

The relationship between tree diameter growth and climate for coniferous species in northern California

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Abstract: The difference between actual and predicted growth rates for the conifer regions of northern California has been observed to vary with climatic changes. This study presents a method to investigate the relationship between growth and climate. Growth variations attributable to biological and cultural factors were removed by using the CACTOS (California conifer timber output simulator) program. The remaining variation was then associated with relative precipitation and temperature for the projected period and the CACTOS calibration period. Climatic data from the current and preceding years were considered. Elevation, stand density, and species were also investigated to determine their effects on the format and magnitude of the relationship between growth and climate. The results of this study, which included tests of stem analysis data taken over 15 years, indicate that growth variation is associated with the climatic changes of winter precipitation and summer temperatures for the region, in addition to biological and cultural factors. Winter precipitation and summer temperatures affect growth in the current and the subsequent years. Moreover, the relationship between climate and growth changes by densities and species. This study provides a basis for using short-term growth data to make long-term growth projections with growth adjusted to long-term climatic conditions.

Résumé : La différence entre les taux de croissance réel et anticipé varie selon les changements climatiques dans les régions de conifères du nord de la Californie. Cet article présente une méthode pour étudier la relation entre la croissance et le climat. Les variations de croissance attribuables aux facteurs biologiques et culturels ont été éliminées à l'aide du programme CACTOS, un programme de simulation de la production de bois chez les conifères de la Californie. La variation résiduelle a été associée à la température et à la précipitation relatives pour la période visée par la simulation et la période de calibration de CACTOS. Les données climatiques de l'année en cours et des années précédentes ont été considérées. L'altitude, la densité du peuplement et l'espèce ont également été considérées pour déterminer la forme et l'ampleur de la relation entre le climat et la croissance. Les résultats de cette étude, qui incluaient des tests avec des données d'analyse de tige prises sur une période de 15 ans, montrent que la variation de croissance est associée aux changements climatiques reflétés dans la précipitation hivernale et les températures estivales de la région, en plus des facteurs biologiques et culturels. La précipitation hivernale et les températures estivales affectent la croissance de l'année en cours et des années subséquentes. De plus, la relation entre le climat et la croissance change selon la densité et l'espèce. Cette étude fournit les bases nécessaires à l'utilisation de données de croissance à court terme pour faire des projections à long terme en ajustant la croissance aux conditions climatiques à long terme.

[Traduit par la Rédaction]

Introduction

Climatic effects on trees and forests have been recognized by a number of researchers investigating the occurrence of species, distribution of plants, and the formation of structural characteristics (formation of growth) (Fuller 1914; McLean 1917). Climatic variations are particularly important in the process of estimating tree height and diameter growth, because characters like stem elongation, formed over long time periods of meristematic activity, are more responsive to climatic influences than characters like repro-

ductive structures that are formed rapidly (Bradshaw 1965). Climatic factors, therefore, must be considered when projecting future growth in trees.

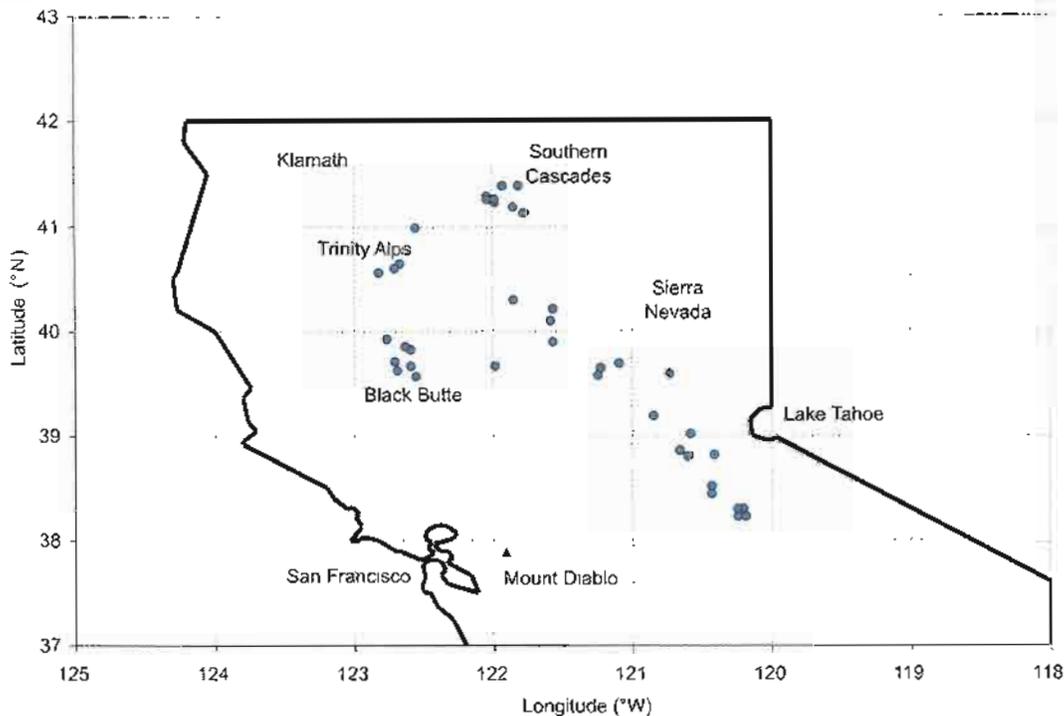
The ability to predict future growth patterns is essential to credible forest management planning (Davis and Johnson 1987; Barrett et al. 1994), and it is especially important in the process of permitting timber harvests where long-term projection is required. The current practice has been to base projections on biological or environmental variables, excluding climatic factors from consideration. Biological variables such as site index, tree age, diameter at breast height (DBH), tree height (HT), and stand density have been used, and environmental variables such as elevation, aspect, and slope have also been considered. Examples of biological and environmental models include CACTOS (Wensel et al. 1986), STEMS (Belcher et al. 1982), PROGNOSIS (Stage 1973; Wykoff et al. 1982), and ORGANON (Hann et al. 1995). The climatic information drawn from these models may not accurately reflect long-term climatic conditions, because

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Fig. 1. Distribution of stem analysis clusters in northern California.



most of the existing models have been fitted to data collected over a short time period. Therefore, growth projections may be over- or under-estimated, especially when attempting to predict long-term growth.

For instance, Jones et al. (1993) correlated an increasing divergence in paper birch (*Betula papyrifera* Marsh.) growth from the STEMS model's (Belcher et al. 1982) growth prediction line from 1984 through 1990 to the climatic stress during the same time period. They declared that the decline episode was preceded by several years of climatic stress with the final mortality in 1990 being due to bronze birch borer activity. In another example, Wensel and Turnbull (1998) used the CACTOS model, calibrated on the period 1980–1985, for the major coniferous species in northern California. They observed that expected growth was consistently higher than actual basal area growth for the time period from 1985 to 1990, ranging from 14 to 32% over estimates for all species studied. The reduced growth was found to be significantly related to the reduced precipitation that had occurred during the study period, as compared with precipitation during the previous 5 years (1980–1985).

In both of the above examples, growth projections would have been more accurate if climatic variations had been considered. If a relationship between growth and climate can be determined and then incorporated into these models, future growth projections can be adjusted for any future precipitation and (or) temperature levels.

Our purpose here is to investigate the effect of climatic changes on annual tree growth for coniferous species in northern California and model this relationship to produce accurate predictions of future growth. A study for the same species in the same area by Wensel and Turnbull (1998) used periodic precipitation for growth predictions in re-measured plots over two time periods. Because they used

two 5-year time periods, only one variable (relative precipitation) could be used in that model. In the current study, we used stem analysis to measure annual growth on felled trees. This gave us 15 years of stem growth data, enabling us to look at more variables. Variables under consideration here included precipitation and temperature. Elevation, density, and species effects on the growth–climate relationship were also investigated.

Growth data

The growth data were obtained from a stem analysis data base collected in 1979 and 1980 by the Northern California Forest Yield Cooperative (Wensel 1982; Biging 1985). We chose to study the variable of annual diameter growth obtained from stem analysis, which is an efficient and accurate way of collecting annual growth data. Our data set consisted of detailed stem analyses of sample trees from young-growth stands of six conifer species: ponderosa pine (*Pinus ponderosa* Laws.); sugar pine (*Pinus lambertiana* Dougl.); Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco); white fir (*Abies concolor* (Gord. & Glend.) Lindl.); red fir (*Abies magnifica* A. Murr.); and incense cedar (*Libocedrus decurrens* Torr.).

The trees were selected in clusters: 31 clusters, each containing three 0.2-acre (1 acre = 0.405 ha) plots, and 8 clusters, each containing two 0.1-acre plots. All trees were free of any recorded history of disturbance from insects, disease, or damage. These plot clusters are distributed across forest lands in the central and northern Sierra, the southern Cascade, the Shasta–Trinity area, and the Black Butte area (Fig. 1).

On each plot, four to six dominant trees, representing the one or two most prevalent species in the stand, were randomly chosen for felling as site index trees for that site. Up to seven additional trees were felled for stem analysis on each plot. These trees were randomly selected but proportional to their representation in the range of diameter classes present on the site.

Annual radial growth increments were determined by digitizing the boundaries of annual rings and averaging their measurements on multiple axes from the pith to the outer edge of a cross section taken at breast height of the tree (Biging and Wensel 1984). Diameter at breast height HT, live crown ratio (LCR), and species were also recorded for each tree, and the elevation and stand density (stocking) was noted for each plot. In terms of DBH, HT, and LCR classes, the trees were distributed in a normal manner over the ranges of 15–92 cm for DBH, 7–46 m for HT, and 0.1–1 for LCR.

Elevations ranged from 853 to 2073 m, but most of the trees studied were growing below 1707 m except for a few trees in one cluster at 2073 m. In terms of basal area density, trees were distributed in a range between 4.59 and 36 m²/ha with most trees growing at the medium level (34–57 m²/ha) and the remainder evenly divided between the low (0–34 m²/ha) and high (>57 m²/ha) levels.

The growth period studied was from 1966 to 1980 inclusive; all the trees used for analysis were felled in late 1980, showing that year's radial growth. Trees with missing inventory data (DBH, HT, LCR) were eliminated. Overall, 541 trees were used in the modeling and testing process.

About half of the clusters were randomly selected for investigation of the growth–climate relationship. These data are hereafter referred to as the fitting data, including 302 trees. The remaining clusters, including 239 trees, are referred to as the testing data and were withheld for testing purposes. Two data sets were tested, although not shown here, to have a similar distribution of observations. Although this testing data set did not provide independent data, it did help test whether a significant relationship from the fitting data is an outcome by chance or guarded against a severely overparameterized model (Neter et al. 1989).

The CACTOS program, version 2.0 (Wensel and Koehler 1985) was used to obtain diameter growth estimates on all plots. This early version of CACTOS has coefficients estimated from the same data as that used for the current study. Growth residuals were computed by subtracting the growth estimate from the observed growth of each tree for each year. In this study, the average growth residual for all trees varied from year to year and were more than 20% above or below the yearly average residual in 9 of the 15 years; in particular, the average growth residual was 80% below the yearly average in 1977 and 80% above the yearly average in 1980. It is this variation that was studied in relation to the climatic variation.

Climate data

In this study, we considered precipitation and temperature to be the major indicators of climatic effects on growth, as other researchers have suggested (Johnson et al. 1988; Holdaway 1990; Jordan and Lockaby 1990; Graumlich 1991; Wensel and Turnblom 1998). Precipitation determines the amount of moisture available in the soil (Powers 1981; Carter et al. 1984; Oliver 1986; Byrne et al. 1987; Allen et al. 1990). Temperature reflects the amount of solar radiation energy available for trees to use in the photosynthetic reaction. Temperature also influences tree growth, because it can affect water availability; high temperatures can reduce growth by enhancing evapotranspiration, resulting in water loss moisture stress (Fritts 1976; Jones et al. 1993).

The forests of northern California are influenced by a Mediterranean climate. During a typical year, there is little or no precipitation during the months of June through September (Koeppel and De Long 1958). Most precipitation (83–90%) is received between October and March (Elford 1970). At higher elevations, much of this precipitation comes in the form of snow, and it can remain for several months before melting, turning into an important source of water for California during the growing season (Koeppel and De Long 1958).

Tree-diameter growth in this region generally starts between March and April when the water supply increases as the snows

melt, although the season can be delayed if snow comes or lingers into those months (Oliver 1986). Tree growth stops around the middle of September, depending upon how much moisture is available in the soil (Fowells 1941). During the growing season, soil moisture gradually decreases and creates a water deficit in well-stocked stands causing trees to quit growing (Zinke 1975). Powers (1981) mentioned that the soil's water-holding capacity is invariably low in summer, even in young plantations. Thus, presumably, a growing season could be extended with additional water, such as that provided by a significant midseason rainfall.

Based on these observations of climatic and growth factors, we designated the period of October through February as winter, March through April as spring, and June through September as summer, because precipitation and temperature in each of these "seasons" has a specific influence on tree growth. The accuracy of these seasonal designations was reinforced by a preliminary growth–climate data analysis, which indicated that those three ranges would give the highest predictive ability for growth variation (Yeh 1997). In keeping with these ranges, we defined a climate year as running from October through September. This definition of climatic year has also been used by some tree-ring researchers (Fritts 1976).

Ideally, climatic data for a growth–climate study would be collected from weather stations located at the growth sites. Unfortunately, on-site weather stations were not available for this study. Instead, we used climate data provided by James Goodridge (California Department of Water Resources (retired)). Additional data were taken from the National Climatic Data Center, Asheville, N.C. Data were taken from stations that could provide complete monthly records for the time period from 1960 to 1980. Monthly records were standardized for each station, based on the average overall measurements in 21 years (1960–1980), and were used to measure the variations in precipitation and temperature from month to month. For example, the monthly precipitation index, Z_{imt} , was computed by the usual standardization equation:

$$[1] \quad Z_{imt} = \frac{P_{imt} - P_i}{\sigma_i}$$

where P_{imt} is the monthly precipitation for station i in month m and year t , $t = 1, 2, \dots, n$ (n is the number of stations); $m = 1, 2, \dots, 12$; $i = 1, 2, \dots, 21$; P_i is the mean, and σ_i is the standard deviation of 21 years of measurements at station i .

Seasonal precipitation is the total precipitation over the months in one season, and seasonal mean temperature is the average mean temperature over the months in one season.

Altogether, precipitation data from 34 stations and temperature data from 32 stations were used; all these stations were distributed in the same geographic area as the growth plots. Since there is large variation in weather over small distances in California because of its diverse topography (McAdie 1903), simply assigning the nearest stations to individual plots is very likely inappropriate and perhaps arbitrary. In a separate study (Yeh et al. 2001), we found that relative precipitation patterns in northern California can be divided into three regions: Black Butte, Klamath, and the sum of the Trinity Alps, Southern Cascade, and Sierra Nevada areas. The climatic variation patterns within each of these regions are statistically similar.

Models and methods

Much research has been conducted to study the relationship between growth and climate based on growth chronologies (time-to-time data) by using time-series analysis (Johnson et al. 1988; Jordan and Lockaby 1990; Orwig and Abrams 1997; Wimmer and Grabner 1997). In particular, dendroclimatic research has a long and fruitful history of such work (Fritts 1976; Cook 1981; Huante et al. 1991; Brown et al. 1992; Rolland 1993). These researchers

used a spline or an exponential function to remove biological growth trends from raw, ring-width chronologies, or they chose to model the relationship using an autoregressive integrated moving average (ARIMA) (Box and Jenkins 1976). These investigators assumed that growth variability due to a tree's biological mechanism and stand dynamics (nonclimatic variations) could be explained by functions with a time variable only.

Alternatively, biological growth variability can be removed by using tree growth models such as CACTOS, STEMS, and PROGNOSIS. These tree growth models provide a logical description of tree growth using tree's and site's characteristics and, therefore, may well explain growth variations that result from nonclimatic growth factors. They also can be used for growth prediction over short periods of time. Our objective here is to learn whether adding two climatic factors (precipitation and temperature) into an existing growth model will improve growth predictions by eliminating climate-based variations from the predictions. Therefore, for this study, we chose an existing growth model, using CACTOS to replace the time-only functions. The model was especially appropriate for use here, because it was originally built on data taken from the same regions and species as used for this study.

Many factors contribute to growth variation: tree or stand and site effects (Wensel and Biging 1988); cultural treatments (replanting, thinning, or site preparation) during a management period; anthropogenic disturbance; some macroclimatic factors like precipitation, temperature, and sunlight (Grewal 1991); and even atmospheric pollution (Larcher 1983). Generally, growth models are designed to quantify the biological processes involved in tree and stand development, and most of them adequately account for factors of tree or stand, site, and cultural activities. The variations not accounted for in these models arise from the macroclimate or from unexpected disturbances such as insect attack, disease, and fire.

We started by using CACTOS to eliminate variations due to trees or stand and other biological factors. Growth plots were chosen for study from among those without anthropogenic or fire disturbances during the period studied, thus preserving a large measure of the climate-induced variation. Then, a climatic response model was fitted to explain the growth variation due to climatic fluctuation. This integrated additive system of using two models was chosen because of its simplicity and because it had proven to be successful in previous studies (Holdaway 1990).

The hypothesis described in the Introduction is that the annual growth residuals from the biological trend prediction are partially due to annual variations in climatic conditions. Since CACTOS was built based on data from the years 1976–1980, under the hypothesis above, if climatic conditions over the whole prediction period are the same as that of the 5-year period (referred to as the base period), then only random variation in the residuals will result. However, if climatic conditions for that prediction period are different from those of the base period, then growth residuals over the prediction period will be correlated with the climatic changes from the base period. Thus, consider the model predicting the observed growth G_{it} of the i th tree at time t :

$$[2] \quad G_{it} = F_B(X_{it}) + r(C_t - C_B) + \varepsilon_{it}$$

where, for a given species, $F_B(X_{it})$ is the growth expected due to tree's biological properties based on the climatic condition in the base period (B); $r(C_t - C_B)$ is growth due to the climatic change for time t , C_t from the climate for the base period, C_B ; and ε_{it} is random error. The climatic condition at time t , C_t , associated with tree i , can be changed from location to location (plot to plot), or even tree to tree, to adjust for microclimatic differences; in that case, C_t can be written as C_{it} .

Equation 2 can be solved in steps. First, we used CACTOS to predict a biological growth trend for each tree. Secondly, after a biological growth trend is determined, growth residual series of each

tree, $G_{it} - F_B(X_{it})$ was computed and then shown by Yeh (1997) to be independent of year within the 15 years of data used. Each time-independent growth residual series was then associated with the climatic function, $r(C_t - C_B)$ that expresses the difference between the climatic effects for any given year and for the base period.

Climatic variables used for eq. 2 were selected from a set of potential independent variables, by doing a conditional stepwise selection process on a portion of the testing data set. The potential variables included all seasonal precipitation, seasonal temperature, and interaction variables for both the current and previous year in consideration of conditioning effects on trees (i.e., persistence of climatic effects on tree structure) (Monserud 1986; Johnson et al. 1988). This gave us a total of 24 variables as the whole set of potential variables. The "conditional" stepwise selection process means that variable selection is based on yearly priority, with the more recent year first. This priority assignment step reduces the large number of potential independent variables and decreases the possibility of spurious correlation between variables. A level of $\alpha = 0.15$, higher than the usual 0.05, was used to avoid having important variables kicked out of the model because of overlapping predictive information contained in the correlated variables of a multiple regression.

Finally, following up eq. 2, let $R_{it} = G_{it} - F_B(X_{it})$ be the growth residual from a growth projection line based on climatic condition B , and replace $C_t - C_B$ with selected climatic variables denoted by M , a regression function was fit to each tree:

$$[3] \quad R_{it} = \beta_{i0} + \beta_{i1}M_1 + \beta_{i2}M_2 + \dots + \beta_{ip}M_p + \varepsilon_{it}$$

where R_{it} was the growth residual of tree i at time t ; β_{ij} 's were coefficients of tree i ; M_1, M_2, \dots, M_p were seasonal climatic variables selected in the stepwise process for tree i ; and ε_{it} was the error term of the model.

The ordinary least squares (OLS) method was used in the regression procedure, because a consistent variability in detrended growth residuals was seen over the years. Each tree i ($i = 1, 2, \dots, n$) had its own regression function with its own set of regression coefficients as shown in eq. 3. For tree i , a set of $b_{i0}, b_{i1}, b_{i2}, \dots, b_{ip}$, and an F value were obtained, where b 's were estimated coefficients of β 's in eq. 3. An average of b_{ij} 's from all n trees, \bar{b}_{ij} , was computed to represent the estimated coefficient of β_{ij} for the overall regression function. For each climatic variable, a t test of the hypothesis that β_{ij} equals zero (no relationship) was executed.

The effects of elevation and density on the growth-climate relationship were tested by first computing a correlation between the residual from the climatic model, $R_{it} - \hat{R}_{it}$, and elevation (or density) E_i (or D_i) for i from 1 to n and for each year to see if elevation was a useful variable in the model. Then, for each coefficient, a correlation was computed between b_{ij} and elevation (or density) from all trees to see if elevation (or density) had an effect on the magnitude of any of the coefficients. That is to test whether elevation or density differences could cause differences in the sensitivity of a growth response to climatic changes. Also, ANOVA (analysis of variance) and post-ANOVA tests for each coefficient were used to see if individual or group of species was different from the others.

Analysis and results

Individual climatic model fitting

Using the average growth residual for trees from one third (80 trees; randomly selected) of the testing data set, the four variables selected through the conditional stepwise process were (i) the precipitation of October through February in the current year ($P_{1,t}$), (ii) the mean temperature of June through

Table 1. Means, standard deviations, and *t* statistics for each parameter of the seasonal climatic variables for the model: $R_{it} = \beta_{i0} + \beta_{i1}P_{1,t} + \beta_{i2}T_{1,t} + \beta_{i3}P_{2,t-1} + \beta_{i4}T_{2,t-1} + \epsilon_{it}$, ($n = 302$; across all six species).

	$H_0: \beta_0 = 0$	$H_0: \beta_1 = 0$	$H_0: \beta_2 = 0$	$H_0: \beta_3 = 0$	$H_0: \beta_4 = 0$
b_i	0.002 59	0.002 38	-0.067 02	0.002 00	-0.023 86
σ_{b_i}	0.000 90	0.000 20	0.008 90	0.000 20	0 006 70
<i>t</i>	2.915	10.486	-7.503	8.186	-3.549
<i>P</i>	<0.0025	<0.0005	<0 0005	<0.0005	<0.0005

Table 2. Estimated coefficient values of the climatic response models for each species group from the fit to the fitting data set.

	b_0	b_1	b_2	b_3	b_4
Pine group	0.006 85	0.002 38	-0.034 63	0.002 00	-0 023 86
Other species	0.000 55	0.002 38	-0.082 58	0.002 00	-0.023 86

September ($T_{1,t}$) in the current year, (iii) the precipitation of October through February from the previous year ($P_{2,t-1}$), and (iv) the mean temperature of June through September from the previous year ($T_{2,t-1}$).

Substituting the four selected climatic variables for M_1, M_2, \dots, M_4 in eq. 3, the new model could be rewritten as follows:

$$[4] \quad R_{it} = \beta_{i0} + \beta_{i1}P_{1,t} + \beta_{i2}T_{1,t} + \beta_{i3}P_{2,t-1} + \beta_{i4}T_{2,t-1} + \epsilon_{it}$$

Each tree of the fitting data set (302 trees) was fit to this model individually. For tree *i*, we had an *F* value and estimates b_{ij} ($i = 0, 1, \dots, 4$) for each of the regression coefficients, β_{ij} .

Table 1 lists the testing results for a hypothesis that each β_j equals 0. All the *t* statistics are significant at a level of $\alpha = 0.05$ ($p < 0.025$), leading us to adopt eq. 4.

Elevation, density, and species effects on the growth-climate relationship

Possible adjustments to eq. 4 for elevation proved to be not significant and was dropped from further consideration. A significant negative correlation was found between stand density and the magnitude of β_1 and β_2 (-0.16 and -0.13, respectively). Although the relations were found to be significant ($\alpha = 0.05$), these relations only explain 2–4% of the variation of each coefficient.

Five logical contrasts formed to test for species effects were (i) pine group (ponderosa pine and sugar pine) versus all others (incense cedar, Douglas-fir, white fir, and red fir); (ii) incense cedar versus the group of Douglas-fir, white fir, and red fir; (iii) Douglas-fir versus white fir and red fir; (iv) ponderosa pine versus sugar pine; and (v) white fir versus red fir. An α level of 0.05 was used for each of the five individual comparisons within each test.

Only the pine group (ponderosa pine and sugar pine) had significantly different values in β_0 ($p < 0.001$) and β_2 ($p < 0.025$) from all the other species group. Therefore, two sets of coefficient estimates were used in the final prediction function, one set for the pine species and another for all the other species. The function then can be written as follows and the coefficient estimates are summarized in Table 2:

$$[5] \quad \hat{R}_i = (I_1b_{01} + I_2b_{02}) + b_1P_{1,t} + (I_1b_{21} + I_2b_{22})T_{1,t} + b_3P_{2,t-1} + b_4T_{2,t-1}$$

where $I_1 = 1$ and $I_2 = 0$ for pine species trees and $I_1 = 0$ and $I_2 = 1$ for other species; b_{01} and b_{21} are estimates of β_0 and β_2 for pine species; b_{02} and b_{22} are estimates of β_0 and β_2 for other species; and $b_1, b_3,$ and b_4 are estimates of $\beta_1, \beta_3,$ and β_4 , same for all the species studied here.

Testing of the climatic response model

Excluding the 80 trees that were used to select the climatic variables from the testing data set (239 trees) withheld at the outset of the study, the remaining (159 trees) was used to test the final climatic models. Since this data set was randomly chosen from the same area with the same period of time, the same climatic observations are applied to this testing data set. Figure 2 shows the difference in annual residuals for the fitting, testing, and predictive series for the pine and other species groups. The differences were not significantly different.

Having satisfied ourselves that this equation fits both data sets and is not just an artifact of the fitting data set, the coefficients were recomputed using all of the data (541 trees). These more robust coefficients are given in Table 3.

Discussion and conclusions

The relationships between tree diameter growth and climate in northern California are clearly statistically significant. Changes in precipitation and temperature can explain about 67% of detrended growth variation in pine species and 74% in the other species studied here. Our investigation of this relationship indicates that (i) winter precipitation and summer temperature are the most influential climatic variables for annual growth prediction, (ii) the climate of the previous year has a conditioning effect on the current year's growth, and (iii) the growth-climate relationship does not change over the elevations tested, but it is likely to change with basal area density and species based on our results. Each of these indications is discussed further below.

- (1) Greater amounts of winter precipitation (positive coefficients) and cooler summer temperatures (negative coefficients) were shown to benefit tree diameter growth.

Fig. 2. The comparison of fitting, testing, and predicted series for each species group.

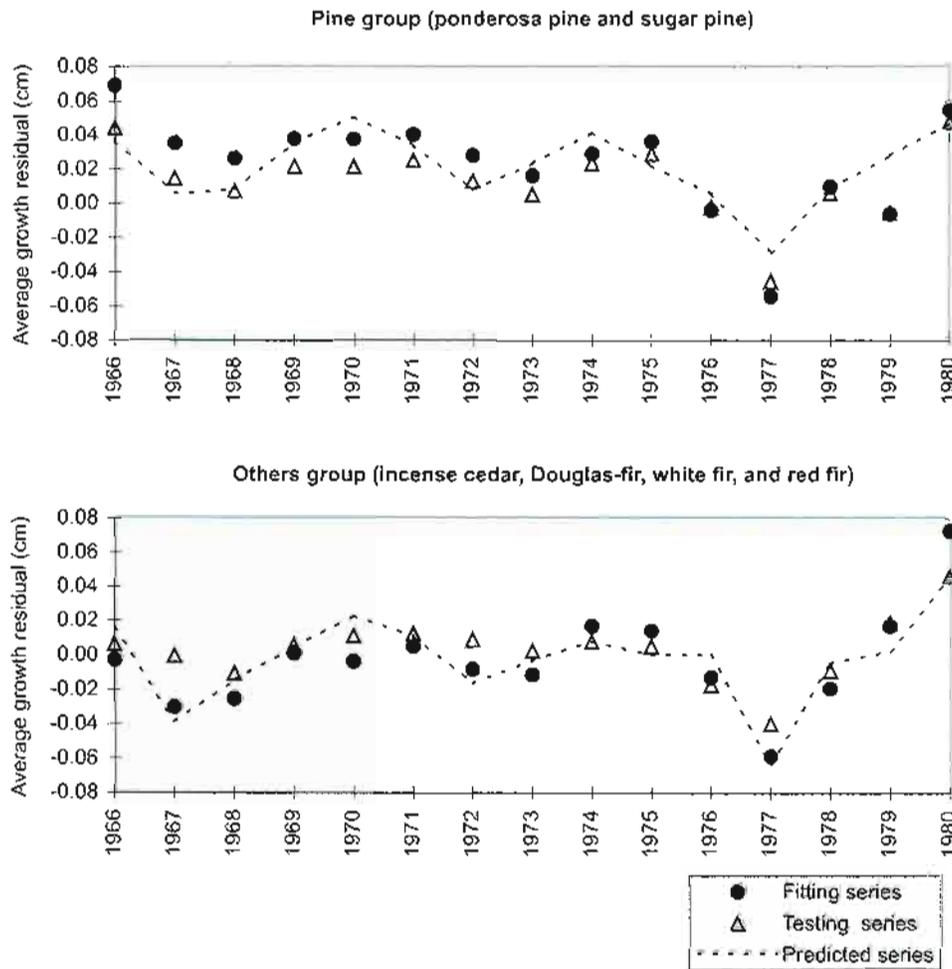


Table 3. Estimated coefficient values of the climatic response models for each species group from the fit to the entire data set.

	b_0	b_1	b_2	b_3	b_4
Pine group	0.004 48	0.002 05	-0.041 64	0.001 67	-0.021 73
Other species	0.000 82	0.002 05	-0.061 03	0.001 67	-0.021 73

More precipitation in winter tends to increase the storage of water for the coming growing season, and lower summer temperatures may decrease water loss, indicating that water supply is the major factor that can limit growth for the six coniferous species studied. Precipitation and temperatures in the spring have no significant influence on growth in the regions we studied, but they may be more important to growth in areas where winter precipitation is limited (Tyron et al. 1957). It is not surprising that summer precipitation showed no significant effect on growth, because in the 15 years studied, little summer precipitation was observed.

- (2) The previous year's climatic variables showed a conditioning effect on the current year's growth. The coefficients for the previous year's climate were smaller in magnitude than for the current year (Table 1), and the correlations were low between the climatic variables for

the 2 years (0.07 for precipitation and -0.18 for temperature). This suggests that, as expected, the current year's climate determines most of the climate-related growth variation. In the study, the conditioning effect was investigated only for the previous year because of limited degrees of freedom.

- (3) We had initially hypothesized that elevation, density (stocking), and species would affect the growth-climate relationship. Our results showed that the relationship does not change within the range of elevations between 853 and 2073 m. This agreed with the study by Fowells (1941). Within the same area as used for this study, Fowells (1941) observed that tree diameter growth at any elevations of the range all starts before or by April at slightly different times. Cessation of growth happens in early to middle September at all elevations except 914 m where growth stops earlier (around late July). It

has been pointed out that elevation has an effect on growth, inasmuch as it influences the timing of growing seasons (Spurr and Barnes 1980). Fowell's observation shows that trees at elevations of from 914 to 1829 m are all within the same "time zone." The magnitudes in the coefficients of the model, therefore, do not change over elevations.

We would be more conservative in applying this model to tree growth at elevations between 1829 and 2073 m, because most of our data came from plots located below 1829 m. At an elevation of 2042 m, Oliver (1986) observed higher levels of precipitation but lesser amounts of diameter growth, because the lingering snow pack delays the start of the growth period at this altitude. Because of the possibility that conditions at higher elevations could "reverse" the growth-climate relationship, we definitely would not apply our model to growth predictions for locations above 2042 m. Of course, those locations would also be out of our data range.

As far as density is concerned, the magnitudes of coefficients tended to be larger for lower density than for higher density. This indicates that trees in low stocking areas tend to take greater advantage of increased precipitation and lower temperatures than trees in high stocking areas. The coefficient estimates could be adjusted for differences in density. However, it is not worthwhile to incorporate the density effect into the climatic model; only about 3% of the variation in coefficient estimates can be reduced by considering the density variable (because of the relatively large variability of coefficient estimates within density). Also, about 74% of trees were from stands of medium stocking (34–57 m³/ha) for the species and locations studied. Therefore, it is risky to apply the magnitude-density relation to a whole range of stocking levels. Thus, density was not used as an explanatory variable in the final climatic model.

For species differences, the four climatic variables selected in eq. 4 were the most significant regardless of species, but the coefficients of intercept and current summer temperatures were different for the pine group versus the others. Although this difference was not strongly justified by the statistical results from using a α level of 0.05 for each of the five individual contrasts, it may be an understandable reflection of the differences in the nature of the species studied. In the regions studied, species are not evenly distributed from plot to plot but occur mostly in clumps. Ponderosa pine, in particular, tends to be found in pure stands in drier areas (Basey et al. 1992). This suggests that the pine species are less disadvantaged than other species by unfavorable climatic conditions, such as water stress that is particularly evident during periods of limited rainfall. These periods are typical of summers in northern California, making summer temperature an indicator of water stress in the area. This may explain why pine species have smaller coefficients for summer temperature than other species.

The relationship between climate and growth defined in our study could help remove climatic effects from growth predictions, so that all growth measures could be adjusted for some long-term average climatic conditions. This is particularly important because the current trend of long-term forest management is to base policy decisions on long-term growth predictions (CDF 1993; Hayes and Cole 1996). In addition, this predictive model could be used to produce

more accurate growth predictions for any hypothesized climatic regime.

This study raises several issues that merit further investigation. First, the model used here to express the growth-climate relationship is a simple linear equation involving precipitation, temperature, and species. This model approximated the relationship well within the range of our data, but it is possible that the climatic effect on growth is an asymptotic process. For example, as precipitation increases, a point might be reached where further increases in precipitation will not increase growth, because after saturating the soil, excess rainfall runs off to rivers (Satterlund 1965). Similarly, as precipitation decreases, growth reduction might also reach an asymptote at some minimum level (Westgate and Boyer 1985). Below the minimum point, further decreases in precipitation might cause an increase in mortality rather than simply a decrease in growth. A similar process may exist for temperature (Baker 1929). Therefore, a more complex model (e.g., a nonlinear function) may possess more biological meaning in expressing the growth-climate relationship, especially near the extremes of climatic conditions. Since we had only 15 years of observation in our data set, we were somewhat limited in the choice of relationship forms.

Secondly, mortality is a part of growth, and it is very likely influenced by climatic conditions. Climatic stress decreases a tree's ability to resist life-threatening attacks from insects or disease (Millers et al. 1989). Climatic stress brought on by dry, hot climatic conditions also makes a tree more vulnerable to fire (Spurr and Barnes 1980). However, it is difficult to estimate how mortality (or stand conditions such as pathogens, pests, fire, etc.) is associated with climatic changes.

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