Effects of ozone and climate on ponderosa pine (Pinus ponderosa) growth in the Colorado Rocky Mountains

DAVID L. PETERSON
National Park Service, Cooperative Park Studies Unit, College of Forest Resources, University of Washington, AR-10, Seattle, WA 98195, U.S.A.

AND

MICHAEL J. ARBAUGH AND LINDSAY J. ROBINSON
USDA Forest Service, Pacific Southwest Research Station, 4955 Canyon Crest Drive, Riverside, CA 92507, U.S.A.

Received June 16, 1992
Accepted February 9, 1993


Long-term radial growth trends of ponderosa pine (Pinus ponderosa var. scopulorum) were studied in second-growth stands in the Front Range of the Colorado Rocky Mountains to determine if there has been any impact from oxidant air pollution. Although ozone concentrations are relatively high at some locations, visible pollutant injury was not found in any trees. Time series of basal area increments are generally homogeneous within stands. Concurrent periods of increasing and decreasing growth can be found in stands throughout the Front Range, which indicates that there are temporal growth trends at the regional level. Most of these trends appear to be related to the effects of stand dynamics and climate. Correlation analysis with climatic variables indicates that soil moisture supply is the dominant factor controlling interannual variation of basal area growth. Palmer hydrological drought index is highly correlated (positively) with growth during the summer months; total precipitation in spring is positively correlated with growth, and mean temperature in spring is negatively correlated with growth. There are no recent changes in growth trends that might be associated with elevated levels of ambient ozone in the Front Range.

PETERSON, D.L., ARBAUGH, M.J., et ROBINSON, L.J. 1993. Effets de l'ozone et du climat sur la croissance du pin de bouleau lourd (Pinus ponderosa var. scopulorum) dans les peuplements de seconde venue situés dans le Front Range des Montagnes Rocheuses du Colorado pour déterminer si les contenus d'ozone dans la pollution de l'air ont eu un impact quelconque. Même si les concentrations d'ozone sont relativement élevées à certains endroits, aucun dommage d'ozone n'était visible chez les arbres. Les séries temporelles d'accroissement en surface terrière sont généralement homogènes à l'intérieur des peuplements. Des périodes simultanées de diminution et d'augmentation de croissance peuvent être identifiées partout à travers le Front Range, ce qui signifie qu'il y a des tendances temporelles dans la croissance au niveau régional. La plupart de ces tendances semblent être reliées à la dynamique des peuplements et au climat. Une analyse de corrélation avec les variables climatiques montre que la disponibilité en eau du sol est le principal facteur qui affecte la croissance en surface terrière d'une année à l'autre. L'indice de sécheresse hydrologique de Palmer est étroitement et positivement corrélé avec la croissance pendant les mois d'été. Au printemps, la précipitation totale et la température moyenne sont respectivement positivement et négativement corrélées avec la croissance. Il n'y a pas de changements récents dans les tendances au niveau de la croissance qui pourraient être associés aux niveaux élevés d'ozone ambiant dans le Front Range.

[Intégration par la rédaction]

Introduction

The effects of atmospheric deposition on forest ecosystems have become a topic of increasing concern in recent years. Foliar damage and growth reductions have been reported for several species (McLaughlin et al. 1982, 1987; Phipps and Whiton 1988; Miller 1992; Peterson and Arbaugh 1992). Reductions in growth of some species have been related to point sources of pollution such as smelters and industrial operations (Thompson 1981; McClanahan and Dochinger 1985; Fox et al. 1986). It is considerably more difficult to associate nonpoint sources of pollution, such as acid precipitation, with growth patterns because of the lack of “control” sites and long-term pollutant concentration data.

Growth reductions in several species of conifers and hardwoods have been correlated with exposure to various air pollutants (McLaughlin 1985). Reductions in the growth of ponderosa pine (Pinus ponderosa var. ponderosa) (Peterson et al. 1989, 1991), Jeffrey pine (Pinus jeffreyi) (Peterson et al. 1987), red spruce (Picea rubens) (Siccama et al. 1982; Hornbeck and Smith 1985; LeBlanc 1990), and several species of pine in the southern United States (Sheffield et al. 1985; Knight 1987) have also been reported, although air pollution is only one of the possible sources of stress in these species.

Although acid precipitation was originally cited as a likely cause of reduced vigor in some forests, recent evidence suggests that oxidants can reduce photosynthesis and productivity of trees even at relatively low exposure levels (Reich and Amundson 1985; Woodman and Cowling 1987; Patterson and Rundel 1989). Ozone is particularly damaging to some species of conifers (Miller and Millican 1971; Benoit et al. 1982; Miller et al. 1983). Ozone injury in conifers is caused by absorption of sublethal amounts of pollutants over a long period of time (Reich and Amundson 1985). Chronic exposure...
to ozone can cause substantial loss of vigor, which can in turn lead to greater susceptibility to additional stresses (such as drought and insects), abnormally high tree mortality, and potential changes in forest structure and function (Miller et al. 1982; Miller 1983; McBride et al. 1985).

Air pollution in urban areas east of the Front Range of the Colorado Rocky Mountains has increased considerably during the past 30 years in association with increasing population. Growth and industrial expansion have been focused in the Denver area, although other municipalities have grown as well. The Denver area is well known for the "brown cloud" of gases trapped under the inversion layer during much of the year. A similar but less severe phenomenon can also be observed in the Boulder and Fort Collins areas of Colorado.

There are few data on air pollution concentrations from areas of the Front Range dominated by coniferous forests. Long-term records of pollutant concentrations are available only from urban areas to the east. Data on sulfur dioxide (two stations) and nitrogen dioxide (three stations) are available for locations between Fort Collins and Colorado Springs (especially near Denver) since 1975 (Colorado Air Pollution Control Division 1986). These data indicate that sulfur dioxide and nitrogen dioxide concentrations are generally low and do not exceed the National Ambient Air Quality Standards (NAAQS) established by the U.S. Environmental Protection Agency; maximum and annual concentrations have remained stable or declined since 1975 (Colorado Air Pollution Control Division 1987).

Ozone (data available from 11 stations in the same area) is the greatest potential air pollution stress to plants in the Front Range. Reactive hydrocarbons and nitrogen oxides produced from the combustion of fossil fuels in metropolitan areas are photochemically oxidized and transported into montane areas to the west. There are many violations of the NAAQS (120 ppb), with highest concentrations in the summer (Colorado Air Pollution Control Division 1986). The highest concentrations (up to 200 ppb) are measured in suburbs of Denver (Colorado Air Pollution Control Division 1987). Only counties between Denver and Fort Collins (Adams, Arapahoe, Boulder, Denver, and Larimer counties) reported violations of the NAAQS in 1986. Data from the southernmost stations near Colorado Springs indicate that there are no violations of the NAAQS, with maximum concentrations well below the standard.

There are few data on gaseous pollutants from montane sites, although we can use data from urban areas and knowledge of climatological patterns to characterize exposure of Front Range coniferous forests to air pollutants. The climate of Colorado frequently produces conditions with poor dispersal of air masses, which results in abnormally high pollutant concentrations in and adjacent to urban areas. Few major storm tracks pass through areas east of the Front Range. The high pressure that is often situated over the state is generally associated with light winds, stable nighttime conditions, and strong subsidence inversions (PEDCO Environmental, Inc. 1981). These conditions lead to poor atmospheric mixing and transport. Strong inversions, with high mountain peaks to the west, produce stable atmospheric conditions with long residence time of certain pollutants. Valley winds often ventilate the Front Range during part of the day, but also recirculate pollutants back into the basin. Dispersion and transport improve significantly only during large-scale weather movements and chinook wind conditions (PEDCO Environmental, Inc. 1981). Wind roses for the Denver area indicate that prevailing winds have a strong southerly component (U.S. Department of Commerce 1963), which suggests that pollutants tend to be transported to montane areas northwest of the city. Wind roses for Colorado Springs in the southern portion of the Front Range Basin have a stronger northerly component (U.S. Department of Commerce 1979), and there is a greater tendency for air masses to be dispersed east of the basin (PEDCO Environmental, Inc. 1981).

Extensive surveys by the USDA Forest Service and the National Park Service have not found pollutant injury symptoms in conifers in the Front Range (James and Staley 1980; unpublished 1987 data from Rocky Mountain National Park supplied by K. Stolte, Air Quality Division, National Park Service). However, ozone levels measured in the Denver area would be high enough to injure ponderosa pine at some locations in California (e.g., Peterson et al. 1991; Miller 1992). Pollutant exposure in the Front Range has apparently not been high enough to produce visible injury, even in sensitive species (Davis and Willhour 1976) such as ponderosa pine. However, there could be some physiological effects that result in loss of vigor and reduced radial growth in the absence of visible symptoms (Reich and Amundson 1985; D.L. Peterson, D.G. Silsbee, M.J. Poth et al., in preparation).

In this study, we used dendroecological analysis to determine if there have been any changes in radial growth of ponderosa pine that might be related to elevated levels of ambient ozone in the Front Range of the Colorado Rocky Mountains. We examined regional growth trends, growth of individual trees and stands, and the relationship between ponderosa pine growth and climate.

Methods

Air-quality data

We characterized ozone exposure for the Front Range of the Colorado Rocky Mountains by acquiring the 1988 air-quality database (our study was conducted in 1988) from the Colorado Air Pollution Control Division in Denver, Colorado. We also acquired the 1988 ozone database for Rocky Mountain National Park from the Air Quality Division of the National Park Service in Lakewood, Colorado. This network of ozone monitors was used to characterize ozone exposure on the east side of the Front Range. Only the monitors at Rocky Mountain National Park and Boulder are located near montane study sites. We assumed that ozone exposure at our study sites would be proportional to the dose measured at valley sites to the east.

We augmented the existing data on ozone exposure by establishing an ozone monitor at Manitou Experimental Forest, which is located just west of the Rampart Range. Instrumentation, calibration, and operation of this ozone monitoring station are described in Zeller and McKinney (1989). We intended that this monitor represent the ozone exposure regime assumed for this "protected" area. Ozone data for all stations were compared by month for April through September 1988 in order to characterize regional patterns of ozone exposure. We also examined the existing database for prior years available from the Colorado Air Pollution Control Division.

Site selection and field data collection

Study sites were selected from a larger group of potential sites determined by an on the ground survey of potential sites. We sampled only in second-growth stands that were greater than 50 years old and

had experienced minimal disturbance since harvest. While most of these stands were originally clear-cut, many stands contain older individuals that were not cut (Table 1). Sampling was stratified in two general groups: exposed and protected. Twenty exposed sites are located across the eastern edge of the Front Range facing the metropolitan areas stretching from Fort Collins to Colorado Springs (Fig. 1). It was assumed that these areas are exposed to abnormally high concentrations of air pollution, especially ozone. Ten protected sites are located to the west of Colorado Springs (CS) that ambient ozone concentrations in 1988 (Zeller and McKinney 1989) were similar to those measured at Colorado Springs to the east. Southwestern dwarf mistletoe (Arceuthobium vaginatum ssp. cryptopodium) is a native parasitic plant commonly found on ponderosa pine in the Front Range (Merrill and Hawksworth 1986). Because moderate and heavy infestations by this plant reduce radial growth (Hawksworth and Shaw 1984), we did not sample any trees rated greater than 3 on a 6-class scale described by Hawksworth (1977).

**Collection and analysis of tree cores**

Two cores were extracted from each sample tree at breast height with an increment borer. Cores were taken from the cross-slope sides of the tree and stored in paper straws until they were processed. Cores were glued into wood mounts and sanded with successively finer grades of sandpaper until individual tracheids were visible under a microscope. Ring widths were measured to the nearest 0.01 mm with an incremental measuring machine equipped with digital encoder. This machine is interfaced with a microcomputer that stores ring widths by year for each core (Robinson and Evans 1980). A video camera attached to a binocular microscope was used to transmit the core image to a monitor.

Cores were included in the database only if they could be confidently cross-dated (Fritts 1976) by accurately associating the rings of each core with a specific year. The last ring measured was formed in 1987, because cores were collected during the growing season of (at 1.4 m), height, dominance based on crown classification (Spurr and Barnes 1980), and needle retention. Needle retention was recorded as the number of years of needles per branch. These estimates were based on a sample of five randomly selected trees per stand, with three randomly selected lower crown branches per tree. Stem density and basal area at each site were determined with 6 circular 0.02-ha quadrats; only trees taller than 1.4 m were included in the sample.

**TABLE 1. Summary of mean diameter, height, and date of earliest cross-dated rings from sample trees**

<table>
<thead>
<tr>
<th>Site</th>
<th>Diameter (cm)</th>
<th>Height (m)</th>
<th>Date of earliest ring</th>
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<td>Mean</td>
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<td>12 (2)</td>
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<td>36.5 (14.4)</td>
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<td>19 (2)</td>
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**NOTE:** One standard deviation is indicated in parentheses for diameter and height.
1988. Cores were initially cross-dated visually by indicating dates directly on the core (Stokes and Smiley 1968; Swetnam et al., 1985). All rings were measured and recorded. Following ring measurement, cross-dating was verified with the program COFECHA (Holmes 1983), which calculates correlation coefficients between the time series of ring widths for a single tree and for an entire collection of trees.

**Data analysis**

Tree-ring series were converted to basal-area increments, and basal-area growth trends were assessed individually for each tree. Growth trends were analyzed with Kalman filter procedures (Kalman 1960; Kalman and Bucy 1961). The Kalman filter is a recursive procedure using state-space formulation of a linear system that allows parameters to be nonstationary with time. It has been used in other studies to detect trends in time-series characteristics of tree growth (Van Deusen 1987, 1990; Visser 1986; Visser and Molenaar 1988, 1992).

We used a version of the Kalman filter that would allow us to accurately detect long-term changes in individual growth (Graybill et al. 1992). The model formulation was:

\[ Y_t = \alpha_0(t) + \alpha_1(t) Y_{t-1} + \alpha_2(t) Y_{t-2} + e_t \]

where \( Y_t \) is basal-area increment at year \( t \); \( \alpha_0(t), \alpha_1(t), \text{ and } \alpha_2(t) \) are parameters analogous to regression coefficients, also referred to as response functions; and \( e_t \) is measurement error at time \( t \). Parameter fluctuations through time were assumed to follow a random walk:

\[ a_i(t) = a_i(t-1) + w_i(t), \quad i = 0, 1, 2 \]

where \( a_i \)'s are model parameters, and \( w_i(t) \) is independent normally distributed random disturbance. Interpretation was based primarily on the parameter \( \alpha_0 \), because it was the parameter most indicative of a trend component. A change in growth trend was defined as a point at which \( \alpha_0(t) \) estimates changed such that a significant trend resulted. A trend was defined as a consistent increase or decrease of \( \alpha_0(t) \) of 10 years or more. Corresponding significant changes in \( a_1(t) \) and \( a_2(t) \) at the same time were used as supporting evidence. Series without significant departures from the stationarity hypothesis or with growth patterns lacking clear trends were considered to have no change. Growth changes were recorded as an increase, decrease, or no change for each tree. They were summarized by site and expressed as frequencies per decade.

In a separate analysis, long-term growth characteristics were examined by dividing basal-area time series of each tree into three time segments: 1900–1929, 1930–1959, and 1960–1987. The proportional changes between periods were calculated as:

\[ D_1 = \frac{B_2 - B_1}{B_1} \]

\[ D_2 = \frac{B_3 - B_2}{B_2} \]

\[ D_3 = \frac{B_3 - B_1}{B_1} \]

where \( B_1 \) is total basal area for 1900–1929, \( B_2 \) is total basal area for 1930–1959, and \( B_3 \) is total basal area for 1960–1987. The most recent time segment is assumed to encompass the period of elevated ambient ozone exposure for mature trees. The 1930–1959 segment is a period during which ozone exposure for mature trees was much lower. The 1900–1929 segment is a period of minimal ozone exposure during which many of the sample trees were in the sapling stage. Using these time segments allowed us to determine the possible effects of ozone, climate, and tree age on growth trends since 1900 (Graybill et al. 1992). Mean changes in \( D_1, D_2, \) and \( D_3 \) between time periods were calculated. Correlations of changes with tree age were also calculated.

An additional analysis examined trends and correlation of radial growth for each site with climatic data from Colorado climate division 4. Detrending of radial growth time series was performed for each tree using exponential and spline functions (program ARSTAN, Cook and Holmes 1985). Remaining persistence in the individual series was removed by fitting the series with an appropriate autoregressive model. The residuals were averaged using Tukey's biweight estimator. The resulting time series of mean growth index values (chronologies) for each site was then used. Climatic data included in the analysis were monthly total precipitation, mean temperature, and Palmer hydrological drought index. The drought index measures long-term relative moisture supply, based on the balance between moisture supply and demand; values normally range between -6 and 6, where positive values indicate periods of greater moisture availability. Pearson product-moment correlations (r) were summarized for all sites for the three time intervals indicated above.

**Results and discussion**

**Ozone concentration data**

We characterized spatial differences in ambient ozone concentrations for the year of the study with data from the Colorado Air Pollution Control Division, Rocky Mountain National Park, and a supplementary site at Manitou Experimental Forest. Some of these data are displayed in Fig. 2, which contains daily maximums and minimums for six stations that cover the north to south expanse of the study area (Fig. 1). Data are displayed for August only, which typically has higher ozone levels than other months. The entire data set for 10 stations can be found in Peterson and Arbaugh (1989).

Air-quality records available since 1975 (Colorado Air Pollution Control Division 1986) indicate that ozone concentrations are generally higher in the central part of the Front Range and lower at the northern and southern extremes (Fig. 2). Monitoring stations in the suburban Denver area (e.g., Arvada (not included in Fig. 2)) consistently had the highest ozone levels during the summer months, with several maximums exceeding 100 ppb at each site. It is interesting to note that Denver exceeded 100 ppb only once during the year, although it has exceeded this level more frequently and at higher levels in previous years (Colorado Air Pollution Control Division 1987). Insolation was reduced considerably in the Front Range during much of the summer as a result of airborne particulates from large wildfires in Yellowstone National Park (personal observation). It is possible that this phenomenon reduced ozone levels in Denver and other areas of the Front Range. There were only seven violations of the NAAQS of 120 ppb in 1988 throughout the Front Range, one of which was at Rocky Mountain National Park. All stations had maximums that exceeded 100 ppb, except the southernmost stations at Colorado Springs and Manitou Experimental Forest.

Ozone levels at mountain locations (Rocky Mountain National Park, Manitou Experimental Forest) were moderate (Fig. 2). For example, maximum concentrations at Rocky Mountain National Park were comparable to those at the valley location (at Fort Collins) to the east. Ozone levels at Manitou Experimental Forest were surprisingly high and comparable to those at Colorado Springs to the east. This was counter to our expectations and challenges our assumption that this area is protected from ozone exposure. It is unclear how circulation patterns would produce this level of exposure at the Manitou site. It is also noteworthy that the mountain and foothill sites have higher minimum ozone values than Denver or other urban areas. This is probably due to the lack of nitrogen oxides from automobile emissions which would normally break down ozone at night (Bohlin 1989). It is difficult, of course, to accurately characterize exposure of forests to ozone because so few data are available from mountain locations.
Site and sample tree characteristics

Stem density varies greatly among sites, ranging from 300 to 2829 stems/ha. Basal area ranges from 11 to 35 m²/ha. Ponderosa pine represents the majority of stem density in most cases, and over 80% of stand basal area in all cases. Stands with high densities generally have large numbers of seedlings or suppressed individuals of ponderosa pine or quaking aspen (Populus tremuloides) in the understory.

Mean diameter of sample trees ranges from 23.5 to 41.3 cm, and mean height ranges from 10 to 19 m (Table 1). The relatively low standard deviations associated with these measurements indicate that there is little variation in the size of trees at most sites. The mean earliest cross-dated tree rings range from 1841 to 1921, with the oldest tree dated to 1765 and the youngest tree to 1937. Seventy-one percent of all sample trees are less than 100 years old.

The data in Table 1 indicate that the stands at most sites are composed of second growth dating from 1880 to 1920. This is a period during which most ponderosa pine stands in the Front Range were harvested, with stands subsequently regenerating naturally. There were also several large wildfires in the Front Range during this period (Veblen and Lorenz 1991) which may have affected some of the stands (fire scars were noted on older trees at several sites). Some stands have several older individuals that survived this period of intensive cutting and fires. These trees were included in our study if they met the sampling criteria. The sample trees in protected sites are slightly older on the average than those in exposed sites (Table 1).

Needle retention

We examined the foliage of each tree in this study to determine if there was any evidence of ozone injury. None of the trees sampled had chlorosis associated with ozone injury. We also collected data on needle retention, because older needles are normally lost in ozone-stressed trees (Peterson et al. 1987;
Peterson and Arbaugh 1988; Miller et al. 1989). Needle retention ranged from 5.6 to 6.8 years per branch, with lowest retention directly west of Denver (Fig. 3). Highest needle retention was near Fort Collins. Sites west of Denver were the only “exposed” sites with less than 6 years needle retention, although some of the “protected” sites also had less than 6 years needle retention. Some sites with high ozone exposure had the lowest needle retention, and some sites with low ozone exposure had the highest needle retention, although there were no significant differences among sites at the p < 0.05 level. It is difficult to relate needle retention to ozone injury because ozone exposure is poorly characterized at mountain locations, and because there is no chlorotic injury. Furthermore, needle retention may be related to genetic and environmental factors not measured in this study. Standard deviations of mean needle retention are relatively low, which suggests that needle retention is uniform within a site.

The ozone exposure levels in the Front Range discussed above are not as high as in other areas where ponderosa pine has visible injury, such as the Los Angeles Basin (Miller and McBride 1988) and southern Sierra Nevada (Peterson and Arbaugh 1988; Peterson et al. 1991). However, the Front Range exposure would normally be considered high enough to cause at least some ozone chlorosis in ponderosa pine, which is a sensitive species. Neither our study nor others (James and Staley 1980; unpublished data from Rocky Mountain National Park supplied by K. Stolte, Air Quality Division, National Park Service) have found evidence of ozone chlorosis in the Front Range. The Rocky Mountain variety of ponderosa pine (var. scopulorum) may be more resistant to ozone injury than the Pacific variety (var. ponderosa) (Aitken et al. 1984).

Tree growth trends

There is a wide variety of growth trends in ponderosa pine within and among stands in the Front Range, although a large number of trees at any given site have similar growth trends. Air-pollution data (Fig. 2) indicate that our original assumption about “protected” sites having lower exposure to ozone than “exposed” sites is probably incorrect. We therefore evaluated growth trends for data that include all sites.

Individual tree growth trends, based on interpretation of \( a_0 \) and other parameters from Kalman filter analysis, are summarized in Figs. 4 and 5. The most striking result of this analysis is the large number of growth decreases in the 1940s. Examination of basal-area growth curves for individual trees shows that this decrease started in the latter half of the decade and continued into the 1950s. This decrease is found in trees of all ages. It is found in at least some trees at each site and occurred in as many as 83% of trees at one site (site 5). There are very few trees with growth increases in the 1940s. A large number of growth decreases are also found in the 1920s, with up to 46% of trees at a site having this trend. These periods of growth decrease are also found in other conifer species of the Front Range (Graybill et al. 1992), as well as in ponderosa pine in northern New Mexico (Swetnam 1987). These growth decreases are almost certainly caused by factors other than air pollution, because they occurred over a long period and started prior to high ambient ozone concentrations.

The only prominent growth increase at any time in this century started in the late 1930s (Fig. 5), despite relatively low precipitation during the early part of the decade. This period of increase was found in some trees at all but two sites and occurred in 61% of trees at one site (site 1). In general, Kalman filter analysis detected far more decreases than increases (Figs. 5 and 6), which suggests that decreases tended to be of greater duration when they occurred. There do not appear to be any particular geographic patterns to growth decreases or increases.

Of greatest interest to this study is the possibility of any recent growth decreases that may be related to air pollution or other causes. There are a large number of sites with growth decreases in the 1960s (maximum of 52% of trees at a site) and 1970s (maximum of 50% of trees at a site). If the number of decreases in the 1960s and 1970s are added, 12 to 82% of the trees per site have decreased growth. This may initially seem to be an important result, but most trees have a sharp growth increase in the 1980s that compensates for lower growth in the previous 2 decades.

Basal-area growth was also evaluated by comparing proportional growth changes (\( D_1, D_2, D_3 \) for the time segments 1900–1929, 1930–1959, and 1960–1987. Absolute and relative values of \( D_1 \) vary widely among sites, with no apparent geographic trend. The mean values of \( D_1, D_2, D_3 \) for all sites combined are 1.03, 0.84, and 2.73, respectively. All values of \( D_1 \) were positive for all sites except two (for \( D_1 \) only). This indicates that basal-area increment generally increases through time on a regional basis, as one might expect for second-growth stands of young to moderate age. Examination of basal-area growth curves for individual trees shows that most trees have a period of increasing basal area during the early years of the time series, which is normal for the juvenile stage of tree growth. The sample trees are survivors of many years of stand competition, and they benefit from the mortality of other trees (Oliver and Larson 1990). In addition, most sample trees have dominant and codominant crown classifications and would therefore be expected to have higher growth rates than more suppressed trees. There are no indications in this analysis of any growth decreases that might be related to recent air-pollution stress.

Relationship of climate to growth

Climate data are helpful in interpreting some of the observed growth trends in the Front Range. The prominent growth decrease in the late 1940s throughout the Front Range appears to be related to a period of low precipitation (Graybill...
et al. 1992). Growth decreases in the latter half of the 1970s may also be related to low precipitation. The 1980s growth increase appears to be related to a period of above-average precipitation during this decade. None of the other growth trends previously discussed have apparent relationships with precipitation patterns. Short-term response of tree growth to extremes in precipitation is apparent in the basal-area time series, although this is normal for most forest sites. For example, high precipitation in 1947 and 1961 is associated with high basal-area growth (large tree rings), and low precipitation in 1951 and 1963 is associated with low growth (small tree rings).

The relationship between climate variables and interannual variation in basal-area growth was investigated with correlation analysis (Fig. 5). Most monthly correlations of ponderosa

**Fig. 4.** Percentage of ponderosa pine at each study site with (A) decreased growth trend and (B) increased growth trend, as indicated by decade. The point at which the decrease or increase started is displayed, rather than the duration of the decrease.

**Fig. 5.** Pearson product–moment correlations of growth index with monthly values of mean temperature, total precipitation, and Palmer hydrological drought index. Correlations are displayed for three time intervals, as indicated.
pine growth with precipitation are positive. Correlations are generally highest during spring, which is a period of relatively high precipitation in the Front Range. Correlations are consistently positive across all time intervals for April through July and tend to be lower for 1900–1929. Spring precipitation is certainly a critical factor for tree growth.

Most monthly correlations of growth with temperature are negative (Fig. 5). Correlations are relatively low, without a strong seasonal pattern. Most correlations during spring are negative, and April temperature for 1930–1959 has the highest negative correlation. The high positive correlation for January temperature during 1960–1986 is difficult to explain. In general, temperature correlations are less important than, and inverse to, precipitation correlations.

The influence of precipitation and temperature on available soil moisture is integrated to some extent in the Palmer hydrological drought index (PHDI). All monthly correlations of growth with PHDI are positive from May through September (Fig. 5), especially during June through August, which corresponds to the primary period of tree shoot elongation and stem growth. This period of high correlation lags behind peak correlation for precipitation, which suggests that spring precipitation strongly affects soil moisture storage in summer. Correlations during autumn and winter tend to be low or negative, which suggests that soil moisture status during these seasons has a small impact on growth; consistently (low) negative correlations for 1930–1986 may reflect a shortened period of growth due to heavy snowpacks in some years. Correlations with PHDI, precipitation, and temperature all suggest that ponderosa pine growth in the Front Range is strongly controlled by soil moisture availability. Similar growth-climate relationships have been found for other conifer species in the Front Range as well (Graybill et al. 1992). The strong correlation of tree growth with soil moisture availability is typical of regions dominated by summer drought (Jordan and Lockaby 1990).

Conclusions

There are some consistent trends in growth of second-growth ponderosa pine in the Front Range of the Colorado Rocky Mountains in this century. The most notable of these is a substantial growth decrease in the late 1940s. This decrease may be related to the relatively warm, dry climate at the time (Graybill et al. 1992). There are also growth decreases in the 1960s and 1970s, most of which are compensated for by growth increases in the 1980s. Most trees have similar growth trends within each site.

The overall growth trend of ponderosa pine in the Front Range is typical of second-growth stand dynamics. Basal-area increment increases rapidly during the early part of the life cycle and then levels off, although it still increases somewhat at most sites. Many older trees remaining from earlier timber harvests have periods of decreasing basal area during this century. Interannual variation in tree growth is correlated with soil moisture availability, which indicates that low spring and summer precipitation can have a major impact on growth.

Ponderosa pine does not appear to have been affected by ozone exposure at the current time. Needle retention is slightly lower west of Denver than at other locations, although there is no evidence of chlorotic injury. The ozone levels experienced in the Front Range would normally produce at least some visible injury symptoms in ponderosa pine in California (Pronos and Vogler 1981; Peterson and Arbaugh 1988; Miller and McBride 1988; Peterson et al. 1989, 1991), but the Rocky Mountain variety of this species may be more resistant to ozone injury (Aitken et al. 1984). Deleterious effects of elevated ozone levels on crown biomass and growth have been documented for ponderosa pine in other areas of the western United States (Ewell et al. 1989; Graybill and Rose 1989; Miller et al. 1989; Peterson et al. 1989). It is unknown whether current levels of ozone exposure in the Front Range are causing physiological stress that is not manifested in visible injury symptoms. Ponderosa pine in the Front Range should continue to be monitored to determine any change in the condition of forest ecosystems exposed to elevated ozone concentrations.

Acknowledgments

We appreciate the assistance of Darren Anderson, Berg Denderian, George Pollock, and David Silsbee with field and laboratory analysis. We thank Doug Fox, Brian Geils, and Ann Lynch of the USDA Forest Service Rocky Mountain Research Station, who assisted with site selection and provided information on the Front Range. Karl Zeller did an excellent job of collecting and analyzing data from the ozone monitor at Manitou Experimental Forest. We appreciate the cooperation of local officials of the Pike, Arapaho, and Roosevelt national forests; Colorado State Parks; and Jefferson County Open Space Parks in allowing us to conduct sampling on lands in their jurisdictions. Edward Cook, Brian Geils, Gregory Ettl, David LeBlanc, Ronda Little, David W. Peterson, and Regina Rochefort provided helpful comments on an earlier version of the manuscript. Review of statistical and dendroecological methods was provided by Lawrence Bednar, Donald Graybill, Douglas Maguire, and Charles Peterson. This research was supported by funds provided by the USDA Forest Service Pacific Southwest Research Station and joint U.S. Environmental Protection Agency (EPA) – USDA Forest Service Forest Response Program. The Forest Response Program is part of the National Acid Precipitation Assessment Program. This paper has not been subject to EPA policy review and should not be construed to represent the policy of the agency.


