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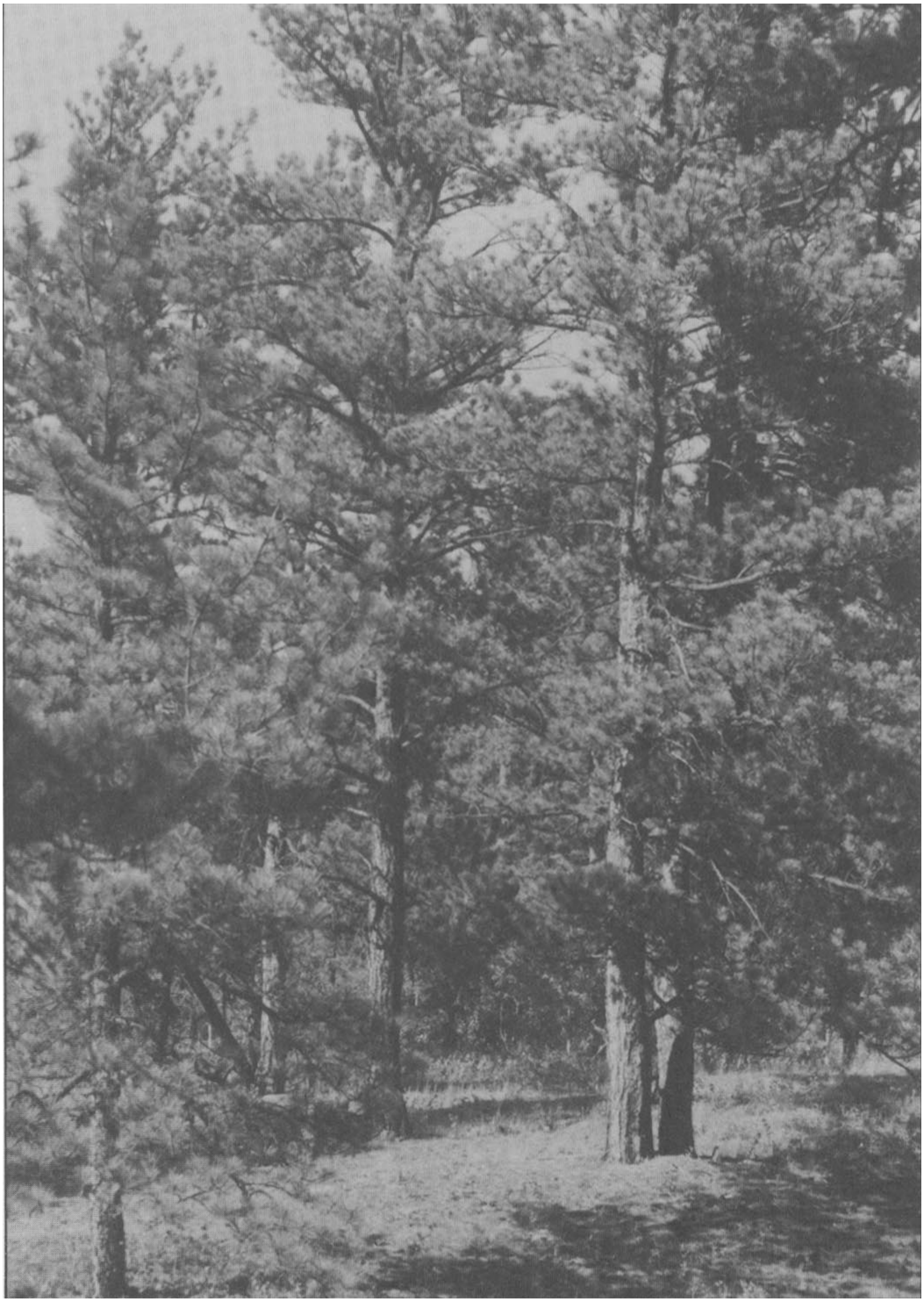
Stemwood Production Patterns in Ponderosa Pine: Effects of Stand Dynamics and Other Factors

Michael J. Arbaugh David L. Peterson



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Retrieval Terms: air pollution, climate, dendroecology, stem analysis, tree growth

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Contents

In Brief . . .

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Growth patterns of vertical stems in nine ponderosa pines from a stand in the southern Sierra Nevada were analyzed for recent changes due to stand dominance position, age, climate, and ozone exposure. Increments in gross bole volume and changes in growth rate were calculated for each tree. Large positive correlations were found between increments in volume growth and basal area at d.b.h. Increments in gross bole volume indicated that some trees declined in growth despite a large release of growth in 1965. Patterns of stemwood distribution along the bole were analyzed by comparing Growth Layer Profiles (GLP's) of ring width and basal area increment series. Spearman correlations were calculated between basal area increments along the bole and normalized bole volume increments. The results indicated that patterns of wood distribution along the bole were associated with age, competitive position, and release from competition. Young trees showed a trend of increasing wood production in the upper bole after release from competition. Older dominant/codominant trees had a similar response, although they previously had had more equal wood distribution along the bole. The opposite pattern was observed for canopy intermediates and suppressed trees. These trees produced more wood in the upper bole area both before and after release from competition. Changes in relationships between seasonal climate variables and annual increments of basal area and volume were also examined. A multiple regression model using winter and spring precipitation adequately explained short-term growth fluctuations during 1920-1955 and predicted growth during 1956-1985 for the trees as a group. A prominent feature of all volume, basal area, and ring width series was a growth response to a selective harvest in 1965. Increments in gross volume increased throughout the bole of all trees after thinning. This increasing trend continued for young and dominant trees but declined for older nondominant trees. It was difficult to determine whether ozone has contributed to these growth declines because the decline pattern was also consistent with competitive suppression. There is no conclusive evidence that growth changes vertically along the bole or through time are due to ozone exposure. This study illustrates the difficulty of assigning causal factors to observed growth patterns, and the need to use several measures of growth response to determine the effect of different environmental factors.

Introduction

The relationship of tree growth to environmental factors has been used to improve tree growth through forest management (Oliver and Larson 1990), to interpret past environmental events and variables (Fritts 1976, Schweingruber 1988), and to detect environmental change (air pollution, hydrologic regime, etc.) using trees as biomonitors (Innes 1990, Peterson and others 1991). Concern over possible impacts of acid precipitation and other air pollutants motivated scientists to study tree growth patterns throughout North America and Europe in the 1980's in an attempt to detect growth changes associated with pollutant stress (Barnard and Lucier 1990). One result of this research demonstrated that individual tree growth patterns are highly variable and that subtle environmental signals are difficult to detect (Cook 1987).

Most studies of tree growth use dendrochronology (Fritts 1976) to evaluate ring width patterns of cores removed from the main stem of trees (normally at d.b.h., 1.4 m above the ground). Cores can be easily extracted without felling the tree. Although ring width data from tree cores can be evaluated for environmental signals, they do not provide as much information as data on volume growth. Where it is possible to remove entire trees, stem volume growth has been shown to be better correlated with environmental effects (LeBlanc 1990, LeBlanc and Raynal 1990). This is logical, because radial growth of tree rings is a one-dimensional measure at one point, while volume represents a three-dimensional measure of growth for the entire stem.

Interpreting tree growth patterns in the southern Sierra Nevada is particularly difficult because of the wide variety of past and current anthropogenic and environmental influences. Many of the lower elevation ponderosa pine forests in this region were harvested some time after 1880, with removal including clearcuts and partial cuts of various intensity. Second growth regenerated naturally, and forests were not actively managed for timber production until the 1950's. Some forest stands have been thinned periodically since that time to enhance wood production in residual uncut trees.

Forests of the southern Sierra Nevada are currently threatened by abnormally high concentrations of ozone. Nitrogen oxides and reactive hydrocarbons produced in the San Francisco Bay region and the Great Central Valley are photochemically oxidized, and transported eastward into the mixed conifer forest of the western edge of the Sierra Nevada (Carroll and Baskett 1979, Ewell and others 1989). Ozone concentrations are high enough to produce visible symptoms of injury in ponderosa pine (*Pinus ponderosa*) and Jeffrey pine (*P. jeffreyi*) throughout the western side of the southern Sierra. There is no clear correlation between ozone injury and conifer growth on a regional basis, although recent growth has been reduced at a few locations with severe injury in Sequoia National Forest and Sequoia National Park (Peterson and others 1987, 1991).

It is often difficult to conclude causal relationships in observational studies because of an inability to separate several plausible explanations. This is especially true for complex data sets (such as this one) that have several spatial and temporal dimensions. In this study we will address this problem by examining several aspects of growth using multiple measures. The presence of pollutive damage will be postulated only when explanations based on stand structure and climate variation do not account for the observed variation in growth. This would occur if changes in growth patterns (outlined below) are observed for several age, canopy classes and time periods, for several of the measures examined.

We believe that the three aspects of bole growth that might be affected by pollutant exposure are: (1) changes in the distribution of wood between the upper and lower bole areas, (2) changes in annual volume increment growth and the rate of volume growth through time, and (3) changes in the growth response-climate relationship. We hypothesize that if high ozone concentrations are affecting bolewood production patterns, a reduction in the total volume increment, the relative amount of wood in lower bole, and/or a change in the relationship between the bole wood volume-climate relationship should occur that is independent of the canopy position class, tree age or other forest structure characteristics.

Ozone damage may also be detectable following a growth release caused by thinning or partial cuts. We expect that a temporary increase in bole volume may occur as the tree responds to increased light and water availability in ozone-affected trees. This growth rate should not persist, however, because of an increasing amount of carbohydrate production being retained for foliage replacement and repair through time as the total canopy biomass increases.

Methods

Site Description

Trees used in this study are from a mixed conifer forest stand located on the Mountain Home District of Sequoia National Forest, California. The stand is located on a west-facing aspect, at 1570 m elevation, on 10-30 percent slopes. Associated vegetation in the overstory includes incense-cedar (*Libocedrus decurrens*), California black oak (*Quercus kelloggii*), and a few sugar pine (*Pinus lambertiana*). Understory species include incense-cedar seedlings and saplings, deerbrush (*Ceanothus integerrimus*), and bearclover (*Chamaebatia foliolosa*). Soils in the area are primarily Xerumbrepts. This portion of the Sierra Nevada has a Mediterranean climate, with warm, dry summers and cool, wet winters; more than 80 percent of annual precipitation falls from November through March.

The study site has been subject to considerable timber management activity. The stand was originally cut or burned around 1880, judging from the age of dominant trees that regenerated after this time. A partial cut removed an unspecified portion of the stand in 1965, and there was a commercial thinning of unspecified volume in 1979.

This area is exposed to elevated ambient ozone concentrations, with the highest levels occurring in the summer months. Composite mean hourly concentrations in adjacent Sequoia National Park range from 40 to 90 ppb, with maximum concentrations of 150 ppb (Peterson and Arbaugh 1988). These values are high when compared to the California State Air Quality Standard of 10 ppb and the U.S. standard of 12 ppb. Comparable values have been measured during limited periods of monitoring in Sequoia National Forest (Vogler 1982).

Data Collection and Measurement

Nine trees with a range of sizes, ages, and ozone injury were harvested at the study site. Basal diameter, d.b.h., total height, and internode lengths were measured for each tree. In addition, ozone injury was characterized for five branches on each sample tree, using the system of Muir and Armentano (1988). This system rates the percent chlorosis of foliage in the lower crown as follows: 0 = 0 percent, 1 = 1-5 percent, 2 = 6-25 percent, 3 = 26-50 percent, 4 = 51-75 percent, 5 = 76-95 percent, 6 = 96-99 percent, 7 = 100 percent.

Sections were removed from the main stem starting at the top of the tree and cut at the midpoint of every second internode for the first 10 years (starting with internode 2), then every fifth internode for the remainder of the tree. Sections were also removed at d.b.h. (1.4 m) and at the tree base. This resulted in 15 to 25 sections being removed for analysis for each tree.

All sections were dried and sanded with successively finer grades of sandpaper until individual tracheids were visible under the microscope. Each section was initially crossdated visually by indicating dates directly on the section (e.g., Stokes and Smiley 1968, Swetnam and others 1985). Radii on the cross-slope sides of each section were measured to the nearest 0.01 mm with an incremental measuring machine equipped with a television camera and monitor. This machine was linked via a digital encoder interfaced to a microcomputer that uses software to store ring width measurements on disk by year for each section (Robinson and Evans 1980).

Following ring measurement, crossdating was verified with the program COFECHA (Holmes 1983), which calculates Pearson product-moment correlations between a single series and a master tree ring series. Crossdating was conducted between sections within a tree, and among sections between trees separately.

Statistical Analysis

Basal area increments were estimated for both cross-slope radii of each section, and averaged to obtain a single estimate for each year-height combination. Volumes were estimated from the basal area increment series by assuming that two basal areas at adjacent heights formed a parabolic section, and then applying Smalian's equation to each section and summing the resulting volumes up the tree by year.

Trees were separated into three groups, based on age and magnitude of stemwood volume growth (*table 1*). Group I includes two trees, both less than 50 years old. All other trees are around 100 years old, with germination dates ranging from 1881 to 1897. Group II includes three trees with crown classes and high growth rates indicative of forest dominants. Group III (codominants to intermediates) includes four trees with smaller crowns or slower growth relative to Group II or both. Pearson product-moment correlations were obtained between the basal area increments at various heights of the bole and tree volume increments through time. Large correlations between basal area increments (b.a.i.) at d.b.h. and the total volume increment for the trees were observed for eight of the nine trees. The low correlation for Tree 10 may indicate that a simple linear relationship between b.a.i. and tree volume may be less reliable for older intermediate trees.

Graphical Analysis of Growth Trends

A descriptive graphical analysis adapted from Fayle and MacDonald (1977) was used to examine the growth patterns of the trees. This analytical approach involves the graphical description of individual tree growth layer profiles (GLP, Fayle 1973) or type 1 sequences (Duff and Nolan 1953). In this type of graph, lines represent one or more years of growth along the height of the bole. Each line is a cumulative measure of growth through time along the bole to that point in time, and the difference of a line from the previous line is a measure of the growth during the time period. The difference between each line in the sequences used in this study represents a time period of 4 or 5 years. The periods chosen are a compromise between completeness of information display and simplification to aid the visual interpretation of patterns. Sequences for both ring width series and basal area increment series were examined.

Table 1–***Descriptive characteristics and group classification of the sample trees.*** r_{dbh} ***is the correlation between basal area increments at d.b.h. and total tree volume.***

Group number[1]	Tree number	Beginning year of growth	Dbh	Height	Ozone injury rating[2]	r_{dbh}
			cm	*m*		
I	13	1937	30.0	15.3	1.2	0.88
I	38	1938	38.5	18.9	0.8	.91
II	2	1883	46.0	23.6	2.4	.97
II	26	1885	47.0	22.1	2.8	.98
II	31	1895	47.5	21.7	1.4	.90
III	5	1881	26.3	20.9	1.8	.89
III	10	1882	31.0	20.2	2.0	.45
III	15	1881	38.0	21.0	1.8	.85
III	25	1897	34.5	22.0	2.4	.96

[1] Group I contains young trees, Group II older stand dominants, and Group III older codominants and intermediates.

[2] Ozone injury rating is a unitless measure, the mean of 5 values per tree. Higher ratings represent higher injury levels. See text for description of rating system (Muir and Armentano 1988).

Stemwood Production Patterns

A graphical examination of allocation patterns along the bole through time was conducted by selecting three 10-year periods of growth (1946-1955, 1966-1975, and 1976-1985) to characterize relative allocation patterns along the bole for each time period. These periods were arbitrarily chosen as equal divisions of the period of common growth for the sample trees. The percent of the maximum b.a.i. was calculated for each period as:

$$\text{Percent Maximum bai}_i = \text{bai}_i / \text{bai}_{max} \times 100$$

where i = height for a single growth period. The result was then smoothed with a cubic spline smoother (to enhance the general trends) and graphed against tree height. This type of presentation is similar to Growth Layer Ratios used by Fayle and MacDonald (1977) except that the ratios are calculated along the bole instead of between time periods.

Spearman correlations (ρ) between the height of each tree section and the annual basal area increment were calculated for each year of growth for each tree to examine the relative allocation of wood in the lower and upper part of the main stem. Spearman correlations were used rather than Pearson correlations to examine changes in the relative amounts of area increments with increasing height. Low correlations indicate that equal allocation of wood was occurring along the tree bole (H_o: $\rho = 0$). Negative correlations indicate that basal area increments were larger for the lower bole area (such as would occur when shading competition is absent). Correlations involving 10 or more sections for a year were retained for further analysis. The maximum one-sided confidence level (n=10) for H_o: $\rho = 0$ versus H_1: $\rho < 0$ for any correlation at $\alpha = 0.05$ was -0.636. Values larger than this were not considered to be significantly different from 0.

The resulting correlations were plotted against time and normalized values of gross volume increments (increments expressed as standard deviations from the mean increment) to examine the pattern of the allocation of wood along the bole.

Relationships Between Annual Volume, Basal Area, and Climate

Annual stemwood volume production was estimated and then used to calculate the proportional change in volume over 10-year periods beginning in 1936 by the following method:

$$P_i = (V_i - V_{i-1}) / V_{i-1}$$

where P_i is the proportional change in volume growth, V_i is total volume for the 10-year period i (where the 1926-1935 is period 0). This calculation indicates the proportional change in growth relative to the previous 10 years of growth (*table 2*).

Climate-Stemwood Growth Relationships

Daily weather records from a nearby National Oceanic and Atmospheric Administration (NOAA) weather station (Giant Forest) were used to calculate mean daily temperatures and total precipitation on a seasonal basis from 1920 through 1985 (e.g., Peterson and others 1987). Seasons were defined as winter (October of the prior calendar year through March), spring (April through June), and summer (July through September).

Each volume series was detrended using the LOWESS algorithm developed by Cleveland (1979) and implemented on the Systat statistical and graphics computer package (Wilkinson 1989). This technique uses locally weighted regressions to estimate the smoothed value for each data point. The amount of smoothing is controlled by the user, and corresponds to the proportion of the total number of sample points used to estimate the smoothed value. Smoothing values of F = .25 were used for this analysis. An intervention function was used with the smoother to remove the sudden increase associated with a partial stand cut that occurred in 1965. A ramp function that started in 1965 and ended in 1968 was found to best fit the increase. Residual series were formed from ratios of the actual volume divided by the trend, then averaged to form a volume index chronology. Autocorrelation coefficients and partial autocorrelation coefficients were calculated and found to be nonsignificant for the residual series.

A multiple regression model was fitted to the chronology using the time interval 1920-1955. Variables were selected using Mallow's Cp criterion (Mallows 1973). This criterion considers both R^2 and model parsimony for model selection. Trends were present in both the response and the predictor variables. Residual analysis indicated that some first order autocorrelation was present for most of the trees, so a full two-step transform method (Harvey 1981) was used for estimation. This method uses Yule-Walker equations to estimate coefficients for autocorrelated errors. The general model form is:

$$y_t = x_t'B + v_t$$
$$v_t = \varepsilon_t - \alpha_1 v_{t-1} - \ldots - \alpha_p v_{t-p}$$

where y_t are the dependent values, x_t is a vector of regressor values, B is the vector of structural parameters, α_i is a vector of coefficients, and ε_t are distributed Gaussian with mean 0 and variance σ^2. All models were estimated using the AUTOREG function of SAS (SAS Institute Inc. 1988). Deviations from expected growth during the second period were examined by

Table 2—***Proportional changes from the previous decade of stemwood volume growth for each tree. Numbers are unitless measures of relative change. Negative values indicate that growth for the decade was less than the growth during the previous decade. Decades are centered at 1940, 1950, 1960, 1970 and 1980.***

Group no.	Tree no.	1936-1945	1946-1955	1956-1965	1966-1975	1976-1985
I	13	I[1]	22.8	1.7	7.3	1.0
I	38	I[1]	48.7	5.6	5.0	1.8
II	2	7.7	0.2	0.5	5.3	0.1
II	26	8.2	0.3	0.2	4.5	0.2
II	31	8.8	0.8	0.1	2.2	0.3
III	5	5.8	-0.1	0.1	3.2	-0.1
III	10	3.5	-0.6	-0.2	4.7	-0.2
III	15	3.9	0.3	0.1	2.2	-0.4
III	25	8.5	0.5	-0.1	4.3	0.3

[1] Indicates incomplete records for 1926-1935 for young trees.

forecasting the model from 1956-1985. Upper and lower 95 percent confidence intervals for the predicted values were calculated and compared with actual values. Forecast error estimates were calculated using results from Baille (1979).

Results and Discussion

Growth Patterns and Vertical Production of Stemwood

Ozone exposure has been shown to affect carbon production and carbon allocation to differing plant structures (Cooley and Mann 1987, McLaughlin and others 1982). Thus it is possible that vertical growth and allocation patterns along the bole might reflect ozone damage that is not observable at d.b.h. These growth patterns may also be associated with competitive effects within the stand and climatic effects on the stand. The approach taken in this study will be to explain the observed patterns as the result of stand dynamics, age, and climate factors when possible. If these explanations are not adequate, then the possibility of ozone effects will be supported.

Because the volume growth trends within each of the three groups of trees were very similar, a single tree was selected for graphical analysis to convey the general growth patterns of that group.

Group I contains two trees that were much younger than the majority of trees. Both were approximately 50 years old and were the two shortest trees in height. The GLP indicates that radial growth was evenly distributed relative to bole height throughout the life of the tree (*fig. 1A*). The post-1965 growth was indicated by an increase in ring width growth over most of the tree bole. The basal area GLP (*fig. 1B*) and production (*table 2*) continued to increase through 1985.

Group II contains three trees that were older canopy dominants. All were within ten years of germination age and had similar heights and growth patterns. Growth trends were more complex than those of Group I. The ring width GLP (*fig. 2A*) indicates that ring widths were larger in the upper portions of the bole during 1930 to 1965. This corresponds to approximately equal basal area increments (*fig. 2B*) along most of the bole. Ring widths were approximately equal, and basal area increments were much greater at the lower bole after 1965.

Group III consists of four codominate or intermediate trees. They were approximately the same age and height as Group II, but their d.b.h. averaged only 70 percent of group II. Growth patterns were quite different from those above (*fig. 3A,B*). They had growth patterns with large ring widths in the lower and upper bole areas before 1945. This pattern varied among the group, but all growth rates were high during this time (*table 2*). Tree growth was reduced in the lower bole relative to the upper bole area during 1945-1965. In the 1965 release, both ring widths and basal area increments increased. However, the pattern of larger ring widths and equal basal area increments in the upper bole area continued through 1985.

Production of wood along the bole changed through time for the trees studied. Spearman correlations and annual volume growth (*fig. 4A*) indicate that years of large relative increases in wood volume were associated with increased wood production towards the base of the trees, whereas low growth years were often associated with equal relative allocation along the bole. The opposite pattern was observed for Tree 10 (*fig. 4B*). The correlations became consistently closer to zero with increasing annual volume. The years associated with these unusual values (correlations >-0.5 and normalized bole volumes >0) are 1968-1971, 1973-1976, and 1982-1985.

Further examination of changes in wood production patterns indicates that each group had distinct changes associated with the release occurring in 1965. Group I patterns in the decade before 1965 indicated that most wood production occurred in the lower bole area (*fig. 5A*). Wood production increased after 1965 in the upper bole area. This trend persisted through 1985, indicating that the crown area may have been gradually expanding after 1965.

Group II had slightly different patterns (*fig. 5B*). Wood production was roughly equal in the middle bole area in the decade before 1965. The decade after 1965 was associated with increased height growth and allocation of wood biomass to the lower bole (similar to Group I). Relative wood production then increased in the upper bole during the last decade.

The Group III growth patterns differ from those of Groups I and II (*fig. 5C*). The general pattern was greater wood production in the upper bole area rather than the lower area. The production was most equal along the bole before 1965. Wood was then increasingly allocated towards the upper bole area after 1965.

Growth Trends in Gross Volume

Gross volume increments were dominated by a release due to a partial cut in 1965 (*fig. 6A,B,C*). This increase was smallest for Group I trees; however, the proportional growth increase was greatest (*table 2*) for this group. Group II trees had the greatest absolute release. Large increases in volume growth occurred after both 1965 and 1979. Volume growth rates increased 220-530 percent and continued at high levels through 1985. Group III trees were characterized by a single growth release period followed by a growth decrease. There was also little response to the thinning of 1979. This resulted in growth rate reductions up to 40 percent for these trees during the last decade.

Relationships Between Climate and Growth

Annual fluctuations in the volume of stemwood were related most directly to winter precipitation (WTP), spring precipitation (SPP), and summer temperature (SMT) of the present year for the sample trees as a group. The model selected in this analysis was:

$$VI = -0.091 + 0.0098*WTP + 0.0078*SPP - 0.033*SMT$$
$$v_t = e_t - 0.34*v_{t-1}$$
$$R^2 = 0.49$$

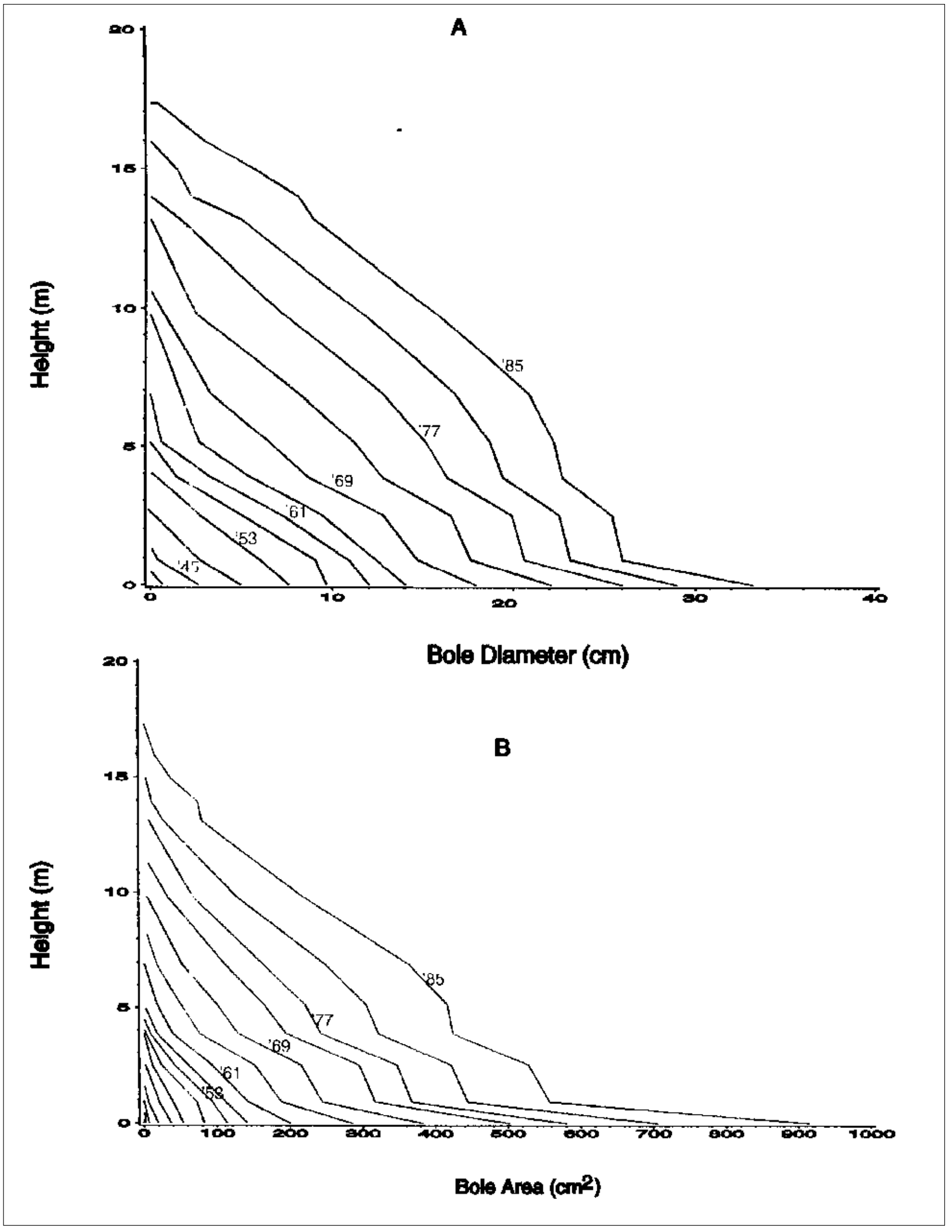

Figure 1—Growth Layer Profiles for Tree 38 in Group I. The width between lines represents the growth that occurred during a 3-year period. The ring width profile is shown in A and the basal area profile is in B. Numbers refer to the last year of growth for the lines to their left.

where VI = Residual annual stemwood volume growth, v_t is the error and e_t is distributed Gaussian $(0,\sigma)$.

These climate variables were significantly correlated with radial growth in previous studies of ponderosa pine and Jeffrey pine in the southern Sierra Nevada (Peterson and others 1987, 1991; Peterson and Arbaugh 1988). No other variables contributed significantly to either the adjusted R^2 or reduced Mallow's Cp criterion. However, the variables selected should be considered to represent local conditions rather than as indicators of functional relationships (Arbaugh and Peterson 1989).

Forecast estimates were calculated for one year ahead during the 1920-1955 period. Estimates were then forecasted without updating through the 1956-1985 period. Forecast confidence intervals indicate that the predictions were consistent with observed values for the later time period (*fig. 7A*). The post-1956 forecast residuals had a significantly ($p = 0.07$) negative mean value (*fig. 7B*), indicating that the model might not be adequate to forecast responses into the distant future.

The model was also fitted to the separate groups. Although model parameters varied between groups, the resulting growth forecast intervals adequately explained the 1956-1985 growth patterns for all groups.

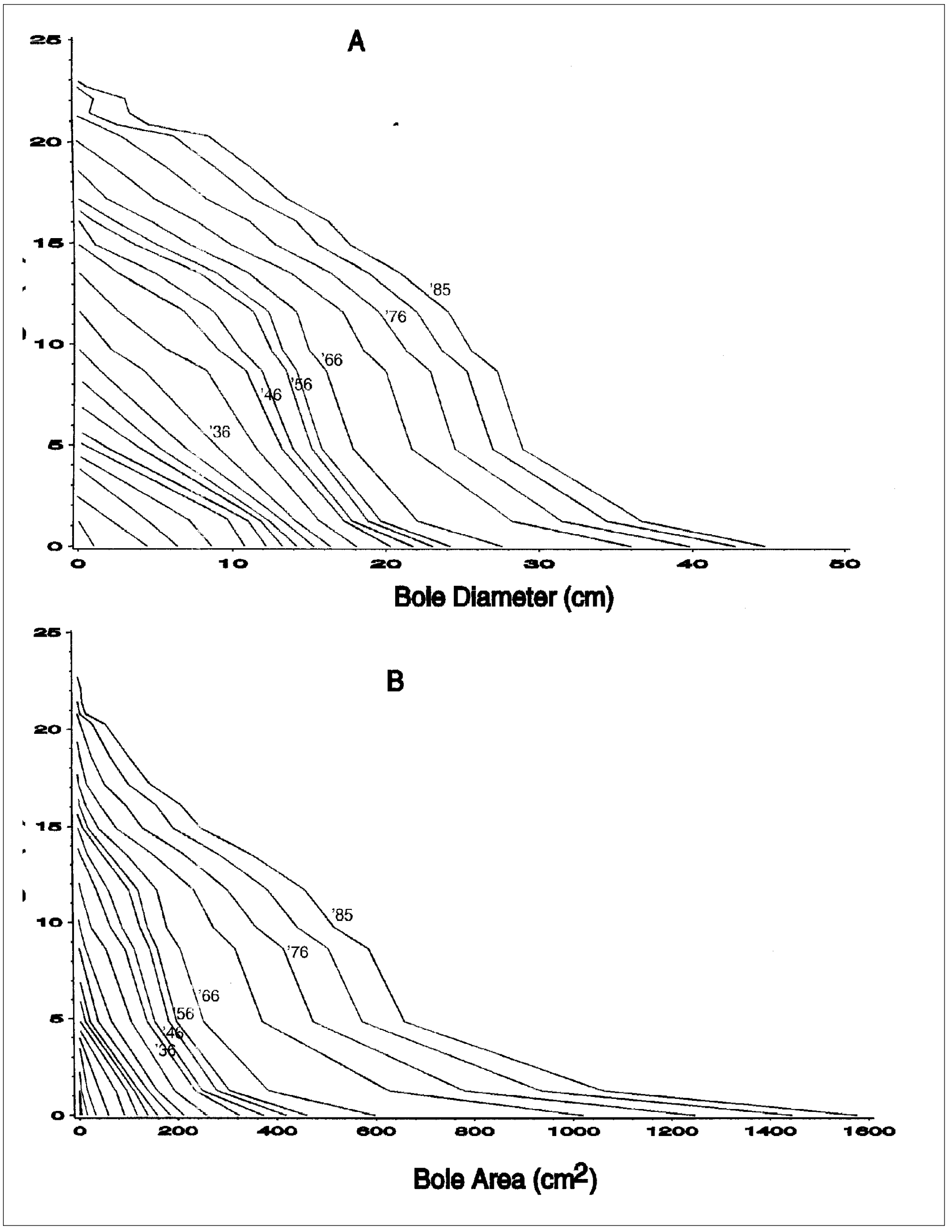

Figure 2—Growth Layer Profiles for Tree 2 in Group II. The width between lines represents the growth that occurred during a 5-year period. The last line represents the growth after 4 years. The ring width profile is shown in A, and the basal area profile is in B. Numbers refer to the last year of growth for the lines to their left.

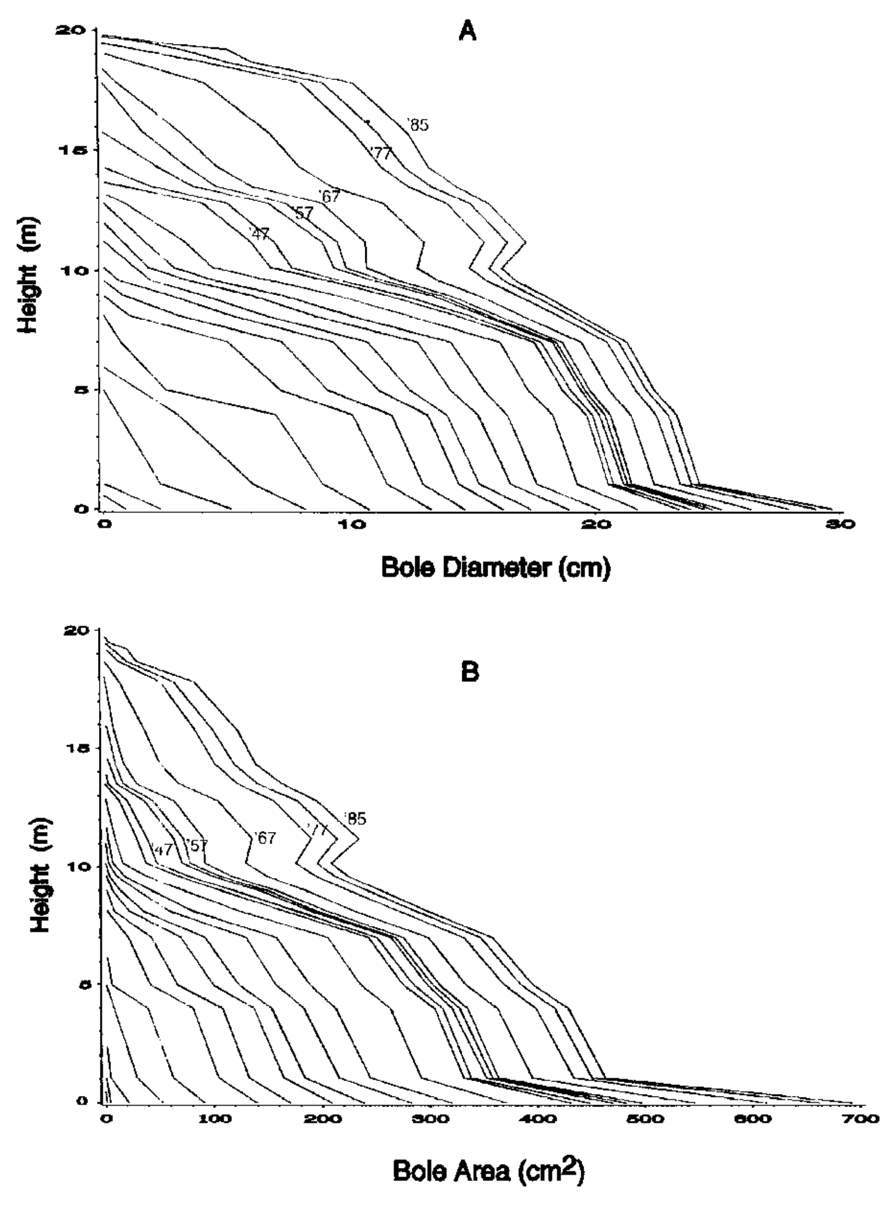

Figure 3—Growth Layer Profiles for Tree 10 in Group III. The lines represent the growth that occurred during a 5-year period. The last line is an average of 3 years of growth. The ring width profile is shown in A, and the basal area profile is in B. Numbers refer to the last year of growth for the lines to their left.

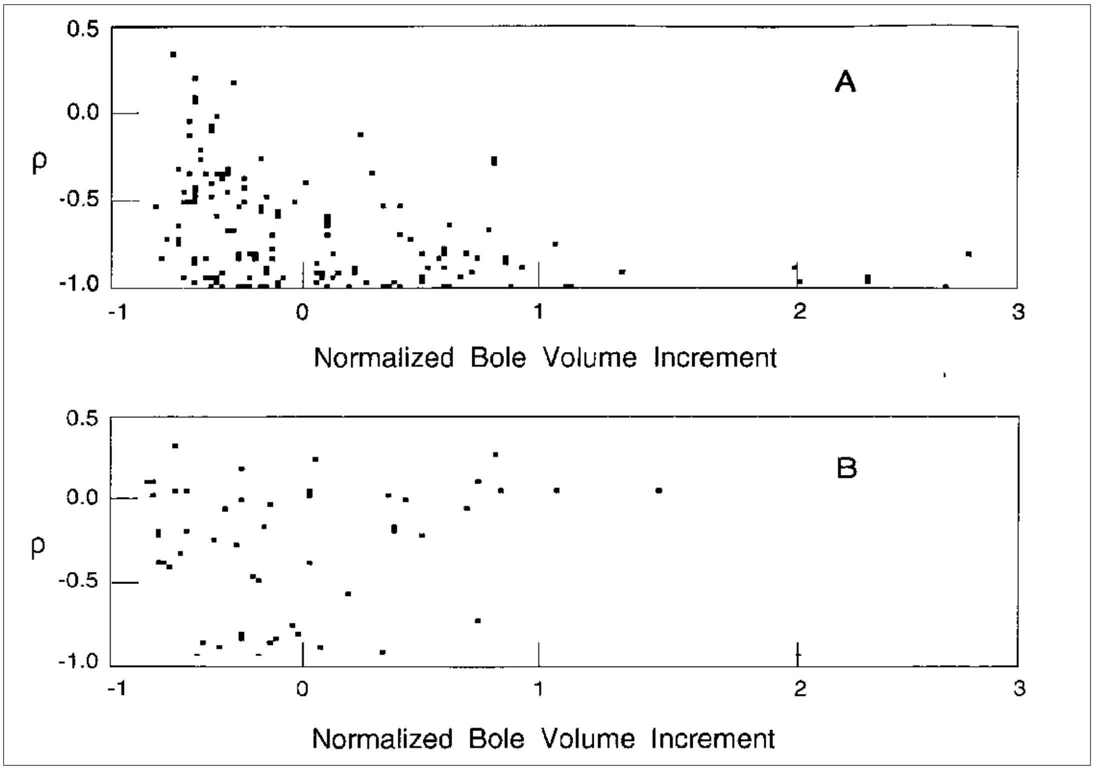

Figure 4—Spearman correlations between height and basal area increment as a function of the normalized stemwood volume growth per year. A, all trees except for Tree 10; B, Tree 10.

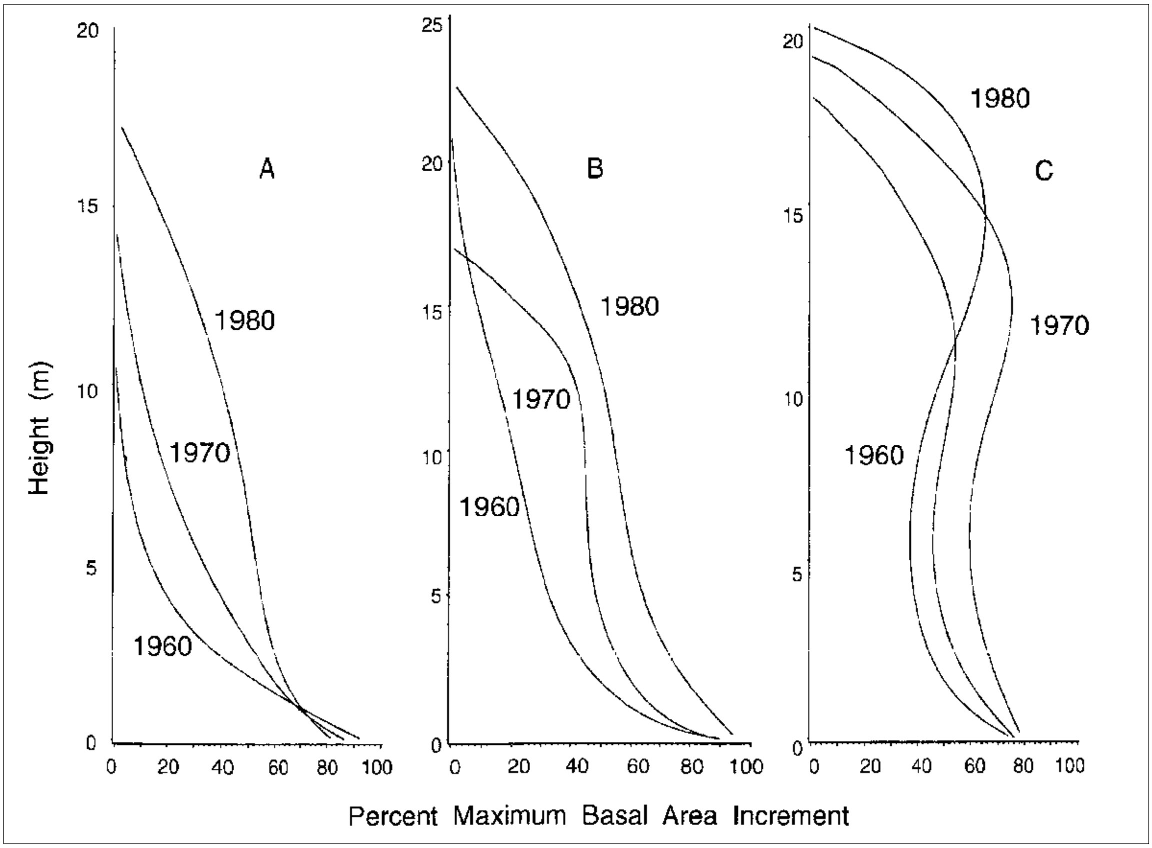

Figure 5—The percent of the growth in maximum b.a.i. growth for three decades at each height (see text). A, Tree 38 (Group I); B, Tree 2 (Group II); C, Tree 10 (Group III). Years indicate the middle year of the decade used for each line.

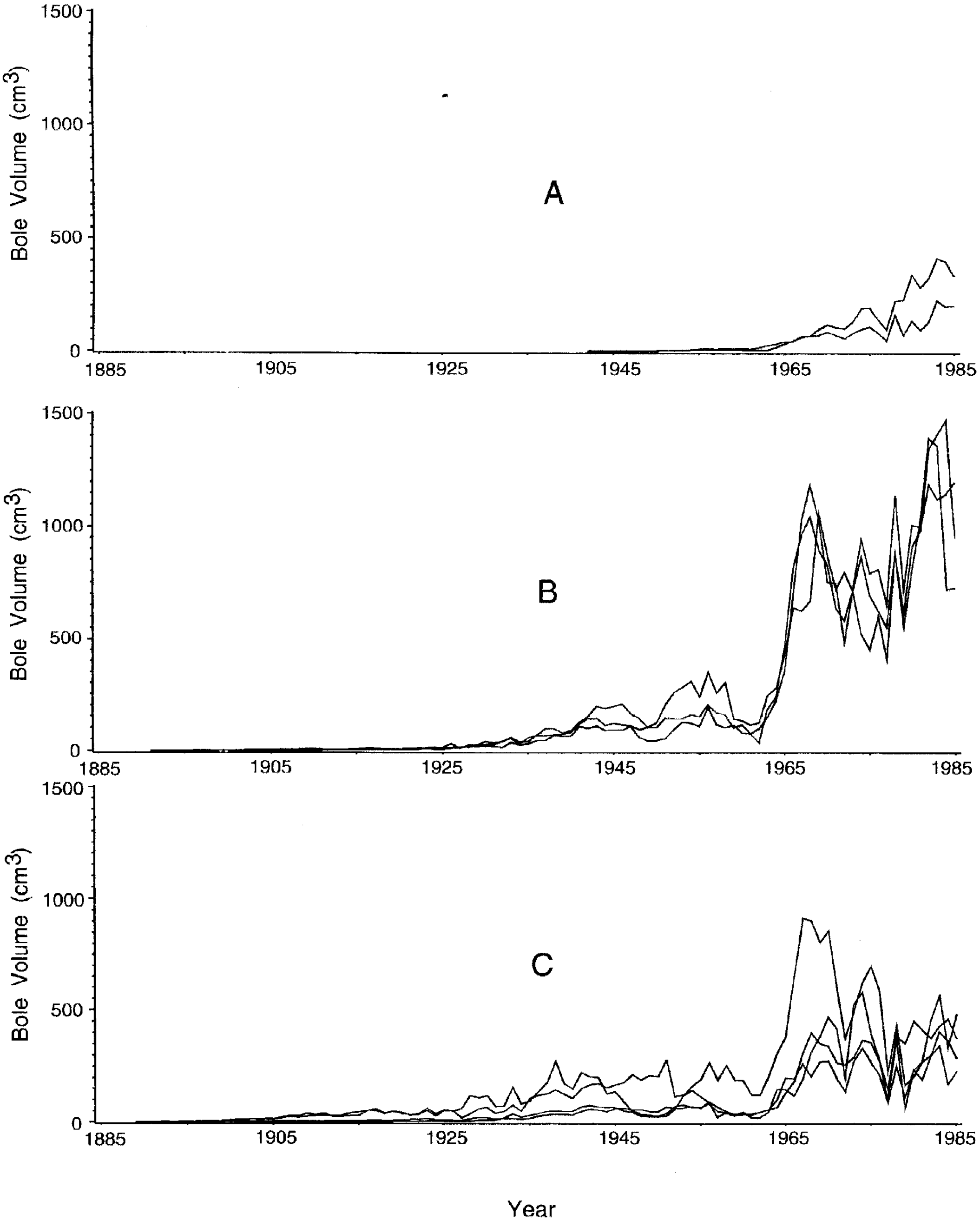

Figure 6—Gross volume increments through time. A, Group I trees; B, Group II trees; C, Group III trees. The sudden increase(s) in growth are due to partial cut in 1965 and in 1979.

Conclusions

Gross volume patterns for Group I and II were consistent with competitive status, including a competitive release around 1965 and a second release in 1979. Relative growth patterns do not indicate unusual or unexplained growth changes for these trees. Growth generally increased through time for both groups. Wood production patterns for these trees are adequately explained by changes in canopy dominance position and wood production rates. No evidence was found that recent ozone exposure affected wood production for these trees (Group I and II).

Growth reductions were observed in less competitive trees (Group III). These patterns could have been caused by stand competition or by elevated ambient ozone. Elevated ozone is known to cause greater growth reductions in older trees than in younger trees for Jeffrey pine in the study area (Peterson and others 1987). Ozone injury has been associated with increased allocation of carbon to foliage and branch production for forest trees (Cooley and Mann 1987, McLaughlin and others 1982). The increased wood production in the upper boles of this group during the last decade of growth is consistent with such an allocation change. Physiological studies show that even slight ozone injury can reduce carbon fixation and productivity in some conifers (Reich and Amundson 1985, Reich 1987). The possibility that ozone may cause greater effects on shaded trees is consistent with the suggestion that subpopulation differences may determine the expression of tree growth reductions (Patterson and Rundel 1989).

The same patterns are also consistent with stand dynamics effects on growth. The growth reductions of Group III may have been caused by the smaller trees receiving less light and other resources. If this group had a smaller removal of competition as a result of management activities, or nearby trees were able to increase height faster than the trees in this group, then the growth rates would be expected to decline and a concentration of foliage in the upper bole area would be expected. This reasoning is supported by the lack of change in wood distribution patterns through time. In addition, the relationship between climate and growth did not vary significantly during the latter decades of growth.

Thus the growth declines observed in this group should not be considered to be evidence for ozone-induced growth changes. Although a decline in volume after the release of 1965 was observed, it can be explained by canopy dominance effects and was not associated with a change in the relationship between climate and growth. It is possible that ozone may cause faster rates of growth reductions or reduce growth to lower levels than would be caused by competitive effects alone. These effects cannot be examined in this study.

The general lack of evidence for growth reductions observed in these trees is consistent with the results of previous studies of ponderosa pine in the Sierra Nevada (Peterson and Arbaugh 1988, Peterson and others 1991). These studies showed that reductions in growth were rare even when severe needle chlorotic injury and reduced needle retention were present.

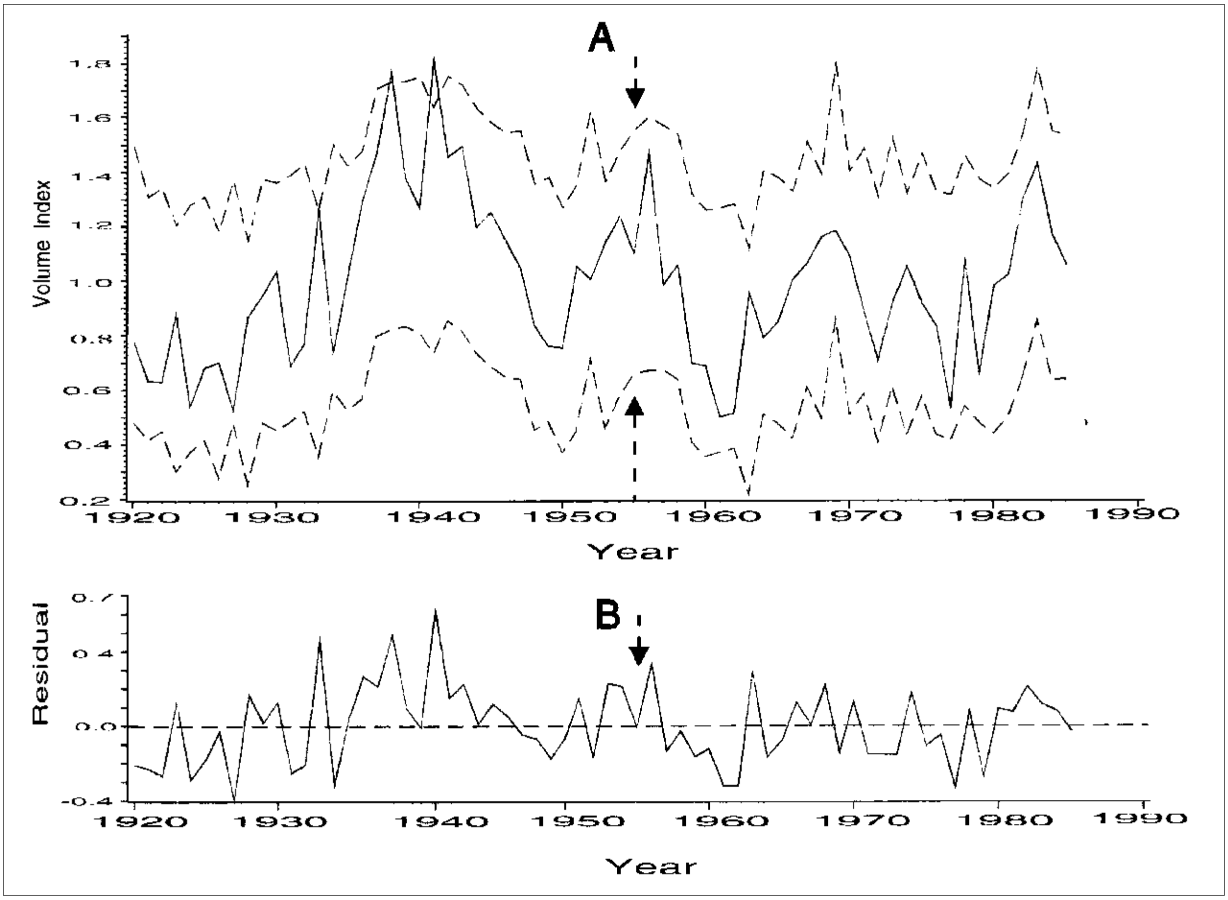

Figure 7—Forecast confidence intervals, volume index and residuals from climatic analysis. A, Forecast confidence intervals (dashed lines) are derived from 1-year-ahead forecasts through 1955 (to the left of the arrows), then are derived from pre-1956 values from 1956-1985. The residual series (B) is the difference between actual and forecasted volume increments.

The results of this study also indicate the importance of considering several aspects of tree growth before inferring causes for observed growth patterns. The gross patterns of volume increments alone (for Group III) might be considered evidence of growth decline due to ozone exposure. However, after considering wood distribution patterns and the climate response, it is equally likely that the decline was due to the effects of stand dynamics.

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