada. Senate Concurrent Resolution No. 44, 1951 General Session, Sacramento. State of California Printing Office.

Muir, J. 1877. On the post glacial history of Sequoia gigantea. Pages 242 – 252 in Proceedings of the American Association for the Advancement of Science.

Nelson, R.M.. Jr., I.H. Sims, and M.S. Abell. 1933. Basal fire wounds on some southern Appalachian hardwoods. Journal of Forestry 31:829 – 837. ’

Nordin, V.J. 1958. Basal fire scars and the occurrence of decay in lodgepole pine. Forestry Chronicle 34:257 – 265.

Otrosina, W.I., Chase T.E., and Cobb, F.W. 1992. Allozyme differentiation of intersterility of Heterobasidion annosum isolated from conifers in the western United States. Phytopathology 82:540-545.

Parmeter, J.R., Jr. 1977. Effects of fire on pathogens. Pages 58 – 64 in H.A. Mooney and C.E. Conrad (technical coordinators). Proceedings of the symposium of fire and fuel management in Mediterranean ecosystems. Palo Alto, CA.

Parmeter, J.R., Jr. 1986. Diseases and insects of giant sequoia. Pages 11 – 13 in C.P. Weatherspoon, Y.R. Iwamoto, and D.D. Piirto (technical coordinators). Management of Giant Sequoia. General Technical Report PSW-95, U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station, Albany, CA.

Parmeter, J.R., Jr., and B. Uhrenholdt. 1975. Some effects of pine needle or grass smoke on fungi. Phytopathology 65:28 – 31.

Parmeter, J.R., Jr., and B. Uhrenholdt. 1976. Effects of smoke on pathogens and other fungi. Tall Timbers Fire Ecology Conference Proceedings 14:299 – 304.

Parsons, D.J. 1990. The giant sequoia fire controversy: the role of science in natural ecosystem management. Pages 257 – 267 in C. van Riper III, T.J. Stholgren, S.D. Veirs, Jr., and S.C. Hillyer (eds.). Examples of resource inventory and monitoring in National Parks of California. Transactions and Proceedings Series No. 8. U.S. Department of the In-terior, National Park Service, Washington, DC.

Parsons, D.J. 1994. Objects or ecosystems? Giant sequoia management in national parks. Pages 109 – 115 in P.S. Aune (technical coordinator). Proceedings of the symposium on giant sequoias: their place in .the ecosystem and society. General Technical Report PSW-GTR-151. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, CA.

Peace, T.R. 1962, Pathology of trees and shrubs. Clarendon Press, Oxford. Piirto, D.D. 1977. Factors associated with tree failure of giant sequoia. Dissertation. University of California. Berkeley.

Piirto, D.D. 1994. Giant sequoia insect, disease and ecosystem interactions. Pages 82 – 89 in P.S. Aune (technical coordinator). Proceedings of the symposium on giant sequoias: their place in the ecosystem and society. General Technical Report PSW-GTR-151, U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, CA.

Piirto, D.D., J.R. Parmeter, Jr. and F.W. Cobb, Jr. 1974. Fomes annosus in giant sequoia. Plant Disease Reporter 58:478.

Piirto, D.D., J.R. Parmeter, Jr., and W.W. Wilcox. 1977. Poria incrassata in giant sequoia. Plant Disease Reporter 61:50. Piirto, D.D., and W.W. Wilcox. 1978. Critical evaluation of the pulsed current resistance meter for detection of decay in wood. Forest Products Journal 28:52 – 57.

Piirto, D.D., J.R. Parmeter, Jr. and W.W. Wilcox. 1984a. Basidiomycete fungi reportedly associated with living or dead giant sequoia and coast redwood. California Forestry and Forest Products No. 55, University of California, Berkeley.

Piirto, D.D., W.W. Wilcox, J.R. Parmeter, Jr., and D.L.Wood. 1984b. Causes of uprooting and breakage of specimen giant sequoia trees. Bulletin 1909. University of California, Berkeley.

Piirto, D.D., and J.R. Parmeter, Jr. 1988. Proposal for funding – biological and management implications of fire-pathogen interactions in the giant sequoia ecosystem. Unpublished report on file at Sequoia and Kings Canyon National Parks, Three Rivers, CA.

Piirto, D.D., and J.R. Parmeter, Jr. 1990. Interim technical report 02 – Biological and management implications of fire-pathogen interactions in the giant sequoia ecosystem. Unpublished report on file at Sequoia and Kings Canyon National Parks, Three Rivers, CA.

Piirto, D.D., K. Piper, and J.R. Parmeter, Jr. 1992a. Final report. Biological and management implications of fire-pathogen interactions in the giant sequoia ecosystem; Part I – fire scar pathogen studies. Unpublished report on file at Sequoia and Kings Canyon National Parks, Three Rivers, CA.

Piirto, D.D., F.W. Cobb, Jr., A. Workinger, W.J. Otrosina, and J.R. Parmeter, Jr. 1992b. Final report. Biological and management implications of fire-pathogen interactions in the giant sequoia ecosystem; Part II – pathogenicity and genetics of Heterobasidion annosum.. Unpublished report on file at Sequoia and Kings Canyon National Parks, Three Rivers, CA.

Piper, K.L. 1992. Biological and management implications of fire-pathogen interactions in the giant sequoia ecosystem: fire scar-pathogen studies. Thesis. California Polytechnic State University, San Luis Obispo.

Reaves, J.L., C.G, Shaw III, and J.E. Mayfield. 1990. The effects of Trichoderma spp. isolated from burned and non-burned forest soils on the growth and development of Armillaria ostoyae in culture. Northwest Science 64:39 – 44. Rogers, R.R. 1997. Personal communication. Sequoia National Forest. Porterville, CA.

Rundel, P.W. 1972. An annotated list of the groves of Sequoiadendron giganteum in the Sierra Nevada, California. American Midland Naturalist 85:478 – 492.

Sequoia and Kings Canyon National Parks. 1992. Fire management plan. Unpublished report on file at Sequoia and Kings Canyon National Parks, Three Rivers, CA.

Stewart, R., S. Keyes, B.A. Waldron, and R.R. Rogers. 1994. Giant sequoia management in the national forests of California. Pages 152 – 158 in P.S. Aune (technical coordinator). Proceedings of the symposium on giant sequoias: their place in the ecosystem and society. General Technical Report PSW-GTR-151, U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, CA.

Swetnam, T. 1993. Fire history and climate change in giant sequoia groves. Science 262:885 – 888.

Wang, C.J.K., F.C. Terracina, and R.A. Zabel. 1989. Fumigant effectiveness in creosote- and penta-treated southern pine poles. State University of New York, Syracuse.

Wang, C.J.K., and R.A. Zabel. 1990. Identification manual for fungi from utility poles in the eastern United States. Allen Press, Inc., Lawrence, KS.

Western Timber Service, Inc. 1970. Sequioa tree inventory. Un-published report on file at Sequoia and Kings Canyon National Parks, Three Rivers, CA.

Wilcox, W.W. 1983. Sensitivity of the ”pick test” for field detection of early wood decay. Forest Products Journal 33: 28-30.

Wilcox, W.W. 1988. Detection of early stages of wood decay with ultrasonic pulse velocity. Forest Products Journal 38: 68-73.

Wilcox, W.W. 1991. Need for non-destructive evaluation (NDE) in detection of decay in structures. General Technical Report PSW-128, U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, CA.

Zagory, D., S.E. Lindow, and J.R. Parmeter, Jr. 1983. Toxicity of smoke to epiphytic ice nucleation active bacteria. Applied Environmental Microbiology 46:114 – 119.

Zagory, D., and J.R. Parmeter. Jr. 1984. Fungitoxicity of smoke. Phytopathology 74:1027 – 1031.

Citation: Piirto, Douglas D., John R. Parmeter, Jr., Fields W. Cobb, Jr., Kevin L. Piper, Amy C. Workinger, and William J. Otrosina. 199S. Biological and management implications of fire-pathogen interactions in the giant sequoia ecosystem. Pages 325 – 336 in Teresa L. Pruden and Leonard A. Brennan (eds.). Fire in ecosystem management: shifting the paradigm from suppression to prescription. Tall Timbers Fire Ecology Conference Proceedings, No. 20. Tall Timbers Research Station, Tallahassee, FL.