VEGETATION PROCESS STUDIES
California Air Resources Board
Integrated Watershed Project

Final Contract Report
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VEGETATION PROCESS STUDIES
Log Meadow,
Sequoia National Park

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ABSTRACT

This work was undertaken to supply baseline data about ecosystem processes that might be affected by acid deposition and air pollution. The project encompasses seven subtopics: stand data and dynamics, lichens studies, tree ring analysis, above ground biomass and production for two dominant *Abies* species and for non-*Abies* species, analytical work related to nutrient pools, below ground production, and population studies.

The work performed included evaluation of thallus morphology of a dominant lichen species, analysis of 25 elements in three important lichens species, analysis of potentially toxic elements in tree rings, the establishment of regressions and evaluation of published regressions for estimating net annual above ground production, determination of element concentrations in plant tissues, quantification of below ground production, and resampling of 10-15 year old permanent plots.

Results included the finding that *Hypogymnia imshaugii* at our site is somewhat convolute, that certain elements were in significantly higher concentrations in H. *imshaugii* than in two other lichen species, that *Abies concolor* tree rings showed a sharp decline in calcium levels in the past 30 years. Above ground production of two *Abies* species is high. Regressions were found for estimating biomass and production of the non-*Abies* species. A substantial body of data was amassed on nutrient pools. Foliar levels of magnesium are low and of aluminum are high in older needles of *A. magnifica* growing on skeletal soils with low pH's, but not on richer soils. This may indicate an sensitivity in such habitats to soil leaching. Below ground biomass was 970 g/m<2> and 2785 g/m<2> in October 1984 and May 1985, respectively. Production of the \<2 mm size class was 158 g/m<2> during the same period. Mycorrhizal colonization was determined and a conversion factor used to estimate production. Burned stands of mixed-conifer forest experienced mortality, shifts in species composition, and changes in basal area. *Sequoiadendron giganteum* reproduced slowly, but had very low mortality and generally increased in basal area. *Calocedrus decurrens* grew and reproduced with surprising rapidity. *Pinus ponderosa* showed relatively high mortality.

Conclusions of the work include the subtle effects of pollution potentially acting in the mixed-conifer forests, as indicated by lichen studies. Foliar levels of magnesium and aluminum may indicate potential sensitivity of *A. magnifica* to pollution on poor soils. Below ground production is rather low and above ground production is high in these forests.

ACKNOWLEDGEMENTS

We acknowledge with thanks the continuing cooperation and logistic support of the staff of Sequoia and Kings Canyon National Parks, particularly Dr. David Parsons and Thomas Stohlgren. This support has been an essential element in the success of our research program. Our work could not have been carried out without the field assistance of a number of individuals. Peter Rabenold, Karen Poulin and Carmelle Crivellone carried out much of the field work on nutrient pools and below ground production. Michael Neuman, David Frew, Justine Rosenthal, and Nancy Sidaras provided the field measurements used to construct the above ground biomass regressions for red and white fir. Sherman Lambert completed the field plot recensuses and drafted the section on population studies.

These biomass and productivity data were a cooperative project completed with joint funding by the California Air Resources Board and the National Aeronautics and Space Administration.

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DISCLAIMER

The statements and conclusions in this report are those of the contractor and not necessarily those of the California Air Resources Board. The mention of commercial products, their source, or their use in connection with material reported herein is not to be construed as either an actual or implied endorsement of such products.

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SUMMARY AND CONCLUSIONS

The short and long-term effects of acid deposition are thought to be one of the most critical environmental issues of the day. California has a great deal at risk in the losses to forest resources that potentially could result from acid deposition and other forms of pollution in the next few years. Evaluation of this risk and development of a plan for managing the resources is properly a matter of high priority for responsible State agencies. The work described in this report provides one element in a group of interrelated, continuing projects on the effects of acid deposition in Sequoia National Park.

During this research we have felt strongly that the most important areas for study are baseline values of above and below ground production. Future efforts by the staff of the Air Resources Board and cooperating scientists to develop mass flow budgets for phosphorus, nitrogen, aluminum, cations and trace elements through terrestrial ecosystems within the watershed will depend on a data base of production studies. Below ground production studies should provide the earliest warning of potentially deleterious effects of acid deposition.

Indications from the lichen studies are that subtle but potentially significant effects of pollution are being experienced in the mixed-conifer forests of Sequoia National Park. The convoluted form of the thallus of Hypogymnia imshaugii has previously been implicated in ozone-induced damage (Sigal and Nash 1983), and certainly ambient ozone levels are moderately high in the Giant Forest area. There are no indications, however, of especially high levels of trace elements which could indicate inputs of toxic combustion products. Soil organisms that mediate crucial soil processes, including decomposition, mineralization, transformation of nutrient ions, and uptake of nutrients, may be suffering pollution effects as well. The manifestations of the effects on these organisms, and the effects on the roots themselves, are much less evident than in the case of the lichens. They will not be observable except by comparison with data bases of the kind being generated by this work.

Nutrient and trace element analyses of tree-ring cores do not exhibit any clear patterns of either build-up of combustion-related pollutants in recent years or declines in cations suggestive of significant leaching of such cations from soils. Cores from Abies concolor do indicate that there are decreasing levels of calcium and strontium over the past 20 years, but this steady decrease could will be a function of physical deposition of calcium in sapwood through time rather than a resultant of soil leaching. We are investigating this pattern in more detail in our ongoing program of research.

The study of above ground production has shown that the mixed-conifer forests, especially those dominated by A. concolor, are among the most productive in the Western United States. The high productivity is in part a consequence of a relatively high fraction of above ground biomass allocated to photosynthetic tissue in A. concolor. Any pollution effects leading to early loss of leaves or reduction in leaf biomass could be expected to seriously impact above ground production of the mixed-conifer forests.

Data for below ground production indicate rather low production values at this site, in comparison to other coniferous forests. This may reflect differences in climate, tree species, and soil fertility. Since above ground production is not notably low, the root/shoot production ratio is lower than that of most coniferous forests. A low ratio of below ground to above ground production is probably a reflection of relatively favorable nutrient conditions at the Log Meadow site. Pollution or acid-related disruptive processes that negatively influence soil nutrient availability, or suppress to any extent the activities of symbiotic organisms such as mycorrhizae, can be expected to change the above ground/ below ground production and biomass ratios. Any photosynthate diverted to below ground processes is lost from the above ground forest, where it figures importantly in human perceptions of the recreational value and in many economically important watershed functions.

Pools of cations in foliage of Abies concolor and A. magnifica over a gradient of needle age does not indicate unusual declines in magnesium and calcium in second year and older needles comparable to what has been reported for conifers from areas of forest decline in New England and Germany. Foliar levels of magnesium from older needles of A. magnifica growing on skeletal soils with low pH's, however, are quite low, perhaps very close to limiting levels. This may indicate an extreme potential sensitivity of this species in such habitats to soil leaching. Such low levels of magnesium were not found on richer, less acid soils. Abies magnifica growing on skeletal soils accumulated high concentrations of aluminum in foliage and bark in comparison to individuals growing on richer soils. This again indicates a great potential sensitivity to pollution effects on poor habitat types.

Our data on stand dynamics in mixed-conifer forests of Sequoia and Kings Canyon National Parks, based on approximately 15-18 years of intervening growth in a series of permanent plots, indicates that burned stands of mixed-conifer forest experienced mortality, shifts in species composition, and changes in basal area. While Sequoiadendron giganteum reproduced slowly, it also had very low mortality and generally increased in basal area. Calocedrus decurrens grew and reproduced with rapidity that was surprising, since it is usually considered a minor species. If such a level of mortality were to continue in the future, the population structure of this species would alter drastically. Since this taxon is known to be sensitive to oxidant pollutants, special attention should be given to documenting future rates and causes of mortality. The unburned sites, which would be considered from a management standpoint to be undisturbed, showed similar kinds of change. Any relationship of the changes to human influences, including pollution, should be investigated.

RECOMMENDATIONS

1. It has been stressed throughout the communications of this project that the collection of baseline data is intrinsically a long-term task. Some of the most important measurements, especially above and below ground production, can be quite variable from year to year. An example is evident in this first year of work. The conventional soil core method for determining below ground production, when used only over one or two growing seasons, leaves doubt about whether the estimated production rates are artifacts of year-to-year variations in standing crop. The quality of future research and regulatory policy will depend strongly on the accuracy and representative nature of the data being generated now. The data base will be in an increasingly stronger position as more years of data are collected.

2. The biological effects of acid deposition and pollution may be expressed in ways that are not anticipated by the rather limited database generated by these early studies. Other kinds of data are required for fullest utilization and interpretation of the baseline production estimates:

3. Nitrogen fixation is a vital ecosystem process that is known to be sensitive to pH and toxic materials. Both leguminous and non-leguminous nitrogen fixation should be quantified, and the responses to pollutants studied.
The pollution responses of the primary producer species should be studied under controlled, greenhouse conditions.

4. The response to pollutants of decomposition, which like other important ecosystem processes is mediated by sensitive microorganisms, should be studied. The dynamics of litterfall are an important component of decomposition processes.

5. The relationship between fire-induced and pollution-induced pH shifts should be studied. The effects of both on critical ecosystem processes, such as above and below ground production, should also be investigated.

6. Mass flow budgets of nutrient and toxic elements should be prepared as an aid in understanding the potential effects of perturbation at the ecosystem and watershed levels.

7. Meeting these objectives will require extensive integration of past, present and future research by many workers. The integration of our biomass and productivity data, and related nutrient pool and flux sizes, with other elements of the Integrated Watershed study will be a critical task for the overall success of this project.

8. A final concern we raise here is the difficulty in establishing causality for any biological effects of reduced productivity which we may find by the end of our project (or on a longer time scale). Regulatory policy related to pollution effects on natural ecosystems requires a clear link between cause and effect. The challenge will be to separate potential effects of acid deposition from effects of oxidant pollutants. The present structure of the Integrated watershed study is not adequate to establish the nature of such links.

INTRODUCTION

This report covers the first year of work on vegetation processes at Sequoia National Park, carried out between May 24, 1984 and August 23, 1985. Our work was undertaken as a study of the base level processes of growth and nutrient dynamics that may be influenced in coming years by acid deposition. This is part of a continuing project, and the first year's findings are difficult to interpret fully if isolated from the continuing work. For this reason, frequent reference will be made to aspects of the project that are still under study.

Detrimental effects have been documented elsewhere, and have been described in reviews and symposia by Mudd and Kozlowski (1975), Hutchinson and Havas (1980), Miller (1980), and Smith (1981). The impacts of air pollution and acid deposition on forest growth is emerging as on of the most significant environmental issues of the decade. Of the economic losses to be suffered from acid deposition in this country, the forest industry in the Eastern United States is expected to bear a substantially larger share than agriculture (Crocker and Regens 1985). The effects will be felt as both localized mortality and loss of wood production, perhaps as much as 5%.

Although experimental work to date has been primarily in Europe and the Eastern United States, acid deposition has been shown to occur in California (Lawson and Wendt 1982). The Sierra Nevada lie in the path of pollutant-laden air from major metropolitan areas, and include the most sensitive regions of California. Past effects of acid deposition on terrestrial processes in the granitic soils of the Sierra Nevada cannot be assessed because of a lack of relevant baseline data. However, there is ample reason to expect future effects on tree growth and vigor, phenology, soil chemistry, soil microbiology, and nutrient cycling processes (Alexander 1980, McColl 1981b, Hutchinson and Havas 1980).

Understanding and documentation of both the short and long-term effects of acid deposition is an essential goal of the State of California. A broad ecosystem study in the form of an integrated watershed study is the most appropriate approach toward this goal, and will provide a basis for future evaluation of the influences of acid deposition in the Sierra Nevada.The work described in this report provides one element in a group of interrelated projects on the effects of acid deposition in Sequoia National Park.

Project objectives

The goal of this project has been the determination of both above and below ground production as a data base against which future changes may be assessed. The research reported here has centered on a small headwater drainage within the watershed of the Marble Fork of the Kaweah river.This montane site (Log Meadow) is a mixed-conifer/stream ecosystem with moderately deep soils high in organic matter.

The objectives of this study are as follows:

1. Species/Community Studies

a. <u>Vegetation</u>. Collection and integration of existing vegetation studies of the Log Meadow site, as well as comparable sites outside the drainage, from a large data base assembled by independent researchers at UCLA, San Jose State University, and UC Berkeley, as well as by National Park Service Staff. These studies were to include quantitative interpretations of understory coverage and species diversities for all groups of vascular plants.

b. Lichens. Assessment of lichen dominance on both tree trunk and rock substrates to determine any patterns which might be related to pollution effects; assessment of unusual patterns of morphological growth in dominant lichen species as an indicator of possible atmospheric pollution; analysis of lichen thalli for concentrations of potentially toxic trace elements.

2. Tree Growth

a. Tree rings. Analysis of sample cores from dominant tree species; analysis of tree ring materials to identify potentially toxic trace elements which might be related to annual growth response.

b. above ground production. Application of dimensional analysis to establish regressions for estimating net annual above ground production in dominant trees.

c. below ground production. Quantification of net annual below ground production by fine roots and mycorrhizae for dominant trees.

d. Population Studies. Resampling of 10-15 year old permanent plots of mixed-conifer vegetation to establish baseline data on mortality by size class for dominant tree species.

During this research we have felt strongly that the most important areas for study are baseline values of above and below ground production. Future efforts by the staff of the Air Resources Board and cooperating scientists to develop mass flow budgets for nitrogen, sulfur, phosphorus, and aluminum through terrestrial ecosystems within the watershed will depend on a data base of production studies. The indirect effects of acid deposition and air pollution act primarily through soil processes. These effects potentially include changes in soil pH and changes in solubility or concentration of both essential and toxic elements. Root growth and function are very sensitive to soil chemistry and may be expected to respond to any changes. Soil microbial activity, including that of mycorrhizal fungi, is also responsive to even subtle changes in soil chemistry. Because of these relationships, we believe belowground production may provide the earliest warning of potentially deleterious effects of acid deposition.

Study area

This study is being carried out in cooperation with the National Park Service. The park is an International Biosphere Reserve, and the National Park Service specifically provides research areas for cooperative work. National Park Service personnel carry out related research activities under their own funding, and help coordinate outside and Park Service researchers. This coordination strengthens the total program and minimizes duplication of effort. The park has been the site of an acid rain monitoring station for the National Atmospheric Deposition Program (NADP) since 1980. The NADP station, located at

Giant Forest, has established that summer pH values are normally below 5.0, and occasionally can drop as low as 3.5. Summer and fall storms usually carry less precipitation than winter storms, when the pH is usually between 4.5 and 5.5. Nitrate is thought to be more significant, relative to sulfate, at Sequoia National Park than in the Northeastern U.S.

The watershed research on vegetation processes has been carried out at two sites within the Marble Fork watershed of Sequoia National Park. The Log Creek drainage of Log Meadow, at 2070 m elevation at its bottom, is a perennial stream drainage about 39 ha in size. Climatic data are being collected by the National Park Service from an outcrop in Giant Forest, approximately 1 km to the south and at a similar elevation. Pollutant levels are being monitored 4 km to the west at an exposed site at 1900 m elevation. The long term mean precipitation for the Giant Forest area is about 1137 mm. Precipitation falls mostly as snow. The Log Meadow site is typical of a *Sequoiadendron giganteum* (giant sequoia) mixed-conifer forest. Other important conifers include *Abies concolor* (white fir) , *A. magnifica* (red fir), *Pinus lambertiana* (sugar pine), *P. jeffreyi* (Jeffrey pine), and *Calocedrus decurrens* (incense cedar). Most soils at Log Meadow are classified as dark brown to dark grayish brown, sandy pachic xerumbrepts. Spring, summer, and fall access is by way of trail (1.5 km) from Crescent Meadow. Winter access is by a 4 km cross country ski trail from Giant Forest. The geography of the Log and Tharp Creek watersheds at Log Meadow are shown in Figure 1. This Figure, prepared by the National Park Service, shows the locations of vegetation plots, flumes, and rain gauges in the watersheds.

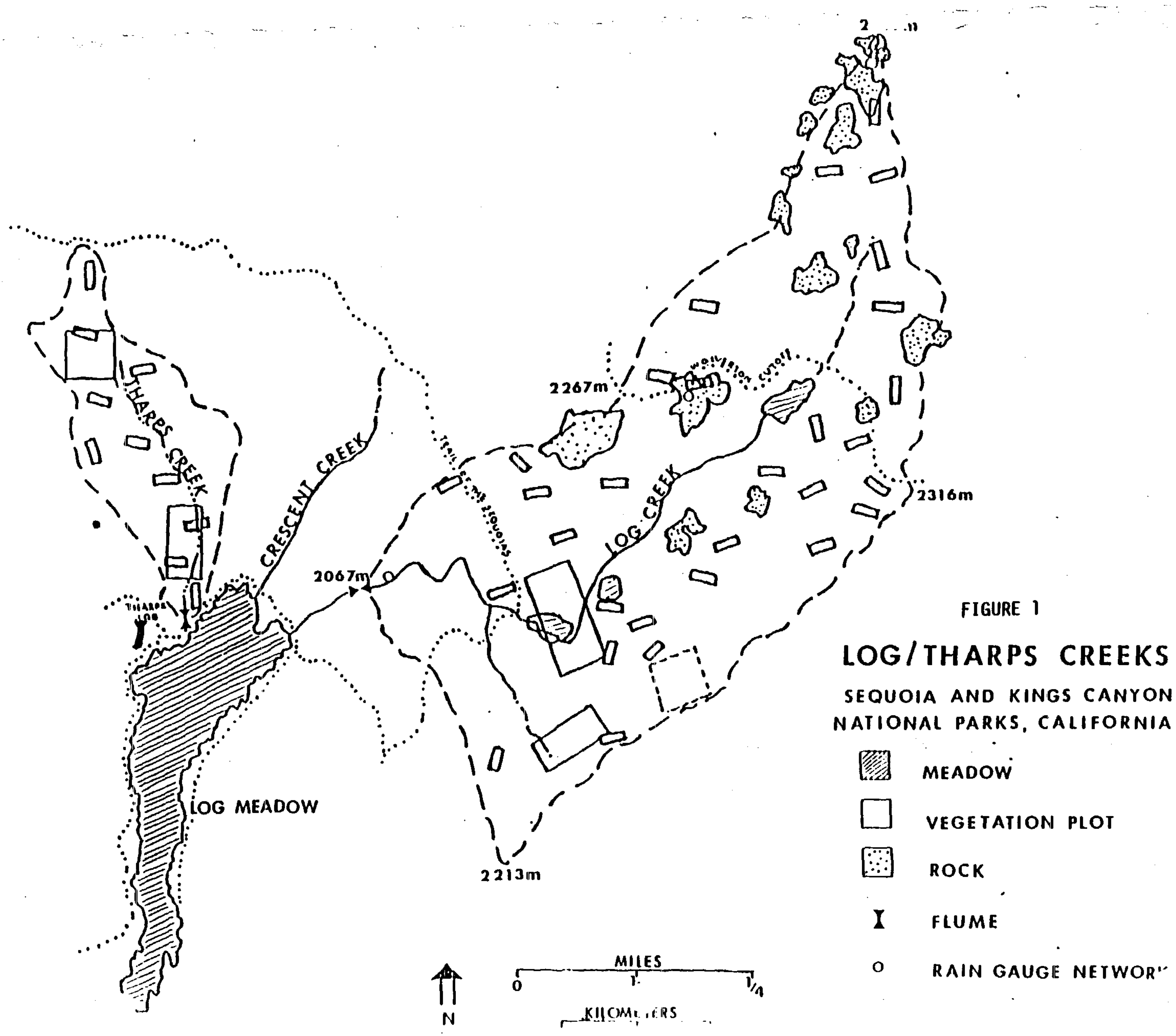

FIGURE 1

LOG/THARPS CREEKS

SEQUOIA AND KINGS CANYON NATIONAL PARKS, CALIFORNIA

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STAND DATA AND DYNAMICS

The primary objective for this portion of the work was to collect data from the above activities and from older data bases, such as those summarized by Rundel et al. (1977), and prepare an updated, detailed description of the vegetation types under study. The final summaries of the data can be expressed in the following form for most stands:

a) distribution of dbh (diameter at breast height) classes for each tree species
b) demographic data on tree population structure
c) relative assessments of tree baselines
d) quantitative assessments of understory coverage

Both small 0.1 ha and 1.0 ha or larger permanent reference stands have been established by the National Park Service in key forest communities (see Figure 1). Every tree in these plots has been tagged, mapped, and measured for dbh and vigor. Shrubs, herbs, and litter accumulation were recorded in subplots. These stands are planned to be periodically resampled by the National Park Service, providing a basis for evaluation of long term growth, mortality, and demography.

The data contributing to these analyses were for the most part generated either by NPS personnel or by researchers from Oregon State University. While it is within the scope of this project to summarize all sources of existing data, the different schedules and short term objectives of NPS researchers make it inappropriate to include their database in our present analysis. The data generated through NPS and other efforts is an important component of the summaries, and must await publication of each unit of research according to the schedules of the individual research efforts. For this reason, we are unable to present detailed data here on the Log Meadow permanent plots. Summary examples of the type of data available are shown in Figure 1 which presents summary data on conifer density and basal area for the 1 ha reference stand at lower Tharp's Creek. Abies concolor is the dominant species, followed by Pinus lambertiana.

Since the specific objectives of this section overlap in some ways with the objectives of the section on tree population studies, we will defer a discussion of the community structure of mixed-conifer stands in the Sequoia-Kings Canyon area until the section of this report dealing with population studies. This section describes the demographic structure of conifers in 39 0.2 ha plots established from 1966-1968 and recensused as part of this project. All of these stands are mixed-conifer vegetation within groves of Sequoiadendron giganteum.

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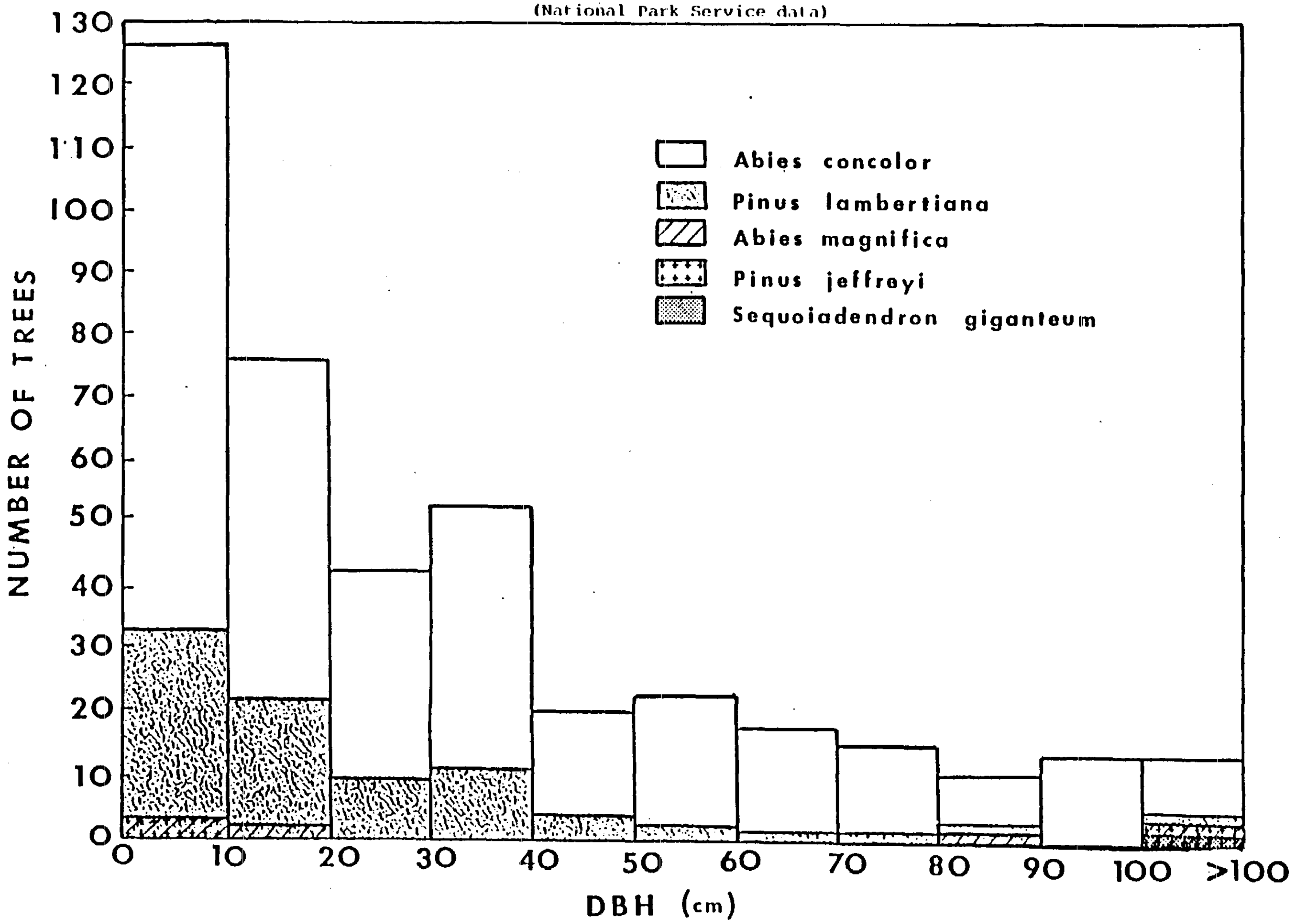
FIGURE 2. **LOWER THARP'S CREEK REFERENCE STAND**

(National Park Service data)



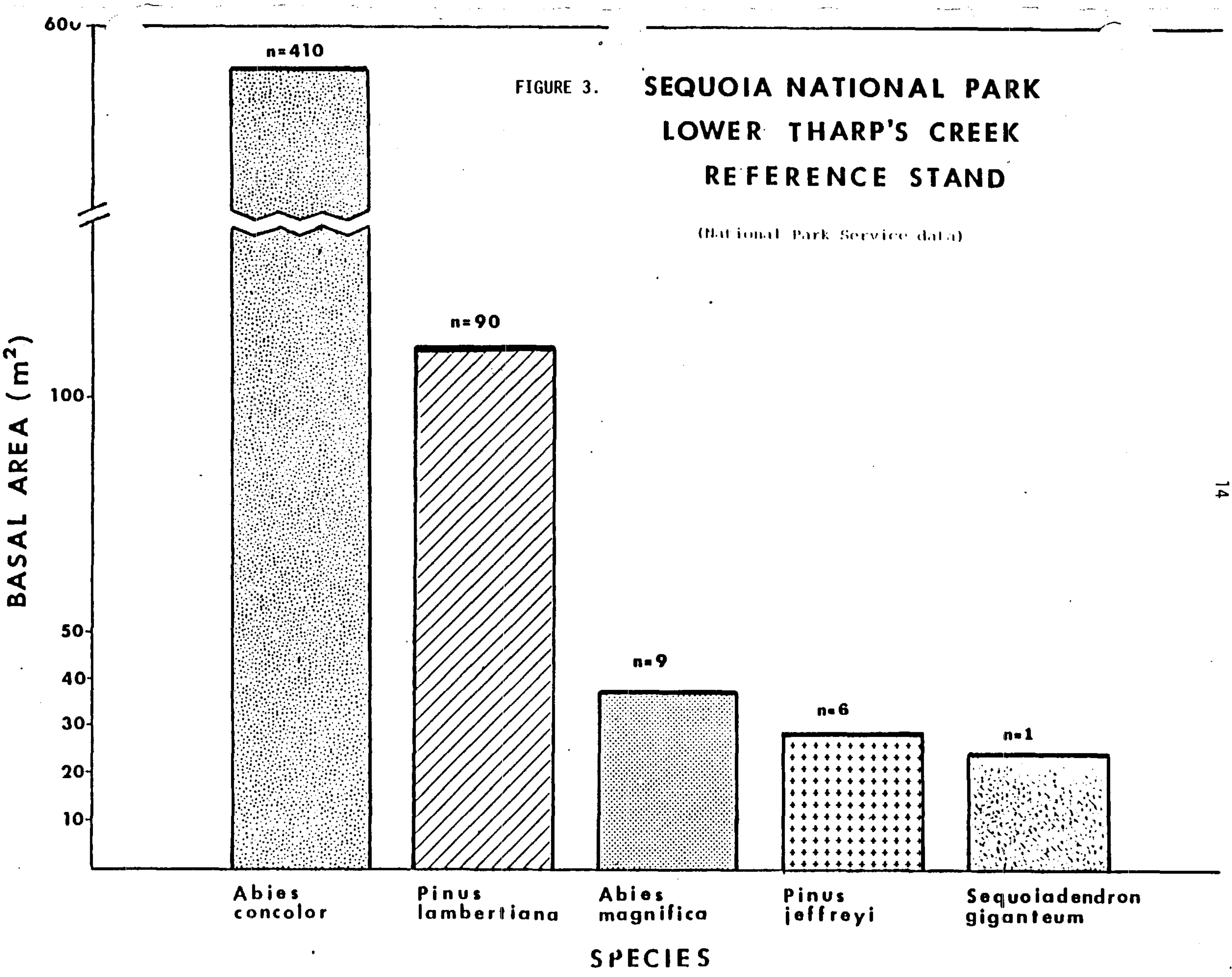


FIGURE 3. SEQUOIA NATIONAL PARK LOWER THARP'S CREEK REFERENCE STAND

(National Park Service data)

LICHENS

The sensitivity of lichens to air pollution is well documented and there is a long history of field studies describing the decline in lichen cover and diversity around cities (see reviews in Ferry 1973). Lichens have been used as bioindicators of air pollution, particularly in European cities, but this approach to pollution monitoring has not been widely used in the United States because of the poor general knowledge of lichen systematics and the general availability of more quantitative pollution monitoring techniques.Nevertheless, appropriate lichen studies can provide a useful means of surveying unstudied areas for potential pollution effects until more quantitative measures of pollution levels are available.

While most pollution-related lichen research is concerned with sulfur dioxide or point source pollutants, lichens are equally good indicators of other kinds of pollution (James 1973). Laboratory determinations of photosynthetic rates indicate sensitivity to ozone (Nash and Sigal 1979) and peroxyacetylnitrate (Sigal and Taylor 1979). Field studies of lichen communities on conifers in the mountains of Southern California have indicated an inverse correlation between oxidant pollution levels and lichen cover (Sigal and Nash 1983).

Lichens may be used as bioindicators of trace pollutants in the atmosphere since they are effective collectors of both dry and wet deposition.Epiphytic lichens have frequently been used to monitor heavy metal concentrations around industrial areas (e.g. Pilegaard 1978). The data collected in such studies, nevertheless, provide a relative measure of ambient concentrations, not an absolute measure. Hydrologic budgets of input and output fluxes are necessary to quantify the later.

In the southern Sierra Nevada lichens do not play an important ecosystem role in either biomass or nitrogen cycling, and in general, the coverage by lichens is small. The only exceptions to this are localized areas of open forest where Letharia vulpina, L. columbiana and Hypogymnia imshaugii may be abundant. Saxicolous lichen cover on rocks is also generally low, although certain crustose species (e.g. Lecidea nevadensis, Rhizocarpon bolanderi, and Caloplaca elegans) may cover a fairly broad local area . Wetmore (1984) has recently published a preliminary checklist of lichens for the foothill and montane areas of Sequoia National Park.His data confirm a rich diversity of crustose lichens, but a low diversity and growth distribution of foliose and fruticose species.

The primary objectives of the study included: 1) a survey of the dominant macrolichen species on conifers; 2) an analysis of morphological characteristics related to possible pollution damage in a dominant lichen species; and 3) analysis of trace element concentrations in dominant lichen species. While we had initially planned to survey the frequency and dominance of lichen coverage on rock substrates, it rapidly became clear that presence or absence of these saxicolous lichens was determined by complex microenvironmental conditions and had little correlation with any possible pollution-related phenomena.

Previous studies of pollution effects on lichens in Southern California have shown that the morphological form of Hypogymnia imshaugii is highly subject to oxidant-related change (Sigal and Nash 1983). Their study found marked deterioration of characteristic thallus morphology in one of the dominant lichen species at sites with high oxidant levels. We selected twenty randomly-selected thalli of this common lichen within each stand sampled at the Log Meadow site. Each thallus was scored for relative bleaching (unbleached, slightly, moderately, or strongly bleached), relative convolution of thallus (unconvoluted, slightly convoluted, moderately convoluted, or strongly convoluted), and fertility. These are morphological characteristics shown by Sigal and Nash (1983) to be of value in indicating pollution effects.

No thallus bleaching was present in any of the 20 thalli examined, but 19 of the thalli would be classified as slightly convoluted and one as moderately convoluted by the criteria of Sigal and Nash (1983). Thus the morphological structure of the thallus form in H. imshaugii at our site is somewhat convolute in its lobing pattern in comparison to typical lobing pattern in this species. We interpret this pattern as an effect of oxidant pollution, but one of relatively to low severity.

Analysis of trace elements were made on pooled, unwashed samples of ten thalli each of Hypogymnia imshaugii, Letharia vulpina, and Bryoria fremontii, important lichens from the mixed-conifer zone. Concentrations of 25 macro- and micronutrients and trace elements were determined, using optical emission spectroscopy in the Laboratory of Biomedical and Environmental Sciences at UCLA.

The three species of macrolichens analyzed were collected from the lower branches of Abies magnifica in the lower Log Creek plots.Two of these species, Letharia vulpina and Bryoria fremontii, are pendulous. The third, Hypogymnia imshaugii, is caespitose.

The results of the trace element analyses are shown in Table 1. The determinations were carried out with ten replicate measurements for each species and appropriate controls. A large number of cations and trace elements are in significantly higher concentrations in H. imshaugii than in the other two species. Since all the lichen collections were from approximately the same height and position in the canopy, it appears that the tufted, upright growth-form of the Hypogymnia is much more effective in trapping dust particles. This is particularly notable for aluminum, silicon and titanium, suggesting that particulate material of soil origin is involved. Surface particulate materials were not systematically removed from the tissue samples, and it is not clear whether the trace elements originated as dry deposition and remain primarily as surface contaminants, or originated as wet deposition that was later incorporated into the tissue. The levels of trace elements shown in Table 1 do not include any unusual levels which might suggest problems of toxic element inputs through the atmosphere. Concentrations of trace elements which would be indicative of combustion-related inputs (e.g. lead, cadmium, and vanadium) were all low. Trace element analyses of Letharia vulpina and Hypogymnia imshaugii from Sequoia National Park have recently been published by Wetmore (1985). These data, collected from samples over a broad area of the park, showed the same general trends as our data with no indications of high levels of toxic trace elements. Wetmore (1985) also measured sulfur concentrations in these lichens and reported no elevated levels.

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Table 1. Trace element concentrations in thallus tissue samples of three macrolichens growing on branches of Abies magnifica in the lower Log Creek Plot, Sequoia National Park. Values (ppm) are means of ten samples analyzed by inductively coupled plasma spectrometry. Samples were not washed before analyses.

	Letharia vulpina	Bryoria fremontii	Hypogymnia enteromorpha
Phosphorus	1307	1533	2087
Sodium	74.1	52.6	386
Potassium	5878	5432	6801
Calcium	1962	1431	5894
Magnesium	662	371	948
Zinc	22.0	14.9	33.8
Copper	2.3	2.9	6.7
Iron	299	183	1334
Manganese	171	104	214
Boron	17.1	30.8	16.9
Aluminum	377	112	2332
Silicon	1896	646	7390
Titanium	21.7	6.0	102
Vanadium	1.4	0.6	3.1
Cobalt	0.6	0.9	1.0
Nickel	0.7	0.7	2.3
Molybdenum	0.1	<0.1	1.2
Chromium	0.6	0.3	2.3
Strontium	14.2	6.0	28.0
Barium	20.1	6.5	43.3
Lead	< 10	< 10	< 15
Cadmium	<0.8	<0.3	<2.0
Silver	<0.1	<0.1	<0.1

TREE RING ANALYSIS

Multivariate regression analyses have proved to be a useful technique in dendroclimatology to describe the growth responses of trees to specific environmental variables (Fritts 1977). The general approach has been to study tree rings in relation to variables in historical records of temperature and precipitation with the assumption that other environmental factors remain the same. The problems of adding possible variables in atmospheric pollutants to these types of multivariate analyses is that long-term records of pollutant levels are generally not available. The approach in such studies has been to assume that if relationships of tree-growth to climate (i.e. temperature and precipitation) differ from an established pattern, then some other environmental variable, such as pollutant level, must be changing. Extreme caution must be used in statistical design of these approaches, since autocorrelation of rings with previous-year's growth can complicate interpretations.

Dendrochronological analyses have proved particularly effective in assessing the effects of point-source pollution on tree growth. Fox and Nash (1980) utilized tree-ring analyses to investigate the growth response of *Larix occidentalis* (western larch) to SO_2 emissions from a lead-zinc smelter at Trail, British Columbia. Their study benefitted from a good documentation of SO_2 emissions in space and time since smelter activities began in 1896 and thus was able to examine the interrelationships of air pollution, climate, and tree growth.

Nonpoint-source pollutants such as ozone, NO_x, or acid deposition (in the broad sense) are much more difficult to deal with in tree-ring studies because of the lack of long-term records. Dendrochronological approaches can be used, however, as an indirect method of assessing the effects of hypothetical changes in levels of atmospheric pollutants. Ashby and Fritts (1972) used this approach to suggest that decreases in tree growth near LaPorte, Indiana, during the 1940's may have been attributable to air pollution. Other examples of this approach are studies by Strand (1980) in Norway, Roman and Raynall (1980) and Puckett (1982) in New York, and Johnson et al. (1981) in New Jersey. These more recent studies have all documented characteristic decreases in tree-growth over the past two and one-half decades which were not attributable to drought, fire, pests, and oxidant air pollutants. They suggest that this change in growth patterns could be the result of physiological stress induced by components of acid deposition. Cogsbill (1977), however, was unable to find any indication of regional effects in a broad tree-ring study in the Northeastern United States.

Ongoing tree-ring studies by the staff of Oak Ridge National Laboratory in the Great Smoky Mountains National Park (Baes and McLaughlin 1984) have demonstrated that trace elements in tree rings can provide evidence of recent and historical air pollution. These tree-ring analyses have revealed decreased growth and greatly increased concentrations of Fe, Al, Cd, Cu, Ti, and Zn in rings formed during the last 20-25 years in relation to values for the previous half century. These increased concentrations of trace elements, in some cases approaching toxic levels, result from increased solubilization of soil elements as well as from anthropogenic origins. The interpretation of trace metal patterns in tree rings rests on the critical assumption that lateral translocation subsequent to initial incorporation into xylem tissues does not occur. Recent studies with *Pinus virginiana* and *Abies balsamea* suggest that this assumption appears to be valid (Hagan in Baes and McLaughlin 1984), although this evidence has not been critically assessed.

The mineral composition of woody tissues in tree rings was analyzed in two cores of *Abies concolor* taken from large trees in Giant Forest near the General Sherman Tree in January 1985. Core AC-1 covered the period 1857-1984, and core AC-2 covered 1792-1984. Individual rings were separated with a teflon-coated razor blade and analyzed individually using an optical emission spectrometer in our laboratory at UCLA. Analytical concentrations were determined for 25 nutrient and trace elements for each year of growth (see appendix I). These data were analyzed statistically to determine time series of mineral concentrations of woody growth rings. Our objective was to test for recent changes in long-term patterns of concentrations which might be related to pollution effects.

Time sequences of mineral compositions were examined to identify outliers that potentially could be very damaging to statistical analyses. Certain years were found to be very unusual in mineral composition in comparison with adjacent years. Resamples of these years suggest unhomogeneous sample collection as the cause of this difference. Data for each anomalous year were replaced by data for an adjacent year. Data were then subjected to a variance-stabilizing transformation:

Where E_0 = estimated concentration of element in ppm
A = "lower limit" of analysis for 10 mg. sample
E = transformed value of concentration

then $E = \log_{10}\{[E_0+((E)_0)^2+(A^2/0.2304))^{05}]/2\}$

For large values of E_0, E is approximately equal to $\log_0 E_0$. For small values of E_0, E is approximately a linear function of E_0.

The transformed time series were then subjected to regression analysis assuming a first degree autoregressive model (SAS procedure AUTOREG was used). The assumption that the deviation of a mineral's concentration from its expected value for a given year is not independent of the deviations in previous years, but is a mixture of an effect proportional to the previous year's deviation and an independent random variable. This assumption permits the observed concentrations to possess an "inertia" whereby they may depend somewhat upon their previous values, and respond less immediately to changes in the expected value of the concentration (the trend line) than they might otherwise.

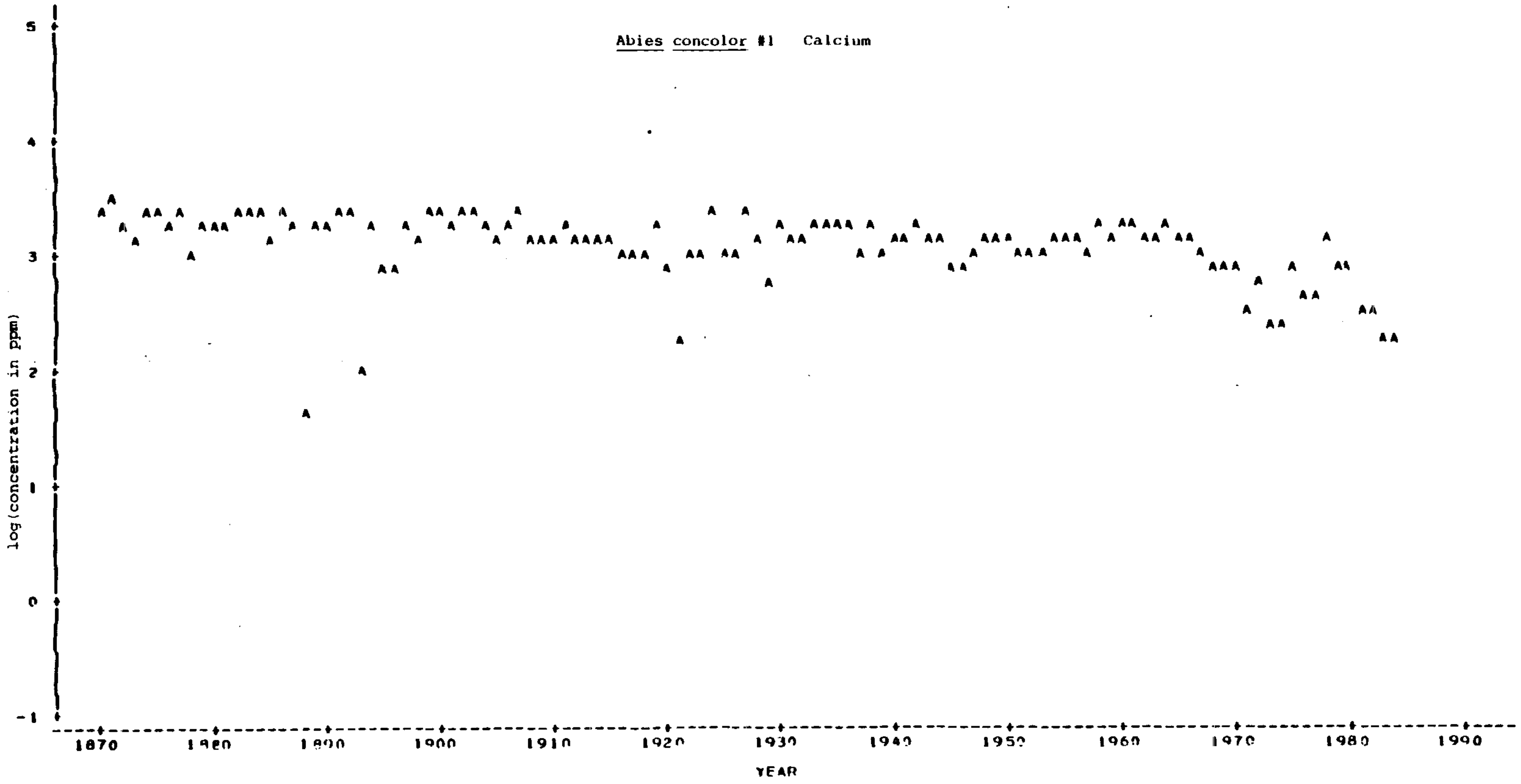
Since it was assumed that the time courses of the expected values of mineral concentrations (the trend lines) could be very complex, the trends were fitted with polynomials of increasing degree. Due to limitations in precision of calculations, it was impractical to fit polynomials of degree higher than five. Fifth degree polynomials were fitted to the long (193 year) record from AC-2, but fourth degree curves were the most complex used for AC-1. It should be emphasized that, had computations been feasible, it probably would have developed that the best fitting polynomials would have been of very high degree, perhaps of a degree about equal to a third to a fifth of the number of years in the record. However, these higher order curves would have emphasized shorter term variations, and would have made it more difficult to test for longer term trends.

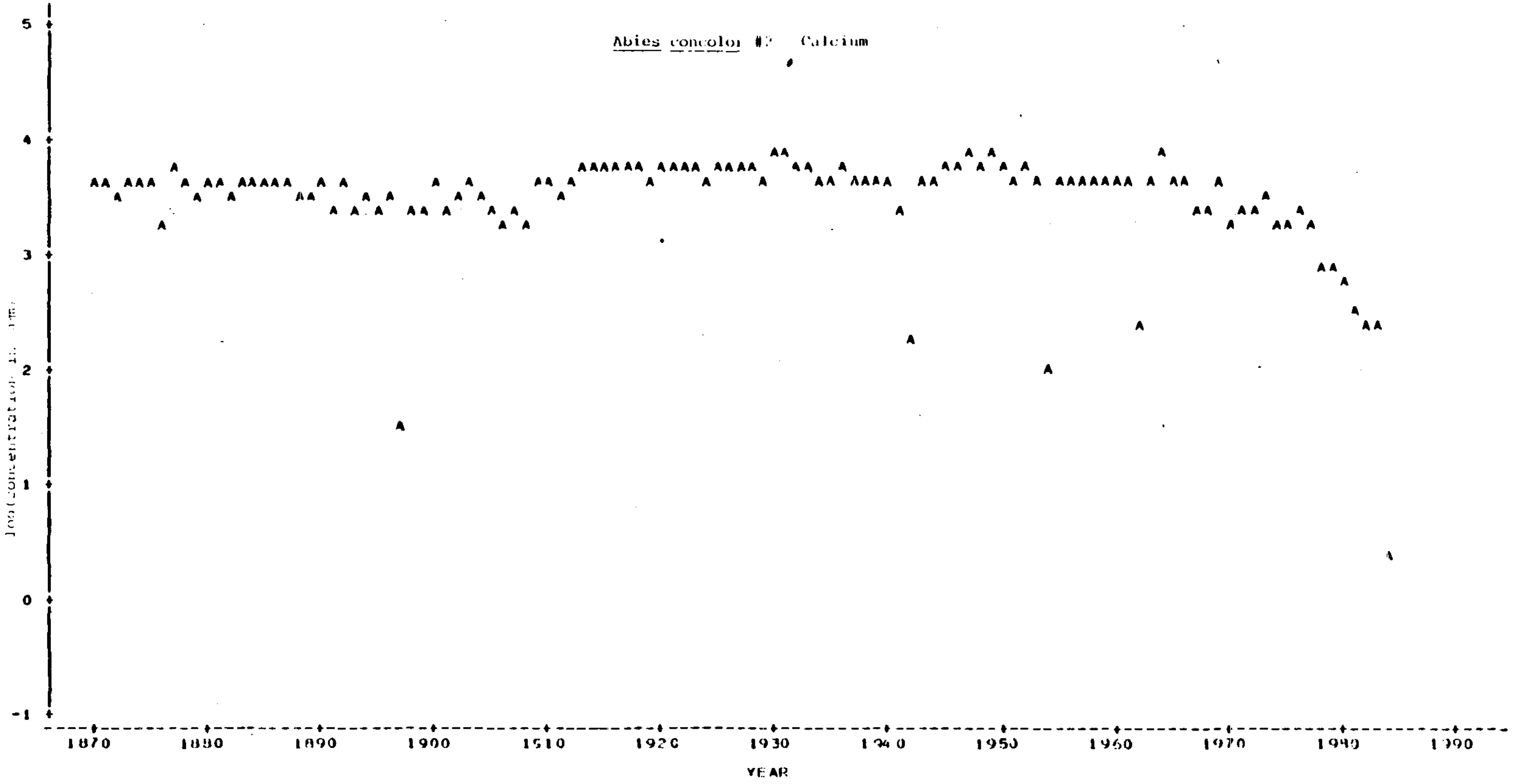
Curves were fitted for six elements. Calcium and magnesium (which would be expected to decrease in availability with soil acidification), manganese and aluminum (which would be expected to increase in availability with soil acidification), and lead and cadmium (which would indicate levels of inputs of combustion-related trace elements). Continuous confidence intervals for the slopes of these trend lines were calculated using the covariance matrices of the estimated curve parameters. Table 2 summarizes the results by reporting on the model of highest degree that was significantly (95% level) better than models of lower degree. Intervals of years with slopes (changes in concentration) significantly different from zero at the 95% level are indicated. Interpretation should be that the mean slope for each period indicated was nonzero, not that the slope was consistently nonzero for the entire interval.

Both of the Abies concolor cores analyzed showed a significant decline in calcium levels of their rings from the early 1950's to the present time (Figure 4, Table 2). This steady decline is more than an order of magnitude. At the present time we do not have sufficient evidence to ascribe a cause to this pattern of decrease, but our best guess is that it is a natural change and is not pollution related. Strontium, a trace element which behaves chemically very much like calcium, showed the same pattern of decline (Figure 5). It seems possible that the period of declining concentrations of these elements represents a sapwood tissue in which strontium and calcium continue to be deposited in the middle lamellae of xylem cell walls. If declining soil acidity were responsible for this pattern, we would expect to see a comparable pattern in magnesium and lithium, which we do not. Neither manganese nor aluminum analyses produced any consistent patterns which we feel could be related to pollution effects. The aluminum concentrations of core AC-1 did show elevated levels over the same recent period (Table 2), but some of this trend may be influenced by trace soil contaminants on rings from 1979-1984. The possibility of such contamination was indicated by slightly elevated levels of silicon (see appendix data sets). Core AC-2 showed a statistically significant elevation of lead over the last 30 years (Table 2) but it is difficult to determine if this change is biologically relevant. The levels involved are low and close to the lower limit of detection for our analysis procedures.

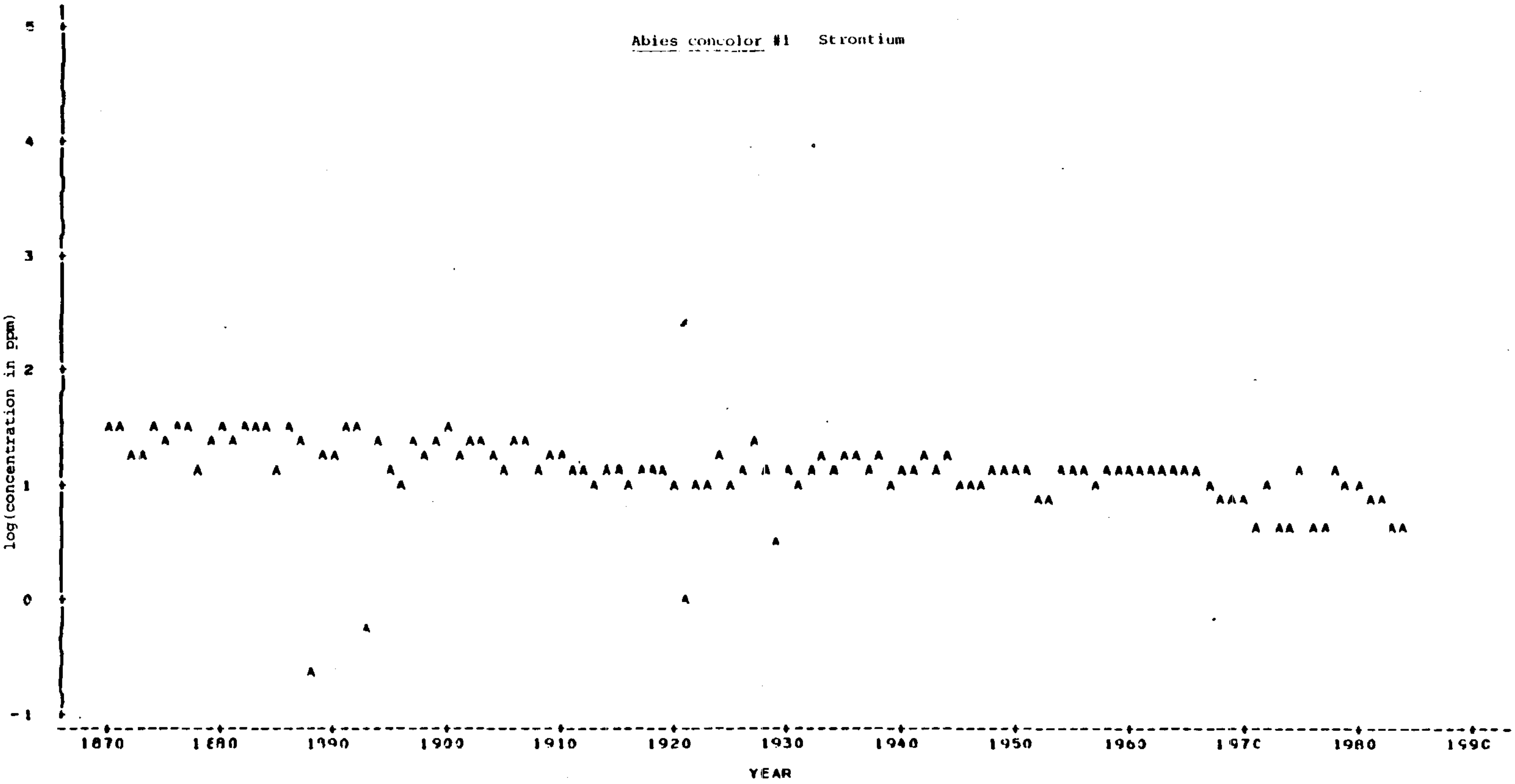
Table 2. Intervals of years in the record period with significant deviations from zero slopes of element concentrations at the 95% confidence level for calcium, magnesium, manganese, aluminum, lead and cadmium. See text for discussion of statistical analyses.

	Abies concolor #1 (1857-1984)			*Abies concolor* #2 (1792-1984)		
Element	Polynomial degree used	Time interval	Slope	Polynomial degree used	Time interval	Slope
Calcium	4	1857-1867	+	5	1792-1793	-
		1881-1917	-		1809-1849	+
		1952-1984	-		1861-1897	-
					1910-1945	+
					1953-1984	-
Magnesium	4	1857-1872	+			
		1881-1940	-	1	1792-1984	-
Manganese	4	1857-1868	+			
		1876-1908	-	2	1792-1838	+
		1916-1958	+		1859-1984	-
		1963-1984	-			
Aluminum	3	1857-1873	+	5	1792-1818	-
		1889-1941	-		1842-1854	+
		1952-1984	+			
Lead	0	none		3	1792-1801	+
					1846-1924	-
					1956-1984	+
Cadmium	0	none		0	none	

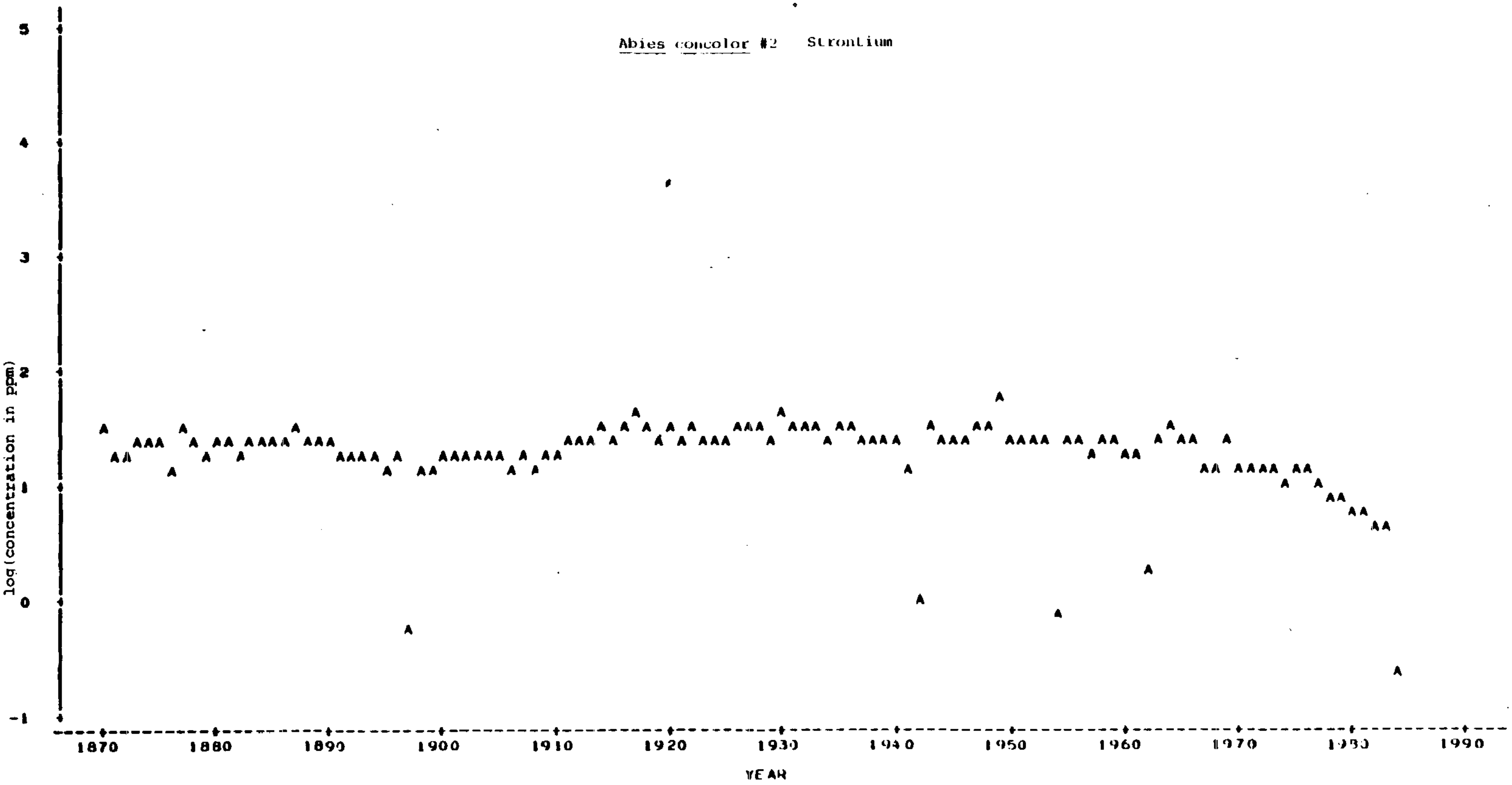

Abies *concolor* #1 Calcium



Abies concolor #2 Calcium
log(concentration in ppm)
5
4
3
2
1
0
-1
1870
1880
1890
1900
1910
1920
1930
1940
1950
1960
1970
1980
1990
YEAR



Abies concolor #1 Strontium



Abies concolor #2 Strontium

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ABOVE GROUND TREE BIOMASS AND PRODUCTION OF TWO ABIES SPECIES

Red and white fir are important components of the montane forests of Pacific North America. They cover more than 1.6 million ha of commercial forest land in California and southern Oregon (Laacke and Fiske 1983). In addition red and white fir forests populate much of the watershed lands for California's 25 million people, and provide recreational cover in such national parks as Yosemite, Bryce, and Sequoia-Kings Canyon. They provide a habitat for more than 123 bird, 60 mammal and 14 amphibian species, of which 8 are listed as sensitive, rare, or endangered (Laacke and Fiske 1983).

Previous studies of biomass in the two fir species have been limited to crude estimates of wood biomass and net production for fir forests by Rundel et al. (1977), based on wood volumes of Schumacher (1926, 1928), and estimates of wood volume in young trees by Ernst and Hann (1984). The present study presents regressions of aboveground biomass, surface area, and production on more readily measured plant parts (e.g. diameter at breast height (DBH)), and representative aerial estimates for fir forests in the southern Sierra Nevada.

This section presents equations for determining above ground biomass and production for the two most common species at Log Meadow, A. concolor and A. magnifica. The equations are of the form $\ln Y = \ln A + B \ln X$. Parameters that could be used as independent variables in the calculation of biomass were diameter at breast height and stem parabolic volume. The equations permitted calculation of several tree components and total above ground biomass. The annual production of the same list of components could be calculated with the same kind of regression equation, and annual increment of stem parabolic volume could also be used as an independent variable. The coefficients of correlation were high for these equations, which were based on sample trees from sites as close as possible to the primary study sites.

White fir (Abies concolor (Gord. and Glend.) Lindl.) occurs in the central Rocky Mountains (Colorado, Utah, Arizona, New Mexico) and in the Pacific Coast ranges, from the San Pedro Martir of Mexico through the Coast Ranges and Sierra Nevada of California to the Cascade and Coast Ranges of Oregon. Some taxonomists consider the coastal form a separate variety (var. lowiana). The coastal form appears to be influenced by hybridization with grand fir (Abies grandis) where the two species overlap in northwestern California and southwestern Oregon (Fowells 1965).

Red fir (Abies magnifica A. Murr.) has a more limited range, from the southern Cascades of Oregon south through the Coast Ranges of California to Lake County (39° N), and south through the Sierra Nevada to the Kern River drainage (35° 40'N). From Mt. Lassen, California, northward red fir is increasingly influenced by hybridization with noble fir (Abies procera). A variety of red fir (var. shastensis Lemm.) has been recognized, centered in this region (Griffin and Critchfield 1972).

At its lowest elevations in California and Oregon, white fir typically occurs in mixed forests with other conifers (e.g. ponderosa pine, sugar pine, Douglas fir, incense cedar -- Pinus ponderosa, P. lambertiana, Pseudotsuga menziesii, Calocedrus decurrens, respectively) and black oak (Quercus kelloggii). In the central portion of its elevation range, white fir may be found in relatively pure stands. At upper elevations, it typically forms mixed stands with red fir, which in turn occurs in pure stands above the elevational tolerance of white fir. Typical elevations for mixed conifer forests in the central Sierra Nevada are 900-1800 m; for white fir alone, 1800-2100; for mixed fir, 2000-2300 m, and for red fir alone, 2200-3000 m. These zones shift with aspect, latitude and longitude, typically occurring at higher elevations in southern latitudes and exposures.

Both species of fir are more shade-tolerant than most of their codominants, with red fir being less shade-tolerant and more frost-tolerant than white fire (Laacke and Fisk 1983). Because of this shade tolerance, mixed-age stands of fir without recent ground fires typically contain a substantial pool of suppressed seedlings and saplings. This is more characteristic of the more shade-tolerant white fir, with red fir tending to reproduce more commonly in canopy gaps (Parker 1985, Ustin et al. 1984). Major reviews of the ecological structure of fir forests include those of Hopkins (1982), Oosting and Billings (1943), Parker (1984) and Rundel et al. (1977).

METHODS

Data Collection

Twelve individuals of each of the two fir species were harvested from Sequoia National Forest during June-August 1984.Red fir individuals were obtained from Shell Mountain and Big Meadow at elevations of 2225-2550 m, white fir from Shell Mountain and east of Whitaker Forest at 1700-2250 m. Eleven of the twelve red fir individuals spanned the following ranges: DBH, 30-100 cm, 62-243 yrs, 16-44 m height. A twelfth individual, a sapling of 5.1 cm DBH, 44 yr age and 2.61 m height, was found to have substantially different biomass proportions than the larger trees and was excluded from final regressions. The twelve white fir individuals spanned the following ranges: DBH, 7-98 cm, 35-157 yrs, 4-42 m height. In the case of white fir, sapling proportions bore allometric relations to those of larger trees, so that final regressions include the smaller size classes.

The dimension analysis system of Whittaker and Woodwell (1968, 1971) was used, with modification, to dissect and analyze tree parts. Trees were felled at approximately 1 m height and further divided into five-six log sections. Dimensions of wood and bark at both ends of each log were measured along four perpendicular axes. Sapwood radii were measured at the top of the basal cut (c. 1 m) and extrapolated to breast height (1.37 m). Because the heartwood perimeter of red fir was particularly irregular, sapwood dimensions were averaged from long and short radii, excluding irregular lobes.

Bark and wood densities were measured for each tree by computing the ratio of bark and wood volumes at c. 1 m (volumetric displacement in water) to oven dry weight (70° C for 24-48 hrs, to constant weight) for samples. Some samples were measured for volume after drying, leading to inflated estimates of specific gravity, especially for bark. The standard error of mean estimates for both wood and bark specific weights, for mixed fresh and oven-dried samples, was less than 4% of the mean in all cases, however. Bark specific gravity typically increases with tree age and height aboveground (Hale 1955, Smith and Kozak 1967). Smith and Kozak (1967), for example, report an average bark specific gravity for Douglas fir (Pseudotsuga menziesii of 0.38 at breast height (20 trees, 10-75 yrs), and 0.31 at half total height. By contrast bark specific gravity of six 10-year-old Douglas firs was 0.21 at half total height.

Both because of the oven-drying of some samples, and the use of breast height samples of mostly older trees, bark specific gravities used here may overestimate stand bark weights by 15-30%. Bark specific gravities used were (mean [std. error]): 0.571 [0.018] for white fir, 0.567 [0.020] for red fir, excluding the 5 cm sapling. No published values exist for direct comparison, though Picea rubens has a reported bark density of 0.49 (Whittaker et al. 1974). Wood specific gravities were 0.431 [0.020] for white fir and 0.388 [0.013] for red fir. This compares with a wood specific gravity of 0.37 reported for white fir in Wenger (1984). Considering that specific gravities further vary with growing conditions and locale, future investigators may wish to modify existing mass equations to reflect specific gravity measurements at particular study sites.

Every branch of each tree was measured for basal diameter, age, and distance from tree top. Six sample branches were taken from different canopy levels in each tree for detailed analysis (72 sample branches per species). On these, branch length, number of current twigs, and oven-dry weight of live and dead branch wood, current twigs, and needles by year were additionally obtained. Because needle growth progressed during the course of the 1984 sampling season, "current" needle growth was taken as that grown during 1983.

To obtain needle surface/weight ratios, 100 needles of each age class were measured from each of lower, middle, and upper canopy positions. Projected needle areas were measured with a LiCor photoelectronic leaf area meter. To obtain the total needle surface, the ratio of the perimeter of magnified needle cross-sections to the width of projected needle area was measured.These ratios (2.26 for white fir, 2.41 for red fir) were multiplied by projected areas to obtain all-sided areas. Needle surface/weight ratios were averaged across age and height classes. These ratios, applied to oven dry needle weights for current and older needles, produced needle area estimates.

Data analysis

In the dimension analysis program, branch surface area is estimated by assuming dichotomous branching, and calculating the number of branchings to achieve a reduction from basal branch diameter to current twig diameter over the length of the branch (Whittaker and Woodwell 1967). The cylindrical surface area of each dichotomous branch segment is then computed. In the case of Abies spp., this method will overestimate branch surface area for two reasons. First, as recognized by Whittaker and Woodwell (1967), branch length is generally the maximum length from base to tip, so that actual lengths to current tips other than the apical one are overestimated. Whittaker and Woodwell (1967) estimated the overestimation factor from this source to be about 1.4 for hardwoods. Second, in the case of the firs, branching pattern consists of a multipinnate pattern with numerous short side shoots that do not develop subsequent branching. As a result, the number of current tips is larger than that of a dichotomous pattern, resulting in a further overestimate of branch surface. Overestimation will increase with tree size. To adjust for these effects, branch surface estimates were reduced by factors of 0.9 - 0.6 for successively larger trees.

Stem bark surface was computed treating each of the six log segments as cylinders, using diameters of log midpoints. Additional surface in bark furrows was ignored.

To obtain regressions on wood production, wood radial increments from disks at c. 1 m height were measured at 5-year intervals on the sample trees. Net bark production was estimated by multiplication of bark dry weight by the wood growth rate (wood dry weight increment/wood dry weight, per log) (Whittaker and Woodwell 1968). Branch growth was estimated by multiplying branch wood and bark dry weight by the slope, B, of the regression of dry weight of the branch on age, and dividing the total by age (Whittaker 1965).

Current leaf production was estimated directly from regressions of current twig and leaf weight of sample branches, and correcting for the proportion of current twig and leaf weight that is twig mass. In these fir species, it was observed that not every leafy branchlet produces new leaves each year. Thus dating needle ages required several procedures. Where current growth (lighter color) occurred, careful observation of bud scale scars from previous years permitted aging of needles. In cases where a branchlet had no termini with current growth, a careful comparison of the sequence of branch segment lengths with that of other branchlets on the sample branch which had current growth permitted anchoring the absolute age of needles. While obtaining current and older needle growth by year is thus a cumbersome procedure in conifers of this growth form, it is important to recognize that mere clipping of all branch tips will vastly overestimate current leaf growth.

To estimate additional mass added to older needles each year, it was noted from the change in specific leaf weight (mass/area) that most additional secondary thickening occurred in leaves of the most recent 10 years (97.7% in white fir, 83.6% in red fir). Using specific leaf weights from the middle of the canopy, an average specific leaf weight was computed, weighted by the proportion of total leaf mass in each age class. Resulting values were 425 g m^{-} for red fir, 446 g m^{-} for white fir. The average annual increase in specific leaf weight for the ten year period, compared to current leaves was computed, and further adjusted for the proportion of secondary thickening occurring in leaves older than ten years. The resulting ratios of older leaf growth to current leaf growth were (in percent) 2.04 for white fir, 1.51 for red fir.

To estimate biomass and production on a stand level, six 60 X 60 m unlogged stands of fir were tallied for DBH and height in Sequoia National Park during July-August 1984. Exact locations of these stands can be obtained from David Peterson (NASA-Ames Research Center, Moffitt Field, CA). Increment cores at breast height were taken from a mean subsample of 12% of trees on each site (range: 6-22%). These values were used to interpolate wood increments per size class for the most recent ten years. Stems were grouped into 10 cm DBH size classes for analysis, except for trees greater than 120 cm DBH, which were analyzed individually. Stem wood parabolic volume increments for these trees were then used as independent variables in production regressions developed from the 23 harvested trees in Sequoia National Forest to estimate production in the Park stands. The small proportion of non-fir species present in these stands were analyzed using regressions based on Abies concolor.

To correct for bias in the arithmetic form of the dependent variable introduced by estimating it from the antilog of a logarithmic regression, all regressions were adjusted by a correction factor. The correction consisted of adding to the intercept, A, in the equation ln Y= A + ln B, the square of the standard error of estimate of Y, in ln units, divided by 2. This correction was made to all regressions at each step of the analysis, and is also incorporated in the regression equations in Appendix I. For a discussion of the statistical basis for this correction, see Finney (1941), Baskerville (1972) and Lee (1982).

FIGURE 6

Percentage of total aboveground biomass and net production in plant tissues of red and white fir, with standard errors. Percentages are means of 11 individuals of Abies magnifica and 12 of Abies concolor.

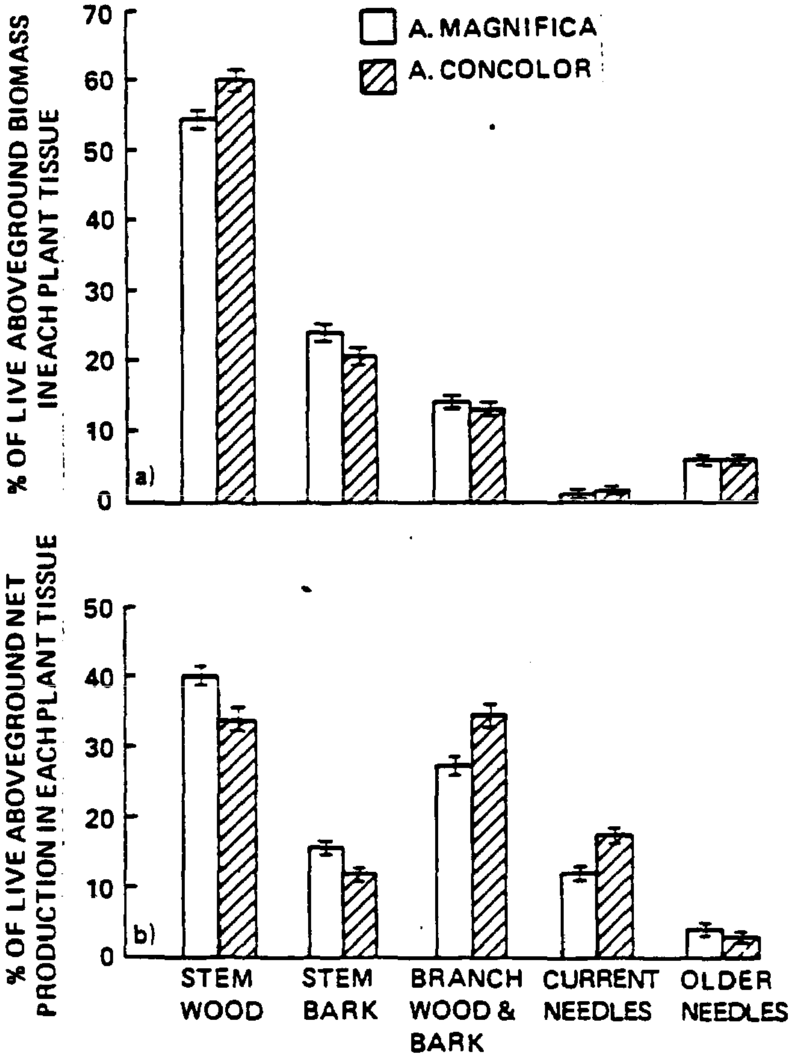
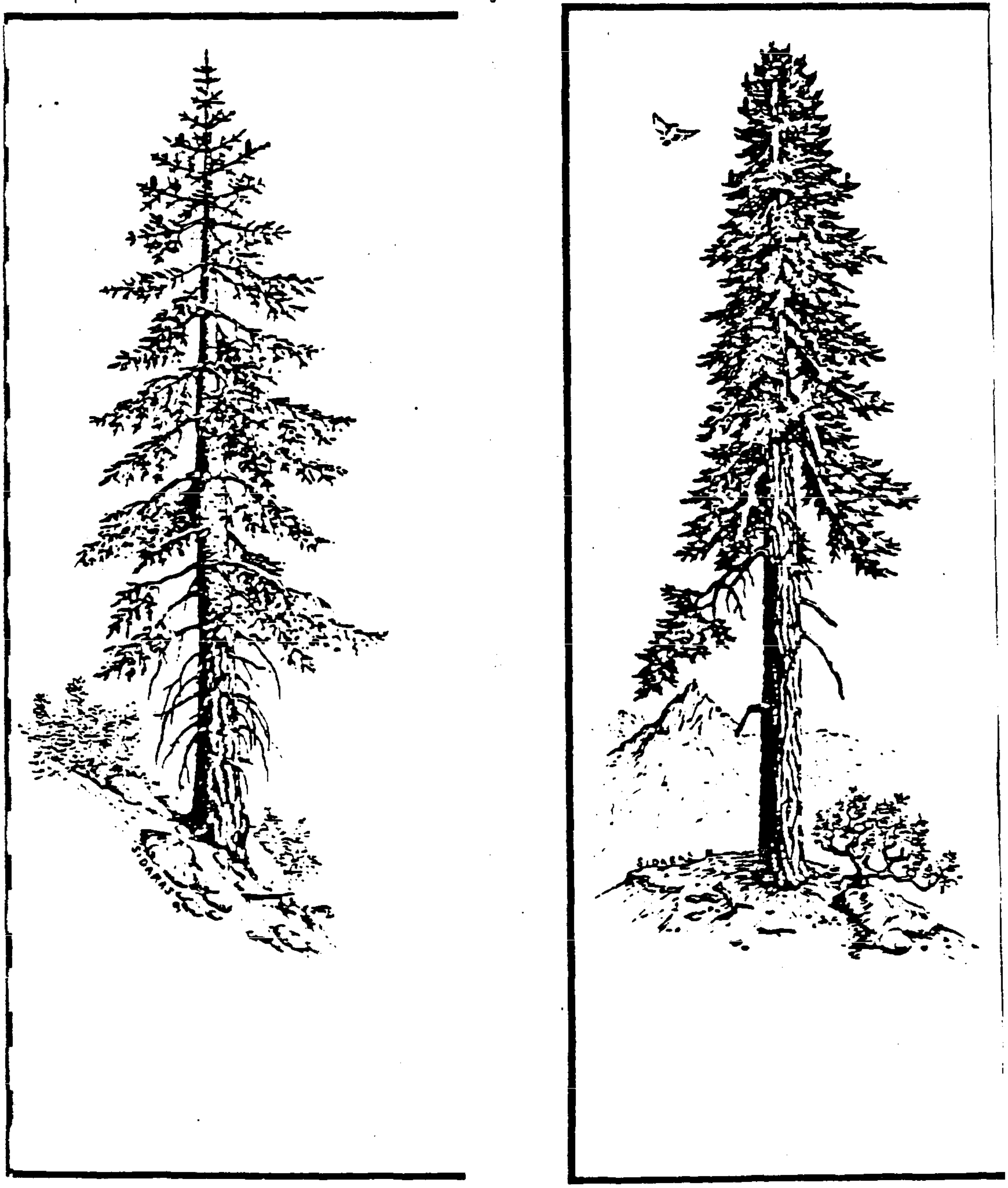


FIGURE 7

Open growth structure of <u>Abies concolor</u> (left) and <u>Abies magnifica</u> (right) in Sequoia National Park. Illustrations by N. Sidaras.



Species-level comparisons

The proportions of total aboveground live mass and production in different plant parts in the two fir species are plotted in Figure 6. If the 11-12 individuals upon which these means are based are assumed to be a random subsample from populations of identical age structure for the two species, then it can be concluded that the two species differ by more than one standard error only in two respects. First, the proportion of bark production is higher in red fir. Since bark masses are not significantly different between the two species, bark shed may be greater in red fir. Second, the proportion of total needle production is higher in white fir, due to higher production in current needles. This is counterbalanced by a shorter needle retention time (maximum age of 24 yr in white fir, 29 yr in red fir), resulting in comparable proportions of leaf mass in the two species.

Compared to other western conifers (e.g. Pseudotsuga menziesii, Abies procera, Pinus ponderosa; Grier and Waring 1974), leaf mass increases more rapidly with sapwood cross-sectional area in the two fir species, red fir having the higher rate of increase. As will be noted in Table 3, this results in the highest proportion of leaf mass to total aboveground mass of the several western conifer forests surveyed (7.0% for red fir forests and 6.1% for mixed fir forests vs. 1.7 - 3.7% for Douglas fir forests, 0.9% for western hemlock-Sitka spruce forests, 2.7% for ponderosa pine and 3.9% for white fir), though the figure is exceeded by young balsam fir (Abies balsamea) forests in the east (13.3%; Sprugel 1984). A visual impression of the denser nature of the canopy in red fir than white fir can be obtained from Figure 7, drawn from open-growth individuals in Sequoia National Park.

In addition to retaining needles for a longer period, red fir individuals tend also to retain live branches longer, as implied by the higher ratio of branch biomass/production in red vs. white fir (Table 3). In general, aboveground biomass accumulation ratios tend to increase in larger, longer-lived individuals. Thus these ratios are higher for red and white fir (44,29) than for red spruce (Picea rubens; 26) in the White Mountains of New Hampshire (Whittaker et al. 1974) or the pygmy conifers of Arizona (Mexican Pinyon pine, Pinus cembroides, 18; Whittaker and Niering 1975) or northern coastal California (Bolander pine, Pinus contorta ssp. bolanderi, 8; Westman and Whittaker 1975).

Appendix II provides information on a portion of the regressions computed by the dimension analysis program. In general, DBH proves to be a robust predictor of dimensions, surface area, and biomass in the two fir species.A slight improvement in prediction of biomass components is obtained by using stem parabolic volume (estimated by basal area X height/2) as the independent variable. More significant improvement in prediction of production variables occurs by use of stem wood annual parabolic volume increment as the independent variable, particularly for red fir. This likely occurs because of the lower shade tolerance of red fir, resulting in more severe suppression of growth if individuals are shaded during a portion of their lifetimes. Hence stem diameter, which will reflect any period of suppression, is a less robust predictor of current production than are current wood growth rates.

Stand-level comparisons

Table 4 presents stand characteristics, biomass and production totals by species for two 0.36 ha stands each of red fir, white fir, and mixed red and white fir from Sequoia National Park. Direct comparisons between forest types are made tenuous by the fact that the stands differ in density, basal area, and environmental attributes. With the exception of a younger, denser white fir stand (No. 13), the remaining fir stands exhibit comparable biomass accumulation ratios (42-59 vs. 27 for No. 13). These ratios are lower than for mature Douglas fir forests (65-70), western hemlock-Sitka spruce (83) or coast redwood stands (93-222), but comparable to 110-130 yr old Douglas fir (52) or Noble fir (53) stands in Oregon (from data in Table 6). They exceed values for 50 yr old Douglas fir (32) or eastern broadleaved forests (14-16) or balsam fir (12) from New York (from data in Table 3). Table 4 also indicates the remarkably low tree species diversity and equitability of the Sierran fir forests.

Table [illegible]

Aboveground biomass accumulation ratios for the two fir species (biomass/net production); means of [illegible] and [illegible] individuals of *A. magnifica* and *A. concolor* respectively.

	Abies magnifica	*Abies concolor*
Stem wood	43.2	60.2
Stem bark	50.1	60.2
Branch wood & bark	26.5	18.8
Current needles	1.0	1.0
Older needles	66.2	49.0
All aboveground parts	43.8	29.3

Table 4

Stand characteristics, biomass, and production by species for six fir stands (3600 m² area) in Sequoia National Park. Height and age are weighted by stem parabolic volume of component tree. Biomass estimated on parabolic volume, production on wood volume annual increment of stems. Parabolic volume was estimated as one-half the basal area times the height of the trunk.

	White fir		Mixed fir		Red fir	
Stand reference no.	13	21	4	25	19	26
Topographic features						
Slope degrees	18	16	<3	11	16	4
Aspect, degrees	250	190	270	110	310	290
Elevation, m	2080	2120	2220	2380	2470	2420

White fir stands

	Size range (DBH, cm)	No. of stems	Weighted mean height, m	Weighted mean age, yr (and range)	Basal area m²/ha	Biomass kg/m²	Production g/m²/yr	Biomass/production
Stand 13								
Abies concolor	4-103	301	29	94(20-200)	78	58.5	2199	26.6
Stand 21								
Abies concolor	5-176	65	49	167(26-220)	91	96.2	1613	
Quercus kelloggii	28	1	7	27 --	0.2	0.05	3	
Pinus lambertiana	41	1	16	48 --	0.4	0.2	13	
Total		67	49		92	96.5	1628	59.3
Mixed fir stands								
Stand 4								
A. magnifica	2-129	118	33	160(40-220)	22	20.8	535	
A. concolor	4-123	42	32	186(40-210)	26	19.5	438	
P. lambertiana	25	2	13	78 (78)	0.3	0.1	6	
P. ponderosa	7-109	2	41	200(25-200)	2.6	2.3	46	
Total		164	33		51	42.8	1026	41.7
Stand 25								
A. magnifica	5-135	46	37	189	(27-240)	28	28.9	416
A. concolor	5-146	60	24	146	(27-200)	18	10.6	340
P. lambertiana	33	31	4	14	64	(64)	0.8	0.4
P. ponderosa	129	1	41	370	--	3.6	3.1	24
Total		111	32			59	43.0	812
	53.0							

Table 4, continued

Red fir stands

	Size range (DBH, cm)	No. of stems	Weighted mean height, m	Weighted mean age, yr (and range)	Basal area m²/ha	Biomass kg/m²	Production g/m²/yr	Biomass/ production
Stand 19								
A. magnifica	5-98	124	25	161 (25-180)		60	39.8	801
P. ponderosa	9	1	5	25	25	0.02	0.004	1
Total		125	25			60	39.8	802
	49.6							
Stand 26								
A. magnifica	5-146	173	33	191 (55-250)	72	65.5		1201
A. concolor	36-72	2	32	178 (130-185)	--	1.4		1.1
Total	25	175	33			73	66.6	1226
	54.3							

The partitioning of biomass and growth by plant parts in the fir forests is illustrated in Table 5. Because of both the higher correlation coefficient of the regression, and the in situ basis of the growth measurement, production values based on estimated volume increment (EVI) are to be preferred over those based on DBH or stem parabolic volume. The youngest white fir stand (No. 13, 94 yr weighted mean age) exhibits the highest net aboveground production of any fir stand. By comparison to the 167 yr weighted mean age white fir stand, the younger stand allocates more energy to current twig and needle growth (30% vs. 23%), less to stem growth (46% vs. 54%), and comparable amounts to branch (20-21%) and older needle growth (3%). The two mature red fir stands (weighted mean ages 161 and 191 yrs), by contrast, exhibited no significant differences in partitioning patterns from each other (49-51%) to stem growth; 23-24% to branch growth, 21-23% to current needles and twigs, and 4-5% to older needle growth). The red fir stands differ from the white fir stand of comparable weighted mean age in devoting slightly more energy to older needle growth, stem bark and branch growth, and less to stem wood growth (32-35% vs. 41% for white fir). These stand level trends reflect the generalizations made about the two fir species above.

Table 5

Stand-level forest structure in six fir forests of Sequoia National Park, 0.36 ha plot.
*= computed from stand census measurements.
SCO= stem conic surface; EVI= estimated volume increment; VPO= stem parabolic volume; DBH= diameter at breast height.

Forest type	Independent variable used in regression	White fir		Mixed fir		Red fir	
Stand reference no.		13	21	4	25	19	26
Area and volume measurements							
Basal area cm^2/m^2	*	78.3	92.0	51.1	50.4	60.1	73.1
Stem parabolic volume (VPO) m^3/m^2	*	0.114	0.224	0.085	0.081	0.074	0.121
Stem wood parabolic volume increment, current year, cm^3/m^2 yr (EVI)	*	1508	1290	764	580	534	892
Weighted mean height, m	*	29.1	48.8	33.2	32.1	24.7	33.2
Biomass estimates Kg/m^2							
Stem wood	DBH	37.9	69.9	29.2	30.3	24.5	35.3
--	VPO	36.0	63.2	24.8	23.6	21.3	34.7
Stem bark	DBH	12.8	22.4	10.8	11.9	10.8	15.7
	VPO	12.3	20.5	9.47	9.60	9.5	15.5
Branch wood & bark	DBH	6.59	9.71	6.48	8.37	6.76	12.0
	VPO	6.97	9.43	6.15	7.05	6.13	11.7
Current twigs	DBH	0.293	0.202	0.095	0.092	0.070	0.084
	VPO	0.294	0.198	0.090	0.084	0.067	0.036
Current needles	DBH	0.341	0.243	0.152	0.146	0.155	0.183
	VPO	0.353	0.238	0.144	0.135	0.146	0.185
Older needles	DBH	2.536	2.960	2.276	2.865	2.958	4.475
	VPO	2.661	2.882	2.186	2.503	2.707	4.443
Total (CMB)	DBH	60.37	105.4	49.00	53.62	45.23	67.74
	VPO	58.50	96.5	42.90	42.96	39.79	66.51

Table 5, continued

Forest type	Independent variable used in regression	White fir		Mixed fir		Red fir	
Stand reference no.		13	21	4	25	19	26
<u>Production estimates</u> g/m^2/yr							
Stem wood	DBH	843	1112	631	649	785	980
	EVI	752	661	375	281	259	429
Stem bark	DBH	279	349	203	213	254	321
	EVI	256	217	146	111	132	198
Branch wood & bark	DBH	439	430	290	346	336	494
	EVI	470	329	227	186	188	291
Current twigs	DBH	283	202	95	92	71	84
	EVI	299	170	93	79	59	81
Current needles	DBH	341	243	152	146	155	183
	EVI	360	205	149	126	127	175
Older needles	DBH	52	60	39	47	45	68
	EVI	62	46	36	28	36	52
Total	DBH	2238	2396	1412	1493	1646	2129
	VPO	2247	2281	1307	1298	1522	2146
	EVI	2199	1628	1026	812	802	1225
<u>Surface area estimates</u>, m^2/m^2							
Stem	SCO	1.05	1.01	0.54	0.49	0.64	0.37
Branches	DBH	10.5	11.6	5.44	5.49	4.33	5.92
Needles, all-sided	DBH	14.53	20.75	15.58	16.45	17.33	25.94
Total		26.1	33.4	21.6	22.4	22.3	32.2

The levels of aboveground biomass and production in the Sierran fir stands are compared to values for other needle-leaved and broad-leaved forests in Table 6. Biomass and production values for the red and white fir forests are comparable to those for other coniferous forests of the Pacific Northwest (Douglas fir, Noble fir, western hemlock-Sitka spruce). Biomass values are 4-7 X greater than for the balsam fir forests of the Adironracks in New York, 3-6 X greater than eastern deciduous forests, and 2-3 X greater than the ponderosa pine forests of Arizona desert mountains. Nevertheless, the Sierran fir forests are still dwarfed in mass by the coast redwoods, which exceed them in biomass by 2-6 X.

White fir forests generally exceed red or mixed fir forests in aboveground production by 1.3-2.7 X. This may reflect in part the more favorable climatic conditions at the lower elevations in which white firs grow.The red fir appears to follow the more energetically and nutritionally conservative strategy of allocating photosynthate to older needles and retaining them longer. Less energy is shunted to stem wood growth, and the red firs generally reach lesser heights at maturity (25-33 m vs. 49 m; Table 4). Indeed, the net production values achieved by white fir forests are at the high end of those reported for coniferous forests, and are exceeded only by <u>Abies sachalinensis</u> of Japan in Table 6. Another key to the high productivity may be the high proportion of total biomass in needles in white fir forests, as noted earlier.

The lower value reported by Whittaker and Niering (1975) for a white fir-Douglas fir stand in the Santa Catalina Mts., Arizona (1110 vs. 1628-2199 g m^2 yr^2 in the Sierras) is an underestimate for at least two reasons. First, Whittaker and Niering did not apply the antilog correction to their calculations, which were based on logarithmic regressions. The mean value of correction factors for white fir in the present study was 1.13 (std. error .01; for red fir, 1.16, std. error .02), implying a 13% underestimation of the Arizona figures on this count alone. Second, their estimation was based on red spruce (Shanks and Clebsch 1962) from eastern forests, a smaller tree with substantially thinner bark and a greater proportion of total production devoted to needles (Whittaker et al. 1974). Beyond these factors, one would expect a lower production for white fir forests in the more arid environment of the Arizona desert mountains.

Table 6

Above ground tree biomass, production, and basal area in a range of forest types

Forest type	Location	Basal area m²/ha, (range)	Age yr.	above ground leaves kg/m²	Woody parts	Total	Net above ground production g/m²/yr	Reference
Needle-leaved forests								
Abies concolor[1]	Sequoia Nat'l pk, CA	83(78-92)	200	3.07	75	78(59-97)	1914(1628-2199)	this study
Abies magnifica[1]	"	67(60-73)	185	3.73	49	53(40-67)	1013(802-1225)	
Mixed *A. concolor*/ *A. magnifica*[1]	" "	50(50-51)	220	2.49	41	43(43)	919(812-1026)	
A. concolor - *Pseudotsuga menziesii*[2]	Ravine of Sta. Catalina Mtns., AZ	59	50-145	1.67	34	36	1110	Whittaker & Niering 1975
Abies grandis	Plantation, U.K. 1956	--	21-24	--	--	26(17-36)	1383(925-1840)	Ovington
Abies sachalinensis	Japan						2320	Kira 1975
Abies balsamea	Adirondack Mtns., NY	60	60	1.6	11	12	[illegible]	[illegible]
[illegible]	Sta. Catalina Mtns., AZ	[illegible]	200-250	[illegible]	75	79	[illegible]	Whittaker & Niering 1975
Tsuga heterophylla-*Picea sitchensis*	Cascade Head, Ore. 1976	98	100-120	0.79	86	87	1033	Funmori et al
Pseudotsuga menziesii *Tsuga heterophylla*	Blue River Ore.	63	90-110	1.1	65	66	1269	"
Abies procera-*Pseudotsuga menziesii* *Abies amabilis*	Wildcat Mtn. Reg. Nat. Area Ore.	98	100-130	1.75	86	88	1658	"

Table 6, continued

Above ground tree biomass, production, and basal area in a range of forest types

Pseudotsuga menziesii	H.J. Andrews Ore.		450	0.89	52	53	820(630-1010)	Grier & Logan 1977
Pseudotsuga menziesii	Cedar River, WA	50(42-57)	22-73	0.79	21	22(13-30)	694(511-877)	Turner & Long 1975
Sequoia sempervirens	On slopes, coastal Northern California	112(89-159)	>500	--	--	115(73-180)	1238(530-1886)	Westman and Whittaker 1975
Sequoia sempervirens	On alluvial flats	247(243-250)	>500	--	--	318(298-330)	1432(1109-1879)	
Pinus ponderosa	low elevation Sta. Catalina Mnts., AZ	46	100-180	0.68	24	25	575	Whittaker and Niering 1975
Broadleaved forests warm temperate deciduous woodlands	Coweeta, GA (S. Appalchian Mnts.)	26(25-26)	>200	0.56	13.4	14.0(13-14)	833	Monk and Day, 1985
cool temperate deciduous hardwoods	Hubbard Brook NH (White Mnts.)	24(22-26)	>250	0.32	13.0	13.3(10-16)	925(751-1095)	Whittaker et al., 1974
Subtropical evergreen hardwoods (*Eucalyptus*)	N. Stradbroke Is., Qld., Australia			0.30	9.7	10.0	1750	Rogers and Westman, 1981 Westman and Rogers, 1977

[1] Production estimates are based on regressions on estimated volume increments. Biomass based on regressions on stem parabolic volume.

[2] All conifer figures based on regressions for *Picea rubens* of Shanks and Clebsch (1962).

[3] Based on regression for *Pinus echinata* of Whittaker et al. 1963.

Leaf area indices of 15-21 for white fir and 17-25 for red fir (Table 4) are comparable to or in excess of the values of 16-20 reported for coast redwoods (Westman and Whittaker 1975). Production / leaf area ratios (g/m^2) are 78 for mature white fir, 151 for younger white fir (stand no. 13) in the Sierra Nevada, and 73 for white fir in the Santa Catalina Mountains of Arizona, compared to 46-48 for red fir, and 72-79 for coast redwoods (Westman and Whittaker 1975). In the Santa Catalinas, values are 54-69 for Douglas fir and 81-98 for ponderosa pine (Whittaker and Niering 1975). White fir forests emerge as more efficient primary producers by this measure than red fir, and comparable to some of the most productive conifer forests reported.

Although red fir forests have higher proportions of leaf biomass than white fir, presumably their lower tolerance to shading, coupled with the more severe environmental stresses of their habitat, prevent them from achieving the net production values of white fir stands. The net photosynthetic rate of Sierran red fir seedlings (3-8 yr old) grown in growth chambers with abundant moisture (Ustin et al. 1984) may be compared with that of Sierran white fir saplings (35 yr old) growing in the field also under conditions of abundant moisture (Rutter 1978). Photosynthetic rates of the two firs are relatively insensitive to temperature within normal field range (Rutter 1978, Ustin et al. 1984). At light saturation (500 microEinsteins $m^{-2}sec^{-1}$, c. 25% of full sunlight), red fir needles exhibit more than twice the net photosynthetic rate of white fir (16.8 vs. 7.5 mg CO_2 dm^{-2} hr^{-1}). At levels of illumination more characteristic of the bulk of canopy needles and the forest floor (50-100 microEinsteins m^{-2} sec^{-1}; Ustin et al. 1984), however, white fir needles sustain a net photosynthetic rate more than double that of red fir (5.7 vs. 0 -2.4 mg CO_2 dm^{-2} hr^{-1}). This increased photosynthetic rate of white fir needles within the shade of the canopy may hold the key to its higher productivity in dense stands.

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ABOVE GROUND BIOMASS AND PRODUCTION OF OTHER SPECIES

While our study was not able to include the other tree species at the study sites, similar equations exist in the literature for biomass of some of the species. These equations were always based on sample trees from other areas, and cannot be expected to estimate biomass with the precision of the *Abies* equations. However, they are useful in that they take into account the form of the tree species, and supply a basis for at least an approximate estimate of biomass. We were able to find no suitable regression equations for some of the species. In these cases we attempted to find equations for species with similar form. Of course, the use of such equations is complicated not only by problems of geographic area, but by whatever differences in form exist between the species of interest and the species for which the regression was intended. Some equations for conifer species of interest to this project are presented in Table 7, based largely on data summarized by Goltz et al. (1979).

Production regressions exist for some conifer species, but production is more dependent than biomass on site characteristics, and the equations based on other geographic areas are unlikely to provide satisfactory estimates in our study area. Biomass estimates can be made at intervals, however, and production estimated from biomass increments.

For the Log Creek plots, we are utilizing a set of dimensional analysis data from comparable or identical species in the Pacific Northwest or Rocky Mountains (Table 7). These existing regressions (see Gholz et al. 1979) which substitute *Chamaecyparis* /*Thuja* for *Calocedrus*, *Pinus ponderosa* for *P. jeffreyi*, and *P. monophylla* for *P. balfouriana* (this will be checked with data for *P. albicaulis*- see below) and old growth *Pseudotsuga menzeisii* for *Sequoiadendron giganteum*. Some data on biomass distribution with branches of *Sequoiadendron* has been collected by T. Stohlgren of the National Park Service.

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Table 7
REGRESSION EQUATIONS FOR ESTIMATING BIOMASS OF SELECTED CONIFEROUS SPECIES

X= DBH in cm
Total above-ground biomass is sum of components given

Species	A	B	authority
Calocedrus decurrens based on			
Chamaecyparis/*Thuja*			Gholz at al. 1979
foliage	-2.617	1.7824	
branches	-3.2661	2.0877	
stem	-2.0927	2.1863	
bark	-4.1934	2.1101	
P. balfouriana based on			
P. edulis			
(Y=ln DBH. C= crown dia in M and S=# stems breast height)			
Miller et al. 1981			
-1.423	1.241	0.347*lnC-0.274lnS	
P. contorta var. *murrayana* based on			
P. contorta			Gholz at al. 1979
foliage	-3.6187	1.8362	
branches	-4.6004	2.3533	
stem	-2.9849	2.4287	
P. jeffreyi based on			
P. ponderosa			Gholz at al. 1979
foliage	-4.2612	2.0967	
branches	-5.3855	2.7185	
stem	-4.4907	2.7587	
bark	-4.2063	2.2312	
Pinus lambertiana			Gholz at al. 1979
foliage	-4.0230	2.0327	
branches	-7.637	3.3648	
stem	-3.984	2.6667	
bark	-5.295	2.6186	
P. monticola based on *P. lambertiana*			
Sequoiadendron giganteum based on old-growth			
Pseudotsuga menzeisii			Gholz at al. 1979
foliage	-2.8462	1.7009	
branches	-3.6941	2.1382	
stem	-3.0396	2.5951	
bark	-4.3103	2.4300	

NUTRIENT POOLS

During 1984-85, we collected preliminary data on concentrations of various nutrients and trace elements in tissues of dominant woody species from mixed-conifer stands. Our focus in these analyses has been to collect appropriate nutrient and trace element data relevant to hypothesized effects of acid deposition on forest trees. At this stage our data has focused on nutrient concentrations, with calculations of pool sizes, an ongoing project this year.

Sampling and methods

For our studies of nutrient and trace element concentrations in mixed-conifer species, we have used two sets of samples for analysis. One set of samples came from carefully subsampled tissues of *Abies concolor* and *A. magnifica* from the trees described previously in this report in the section on biomass and productivity. These trees were collected from the Sequoia National Forest adjacent to Kings Canyon National Park. Individual analyses were made of samples of seven woody tissue types, each replicated from five trees of each species. Three replicates of each sample were run. These were bark, sapwood, heartwood, branchwood, branch bark, old twigs and current twigs. Additionally, foliage samples separated by age class were collected from four trees of each species to provide material to analyze age related effects on foliage nutrient concentrations. We used optical emission spectroscopy to provide quantitative analyses of 25 elements in these tissues. We are currently in the process of completing nitrogen and sulfur analyses of these same tissue samples.

A second set of samples of mixed-conifer tissues came from the Log Creek site in Giant Forest. Nitrogen and phosphorus concentrations of nine tissue types (heartwood, sapwood, bark, branchwood, old stems, current stems, old foliage, new foliage, reproductive tissue) were determined for seven dominant species collected in October 1983 by National Park Service staff. Therefore, we concentrated our analytical effort here on the developmental change in nutrient and trace element concentrations of new foliage collected at seven dates over the course of the summer growing season.We analyzed samples from ten trees and shrubs (see below), as well as concentrations in eight dominant species of herbaceous perennials on a single date in July, 1984. Each sample analysis was replicated three times.

Concentrations of nitrogen in tissue pools at Log Creek show expected patterns (Table 8). The five conifer species samples (*Abies concolor*, *A. magnifica*, *Sequoiadendron giganteum*, *Pinus lambertiana* and *P. jeffreyi*) all had similar patterns of nitrogen concentration, as did the sclerophyllous *Arctostaphylos patula*. *Ceanothus cordulatus*, a nitrogen-fixing shrub, had higher concentrations in all compartments. It is interesting to note the higher levels of nitrogen in sapwood than heartwood. For phosphorus (Table 9), the values are relatively similar for all of the species. A few values seem surprisingly low, however, and need to be rechecked. These include the low concentration reported for current needles of *P. lambertiana* and for bark of *A. magnifica*. Our analyses of bark of this species from our collections from Sequoia National Forest had a mean value of 1.8 mg g^{-1} dry weight, similar to that for *A. concolor* in Table 9.

Comparative studies of concentrations of trace elements in trunk tissues of *Abies concolor* and *A. magnifica*, collected in the Sequoia National forest, indicated a number of interesting patterns (Tables 10 and 11). In both species, bark concentrations of aluminum, phosphorus, calcium, and magnesium were significantly higher than in heartwood or sapwood, while other elements did not show this type of localization. Despite this apparent dichotomy between cation and trace element concentrations of heartwood and sapwood samples from these analyses, we surprisingly could not observe a similar trend in the tree cores of *Abies concolor* analyzed from Giant Forest. More study is clearly needed here to determine if site specific effects are responsible. Three trace metals indicative of combustion-related pollution (copper, zinc, and lead) were all low and close to our limits of detection. Vanadium concentrations, not shown in Tables 10 and 11, were at or below our analysis limit of 1 ppm.

We have made a special effort to investigate aluminum concentrations in fir tissues because of the suggestions in the literature that aluminum accumulation in the roots of trees may be an important factor in forest decline in Western Europe. Absolute concentrations of aluminum in roots of *Abies* were no higher than those in adjacent hardwoods (Table 12). Since there is always the possibility of contamination of field tissues by soil particles, we have calculated a Al/Ti ratio for each tissue as a relative measure of accumulation. The Al/Ti ratio of the soil is approximately 12.5:1. We have calculated a value for relative aluminum enrichment as the tissue Al/Ti ratio over that of the soil. This enrichment index makes no assumptions on the relative solubility of titanium and aluminum in soils, but rather serves as a useful relative index of enrichment.

Table 8. Nitrogen concentrations (mg g^{-1} dry wt.) in tissue pools of dominant woody species at the Log Creek site, Sequoia National Park. Values are for pooled samples collected from ten individuals of each species in October, 1983, by the Sequoia National Park staff

	Heartwood	Sapwood	Bark	Branchwood	Old stems	Current stems	Old needles/ leaves	Current needles/ leaves	Reproductive tissues
Abies concolor	<0.1	0.5	1.8	2.5	5.2	6.9	8.9	8.1	9.6
Abies magnifica	ND	0.2	1.0	3.0	4.5	8.4	9.5	10.0	ND
Sequoiadendron giganteum	<0.1	2.5	2.5	2.5	- 5.4* -		7.5	11.0	ND
Pinus lambertiana	<0.1	0.4	1.7	4.5	6.0	8.3	12.3	10.2	ND
Pinus jeffreyi	1.3	1.8	2.3	3.5	5.7	10.3	12.0	10.7	7.4
Ceanothus cordulatus	-	-	-	6.3	8.8	10.7	24.7	27.4	17.7
Arctostaphylos patula	-	-	-	3.3	5.3	6.0	8.7	11.3	7.5

*Old and current stem growth not differentiated

Table 9. Phosphorus concentrations (mg g^{-1} dry wt.) in tissue pools of dominant woody species at the Log Creek site, Sequoia National Park. Values are for pooled samples collected from ten individuals of each species in October, 1983, by the Sequoia National Park staff.

	Heartwood	Sapwood	Bark	Branchwood	Old stems	Current stems	Old needles/ leaves	Current needles/ leaves	Reproductive tissues
<u>Abies concolor</u>	0.1	<0.1	2.1	0.4	0.9	1.5	1.0	1.4	1.6
<u>Abies magnifica</u>	ND	0.1	0.8	0.3	0.8	1.9	1.1	1.9	ND
<u>Sequoiadendron giganteum</u>	0.1	0.1	0.1	0.1	- 0.6 -*		0.6	1.6	ND
<u>Pinus lambertiana</u>	<0.1	<0.1	0.1	0.3	0.9	1.6	1.3	0.8	ND
<u>Pinus jeffreyi</u>	0.3	0.4	0.3	0.8	1.3	2.0	1.5	1.9	0.7
<u>Ceanothus cordulatus</u>	-	-	-	0.5	0.8	1.2	1.4	1.6	2.0
<u>Arctostaphylos patula</u>	-	-	-	0.5	0.9	1.2	1.5	1.4	1.6

*Old and current stem growth not differentiated

Table 10. Comparative concentrations of nutrients and trace elements in trunk tissues of *Abies concolor*. Values (ppm) are means (standard diviation in parentheses) of five different trees, collected from Shell Mountain, Sequoia National Forest at elevations of 1200-2250 m.

	Heartwood	Sapwood	Bark
Aluminum	11.8	7.9	151
Phosphorus	50	106	2093
Calcium	2513	1559	10705
Magnesium	270	100	737
Potassium	11417	1899	4280
Sodium	79	19	8.4
Iron	157	274	153
Copper	4.8	9.9	10.6
Zinc	5.9	9.3	9.9
Lead	2.7	4.7	4.9

Table 11. Comparative concentrations of nutrient and trace elements in trunk tissues of Abies magnifica. Values (ppm) are means of replicate analyses from five different trees, collected from Shell Mountain and Big Meadow, Sequoia National Forest, at elevations of 2225-2550 m. Standard deviations are given in parentheses.

	Heartwood	Sapwood	Bark
Aluminum	8.5(2.7)	11.1(5.7)	92.3(42.4)
Phosphorus	2.7(4.4)	157(155)	1776(314)
Calcium	1248(813)	872(422)	3483(1068)
Magnesium	246(89)	147(35)	525(78)
Potassium	3335(645)	2902(607)	4498(814)
Sodium	3.3(3.5)	2.9(2.2)	3.8(4.4)
Iron	121(59)	169(129)	145(29)
Copper	3.7(1.4)	3.6(1.1)	9.0(2.6)
Zinc	4.8(2.9)	6.4(3.7)	8.8(5.4)
Lead	1.9(2.5)	3.6(2.6)	2.2(3.5)

Table 12. Aluminum concentration and enrichment in fine roots of *Abies* and understory hardwood at Log Creek, Sequoia National Park.

	Al ($\mu g\ g^{-1}$)	Al:Ti ratio	Al enrichment
Abies roots	2686	31.1	2.5
hardwood roots	2100	20.2	1.6

Table 13. Aluminum concentrations and enrichment in tissues of *Abies concolor* and *Abies magnifica* collected from the Sequoia National Forest. Values are means of three replicates each of five trees for woody tissues and four trees for needles.

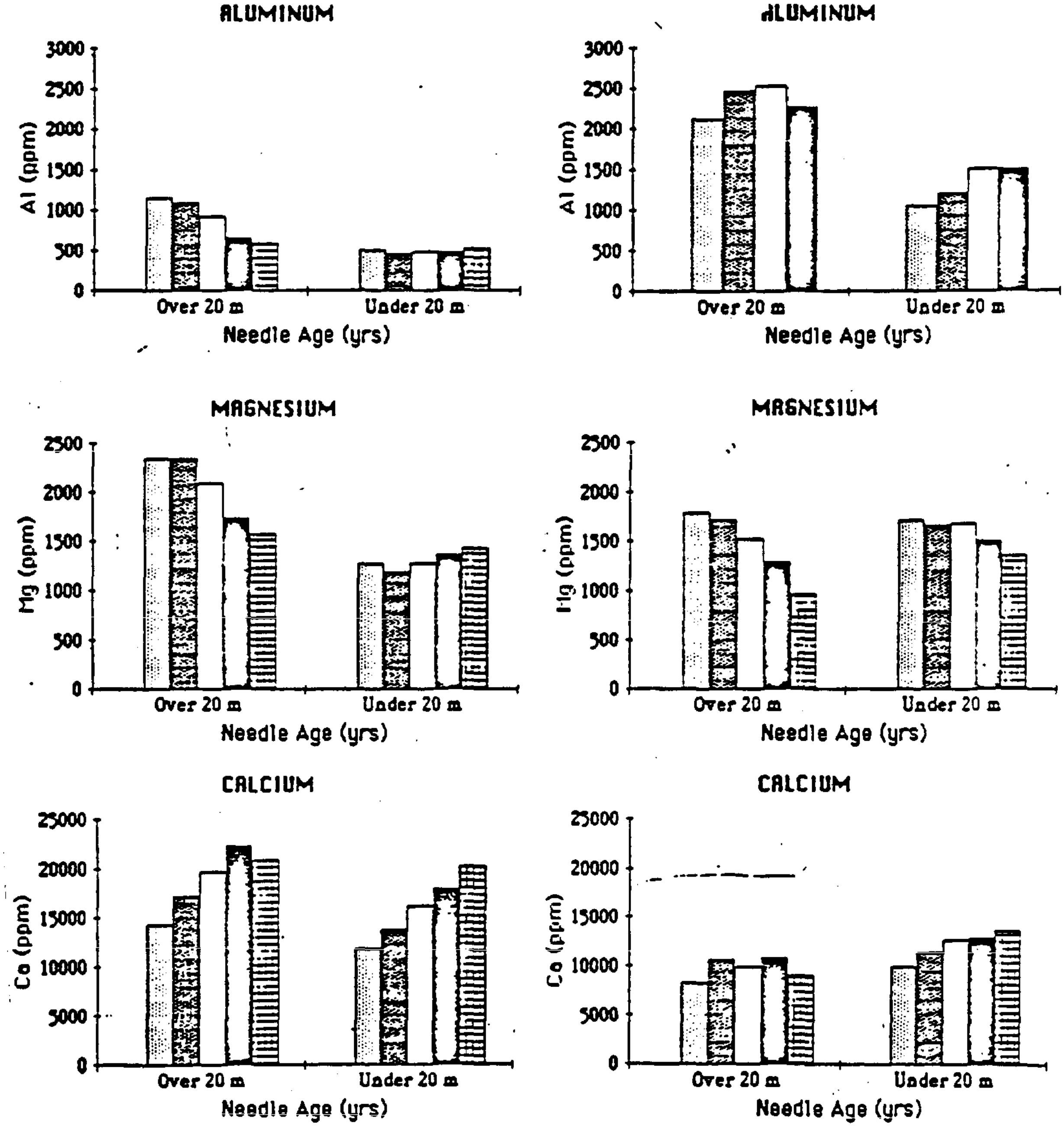
	Abies concolor		*Abies magnifica*	
	Al (ppm)	Al enrichment	Al (ppm)	Al enrichment
Heartwood	11.8	*	8.5	2.0
Sapwood	7.9	*	11.1	2.5
Bark	151	3.6	92.3	22.8
Branch wood	14.6	*	131	3.9
Branch bark	872	5.1	284	7.5
Older twigs	574	3.2	748	3.5
Current twigs	567	5.0	493	4.4
5-yr needles (>20 m in canopy)	579	4.9	2101	33.6
5-yr needles (<20 m in canopy)	523	2.6	2191	25.3
Current (1-yr) needles (>20 m)	1155	9.3	1030	31.2
Current (1-yr) needles (<20 m)	499	3.4	1491	33.9

Values of aluminum enrichment vary little between above ground tissues in white fir, but in red fir there is an interesting difference. Trunk bark and foliage in the latter species serve as sinks for aluminum, with mean enrichment values about six times greater than in other tissues (Table 13). Aluminum concentrations often increase with foliage age in the canopy, with absolute values as high as 5000 ppm. These high values of aluminum in needles of Abies magnifica in samples from Shell Mountain in the Sequoia National Forest were not matched in comparable tissues from Log Creek. These needles had no indications of aluminum accumulation.

Figure 8 presents data on foliage element concentrations for Abies concolor (left hand column) and A. magnifica (right hand column) in relation to needle age (1 to 5 years) and crown position (upper or lower). The values presented in these tables are means of analyses of four individual trees, each replicated three times. Aluminum concentrations are consistently higher, and calcium concentrations consistently lower in A. magnifica in comparison to A. concolor. For the other four elements shown, concentrations are comparable between the two species. As mentioned above, the needle concentrations of aluminum in A. magnifica are remarkably high in upper foliage, but much lower in foliage collected below 20 m in the canopy. All of the cations sampled for both species occurred at reasonable concentrations, suggesting that they are not limiting for growth.Concentrations of magnesium in 5-10 year old needles of A. magnifica from this site, however, did drop to 400-800 ppm. This level would be expected to be borderline to limiting concentrations.

Because of the ongoing nature of our trace element studies, we report our data on selected cations and trace elements in developing foliage, of Log Creek species without any significant discussion (see Appendix). Concentrations of aluminum and trace metals were consistently low. Cations do not appear to be at potentially limiting levels. It is not clear at this stage if the lack of clear patterns of change with time for most elements represents subsampling variability or whether it can be correlated with phenological or physiological parameter.

Figure 8. Nutrient concentrations in one to five-year old needles of Abies concolor (left column) and Abies magnifica (right column). Each bar of the histogram corresponds to a one year cohort of needles, with 1-year old needles on the left and 5-year old needles on the right. Ranges of needle concentrations are shown sepaately for upper canopy (over 20 m) branches and lower canopy (less than 20 m) branches.



Note: All values shown are means of samples analyzed individually from four trees for each species.

FIGURE 8 (Continued)

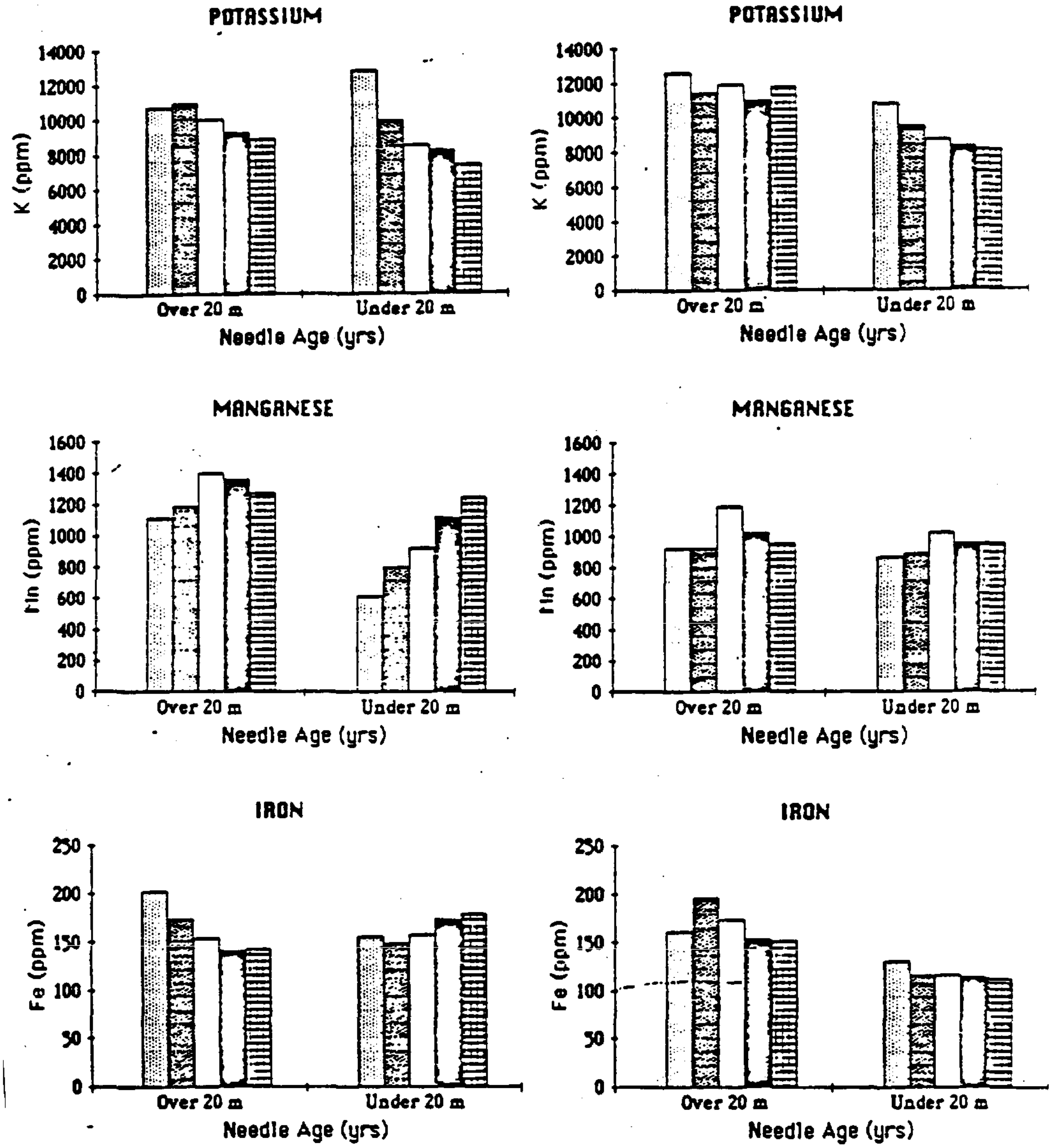


Table 14. Nitrogen concentrations (mg g^{-1} dry wt.) in tissue parts of dominant woody species at the Emerald Lake site, Sequoia National Park. Values are for pooled samples collected from ten individuals of each species in October 1983, by the Sequoia National Park staff.

	Heartwood	Sapwood	Bark	Branchwood	Old stems	Current stems	Old needles/ leaves	Current needles/ leaves	Reproductive tissues
Pinus contorta ssp. murrayana	ND	ND	ND	3.7	6.6	13.4	11.8	12.6	ND
Pinus monticola	1.0	1.5	2.5	3.0	6.3	12.0	11.3	11.1	ND
Abies magnifica	ND	ND	ND	2.8	5.5	11.8	10.3	13.0	ND
Salix orestera	-	-	-	5.3	10.5	15.8	-	19.3	12.7
Chrysolepis sempervirens	-	-	-	3.7	8.0	12.3	13.7	15.4	ND
Phyllodoce breweri	-	-	-	5.0	6.5	12.6	10.6	14.1	12.3

Table 15. Phosphorus concentrations (mg g^{-1} dry st.) in tissue parts of dominant woody species at the Emerald Lake site, Sequoia National Park. Values are for pooled samples collected from ten individuals of each species in October 1983, by the Sequoia National Park staff

	Heartwood	Sapwood	Bark	Branchwood	Old stems	Current stems	Old needles/ leaves	Current needles/ leaves	Reproductive tissues
Pinus contorta ssp. *murrayana*	ND	ND	ND	0.8	1.2	2.0	1.2	2.0	ND
Pinus monticola	0.6	0.8	0.7	1.0	0.9	2.2	1.8	2.0	ND
Abies magnifica	ND	ND	ND	1.0	0.7	2.9	1.6	1.8	ND
Salix orestera	-	-	-	0.9	1.3	1.5	-	1.7	1.6
Chrysolepis sempervirens	-	-	-	1.0	0.3	1.4	1.4	2.0	ND
Phyllodoce breweri	-	-	-	1.0	1.3	2.0	1.4	1.8	2.1

BELOW GROUND PRODUCTION

The objectives of the below ground portion of the project were:

1) Estimate the yearly production of fine roots in the upper soil layers at the mixed-conifer site.

2) Obtain an estimate of the fraction of new root length colonized by ecto- and vesicular-arbuscular mycorrhizal fungi.

3) Using a correction factor for weight of fungal tissue per unit of colonized root length, estimate yearly production of symbiotic fungal tissue.

The plots were laid out and field work begun in June and July of 1984, as soon as administrative and personnel considerations allowed. The three 25 by 25 meter square plots are in a small drainage above Log Meadow, in an area heavily used by park service and outside researchers. They are situated between the large permanent plots of the a group from Oregon State University and some plots used for decomposition studies by NASA researchers.

Yearly production of fine roots

The first objective was met through application of the plane intercept method, a procedure for estimating root production. The theory of the technique was described in detail in the proposal. The methodology has been refined by much practical experience gained since that proposal was written. Appendix IV gives a discussion of the method and the field techniques that have evolved through use of it in this project, in a Colorado shortgrass prairie, and in a California desert ecosystem.

Certain unexpected difficulties were encountered in the use of the technique. The screens were marked with flagging tape for easy relocation. The flags proved attractive to park animals, and a number of screens were harvested ahead of schedule by the bears. There was no root growth whatever from July through October, and the set of 90 screens per plot installed on July 4 was conserved to monitor winter and spring root growth. No screens could be located under the snow on the January 10 sample date. Some soil cores taken at that time turned up only older, decomposed roots in the small size classes, except for a single example of fine angiosperm roots. This suggests that root growth of the conifers still had not begun. Recovery of the screens, even when marked with flagging tape, proved unexpectedly difficult. As of this writing, 1984 screens are still being found in the course of other activities at the site. Some of these delayed harvests will be reported in connection with work taking place outside this funding period. Counts from surviving screens, and accompanying calculations, are shown in Table 16. They indicated a production rate of 17.5 g/m^2 during the one-year period from July 4, 1984, to July 18, 1985.

The plane intercept technique was supplemented by soil cores taken on two harvest dates. While the cores were not part of the original plan, we decided to add them to the schedule because the plane intercept technique by itself does not provide an estimate of root standing crop. Production remains the parameter of primary interest, but the perspective provided by standing crop allows more meaningful comparisons with studies published elsewhere.

The soil cores were taken the week of October 16, 1984, and the last week of May, 1985. The roots were washed out of the soil, oven-dried, and sorted into size classes as shown in Tables 17 and 18. The class boundaries conform to those of Santantonio et al. (1977), to make them comparable to that and other ecosystem work in coniferous forests. No attempt was made to sort live from dead biomass. Biomass in five root size classes and on two harvest dates is summarized in Figure 9. Both biomass and length of root in each size class are given in Table 17 for the October 1984 harvest. Biomass in each size class is given in Table 18 for the May 1985 harvest.

Table 16
SCREEN INTERCEPT COUNTS

SITE: LOG CREEK
INSERTED: JULY 1984 FIBERGLASS SCREENS

HARVEST: JUL 18, 85 1 YEAR

PLOT	MEAN # INTCPTS	LENGTH CM/M2	g/M2
1	1.2	8250	26.71
2	0.0	0	0.00
3	1.1	7955	25.76
HARVEST MEAN:		5401	17.49

Table 17
ROOT BIOMASS AND LENGTH, OCT 1984
Log Creek, Sequoia National Park

	Root diameter <2		2-5mm		5-10mm		10-20mm		20-50mm		Totals
Plot	g/m²	cm/m²	g/m²	cm/m²	g/m²	cm/m²	g/m²	cm/m²	g/m²	cm/m²	g/m²
1	361.3	139429	273.9	9164	119.0	787	114.0	255	0.0	0	868.2
2	362.4	102417	229.1	8184	180.5	1474	158.2	436	99.1	90	1029
3	591.4	140448	272.7	10972	159.9	13623	96.8	210	0.0	0	1023
MEAN	[illegible]	127431	258.2	9440	153.1	1208	119.7	300.3	29.7	[illegible]	[illegible]
ST DEV	127.7	60293	97.2	5152	101.2	794	193.9	459	162.7	145	

Table 18
ROOT BIOMASS, MAY 1985
LOG MEADOW

31 MAY 85 PLOT 1	ROOT DIAMETER CLASSES, mm					TOTAL
PLOT #	<2	2-5	5-10	10-20	20-50	g/m^2(30cm)
1	949.0	455.8	236.5	252.8	320.5	2215
2	408.3	242.8	150.6	98.5	2502	3402
3	342.3	222.6	223.3	317.6	1631	2737
MEAN	566.5	307.1	203.5	223.0	1484	2785

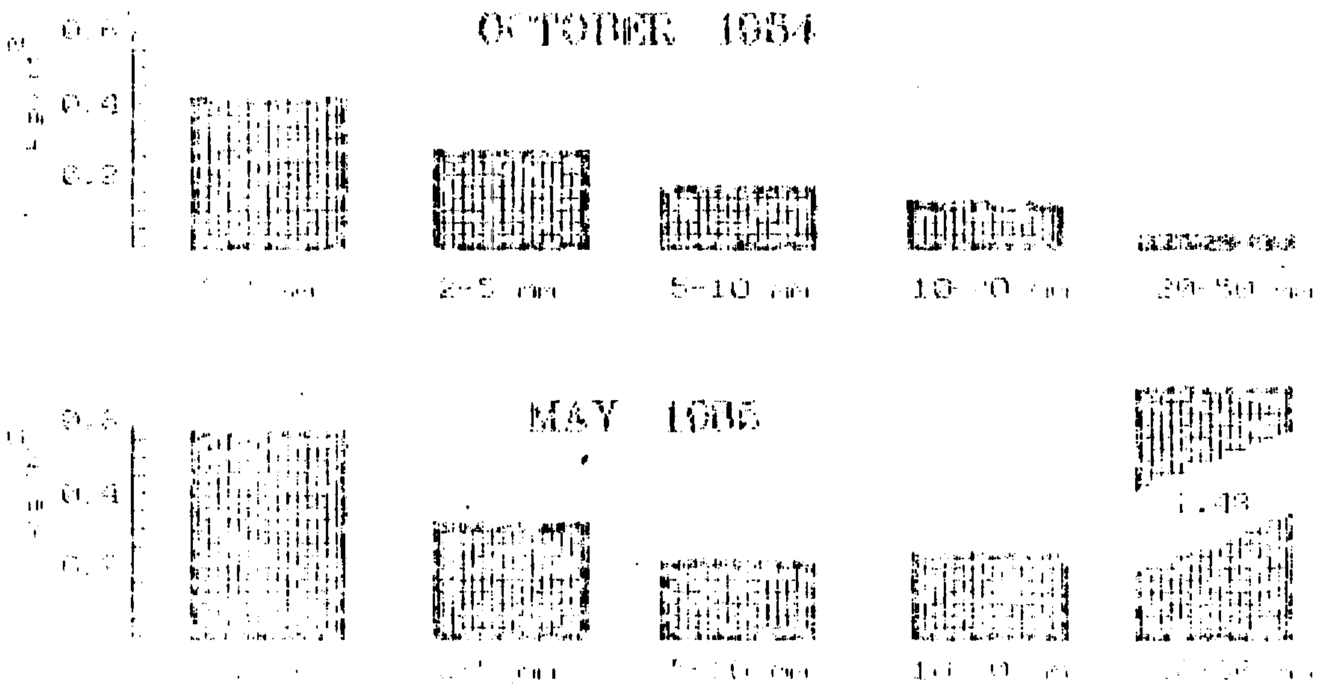
Table 19
MYCORRHIZAL COLONIZATION
LOG MEADOW

31 MAY 85		LENGTH/LENGTH		BIOMASS OF	BIOMASS
PLOT #	<2mm ROOTS	ECTO	VAM	MYC. FUNGI	g/m2(30cm)
1	29.815	0.004	0.000	0.051	1.634
2	12.827	0.003	0.002	0.021	0.682
3	10.754	0.006	0.000	0.029	0.923

Figure 9

ROOT BIOMASS IN FIVE DIAMETER CLASSES

Log Creek, Sequoia National Park



The plane intercept method provides a direct determination of root growth, but registers only the growth of the finest size class. A supplementary estimate of belowground production can be made from the cores, using as a basis the assumption that differences in standing crop between sample dates must represent root production. An increase indicates that the new root growth took place between sample dates. A decrease would indicate that it occurred at a different time of year and only decomposition was registered by that data set. The mean biomass for the three plots in October, 1984, was 970 g/m^2. That for May 1985 was 2785 g/m^2. This suggests that 1815 g/m^2 grew at some time between sample dates.A figure that considers only the \<2 mm size class indicates a positive increment of 158 g/m^2. This calculation requires that root growth in 1984 and 1985 were identical, an unconfirmed assumption. With a single season's data, it is impossible to distinguish year-to-year variation from real production with these methods.

Previous studies of fine root production in coniferous forests have indicated higher production values than found in this study. Fogel and Hunt (1983) observed no fine root production in the first year of their work in a western Oregon stand of Pseudotsuga menziesii, but found 379 g/m^2 during the second year. Persson (1978), in a Swedish plantation of Pinus sylvestris, found 183 g/m^2 fine root production. Person (1980) found 218 g/m^2 in similar conditions. Vogt et al (1982) found between 571 and 1196 g/m^2 in subalpine stands of Abies amabilis in western Washington. The methods of all these studies resembled the core method used in the present project. Our soil core results are comparable to the lower values found in other projects, but the plane-intercept results are an order of magnitude lower. Persson (1979), reported an experiment in which a second method was used along with soil cores. The results from his ingrowth cores were very different from the soil core results, underscoring the strong and somewhat disturbing dependence of root production on the method being used.

Fraction of new root length colonized by mycorrhizae

Mycorrhizal colonization, as originally planned, was to be determined by evaluation of roots passing through the plane of the screen. It turned out that the roots that passed through the screen were usually extension roots that kept growing. The short mycorrhizal side roots tended not to pass through the screens, and the estimates made in this way were almost certainly much too low. The anticipated use of this method was based on experience with Vesicular-arbuscular mycorrhizae in other projects. Because of the unexpected difficulty, an alternative method for determining rate of mycorrhizal colonization was used. Samples of the smallest root fraction from the soil cores were cleared and stained (Phillips and Hayman 1970) and examined microscopically while superimposed on a fine grid. Intersections of roots with the grid line were counted and scored mycorrhizal or nonmycorrhizal. Because grid intercepts are a measure of length (Marsh 1971), the parameter (mycorrhizal/total intercepts) multiplied by 100 gives a length/length percent determination of colonization. For both ecto and vesicular-arbuscular mycorrhizae, percent infection means length of colonized root divided by total root length, times 100. This is more conventional for vesicular arbuscular than for ectomycorrhizae, but was used here for ectomycorrhizae because it provides a basis for estimating fungal biomass and production.

Biomass of mycorrhizal fungi

There was no direct measurement of this parameter in this project, and this parameter has not been measured with confidence in any ecosystem study of ECM. The data of Fogel and Hunt (1983) included all soil fungi, since there was no clear basis for distinguishing ectomycorrhizal hyphae from saprophytes. The approximation used in this study is to accept the value used by Vogt et al. (1982) for the fungal share of total root weight: 40%. We have assumed that the 40% accounts for both internal and external mycelium. While VAM hyphae can be distinguished from other soil fungi, there are nonetheless very few field data on which to base an estimate of external VAM mycelium. Sanders et al. (1977) reported 3.6 micrograms per cm of mycorrhizal root length, in pot culture conditions. Nicolson and Johnston (1979) found between 0.2 and 1.6 g external mycelium per liter of Scottish dune sand, with an extreme value of 4.5 g/l. A recent unpublished study by St. John showed a low of 8.4 g/m^2 in October and a high of 18.6 g/m^2 in August. If recalculated to give comparable units, the data of St. John come out about an order of magnitude higher than those of Sanders et al., and those of Nicolson and Johnston between one and two orders of magnitude higher still. Because the present project is being done at a field site where external mycelium is expected to be low, the value of Sanders et al. (1977) is probably the most appropriate comparison. That conversion factor is reflected in Table 19.

In addition to the external mycelium, internal structures must be included in the estimate of fungal biomass. Fogel and Hunt (1983) considered in their work that 40% of the ectomycorrhizal tissue was fungal. We have used this figure to include both root- and soil-borne fungal tissue.Hepper (1977) found in her experiments with VAM that internal fungal tissue constituted 2.5% of the weight of colonized roots, and we have used her value for our calculations. Both internal and external mycelium are accounted for in this way by the calculations in Table 19.

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POPULATION STUDIES

The Sequoia-mixed conifer forests are an important economic and unique biological resource (Rundel et al. 1977), covering extensive acreage in the western Sierra Nevada. These forests include the largest trees in North America and the last remaining natural habitat of <u>Sequoiadendron giganteum</u> (giant Sequoia). All but a few stands are in Sequoia and Kings Canyon National Parks.

These forests are subject to periodic disturbances of several types. The disturbances range from irregular fires to oxidant pollution (Miller et al., 1972). The few stands outside the National Parks face additional pressures of logging and grazing. To soundly manage these unique forests we must understand the complex successional processes that result from these forms of disturbance.

Gleason (1926) articulated the importance of individuals and local populations as functional units of succession. Modern successional studies should address the population dynamics of the involved species (Drury and Nisbet, 1973; Shugart, 1985). This approach has received limited application in forest successional studies because of the complex requirements in collecting relevant data. This scarcity of work is reflected in the limited number of appropriate data sets available (e.g., Leak, 1970; Horn, 1974). Theoretical models of forest succession for mixed-conifer forests in the Sierra Nevada have been proposed by Bonnickson and Stone (1982) and by Kercher and Axelrod (1984), but lack empirical data, especially on attributes of population structure.

Western Timber Service (1970) established 100 permanent plots from 1966 to 1969 to quantify the forest structure and timber types present in the <u>Sequoiadendron giganteum</u> groves of Sequoia and Kings Canyon National Parks. These surveys recorded dbh (diameter at breast height) on all tree species present in each 20 x 100 m plot. Although the primary goal was vegetation-type description, the plots were permanently marked for later use in long-term successional studies.

There are three objectives to this research: 1) to examine the rate of succession in plots; 2) to detect evidence of mortality that might be related to pollution; and 3) to demonstrate the detailed effects of fire upon succession.

Preliminary data has shown succession to be occurring at an unexpectedly rapid rate in stands that, from a management standpoint, were considered undisturbed. The documented presence of oxidant pollution (Miller et al. 1972) suggests that the entire Sequoia-mixed conifer forest receives a chronic disturbance that may be affecting changes. Williams et al. (1977) and Williams (1983), for example, have recorded oxidant-induced disease in the area. This study will examine the possibility that our records include effects of oxidant upon forest successional processes in greater breath than any previous research. The data base is sufficiently diverse to analyze succession over the full comprehensive examination of the successional process.

METHODS AND MATERIALS

From 1966 to 1969, 100 permanent plots (Tables 20, 21), 100 x 20 m rectangles, were established as part of the Sequoia Inventory Project at Sequoia and Kings Canyon National Parks (Western Timber Service, 1970) (figure 10a). The plots were created to quantify typical forest structures present within Sequoia-mixed conifer forests. Every standing tree stem, living and dead, was recorded by species and diameter increment class (2-inch and 4-inch increment). The largest concentration of permanent plots are the 6 of the Redwood Mountain-Big Stump-Grant's Grove area (figure 10b). The region is geographically close enough to be considered climatically and topographically similar (Harvey et al. 1980).

The Redwood Mountain grove, which contains 51 permanent plots, has recently received extensive use in burning experiments. Grant's Grove has been protected since 1936 (Hartesveldt et al. 1975) and it, too, has been treated in part with controlled burns. The Big Stump grove became part of the park in 1963 and permanent plots were all unburned through our field resampling.

We selected 18 unburned plots (Table 20) and 21 burned plots (Table 21) from the Redwood Mountain-Big Stump-Grant's Grove region which represented the moisture-topographical diversity of the area and were relocatable without any ambiguity in boundary. Several of the original plots could not be relocated accurately and they had to be eliminated from the study. Three subjective moisture classifications were recognized based entirely on physical characteristics. Xeric plots were generally on steep dry exposures or rocky saddles. Wet mesic plots were those with permanent water with the plot boundaries. Dry mesic plots were those of intermediate character.

Those plots accurately relocatable from the original orientation instructions were gridded off into 5 x 5 m squares and all standing stems of 5 cm height and greater were measured and mapped. Diameters greater than zero were recorded to the nearest 0.25 cm. at breast height (1.6 m). Stems less than 1.6 m height were recorded by height to the nearest 2.0 cm. Some of the stems were spatially recorded as counts per subquadrat.Stumps and fallen dead stems were usually mapped and measured as well to confirm mortality records. Plot topography, general condition and other standard physical parameters were recorded. Recent fire records obtained from Resource Management Department, Sequoia and Kings Canyon National Parks, were used to identify plots which had natural or prescribed burns since the original survey.

RESULTS AND DISCUSSION

Most of the unburned plots showed considerable change in actual count (Table 22) and basal areas (Table 23). The general trend was an increase in both attributes, although there was some specific variation. The burned plots also showed considerable change but the general trend was a substantial decline in stem number (Table 24) and a less pronounced loss in specific basal area (Table 25).

When the plots are pooled by available moisture type, similar trends appear with some deviation. The unburned plots had general increases in basal area (figure 11), but specific variations are apparent. These differences were sufficiently strong to shift the relative dominance of the available moisture groups (Figure 12). The burned plot results, when pooled by available moisture class, show the overall loss, but interesting individuality is present (Figure 13). Even with shifts in relative dominance (Figure 14), rank order remained the same in all but the wet mesic group (Figure 14c).

Recruitment of new individuals into the zero diameter class was recorded by stem counts. This method represents the recruitment of the last few years, but may be biased toward species with recent large seed crops.Nonetheless, several patterns of specific differences emerged in the burned and unburned comparison (Figure 15). Generally, the total recruitment was about equal but the species representations were distinctly different in burned and unburned plots.

Rates of mortality were arranged by size class and available moisture category for unburned (Table 26) and burned (Table 27) plots. In agreement with widely accepted predictions (e.g., Whittaker 1975, Pianka 1983), the mortality was generally highest in the smallest size classes. However, there were exceptions, particularly in the unburned plots. The mortality in the smaller size classes was substantially higher in the burned plots, as would be expected. Even though the mature stems had similar mortality rates in both fire treatments, these large mature stems are especially important as the source of future reproduction. Since they should have sufficient root development to obscure local physical habitat differences, they were pooled for a direct burned and unburned comparison (Figure 16).

Pinus ponderosa/jeffreyi (a hybrid of ponderosa and Jeffrey pine), the species with fewest individuals in the original plots, declined in basal area and number regardless of burn treatment. The losses in basal area were sufficient to promote concern over the future of this species as a member of the Sequoia-mixed conifer forest type. The downward shift in relative dominance has made Pinus ponderosa/jeffreyi the least important species in all but the xeric plots; even there (e.g., GT4), the decline is pronounced. The loss in basal area can be easily attributed to mature stem losses in both burn and unburned plots. Recruitment is still occurring in unburned plots, but with a mature stem mortality rate of 2.7% a year it is doubtful that replacement is currently possible. As the species most vulnerable to oxidant pollution (Miller 1973, Williams 1983), the high rate of mortality deserves special attention in future research.

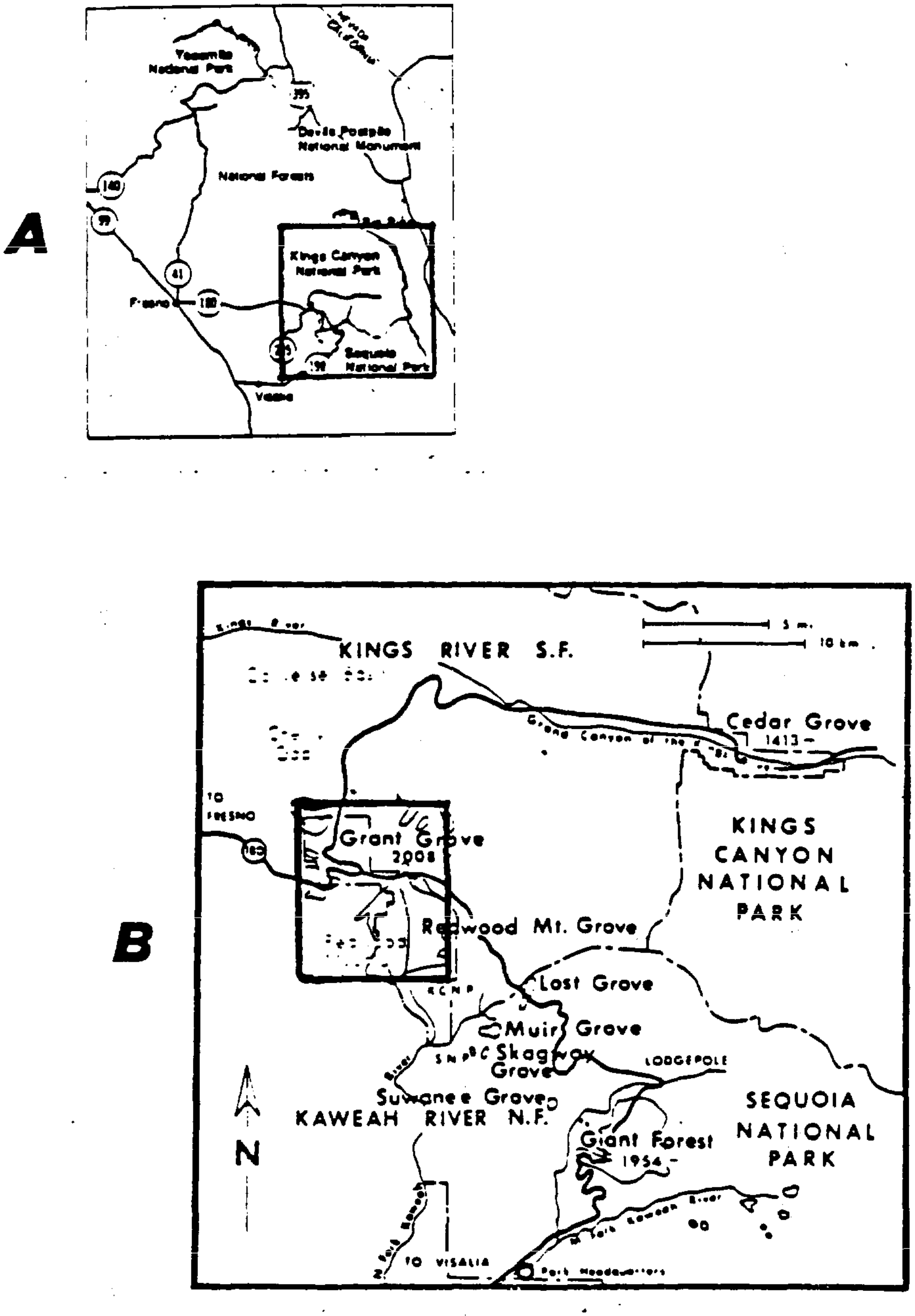


FIGURE 10

Location of the study area (A), Sequoia and Kings Canyon National Parks, and the perimeter boundary of the sample plots (B).

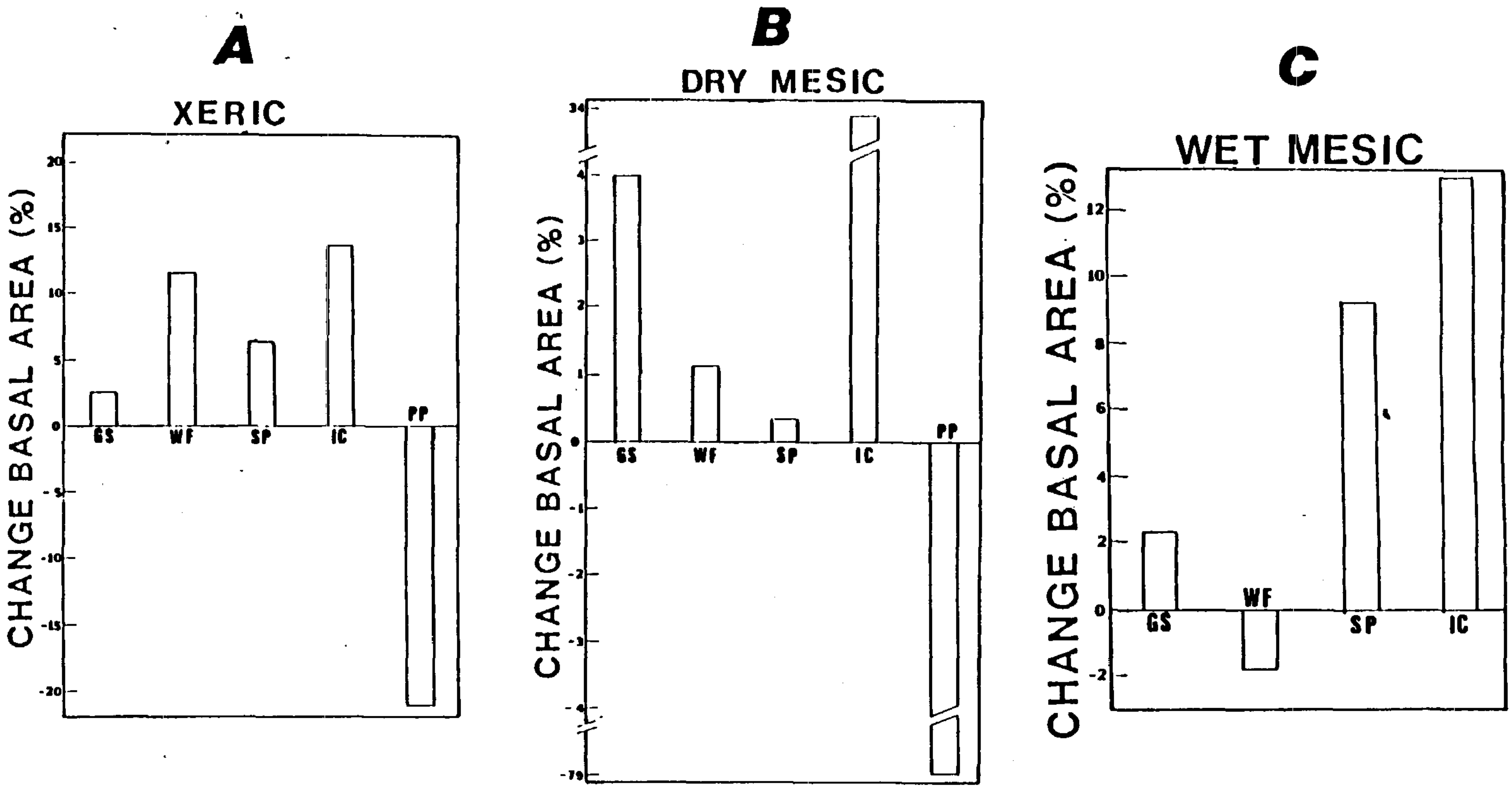


FIGURE 11

Species changes in basal area, pooled into available moisture classification groups, since permanent plot establishment at unburned stands.

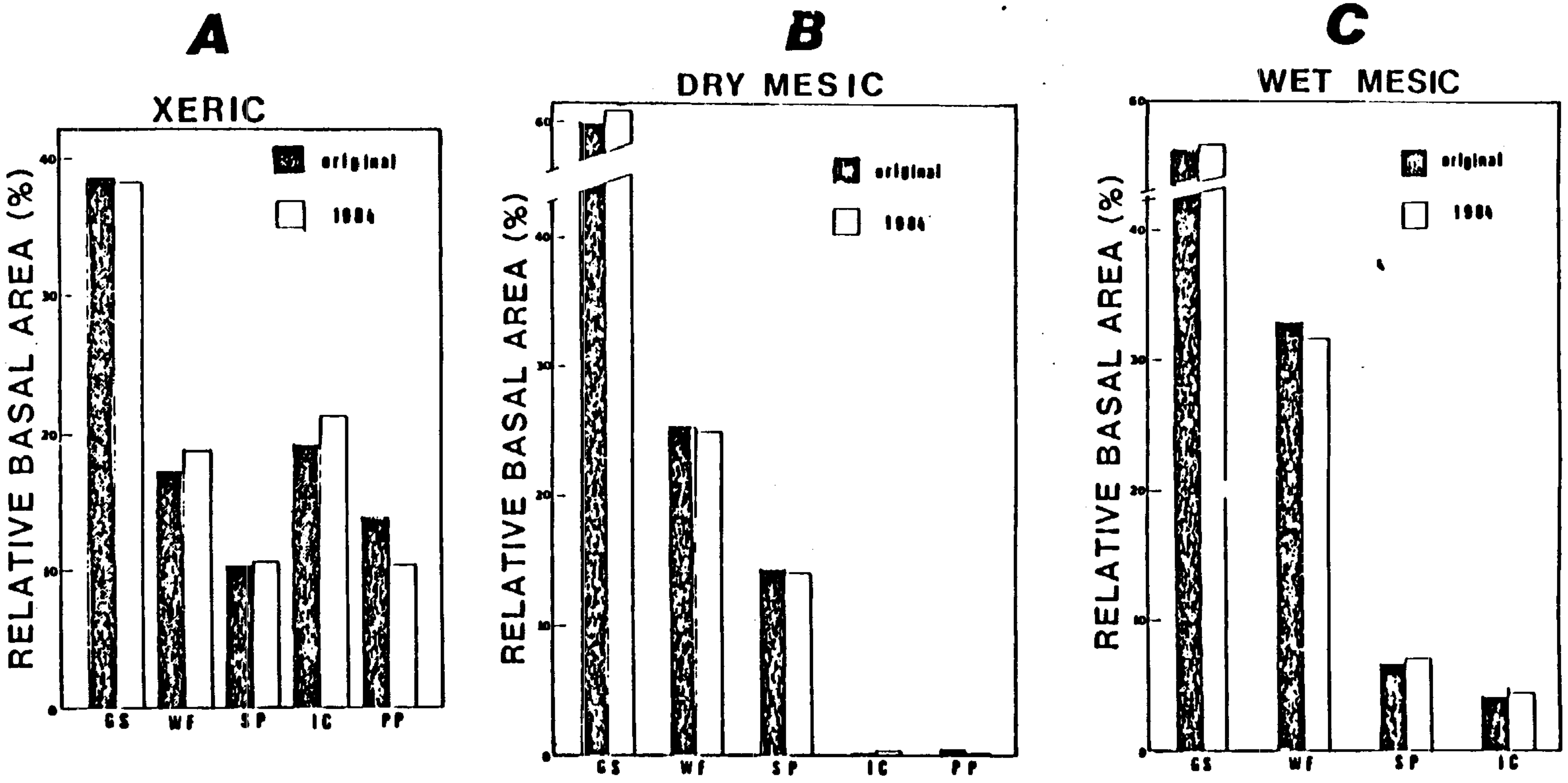


FIGURE 12

Relative dominance of coniferous tree species pooled into available moisture classification groups of unburned permanent plots.

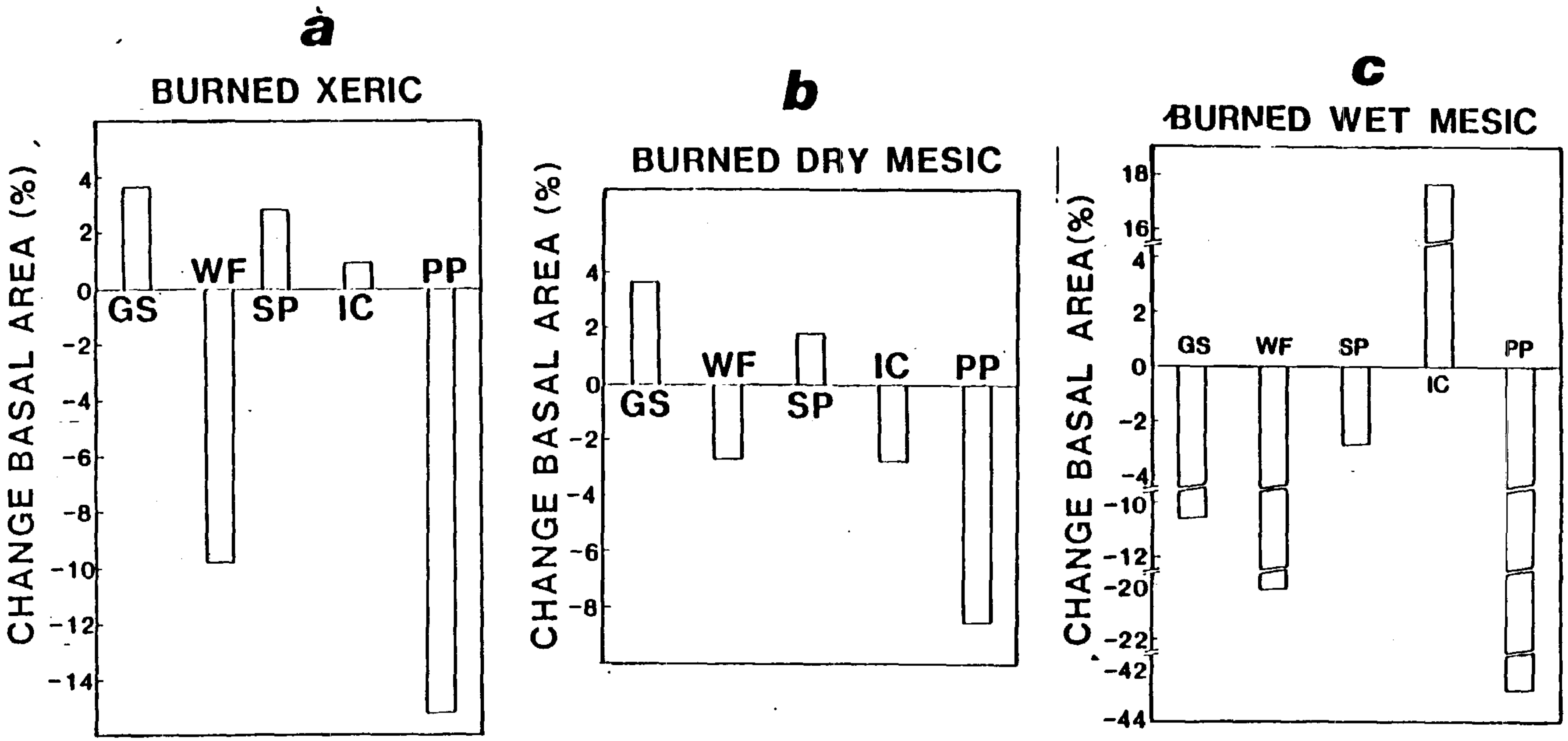


FIGURE 13

Species changes in basal area at burned stands pooled into available moisture classification groups since permanent plot establishment.

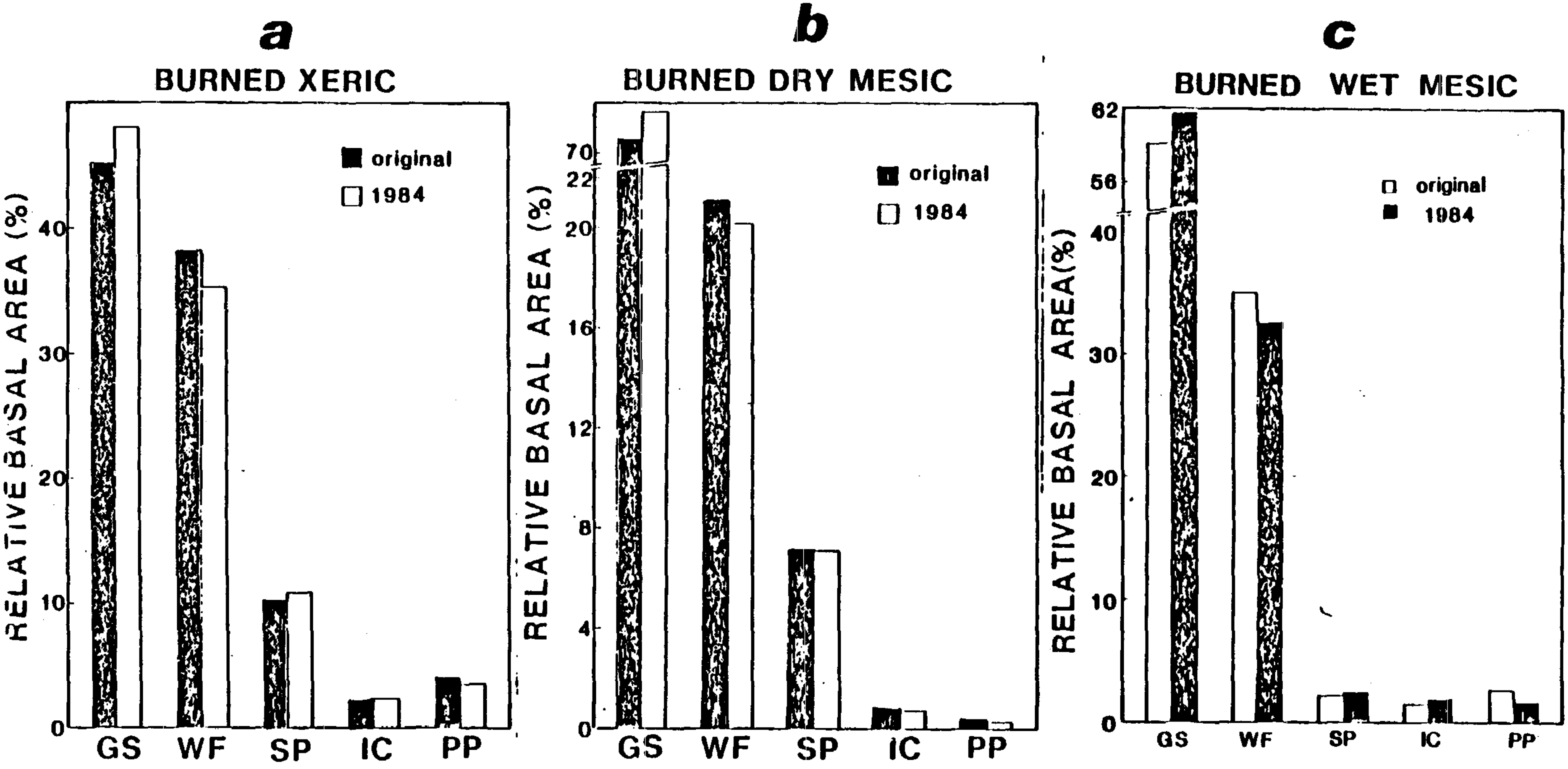


FIGURE 14

Relative dominance at burned permanent plots pooled into available moisture classification groups.

FIGURE 15

Zero class stem (2.5 diameter at S.D.B.H.) recruitment rates at burned and unburned permanent plots.

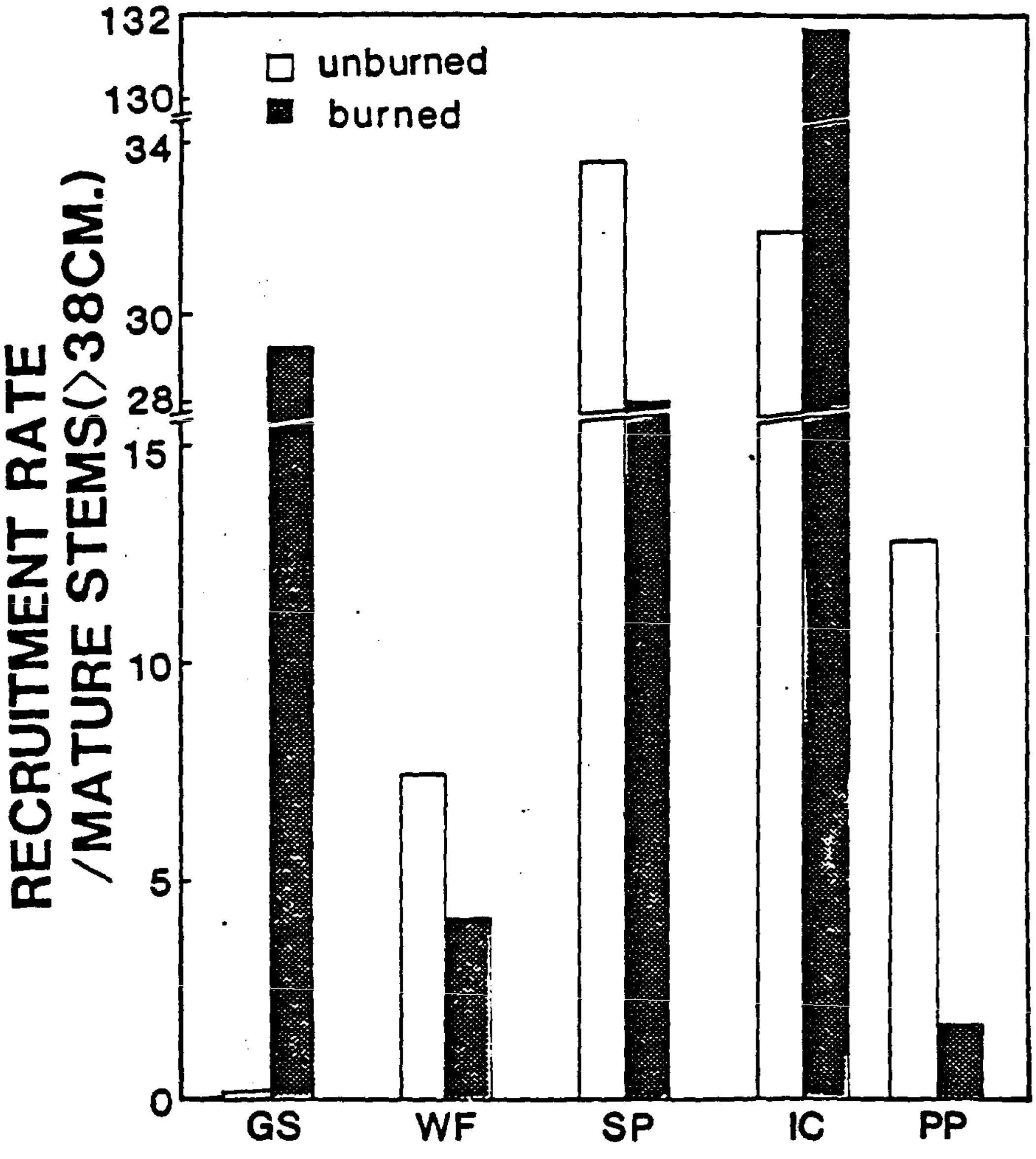
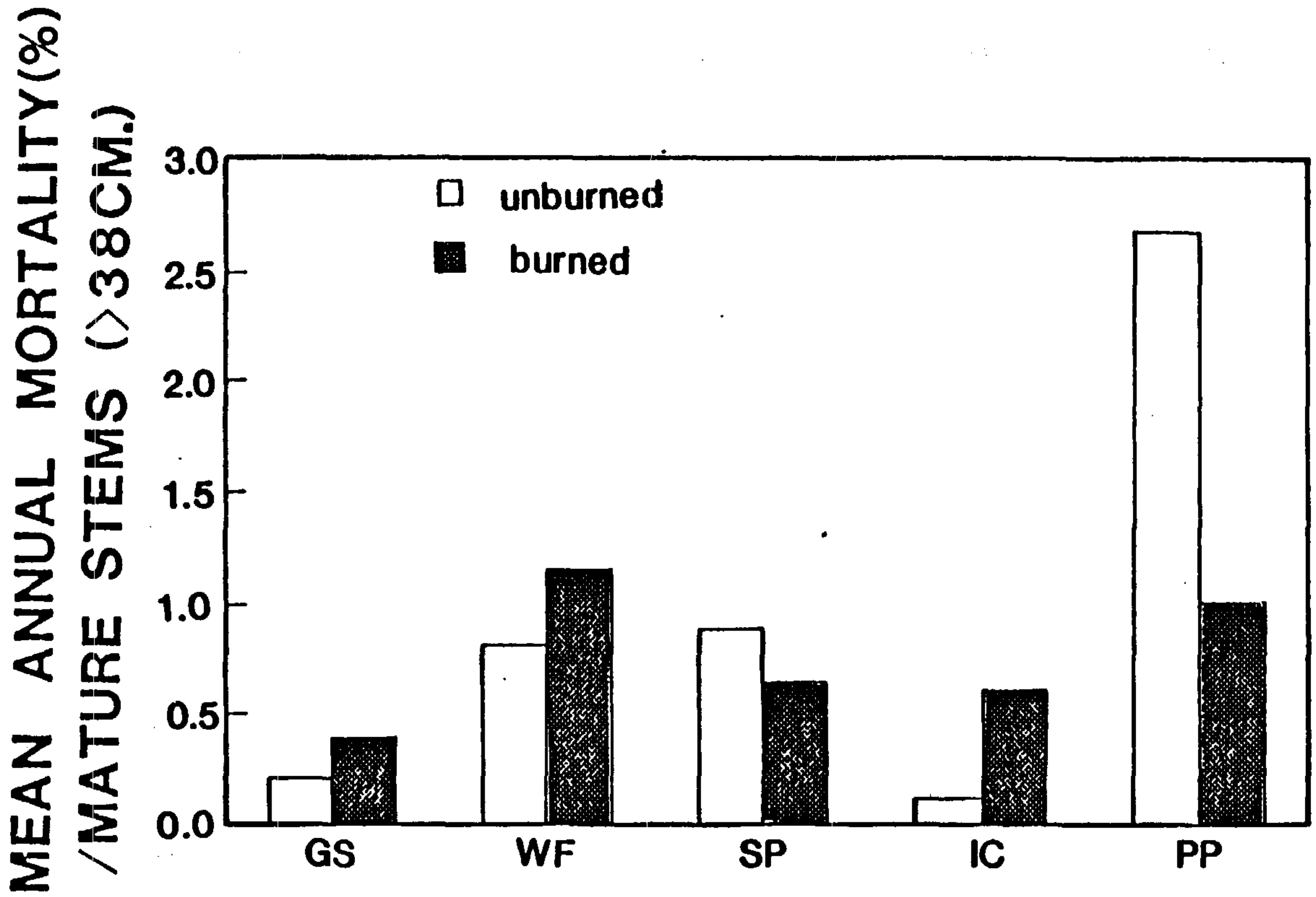


FIGURE 16. Comparative mortality rates at burned and unburned permanent plots of mature tree stems (> 38 cm. diameter at S.D.B.H.).



Calocedrus decurrens (incense cedar) was best represented on the xeric and wet mesic plots. On unburned plots it increased consistently in basal area and number.The large, well-established populations were not widespread but the species was vigorous throughout the unburned sample. The dramatic increases in basal area were somewhat surprising. *Calocedrus decurrens* is considered a tolerant species (Harlow et al. 1979) but it is also considered the slowest growing of the sample group (Fowells 1941, 1965). The increase in *Calocedrus decurrens* has been noted in a few literature references (e.g., Sellers 1970, Parsons and DeBenedetti 1979), but many considered the species of too little importance for more than casual mention (Bonnickson, 1975; Bonnickson and Stone, 1982). With the high rate of recruitment and low rate of mortality found in this study, *Calocedrus decurrens* appears to be a species of increasing importance in the Sequoia-mixed conifer forest. There were some heavy losses on burned plots but *Calocedrus decurrens* increased even there. Only *Sequoiadendron giganteum* had a lower rate of mortality on burned plots and no species of the study had a higher rate of recruitment.

Abies concolor (white fir) is generally considered the dominant species in Sequoia-mixed conifer forests and it was the best represented tree of this study. With some local variation *A. concolor* increased on unburned plots but the mortality rate of mature stems was higher than several other species. The recruitment rate of *A. concolor* was near the lowest in both fire treatments. The results raise doubts about the reputed role of *A. concolor* as the dominant tree species in the absence of fire (Vankat and Major 1978, Bonnickson and Stone 1982).

Abies concolor is considered intolerant of fire (Harvey et al. 1980, St. John 1976) and our results strongly support that conclusion. *Abies concolor* suffered the highest rate of mature stem mortality in the burned sample. On burned plots *A. concolor* consistently declined in relative dominance. Only *Pinus ponderosa/jeffreyi* endured greater basal area losses.

Pinus lambertiana (sugar pine, contrary to expectations (Fowells 1965), was best represented on plots with higher available moisture. Recruitment rates were high on both burned and unburned plots but mortality rates were also consistently high. The net result was a modest increase in *P. lambertiana* relative dominance on most plots. *Pinus lambertiana* is considered a tolerant species (Spurr and Barnes 1980). The predicted fire resistance of this species held true in our study. The high unburned mortality rates raised a question of oxidant pollution as a possible factor in *P. lambertiana* mortality.

Sequoiadendron giganteum had almost no recruitment on unburned plots, in agreement with previous studies (Harvey et al. 1980), but the species maintained sable codominant populations. The mortality was locally high but the attrition was more or less restricted to small stems that grew in high density. Basal area increased consistently and the exceptions were mostly the wet mesic burned plots where stems can easily topple. On all but the unburned xeric plots *S. giganteum* increased in relative dominance.The mortality rates of large stems for *S. giganteum* was low in unburned plots and the lowest of the study group under burned treatments. The recruitment became robust following a fire and, in general, the species appears to have stable populations under all recent park conditions.

Table 20. Physical site characteristics of unburned permanent plots.

Grove	ID Number[t]	Date of Estimation	Elevation (m)	Aspect	Slope	Topographic position*	Moisture
Big Stump	(BS1)	5/68	1920	360°	15°	L	W-M
Big Stump	(BS3)	5/68	1920	351°	15°	L	D-M
Big Stump	(BS4)	9/67	1951	86°	20°	L	W-M
Big Stump	(BS5)	5/68	1834	180°	30°	T	X
Big Stump	(BS6)	9/67	1905	356°	25°	T	X
Grants Grove	(GT1)	7/67	1905	200°	25°	L	D-M
Grants Grove	(GT2)	7/67	1829	180°	40°	U	X
Grants Grove	(GT3)	7/67	1768	88°	5°	B	W-M
Grants Grove	(GT4)	7/67	1829	200°	45°	T	X
Redwood Mt.	(RW2)	8/69	1738	204°	35°	U	X
Redwood Mt.	(RW23)	9/68	1905	210°	10°	UT	D-M
Redwood Mt.	(RW26)	9/68	1661	210°	30°	L	D-M
Redwood Mt.	(RW27)	9/68	1661	200°	5°	ML	W-M
Redwood Mt.	(RW37)	9/68	1722	180°	30°	U	D-M
Redwood Mt.	(RW38)	9/68	1783	20°	5°	LM	W-M
Redwood Mt.	(RW42)	9/68	1859	170°	15°	LB	W-M
Redwood Mt.	(RW47)	9/68	1738	240°	35°	U	D-M
Redwood Mt.	(RW50)	8/69	1874	227°	40°	U	X

t = from Western Timber Service, 1970

* = L-lower slope, U-upper slope, T-ridgetop, B-bottom, M-meadow, R-rocky

** = X-xeric, D-M-dry mesic, W-M-wet mesic

Table 21. Physical site characteristics of the permanent plots that have been burned since establishment.

Grove	ID^{t}	Date of Estimation	Elevation (m)	Aspect	Slope	Topographic position*	Moisture	Burned
Grants Grove	(GT5)	7/69	1905	185°	30°	U	Xeric	1982
Grants Grove	(GT7)	7/69	1874	174°	25°	U	Dry-mesic	1982
Redwood Mt.	(RW5)	7/68	1951	120°	30°	UT	Xeric	1977
Redwood Mt.	(RW14)	5/68	2057	174°	45°	UR	Xeric	1977
Redwood Mt.	(RW16)	5/68	1996	140°	30°	UT	Dry-mesic	1977
Redwood Mt.	(RW17)	5/68	1966	185°	32°	UT	Xeric	1977
Redwood Mt.	(RW18)	7/68	1844	165°	10°	L	Wet-mesic	1981
Redwood Mt.	(RW19)	7/68	1813	170°	5°	M	Wet-mesic	1977
Redwood Mt.	(RW20)	7/68	1829	225°	30°	LB	Wet-mesic	1980
Redwood Mt.	(RW21)	7/69	2027	210°	15°	T	Dry-mesic	1977
Redwood Mt.	(RW25)	7/68	1920	354°	32°	U	Dry-mesic	1969
Redwood Mt.	(RW28)	7/68	1691	240°	30°	U	Xeric	1971
Redwood Mt.	(RW29)	7/68	1768	320°	35°	RT	Xeric	1972
Redwood Mt.	(RW32)	8/68	1874	290°	35°	U	Xeric	1977
Redwood Mt.	(RW33)	8/68	1951	234°	25°	U	Dry-mesic	1977
Redwood Mt.	(RW40)	7/68	1874	165°	15°	B	Wet-mesic	1980
Redwood Mt.	(RW41)	7/68	1996	185°	35°	UM	Dry-mesic	1980
Redwood Mt.	(RW44)	9/68	1707	126°	10°	U	Wet-mesic	1977
Redwood Mt.	(RW45	9/68	1707	80°	32°	U	Dry-mesic	1977
Redwood Mt.	(RW48)	9/68	1691	135°	30°	L	Wet-mesic	1977
Redwood Mt.	(RW49)	9/68	1676	150°	30°	L	Wet-mesic	1977

t - from Western Tmber Service, 1970 * - L = lower slope, U = upper slope,
T = ridgetop, R = rocky, B = bottomland,
M = meadow

Table 22. Actual stem counts (original/1934) of living coniferous stem (≥3 cms) at each unburned plot.

	Xeric Plots						Dry Mesic Plots						Wet Mesic Plots						GRAND
Species	GT4	BS6	RW2	RW50	BS5	GT2	RW47	RW23	RW26	GT1	BS3	RW37	GT3	BS4	BS1	RW38	RW42	RW27	TOTALS
PP	16	8	5	0	3	1	1	0	0	0	3	1	0	0	0	0	0	0	38
	15	7	6	0	3	1	0	0	0	0	1	0	0	0	0	0	0	0	33
IC	8	35	15	20	17	2	4	1	2	0	0	4	20	11	1	2	0	0	142
	18	39	21	20	18	12	6	1	2	1	0	5	33	13	4	2	0	2	197
WF	11	25	25	78	21	97	35	64	47	73	51	121	44	42	45	150	50	55	1034
	15	26	35	71	21	99	62	70	55	83	50	110	51	35	66	185	68	65	1167
SP	3	5	9	3	6	15	9	38	66	17	6	19	36	5	7	17	16	14	291
	8	6	10	6	6	15	12	36	81	15	5	29	27	5	8	27	14	24	334
GS	0	1	5	0	22	2	13	82	6	2	62	69	8	12	0	0	34	23	341
	0	1	5	0	22	4	12	75	6	2	49	47	12	12	0	0	35	20	302

PP = *Pinus ponderosa*

IC = *Calocedrus decurrens*

WF = *Abies concolor*

SP = *Pinus lambertiana*

GS = *Sequoiadendron giganteum*

Table 23. Basal area (meters^2), (original 1984) of coniferous species at each unburned plot.

	Xeric Plots						Dry Mesic Plots						Wet Mesic Plots						GRAND
Species	GT4	BS6	RW2	RW50	BS5	GT2	RW47	RW23	RW26	GT1	BS3	RW37	GT3	BS4	BS1	RW38	RW42	RW27	TOTALS
PP	5.45	2.01	2.70	0.0	0.68	2.48	0.40	0.0	0.0	0.0	0.21	0.0	0.0	0.0	0.0	0.0	0.0	0.0	13.94
	2.35	2.57	2.01	0.0	0.85	2.48	0.0	0.0	0.0	0.0	0.13	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10.39
IC	4.91	4.26	3.01	2.99	1.92	1.33	0.22	0.01	0.03	0.0	0.0	0.04	4.12	0.06	0.01	0.00	0.0	0.0	23.45
	5.45	4.78	3.60	3.07	2.52	1.49	0.28	0.01	0.04	0.0	0.0	0.06	4.49	0.79	0.05	0.01	0.0	0.0	26.65
WF	0.05	1.87	1.46	7.02	1.44	4.81	6.95	5.19	7.74	4.42	4.38	4.17	2.85	5.56	7.34	6.73	10.05	5.19	87.35
	1.70	2.37	2.09	6.87	1.71	5.37	6.38	3.94	8.29	4.86	5.16	4.56	2.56	5.41	7.37	7.27	9.06	4.59	88.95
SP	0.61	0.92	0.04	2.97	0.84	4.51	2.09	4.25	2.55	1.48	3.24	5.01	1.42	0.54	0.09	2.97	2.36	0.25	36.13
	0.72	1.21	0.09	2.97	0.86	4.66	0.89	4.50	2.99	1.64	3.56	5.10	1.65	0.57	0.23	3.20	2.26	0.42	37.53
GS	0.0	0.0	0.57	0.0	9.83	26.62	0.72	1.77	16.30	14.74	14.07	30.81	13.47	5.26	0.0	0.0	3.84	41.92	179.93
	0.0	0.0	0.81	0.0	10,47	26.64	0.88	2.29	16.44	14.74	16.58	30.62	13.82	5.80	0.0	0.0	4.08	42.48	185.67

Note: Abbreviations as in Table 22.

Table 24. Actual counts (original 1984) of living coniferous stems (>3 cms) on burned plots.
(stems >3 cm diameter S.D.B.H.)

	XERIC PLOTS							DRY MESIC PLOTS							WET MESIC PLOTS							GRAND
Species	RW28	GT5	RW29	RW14	RW32	RW17	RW5	GT7	RW41	RW33	RW16	RW25	RW45	RW21	RW40	RW20	RW48	RW49	RW44	RW18	RW19	TOTALS
PP	0	4	0	3	1	0	0	0	4	0	0	0	0	0	3	0	0	0	0	0	0	15
	0	4	0	1	1	0	0	0	3	0	0	0	0	0	2	0	0	0	0	0	0	11
IC	42	5	18	3	9	3	0	36	10	3	4	1	0	0	15	12	2	1	1	0	1	166
	32	5	20	4	2	2	0	22	9	0	4	0	0	0	20	17	1	0	0	0	2	140
WF	84	35	103	43	86	45	87	130	42	69	59	81	35	20	56	26	42	61	48	30	17	1199
	47	29	70	31	45	21	25	68	54	24	31	29	36	19	60	32	20	21	42	9	12	725
SP	5	14	16	1	10	4	10	34	15	7	10	4	9	8	19	3	2	26	4	6	3	210
	4	15	13	1	3	3	5	15	12	4	8	2	2	3	15	7	2	2	1	2	3	122
GS	1	1	4	1	7	1	5	3	15	2	3	12	5	7	13	16	5	5	3	3	17	129
	0	2	4	1	7	1	5	3	14	2	3	12	5	7	11	16	4	3	2	3	18	123

Note: Abbreviations as in Table 22.

Table 25. Basal areas (meter^2) of coniferous species on burned plots (original 1984)

	Xeric plots							Dry mesic plots							Wet mesic plots							GRAND
Species	RW28	GT5	RW29	RW14	RW32	RW17	RW5	GT7	RW41	RW33	RW16	RW25	RW45	RW21	RW40	RW20	RW48	RW49	RW44	RW18	RW19	TOTAL
PP	0.0	3.19	0.0	1.62	0.52	0.0	0.0	0.0	0.86	0.0	0.0	0.0	0.0	0.0	3.19	0.0	0.0	0.0	0.0	0.0	0.0	9.35
	0.0	3.32	0.0	0.29	0.66	0.0	0.0	0.0	0.79	0.0	0.0	0.0	0.0	0.0	1.82	0.0	0.0	0.0	0.0	0.0	0.0	7.12
IC	1.49	0.11	0.86	0.17	0.24	0.02	0.0	1.42	0.25	0.04	0.05	0.00	0.0	0.0	0.91	0.75	0.02	0.01	0.01	0.0	0.02	6.37
	1.47	0.20	0.97	0.05	0.20	0.02	0.0	1.51	0.14	0.0	0.07	0.0	0.0	0.0	0.97	1.00	0.02	0.0	0.0	0.0	0.03	6.65
WF	7.11	1.90	1.91	15.57	8.35	9.47	6.71	6.93	3.07	7.04	5.18	6.61	8.68	7.69	5.66	6.14	11.67	10.31	5.84	2.93	3.20	142.76
	6.32	2.27	2.59	12.53	9.30	6.63	6.32	6.23	4.24	5.57	5.71	6.40	9.31	7.33	6.17	6.70	7.48	6.08	6.46	2.54	0.29	127.36
SP	1.07	6.68	0.68	0.52	2.17	0.51	2.20	3.91	1.54	2.15	6.31	0.37	0.14	1.12	0.30	0.14	0.86	0.24	0.25	0.97	0.02	32.12
	1.15	7.00	0.83	0.66	2.21	0.47	1.90	4.16	1.67	2.20	6.37	0.33	0.02	1.04	0.23	0.16	1.01	0.05	0.29	0.92	0.03	32.70
GS	0.66	8.83	0.47	4.67	9.14	6.02	29.79	0.36	12.91	11.11	25.75	15.23	35.75	52.53	2.28	2.59	11.59	18.08	16.67	12.52	13.40	291.15
	0.0	8.83	0.60	4.67	10.77	7.30	30.41	0.53	13.02	11.11	26.57	15.44	38.06	54.46	2.50	3.51	8.51	17.72	10.57	12.52	13.65	290.75

Note: Abbreviations as in Table 22.

Table 26. Unburned plot mean annual mortality rates (%) by size class and habitat type

	GS %	WF %	SP %	IC %	PP %
Seedlings		(8-17 cm, diameter at S.D.B.H)			
xeric	0.000	0.513	1.466	0.660	1.319
dry-mesic	2.069	0.642	1.099	0.000	-
wet-mesic	0.507	0.258	1.649	0.000	-
TOTAL	1.860	0.458	1.305	0.388	1.319
Saplings		(18-28 cm, diameter at S.D.B.H)			
xeric	0.000	0.535	4.398	0.000	2.199
dry-mesic	1.277	0.905	1.237	0.000	6.596+
wet-mesic	1.649	0.916	1.799	0.000	-
TOTAL	1.346	0.798	1.759	0.000	3.958
Poles		(29-38 cm, diameter at S.D.B.H)			
xeric	0.000	0.600	0.000	0.000	0.000
dry-mesic	0.314	1.360	3.769	0.000	-
wet-mesic	0.825	1.721	0.000	0.000	-
TOTAL	0.400	1.361	1.759	0.000	0.000
Mature		(>38 cm, diameter at S.D.B.H)			
xeric	0.000	0.694	0.776	0.000	2.639
dry-mesic	0.471	0.679	0.977	0.000	3.298
wet-mesic	0.000	0.954	0.880	0.942	-
TOTAL	0.202	0.803	0.894	0.124	2.698

Note: Abbreviations as in Table 22.

Table 27. Burned mean annual mortality rate (%) by size class and habitat type

	GS	WF	SP	IC	PP
	%	%	%	%	%
Seedlings		(8-17 cm, diameter at S.D.B.H)			
xeric	-	3.455	2.500	2.222	6.667+
dry-mesic	0.000	4.386	4.561	2.293	-
wet-mesic	0.952	3.978	4.103	1.429	-
TOTAL	0.555	3.898	3.825	2.262	6.667+
Saplings		(18-28 cm, diameter at S.D.B.H)			
xeric	0.000	3.379	2.500	1.053	-
dry-mesic	0.000	2.937	4.000	2.051	-
wet-mesic	0.000	3.611	6.667+	0.000	-
TOTAL	0.000	3.252	4.267	1.458	-
Poles		(29-38 cm, diameter at S.D.B.H)			
xeric	-	2.105	4.444	1.667	-
dry-mesic	0.000	2.167	1.667	2.857	6.667+
wet-mesic	0.000	3.333	6.667+	1.333	-
TOTAL	0.000	2.469	3.636	2.083	6.667+
Mature		(>38 cm, diameter at S.D.B.H)			
xeric	0.392	1.176	0.952	1.333	0.952
dry-mesic	0.424	0.580	0.000	0.000	
wet-mesic	0.667	1.931	0.000	0.000	2.222
TOTAL	0.397	1.171	0.654	0.606	1.026

Note: Abbreviations as in Table 22.

The burn treatments were most detrimental to Abies concolor. Pinus lambertiana suffered high small stem mortality but mature stems survived comparatively well. Pinus ponderosa/jeffreyi had substantially lower mature stem mortality with fire, but the largest population was on an unburned plot. The pines are generally considered fire resistant. Perhaps the removal of younger stems relieves some stress, although this explanation suggests adult-juvenile competition. The release of mineral into the soil following the fire is an alternative explanation (St. John and Rundel 1976). Calocedrus decurrens has thin-barked juvenile stems so the high fire mortality was not surprising. The species was relatively successful in spite of fire mortality. Burning favored other species at the expense of Abies concolor, in accordance with the management goal.

The results on unburned plots may point to a problem. The successional pattern showed C. decurrens increasing and P. ponderosa/jeffreyi decreasing dramatically. Abies concolor and P. lambertiana were not in serious decline but the mortality rates were high. A fire, as an intense disturbance, would be expected to cause large shifts in dominance and high mortalities in a short period of time, but there are changes of equal intensity occurring in the "undisturbed" stands. Until we understand what is causing them, we have little possibility of controlling the outcome. The species most susceptible to oxidant pollution suffered the highest mortality rates, and the two most resistant species, S. giganteum and C. decurrens, had distinctively low mortality rates. The evidence in this study is far from conclusive but suggests damage from oxidant pollution.

Conclusions

1. As expected, burned stands experienced significant mortalities and changes in basal area, but similar changes were recorded as well in the absence of fire. The implication is that stands that are unburned are not necessarily undisturbed.

2. Species responses to fire were in general agreement with literature predictions. Fire adapted species (Sequoiadendron giganteum, Pinus lambertiana and P. ponderosa/jeffreyi), suffered lower mortalities than thin barked Abies concolor in burned plots. Sequoiadendron reproduction appeared fire dependent, in confirmation of previous studies.

3. Sequoiadendron reproduced poorly but it suffered low mortality and showed consistent increase in basal area. Abies concolor was numerically dominant but reproduction was low and mortality high. Pinus lambertiana reproduced abundantly but mortality was higher than would be expected for a tolerant species. Calocedrus decurrens, a minor species in most current Sequoia-mixed conifer models, displayed traits of a dominant species. Mortality was low, reproduction was high and growth was the highest of any species. Pinus ponderosa/jeffreyi shows signs of serious decline in the small sample size studied. The high mortality rates for mature stems are unsustainable if the populations are to continue in Sequoia-mixed conifer forests.

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