Evaluating the effect of climate in a Sierran Mixed Conifer forest

Aimee Sprague
Honors Research Thesis

ABSTRACT

Forest growth and yield models such as CACTOS and PROGNOSIS have typically modeled future growth dynamics using unchanging climatic data. These models, applied to a future where the climate is changing, can lead to important discrepancies between actual and predicted growth rates. Yeh and Wensel (2000) first examined these discrepancies in CACTOS performance. They identified summer temperature and winter precipitation as key climatic variables influencing tree growth and developed indices to adjust growth based on the climate. However, the relationships established by Yeh and Wensel were formulated using the CACTOS growth simulator, an input-intensive growth and yield model. No independent validation of the climate-growth indices was conducted. This study examines the reliability of Yeh and Wensel's climate adjustments to the growth model for forest management applications. Biological growth signals were removed from long-term annual growth records. These empirical records were derived from tree ring analyses. A smoothing spline was used to quantify the biological growth signal (i.e., low-frequency variation in increment). A climate signal (i.e. the residual) was derived by subtracting this spline from the long-term record. The resulting residuals were correlated against the predicted climate growth signal as given by Yeh and Wensel's model. The correlation of climatic influence on growth for different species and crown classes was also considered. The results of this study indicate that Yeh and Wensel's model provides growth estimates that reliably inform management decisions. However, the relationship between climate and growth is stronger in dominant tree classes, indicating that climate more predictably affects more dominant trees. For sub-dominant trees, climatic variables had little correlation. It does not appear that competition between dominant and sub-dominant trees is confounding the correlation between sub-dominant tree growth and climate. Suppressed or understory tree growth may be more dependent on edaphic and/or microclimate gradients.

INTRODUCTION

Climate has a profound influence on the growth and distribution of forest ecosystems in California (Lenihan *et al*. 2003, Field *et al*. 1999). Understanding the magnitude of this influence, especially in light of the expected global climate change, is important for effective forest management. In California, temperatures are expected to increase anywhere from 2.2 to 4.0 degrees C (Hayhoe *et al*. 2004). Recent studies examining the relationship between rising temperatures and tree growth are conflicting. In 2003, Lenihan *et al*. found that, under all modeled climate change scenarios, we can expect an increase in total productivity and "a widespread expansion of forest" in the future (Lenihan *et al*. 2003); this study used a general biogeochemical simulator to predict vegetation shifts throughout California. In contrast, Battles *et al*. (2006) found that increased temperatures caused a significant reduction in conifer tree growth (and therefore forest productivity) under all conservative climate change scenarios. Unlike Lenihan *et al*., this study looked at only one forest type in one county of California. Both studies agree that changing climatic factors will have a substantial impact on forests; however, Lenihan *et al*.'s study lacks specificity, while Battles *et al*.'s is specific to one area and cannot be readily applied to other forest types.

Until recently, projections of forest growth and yield excluded climatic factors and instead considered only biological and edaphic factors. These models, such as CACTOS (Wensel *et al*. 1988), STEMS (Belcher *et al*. 1982), and PROGNOSIS (Stage 1973; Wykoff *et al*. 1982) typically assume future climate to be the same as past climates. Furthermore, many of these models were built from data collected for short growth periods, and may have been inaccurate at predicting long-term growth projections (Yeh and Wensel 2000). In 2000, Yeh and Wensel attempted to address this oversight by developing a model that would work in conjunction with CACTOS to produce more accurate projections of future growth by including key aspects of the climate as predictors. This model includes two versions: one for pine species, and one for all other species.

A cause for skepticism in the accuracy of Yeh and Wensel's model arises in their testing data. On-site weather stations were not available for collection of precise climatic data at the time of the study. Instead, Yeh and Wensel interpolated weather data collected from a variety of stations in the same region as the forest sites where the growth data was collected. Additionally, the authors formulated their model specifically for use with CACTOS, which requires a great deal of site-specific information (such as site index). Furthermore, CACTOS itself was formulated specifically for growth modeling in Sierran mixed conifer forests, and may not be appropriate for use in other forest ecosystems.

Like Yeh and Wensel, dendrochronology also recognizes that growth signals due to climate are separate from those due to biological or edaphic factors. While Yeh and Wensel developed a climate signal model for use in addition to an existing, site-specific biological model (CACTOS), dendrochronology uses a different approach. Dendrochronology assumes that raw increment growth can be separated into two signals: growth due to climatic factors, which may be highly variable from year to year, and growth due to biological factors, which may change slowly to reach a stationary mean level (Cook and Peters 1981). In this way, low frequency signals (biological) can be subtracted from the total growth signal to leave only the high frequency signal (climate). This method is known as the "smoothing spline" (Cook and Peters 1981). The smoothing spline is widely useful, as it can be applied to any tree species that records produces annual rings.

If both the Yeh and Wensel and smoothing spline models are used to estimate climate signals using real data, and these two signals are significantly correlated, then site-specific growth and yield models such as CACTOS would not be necessary for more general growth projections. Yeh and Wensel's model alone would prove accurate and reliable for a wide range of forest types, as well as some management options.
Different crown classes of trees may respond differently to climate variations. The levels of precipitation received by understory trees, for example, may be a direct result of levels intercepted by overstory trees. No existing models to date, including Yeh and Wensel's model, CACTOS, or the smoothing spline, address the potential differences in climate growth response among different crown classes within the same species.

This study tests the following hypotheses: 1) Using the smoothing spline as a testing model, how accurate and useful is Yeh and Wensel's growth model (for both "pine" and "other species" versions?) Evidence of the validity of this model would be a statistically significant, positive correlation (at a 95% level) between the smoothing spline climate signal and Yeh and Wensel's climate signal, across several species. 2) How does climate affect the growth of different crown classes of the same species? It is hypothesized that the dominant trees would determine the growth response of the subdominant trees along a gradient, with the suppressed and understory trees being the most dramatically affected by climate variation. Evidence of this would be a statistically significant, negative correlation (at a 95% level) between the growth of the dominant trees and the growth of other crown classes, with the least dominant classes showing the most negative correlation.

SITES

Data for this study was collected at Blodgett Forest Research Station (BFRS) in El Dorado County, on the western slope of the Sierra Nevada mountain range in northern California (38° 52′ N; 120° 40′ W). The BFRS central property consists of 1,219 ha (3,011 ac) of

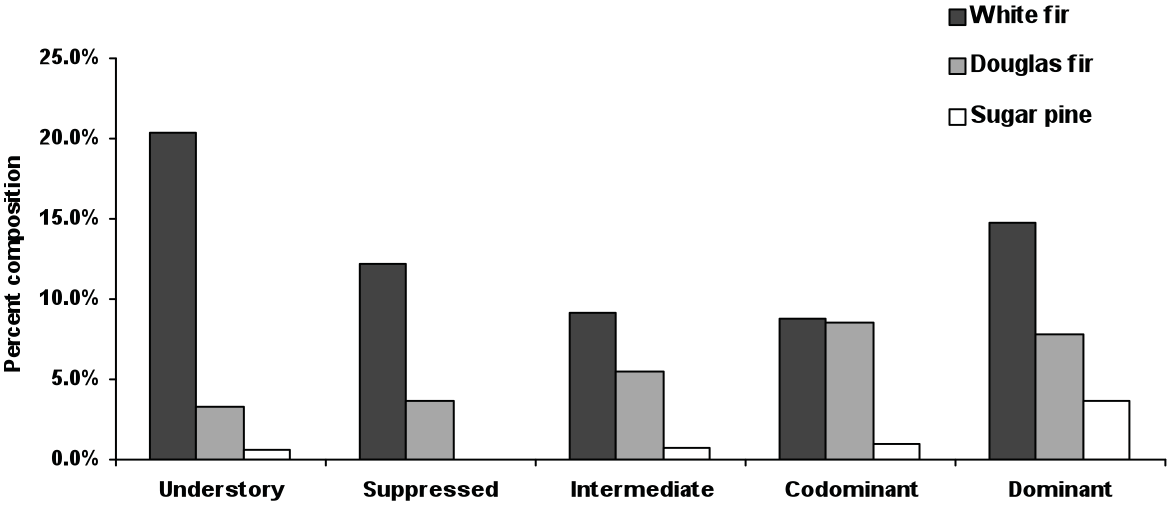

Figure 1: Forest composition of Blodgett Forest Research Station reserve stands by size class. Only three species specific to this study (white fir, Douglas-fir, and sugar pine) are included.

Crown Class	*Total number of trees*	*Mean DBH(cm)*	*DBH range (cm)*	*Mean height (m)*	*Standard Error of height (m)*
Understory	125	5.65	0.0 – 11.91	2.7	0.36
Suppressed	82	11.5	11.92 – 19.56	9.1	0.59
Intermediate	80	19.33	19.57 – 33.0	15.2	1.0
Codominant	95	23.88	33.1-50.8	24.7	1.6
Dominant	136	48.0	>50.8	38.1	1.5

Table 1: Mean height, diameter at breast height (DBH), and range of height by crown class for all species.

mixed conifer forest divided in 109 management compartments (size range: 8–80 ha [20-198 ac]). The mixed conifer forest type is composed of variable proportions of *Abies concolor* (white fir), *Pseudotsuga menziesii* var. *menziesii* (Douglas-fir), *Pinus lambertiana* (sugar pine), *Pinus ponderosa* (Pacific ponderosa pine), *Calocedrus decurrens* (incense cedar), and *Quercus kelloggii* (California black oak) (Battles *et al*. 2006). All species of the Sierra mixed conifer forest type are represented at BFRS.

The terrain in Blodgett Forest is flat or gently sloping and elevation varies from 1,188 m to 1,463 m (3,898 ft to 4,800 ft). The climate is characterized by cool, wet winters and warm, dry summers. Mean annual precipitation is 158 cm (62.2 in); 78% falls between November and March, 35% as snow. The mineral soil is a well-drained, sandy loam that supports a productive site in terms of tree volume growth. Between 1900 and 1913, most of the Forest was logged and then burned to reduce logging slash. The University of California, Berkeley, has operated Blodgett Forest as a research and teaching facility since 1933.

GROWTH

For this study, data was collected in the reserve stands of BFRS, located at compartments 292, 160, and 220. The reserve stands have remained unmanaged since 1913, with the exception of fire suppression. Forest composition by species and size class for compartments 220, 292 and 160 is well mixed, with white fir comprising the most understory and dominant trees (Figure 1). Crown classes were determined using BRFS forest inventory protocol. Average height and average diameter at breast height (DBH) of understory class is 2.7 m (8.9 ft) and 5.65 cm (2.24 in), respectively; average height and average DBH of the dominant class is 38.1 m (125.0 ft) and 48 cm (18.9 in) respectively (Table 1). In terms of basal area, white fir and incense cedar are the most abundant species in the stands (Table 2).

The radial increment growth data used in this study was collected for a related study designed to predict the likelihood mortality (Das *et al*. 2007). In the mortality study, live tree increment cores were

Species	Percent of total basal area (total = 104.8 m^2/ha)
White fir	26%
Douglas-fir	18%
Sugar pine	10%
Ponderosa pine	16%
Incense cedar	25%

Table 2: Relative dominance all five species present in the reserve stands of Blodgett Forest Research Station.

collected to match a sample of cores taken from dead trees, but were otherwise collected without bias. (See discussion for more details on potential biases). The minimum tree sizes included in this analysis were at least 1.37 m (4.5 ft) in height.

All cores were collected on the sides of the tree parallel to the slope of the plot, generally below 1m (3.28 ft) in height and above any basal swell. For live trees greater than 60 cm (24 in) DBH, two samples were collected from opposite sides of the tree. The two cores from the larger trees were used in developing the master chronology for the species at the site. For all other trees, at least one good core was obtained. Cores were sanded until individual cells were visible under magnification.

Tree rings were then measured to 0.01 mm (3.9 x 10-3 in) using a dissecting microscope and a sliding stage micrometer. Master chronologies were built for each species using all live trees greater than 60 cm (24 in) DBH with the aid of COFECHA (Grissino-Mayer 2001). Errors (missing or false rings) were then identified in the remaining cores by comparing them against the chronology using COFECHA (Grissino-Mayer 2001). Corrections were made after errors were confirmed by visual inspection of the core. This check was done for all cores that could be cross-dated.

The growth data was analyzed for years 1964-2003, for all trees with growth data for every year. Trees with missing increment data for any of those years were excluded from this study. The total trees analyzed included 91 white fir from compartment 220, 55 Douglas-fir from compartment 220, and 67 sugar pine (12 from compartment 220, 42 from compartment 229, 3 from compartment 160).

Yeh and Wensel (2000) hypothesized that the climate parameters most influential in predicting annual increment growth included winter precipitation and summer temperature from the current and previous climate year. Yeh and Wensel (2000) provide a more detailed description of why those variables are thought to be the most important predictors of climate signals. Briefly, temperature is an indicator of the amount of solar radiation energy available to the trees, as well as enhanced levels of evapotranspiration in forest ecosystems. Precipitation determines the amount of moisture available to trees in the soil. Water stress, therefore, is the primary driver of tree growth; this fact is accounted for in Yeh and Wensel's model (Table 3). Based on the period of water supply for trees in mixed conifer forests, Yeh and Wensel defined the winter season as October through February, and the summer season as June through September. The "climate year" is therefore the water year of California: October through September. Seasonal precipitation is the total precipitation over the months in a season, and seasonal mean temperature is the average mean temperature over the months in one season.

Climate Data

The BFRS weather station is centrally located on the BFRS property, and has been recording daily precipitation and temperature data since 1961. Temperature data for months June through September, for years 1964 through 2003, were obtained from the on-site BFRS weather station. Where the temperature data were missing from the record (i.e. was not recorded due to a technical error), supplemental temperature data were obtained from the Parameter-elevation Regressions on Independent Slopes Model (PRISM), which uses real measurements of precipitation and temperature to produce continuous estimates of climatic parameters (http://www.prism.oregonstate.edu/). Eleven out of the total 468 months evaluated required estimated temperatures from PRISM, resulting in 2.3% temperature data extrapolation.

Precipitation data for the months October through February, for years 1964 through 2003, were obtained from the same BFRS weather station. No precipitation data were missing for these years.

MODELS AND METHODS

Once growth and climatic data were obtained, Yeh and Wensel's model could be validated using increment cores and on-site weather data. First, climatic data was applied to Yeh and Wensel's model to generate a predicted climatic response signal:

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

Where R_{it} is the radial growth residual due to climate of tree *i* at time *t*; β_{i0}, β_{i1}, β_{i2}, β_{i3}, and β_{i4} are estimated coefficients for tree *i*; $P_{1,t}$ is seasonal winter precipitation in the current year; $T_{1,t}$ is the seasonal mean summer temperature in the current year; $P_{2,t-1}$ is seasonal winter precipitation in the previous year; $T_{2,t-1}$ is the seasonal mean summer temperature in the previous year; and ε_{it} is the error term of the model. The coefficient values β_{i0}, β_{i1}, β_{i2}, β_{i3}, and β_{i4} are shown below in Table 3. The values show the relatively greater negative effect of extreme temperature on growth, compared to precipitation.

To test Yeh and Wensel's model, a different approach was used to estimate the climatic signal. As previously mentioned, raw increment growth can be separated into climatic and biological growth signals. Once biological growth is removed, only growth variance due to climate should remain. This is achieved by subtracting biological growth from the total increment growth (see Figure 2). Instead of using CACTOS to remove this signal, as did Yeh and Wensel, a more generalized model was used to see a) if Yeh and Wensel's predictive series would accurately predict real growth trends in the past, and therefore reliably predict future estimates, and; b) if Yeh and Wensel's predictive series can still be widely useful in forest ecosystems where detailed growth and yield models like CACTOS are unavailable.

	b0	*b1*	*b2*	*b3*	*b4*
Pine Group	0.00685	0.00238	-0.03463	0.00200	-0.02386
All Other Species	0.00055	0.00238	-0.08258	0.00200	-0.02386

Table 3: Yeh and Wensel (2000) estimated coefficient values of the climatic response models for each species group.

For this study, the smoothing spline (Cook and Peters, 1981) was used to generate biological response signals. The smoothing spline approximates growth rates of low variability over time, as a centrally weighted, moving average. It is useful for modeling biological response signals, as it was developed to approximate functions that are disjointed or episodic – just like tree growth over time.

To initially test Yeh and Wensel's model, data from white fir was used, as the data set for white fir better represented a range of crown classes than Douglas-fir or sugar pine. Climatic data was applied to Yeh and Wensel's "Other Species" model (Table 3), generating the predicted climate signal for years 1964-2003. For the testing series, raw increment growth and the smoothing spline were used to approximate the biological growth response. The smoothing spline data was subtracted from the total increment growth data. The result was the testing climatic response for all white fir trees and all years, 1964-2003. This result was averaged yearly for all trees to get a general idea of how well the testing series correlated with Yeh and Wensel's predicted climatic signal (R_{it}) for white fir in years 1964-2003. This test was then applied to Douglas-fir and sugar pine, to determine if Yeh and Wensel's model remained accurate for other species.

The testing series (white fir) was stratified into crown classes, in order to view the predicted and testing climatic signals of understory, suppressed, intermediate, codominant, and dominant trees of the same species. Climatic response data for each crown class (averaged for each year) were normalized so that all data was directly comparable. (Normalization is the difference between the grand mean of all years and each year, to examine variation from average).

To examine the relationship between various crown classes, all classes for which there were sufficient data were correlated against that of the dominant crown class, to determine if the growth of each crown class was negatively correlated with that of the dominant class. This was done using both total increment data, and biological data alone.

Total increment growth data were separated by crown class, averaged for each year, normalized, and correlated against total increment growth of the dominant crown class.

When it was determined that the correlation of growth and climate was weaker for the sub-dominant trees, it was thought that perhaps competition with the dominant trees was driving the growth response, rather than climate. To test this hypothesis, biological response data alone were separated by crown class, normalized, averaged for each year, and correlated against the bio-

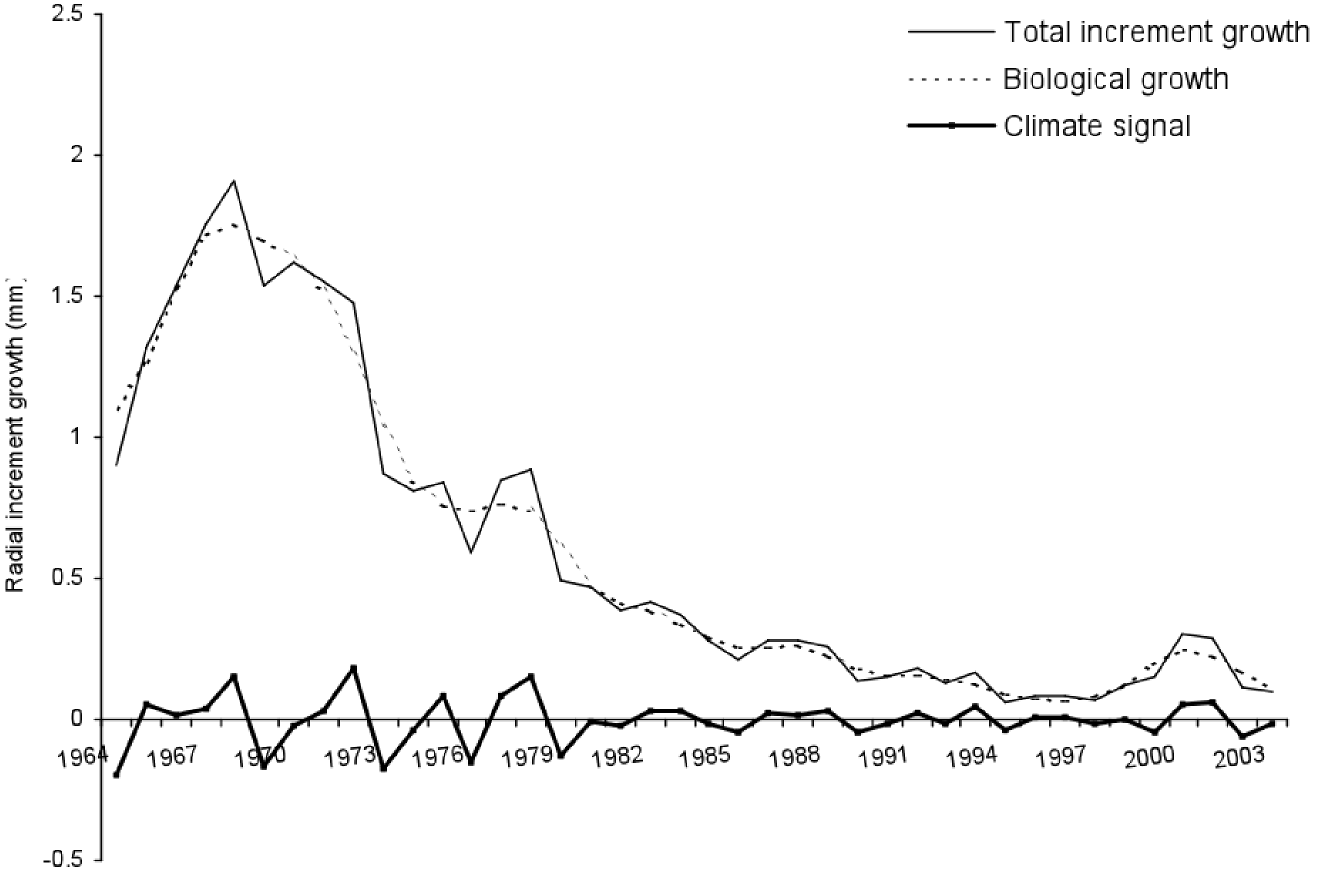

Figure 2: An example of the testing climate signal, approximated by subtracting the biological data (approximated by the smoothing spline) from total radial increment growth. Growth data shown here is from a dominant Douglas-fir tree.

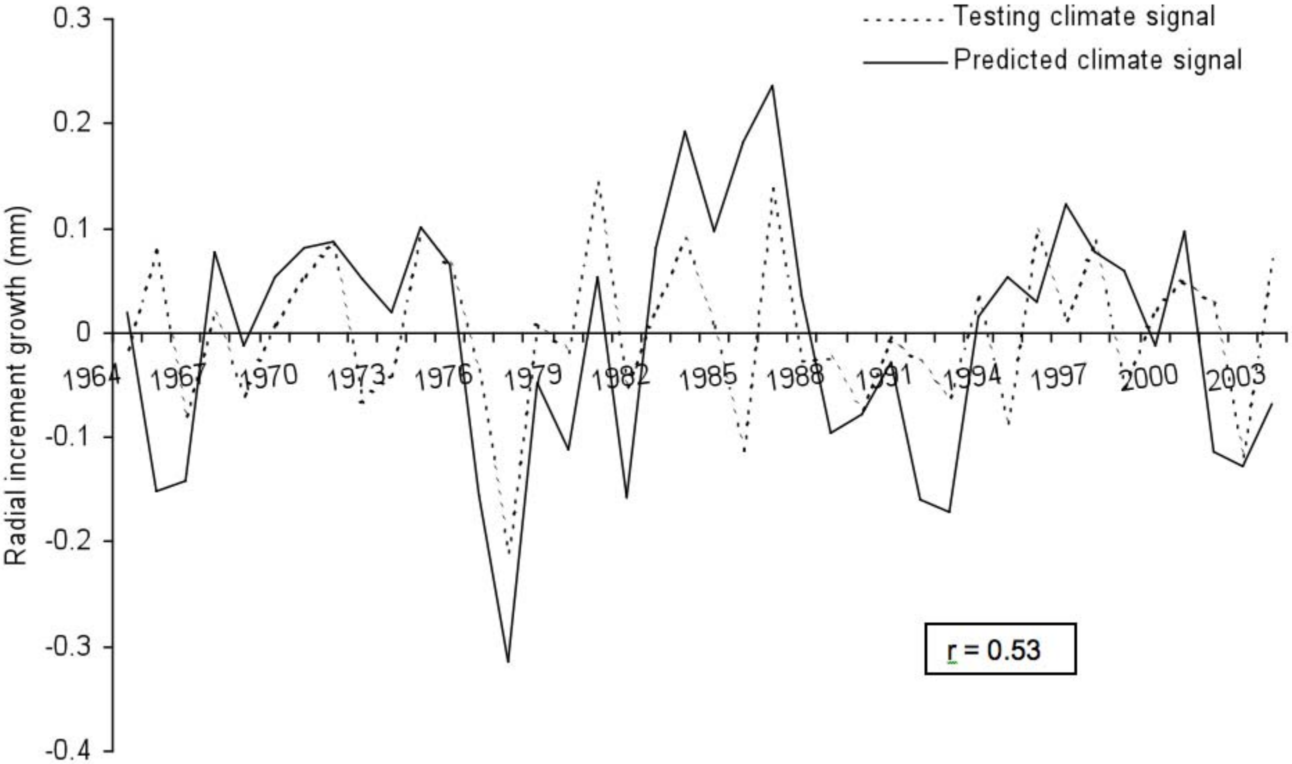

Figure 3: The predicted climate signal (from Yeh and Wensel) and testing climate signal (from the smoothing spline) for all white fir trees, all crown classes, years 1964-2003. The predicted and testing series show an overall correlation of 0.53.

Species	n	r	t	p
White fir	91	0.534	5.90	<0.001
Douglas-fir	67	0.408	3.20	<0.001
Sugar pine	55	0.407	3.58	<0.001

Table 4: Correlation coefficients and levels of significance of predicted average growth for white fir, Douglas-fir, and sugar pine, and the testing residuals. In this table, t is the t statistic, and p is the probability that one would observe these results by chance if the test were run infinitely.

Species and size classes	R value
White fir	
Understory	-0.182
Suppressed	0.213
Intermediate	0.259
Codominant	0.412
Dominant	0.584
Douglas-fir	
Intermediate	0.149
Codominant	0.227
Dominant	0.387
Sugar pine	
Codominant	-0.093
Dominant	0.406

Table 5: Correlation coefficients of predicted average growth for different crown classes of white fir, Douglas-fir and sugar pine, and their respective testing residuals.

logical response data of the dominant class, to determine if the growth response variation was largely due to biological and edaphic factors alone.

Finally, all tests with respect to crown class were performed for Douglas-fir and sugar pine, to determine how climate affects the growth signals of their respective crown classes. It should be noted that the growth data for Douglas-fir and sugar pine did not reflect as complete a representation of various crown classes as did that of white fir.

To test the signficance of correlation, the Pearson correlation was used to determine the measure of strength of relationship between two variables, and probability levels were determined to estimate the significance of those relationships.

RESULTS

Yeh and Wensel's model was a reliable predictor of the overall climate response for the testing series, white fir (Figure 3, Table 4) as well as Douglas-fir and sugar pine (Table 4). Points of reference include the year 1977, the driest year in recorded hydrologic history (http://watersupplyconditions.water.ca.gov/factsheet.cfm), and 1983, a significant wet year (http://watershed.org/news/win_91/rainfall.html). These reference years help demonstrate visually the relative reliability of Yeh and Wensel's model.

The climate responses of the dominant crown classes were positively correlated to the predicted response (Figure 4), while the sub-dominant crown classes were weakly or negatively correlated (Table 5), indicating that growth of the sub-dominant crown classes was less impacted by climatic factors. While the trend seen among the various crown classes of Douglas-fir and sugar pine was similar to that of white fir, the patterns are not as striking.

The correlation of total increment growth signals of all crown classes to the dominant class signal was more positive for the dominant crown classes than the sub-dominant crown classes (Table 6). The same trend was found in comparing biological growth signals (Table 7). There was insufficient data to report for all crown classes of sugar pine.

DISCUSSION

The testing of Yeh and Wensel's model and the questions investigated thereafter lead to the following conclusions: (*i.*) There was a statistically significant, positive correlation (at the 95% level) for the white fir predicted and testing data, as well as for Douglas-fir and sugar pine species, verifying that Yeh and Wensel's model is accurate and reliable. (*ii.*) The relationship between climate and growth is stronger in dominant crown classes, indicating that climate more predictably affects dominant trees. (*iii.*) The growth response of the sub-dominant crown classes was not negatively correlated with that of the dominant crown class, indicating that there is no significant relationship between the climate and biological growth of dominant trees and that of suppressed or understory trees. It does not appear that competition between dominant and sub-dominant trees, rather than climate, determines the growth of suppressed or understory trees; instead, microclimate may be the most important driver of sub-dominant tree growth.

1) Since the testing data was strongly and sig-

Species	Suppressed	Intermediate	Codominant
White fir	0.088	0.609	0.862
Douglas-fir	0.371	0.527	0.900
Sugar pine	-	-	0.813

Table 6: Correlation coefficient for normalized total increment growth for three crown classes and normalized total increment growth for the dominant crown class, years 1964-2003.

Species	Suppressed	Intermediate	Codominant
White fir	-0.007	0.682	0.886
Douglas-fir	0.368	0.630	0.920
Sugar pine	-	-	0.912

Table 7: Correlation coefficient for normalized biological growth for three crown classes and normalized biological growth for the dominant crown class, years 1964-2003.

nificantly correlated to the predicted data, Yeh and Wensel's model is reliable and can be used for a wide variety of management applications. This model is not data-intensive, unlike previous models; the only data required are temperature and precipitation. Even without an on-site weather station, climate data can be obtained online through programs such as PRISM (http://www.prism.oregonstate.edu/). Futhermore, if the expected climate response of a forest is known, forest management can be handled more effectively by controlling for other factors which, unlike climate, are feasible to manipulate, such as fire regime, stand density, and species composition.

The correlation of the testing sugar pine data with Yeh and Wensel's pine model was not as strong, though still statistically significant. It is possible that the pine model incorrectly assumed pine species are less disadvantaged than "other species" by summer temperature (Table 3), and therefore predicted less of a climatic response than was observed. There is conflicting literature on the response of pine species to unfavorable climatic conditions. It was suggested by Phipps (1982) that shade-tolerant species (such as white fir) are more sensitive to climatic variation than other species. However, Orwig and Abrams (1997) found that Virginia pine (*Pinus virginiana*) was the least impacted by drought on dry-mesic sites, but more impacted than other species on mesic sites, indicating that location is a major factor in growth response. More likely, the weaker correlation is due to a data deficiency in this study. Since the increment data was obtained from a previous mortality study, a wide range of crown classes for sugar pine was not available. As such, only codominant and dominant crown classes were used to approximate the testing data. It does seem like this should bias the study toward a more positive correlation, since it was shown that dominant trees track climate more accurately; however, Yeh and Wensel's model was developed using a wider range of crown classes that included sub-dominant trees, and this may explain the difference in correlation.

Yeh and Wensel (2000) cover the limitations of this model in depth in their study. Briefly, the potential problems in applying this model widely are: (*i.*) the model assumes the affect of climate on growth to be linear, when it is possible that it is asymptotic. For example, as precipitation declines, growth may reach a minimum level, beyond which the tree will not survive. These kinds of ecological responses are not accounted for in the model. (*ii.*) The model does estimate growth stress due to unfavorable climate, but does not estimate mortality. The stress from unfavorable climate may render the trees unable to defend against pests and pathogens (Battles *et al*. 2006) and cause mortality, where Yeh and Wensel's model would predict recovery in the following year.

2) The results indicate that climate more predictably affects dominant class trees. This conclusion is also met by a large body of conflicting literature. It has been demonstrated in several studies that understory trees are much more responsive and vulnerable to climatic stressors than dominant trees (Pichler and Oberhuber 2007, Orwig and Abrams 1997, Abrams and Mostoller 1995, Hanson and Weltzin 2000). Some of the literature indicates that dominant trees are more susceptible to climatic stressors due to greater losses during evapotranspiration (Thompson and Hinckley 1977, Liu and Muller 1993). There are still further

studies that suggest light, and not climatic factors, seems to be the most important determinant of sub-dominant tree proliferation (Coomes and Allen 2007, Drobyshev and Nihlgard 2000).

One explanation for this result may be that the dominant trees are "favorably positioned" and as such have access to a larger portion of available precipitation. Because of this access, dominant trees are more vulnerable to significant changes in total precipitation, whereas suppressed or understory trees may not experience these fluxuations, as precipitation has already been mostly sequestered by dominant trees (Wensel and Turnblom 1988).

Since Yeh and Wensel collected growth data representative of a range of crown classes for their study, it seems unlikely that these data are biased due to error in the model. Therefore, the data in this study only support the fact that crown class dynamics are complex and likely involve many climatic, biological and edaphic factors.

Despite the conflicting literature, it can be assumed for this study that Yeh and Wensel's model is more reliably accurate at predicting growth of dominant trees than sub-dominant trees. In terms of management, this may mean that Yeh and Wensel's model is useful for predicting the growth of dominant trees within stands (example: trees left in shelterwood management practices), and not as useful for other applications, such as predicting growth of even-aged stands or plantations. It may also not apply to stands that have been heavily managed, as the testing climate signal was generated using data from a totally unmanaged stand.

3) Neither the total nor biological growth signals of the sub-dominant crown classes followed the dominant class signals. This was explored after discovering that the climate signal of sub-dominant crownsize classes did not follow the predicted climate signal as well as the dominant class. It was thought that if the climatic signal of the dominant class was not driving the growth of the sub-dominant trees, perhaps the biological signal alone (more precisely, competition) could explain the trend. In running this test, it was expected that the biological growth of the dominant and sub-dominant trees would show an inverse relationship, due to the dominant trees' better access to light and nutrients. This was not the case. The sub-dominant crown classes did not appear to be influenced, inversely or otherwise conclusively, by any growth signal of the dominant class. It seems, then, that microclimate is the most important determinant of sub-dominant tree growth, as supported by the conflicting literature in (2). This may include susceptibility to shading, desiccation, and nutrient availability, all which may occur in varying degrees from one small tree site to the next. This conclusion is also supported by Nick Brown in his study, who said that whether a smaller tree survives depends on "its reaction to a whole sequence of unpredictable microclimatic events" (Brown 1993).

Acknowledgments

The author would like to thank John Battles for his patience and exhaustive guidance in all aspects of this study, Adrian Das and the good people of Blodgett Forest Research Station for data, Battles Lab graduate students for the admittance into their territory, and Jordan Wolfe and Morgan Trieger for their very necessary encouragement.

REFERENCES

Abrams, M.D., Mostoller, S.A. 1995. Drought-year gas exchange, leaf structure and nitrogen in contrasting successional tree species in high and low light environments. Tree Physiol 15:361–370

Battles, J. J., T. Robards, A. Das, K. Waring, J. K. Gilless, F. Schurr, J. LeBlanc, G. Biging, and C. Simon. 2006. Climate Change Impact on Forest Resources. Public Interest Energy Research, California Energy Commission. CEC-500-2005-193-SF.

Belcher, D.M., Holdaway, M.R., and Brand, G.J. 1982. A description of STEMS—the stand and tree evaluation and modeling system. USDA For. Serv. Gen. Tech. Rep. NC-79.

Brown, N. 1993. The implications of climate and gap microclimate for seedling growth conditions in a Bornean lowland rain forest. Journal of Tropical Ecology 9:153-168.

California Department of Water Resources. *California Drought*. 8 December 2007. <http://watersupplyconditions.water.ca.gov/factsheet.cfm>

Cook, E.R., and Peters, K. 1981. The smoothing spline: a new approach to standardizing forest interior tree-ring width series for dendroclimatic studies. Tree-Ring Bull. 41: 45–54.

Coomes, D. and Allen, R. 2007. Effects of size, competition and altitude on tree growth. Journal of Ecology 95: 1084-1097.

Drobyshev, I., and Nihlgård, B. 2000. Growth response of spruce saplings in relation to climatic conditions along a gradient of gap size. Can. J. For. Res. 30: 930–938.

Field, C.B., G.C. Daily, F.W. Davis, S. Gaines, P.A. Matson, J. Melack, and N.L. Miller, 1999. Confronting climate change in California: Ecological Impacts on the Golden State. Union of Concerned Scientists, Cambridge, MA and Ecological Society of America, Washington D.C.

Goodridge, Jim. *One Hundred Years of Rainfall Trends in California*. 8 December 2007. <(http://watershed.org/news/win_91/rainfall.html>

Grissino-Mayer, H.D. 2001. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. Tree-Ring Research 57:205-221.

Hanson, P.J., J.F. Weltzin. 2000. Drought disturbance from climate change: response of United States forests. The Science of Total Environment 262: 205-220.

Hayhoe, K., D. Cayan, C. B. Field, P. C. Frumhoff, E. P. Maurer, N. L. Miller, S. C. Moser, S. H. Schneider, K. N. Cahill, E. E. Cleland, L. Dale, R. Drapek, R. M. Hanemann, L. S. Kalkstein, J. Lenihan, C. K. Lunch, R. P. Neilson, S. C. Sheridan, and J. H. Verville. 2004. Emissions pathways, climate change, and impacts on California. Proceedings of the National Academy of Sciences of the United States of America 101: 12422–12427.

Lenihan, J. M., R. Drapek, D. Bachelet, and R. P. Neilson. 2003. Climate change effects on vegetation distribution, carbon, and fire in California. Ecological Applications 13: 1667–1681.

Das, A., J. J. Battles, N. L. Stephenson, and P. J. van Mantgem. In review. A dendroecological approach to understanding tree mortality: A study of two tree species in the Sierra Nevada.

Liu, Y., Muller, R.N. 1993. Effect of drought and frost on radial growth of overstory and understory stems in a deciduous forest. Am Midl Nat 129:19–25

Oregon State University. *PRISM Group.* 6 May 2007. July 2007. <http://www.prism.oregonstate.edu/>

Orwig, D. A, and M. D Abrams. 1997. Variation in radial growth responses to drought among species, site, and canopy strata. Trees 11:474–484.

Phipps, R.L. 1982. Comments on interpretation of climatic information from tree rings, eastern North America. Tree-ring Bull 42:11–22

Pichler, P. and Oberhuber, W. 2007 Radial growth response of coniferous forest trees in an inner Alpine environment to heat-wave in 2003. Forest Ecology and Management 242:2, 688-699.

Thompson DR, Hinckley TM (1977) Effect of vertical and temporal variations in stand microclimate and soil moisture on water status of several species in an oak-hickory forest. Am Midl Nat 97:373–380

Wensel, L.C., and Biging, G.S. 1988. The CACTOS system for individual-tree growth simulation in the mixed conifer forests of California. In Forest growth modeling and prediction. Vol. 1.Edited by A.R. Ek, S.R. Shifley, and T.E. Burk. USDA For. Serv. Gen. Tech. Rep. NC-120. pp. 175–183.

Wensel, L.C. and Turnblom, E.C. 1998. Adjustment of estimated tree growth rates in northern California conifers for changes in precipitation levels. Can. J. For. Res. 28: 1241–1248.

Wykoff, W.R., Crookston, N.L., and Stage, A.R. 1982. User's guide to the PROGNOSIS model. USDA For. Serv. Gen. Tech. Rep. INT-133.Stage, A.R. 1973. PROGNOSIS model for stand development. USDA For. Serv. Res. Pap. INT-137.

Yeh, H-Y., and L. C. Wensel. 2000. The relationship between tree diameter growth and climate for coniferous species in northern California. Canadian Journal of Forest Research 30: 1463–1471.