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Relations of Climate and Radial Increment of Western Hemlock in an Old-growth Douglas-fir Forest in Southern Washington

Abstract

The objective of this study was to examine the association of western hemlock (*Tsuga heterophylla*) growth to climate across structural levels in an old-growth forest. The canopy vertical gradient was sectioned into six 10-m height classes with western hemlock growth examined in the top five levels. All trees in a 4.0 ha plot (n = 645), greater than 15cm diameter at breast height (DBH) were cored for the recent 20-year growth record. Growth chronologies representing each height class were correlated to 10 climatic variables. The 40-50m height class exhibited the highest correlations to climate and the 10-20m height class exhibited the lowest. When moving averages of 3 and 5 years were applied to the growth index and climatic variables, the correlations of height class one (10-20m) became the strongest suggesting that growth of canopy dominants is determined by short term climatic conditions while understory growth was influenced by longer term climatic conditions. Understory growth at the 5-year temporal scale was strongly ($-0.6 > R < -0.8$) and negatively correlated to temperature while its correlation to precipitation was strongly positive. The annual depth of snow at the 5-year time scale was the only climatic variable to affect growth similarly for all height classes, indicating consecutive years of deep snow had a negative impact upon western hemlock productivity.

Understanding effects of canopy structure upon the relationships between climate and tree growth can improve interpretation of past climatic conditions and stand dynamics from long tree cores. The climatic signal for stand chronologies that experienced suppression or competition could be adjusted for typical changes that occur with tree ascension to canopy dominance. Current uses of universal climate-growth relationships in forest ecosystems (e.g., gap family models), especially in structurally diverse old-growth stands, provide a questionable picture of forest growth and dynamics.

Introduction

The relationship between the formation of tree rings and climate is well established and can be used to investigate changing stand conditions related to disturbance, stand development or climatic variation (Fritts 1976, Hughes et al. 1982, Fritts and Swetnam 1989, Brakel and Visser 1996). For example, the climatic record of a drought is commonly found in a tree ring series with the formation of relatively narrow rings (Fritts and Swetnam 1989, Cook and Kairiukstis 1990, Lane 1991). However, growth-limiting factors can be interactive and complex depending upon the variation of environment experienced by a given tree through space (canopy position) and time (maturity or age). By measuring and comparing changes in tree ring characteristics sampled along particular ecological gradients we can gain insights into the interaction of climate and stand structure. An old-growth stand provides the ideal vertical depth required for a clear separation of ecological gradients associated with stand structure. However, the complexity of multiple canopy layers and the scale of heterogeneity characteristic of a temperate old-growth rain forest requires intense and large scale tree sampling (Spies et al. 1990).

Most of the unique compositional and functional attributes of old-growth are derived from their structural characteristics. Stand structure in old-growth includes a wide ranges of tree sizes, deep canopies, and abundant dead wood (Franklin et al. 1981, Smith and Long 1989, Franklin and Spies 1991, Tappeiner et al. 1997). Canopy gaps are a main feature of the canopy layers and contribute greatly to the horizontal and vertical complexity that is found in an old-growth forest stand (Oliver and Larson 1990, Lertzman et al. 1996, Song et al. 1997). Structural understory heterogeneity is closely related to, and highly dependent upon, the architecture of the canopy layers (Song 1998). Since complex structural attributes affect ecosystem functions such as growing conditions, we hypothesized that radial growth response would vary depending on the vertical and horizontal position of a tree in the canopy.

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Earlier dendroecological investigations into the role of climate on the radial growth of the forest stand have been limited to analysis of canopy dominants as it was believed that these trees exhibit the clearest climatic signals and contain the longest records (Fritts 1976, Brubaker 1980). Dendroecological investigations into stand dynamics have been avoided in closed canopy systems because the climatic signal in understory trees was thought to be obscured or weakened by the presence of intense competition. Incorrect estimations of the future effects of climate change and the past interpolations of climatic conditions may occur by assuming a uniform response to climate among all height classes. Understanding the effects of stand structure upon tree growth at all levels of the forest canopy will begin to unravel the complex nature of old-growth function. Given these insights and the lack of research in this area, we attempted to reveal the nature of growth rate and climatic relationships at various height levels.

The objectives of this study were to: 1) examine the correlation of climatic variables to the growth of western hemlock from five height classes over a 20-year period, 2) construct predictive models of growth for each height class using climatic variables, 3) examine the correlations between climate and growth among height classes at the larger temporal scales of three and five years. We hypothesized that growth rates of each height class have unique correlations to climatic variables.

Methods

Study Site

The four-hectare study plot is located in the T. T. Munger Research Natural Area at the Wind River Experimental Forest near Carson, Washington. The plot is in the Wind River valley at 355 m elevation, deep within the southern Washington Cascade Range (45.49° N, -121.58° W). It is located on gentle topography near the base of Trout Creek Hill, an extinct volcanic cone. Soils are coarse textured (Shotty loamy sands and sandy loams) Inceptisols developing in two to three meters of volcanic ejecta over basalt bedrock. A seasonally intermittent stream runs through the center of the study site from west to east. The region is characterized by a climate with wet winters, and dry summers. Annual precipitation is 2528 mm with less than 10% occurring between June and September. Average annual snowfall is 2330 mm. Mean annual temperature is 8.7° C. This 500-year-old forest is dominated by Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*). Other tree species include western redcedar (*Thuja plicata*), Pacific silver fir (*Abies amabilis*), noble fir (*Abies procera*), and grand fir (*Abies grandis*).

Dendroecological Methods and Data Analysis

A tree's canopy position or relative height defines its physiological maturity better than chronological age (Fritts 1976, Kramer and Kozlowski 1979, Cook and Kairiukstis 1990). Therefore, we defined the ecological gradient for analysis along height classes rather than diameter at breast height (DBH) classes. We obtained estimates of height from tree diameter using a non-linear regression model developed by Song (1998) (Figure 1). We then sorted all tree species into six 10-m height classes. Western hemlock was chosen for analysis since it was present in all height classes (Table 1). Height class 2-10m was not core sampled and not included in any analysis. The remaining height classes one, two, three, four, and five represent trees with heights ranging from 10-20m, 20-30m, 30-40m, 40-50m, and 50-60m respectively. Height classes one, two, three, four, and five contain n = 175, 124, 111, 164, and 59 trees, respectively.

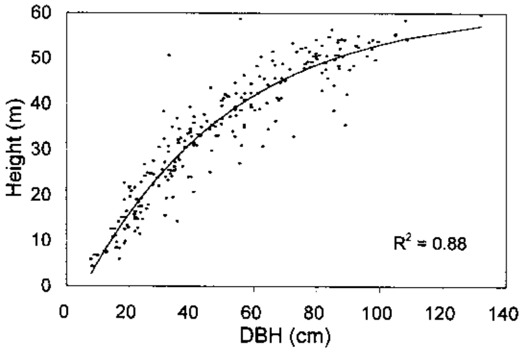

Figure 1. Non-linear regression relationship of western hemlock DBH and height. Model (*Height* = 61.50949137 – 69.5364329 * $e^{(0.02108786 \cdot DBH)}$) has a r^2 = 0.88. Model developed by Song (1998).

We took one increment core from the north face of each live western hemlock tree >15 cm at 1.37m or higher (n = 645) in the 4 hectare study plot. A second core 45 degrees from the first was

TABLE 1. Height class frequency distribution (trees per hectare) of major tree species in an old-growth Douglas-fir forest near the Wind River Canopy Crane research area in south central WA.

Height Class	Pacific silver fir	grand fir	Western red cedar	Douglas-fir	Pacific yew	western hemlock
2-10m	34		4		105	93
10-20m	7	1	2		10	49
20-30m	2	2	1		1	30
30-40m		4	2	1		28
40-50m		2	2	6		42
50-60m		1	1	21		14

taken from 26 trees that had obvious physical damage to the bole face or a rotted core. We took core samples 4-7 cm in length in order to capture at least the last 20 annual growth rings. We sealed the cores in numbered plastic straws and stored them frozen to prevent rotting, breaking, and cracking. We mounted thawed cores on grooved boards for sanding and ease of measurement following the techniques set forth by Stokes and Smiley (1968).

Crossdating is a procedure that insures that each ring increment is placed in its proper time sequence (Fritts 1976). A common crossdating technique is to match ring width patterns in one ring series with ring patterns in an established site chronology. This method was not applied due to the short growth record collected, and lack of conspicuous marker years or width patterns. Crossdating techniques employed in this study consisted of careful inspection of the core samples for signs of false and missing rings (Stokes and Smiley 1968). Samples exhibiting the characteristics of a false ring were removed from the analysis (n = 12). Missing rings, usually due to stress from climate or other factors, can fail to show an early-latewood pattern entirely and must be compared to other samples for confirmation (Stokes and Smiley 1968). Since a site chronology was not established and direct comparison was not possible, missing rings may be present and misrepresenting the true ring series. A recount and comparison of 20% of the core samples was performed in order to insure proper measuring technique and prevent measuring errors such as misalignment of ring widths, inaccuracy, and imprecision. It is assumed that the quantity and intensity of the sampling will average the dating errors caused by only taking one core per tree and not crossdating to a site chronology.

Tree ring widths vary with fluctuations in the environment and systematically with changes in tree age and height. Standardization is required to correct ring widths for the changing age and geometry of the tree; transformed values are ring-width indices (Fritts 1976). Van Deusen (1987) introduced a method of standardization, named "differencing", that requires little subjectivity and can be used to process large numbers of cores automatically.

$$\text{Log}\,[R(t)] - \text{Log}\,[R(t-1)] = \Delta\text{Log}\,[\text{R(t)}] \qquad (1)$$

Where: R = growth increment, t = time (year)

This method creates a first difference by taking the difference of natural log transformation of the growth increment of one year from the previous year. The log transformation puts the ring series on a relative scale. The first difference is a first derivative that can be viewed as a growth rate. The resulting index has a mean of zero and is the relative rate of change in ring width from one year to the next (Van Deusen 1987). Comparing two trees of differing sizes, ages, and growth rates before and after standardization indicates that these effects are removed (Figure 2a and 2b).

For the final step in the data transformation, we averaged the detrended tree ring indices in each height class for each year to produce height class chronologies. This averaging removes the effects of local disturbance, random error and amplifies the climatic signal desired for analysis (Fritts 1976, Cook and Kairiukstis 1990, Van Deusen 1990). To insure that the effects of outliers did not influence the variance and bias of the mean a biweight robust mean procedure, with five

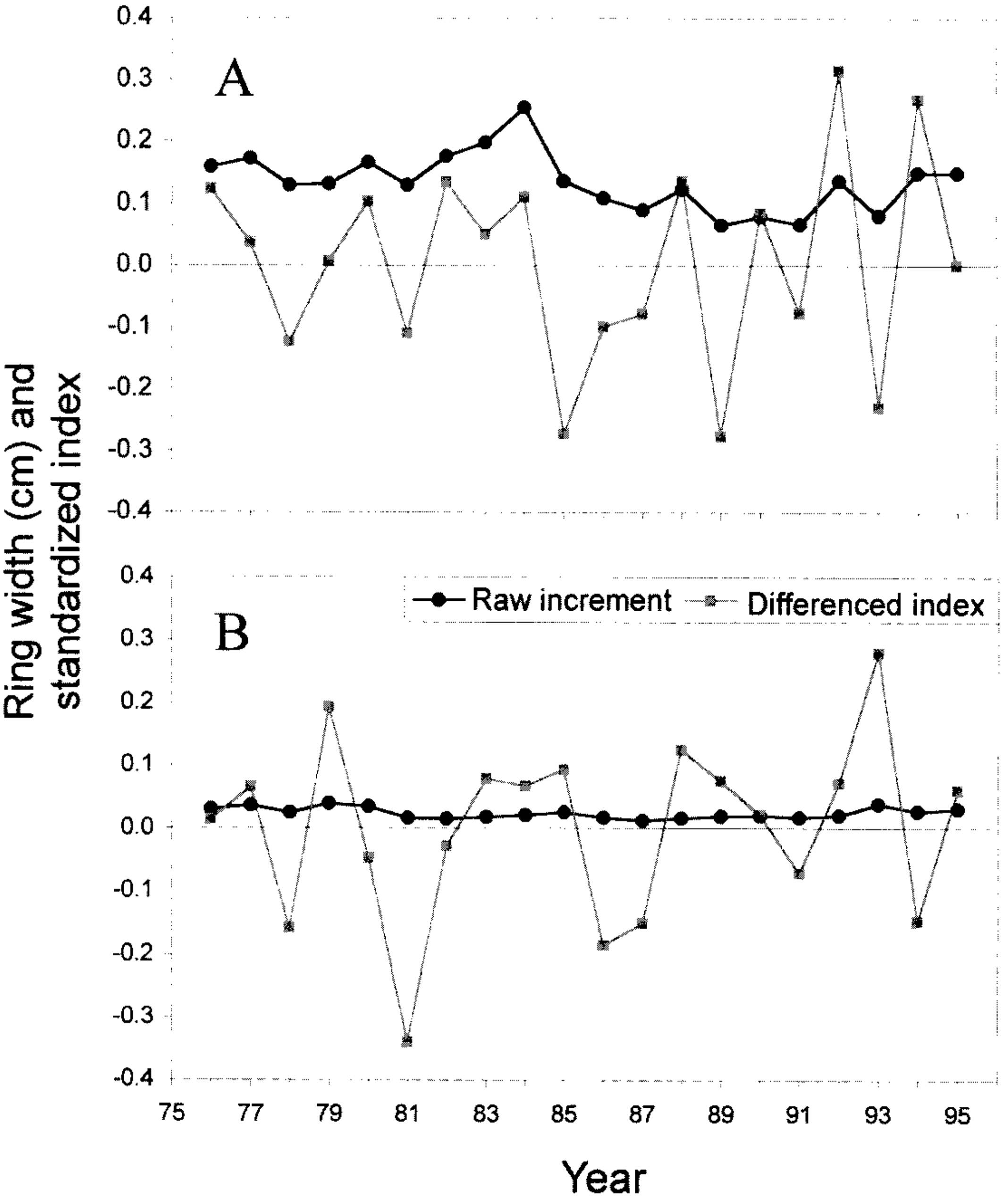

Figure 2. Comparison of standardization effect upon two increment cores from different canopy levels. Standardization effect upon a vigorously growing western hemlock single tree ring series (tree #4374) from the fourth height class (40-50m)(A). Standardization effect upon a complacent or suppressed single western hemlock tree ring series (tree #5156) from height class one (10-20m) (B).

iterations, was used to obtain the final chronologies (Cook and Kairiukstis 1990). The biweight mean procedure was also used to average the raw ring series data for each height class to compare the effects of the standardization and observe ring characteristics within each height class (Figure 3). The comparison of transformed data or chronologies (Figure 4) illustrates the resulting stan-

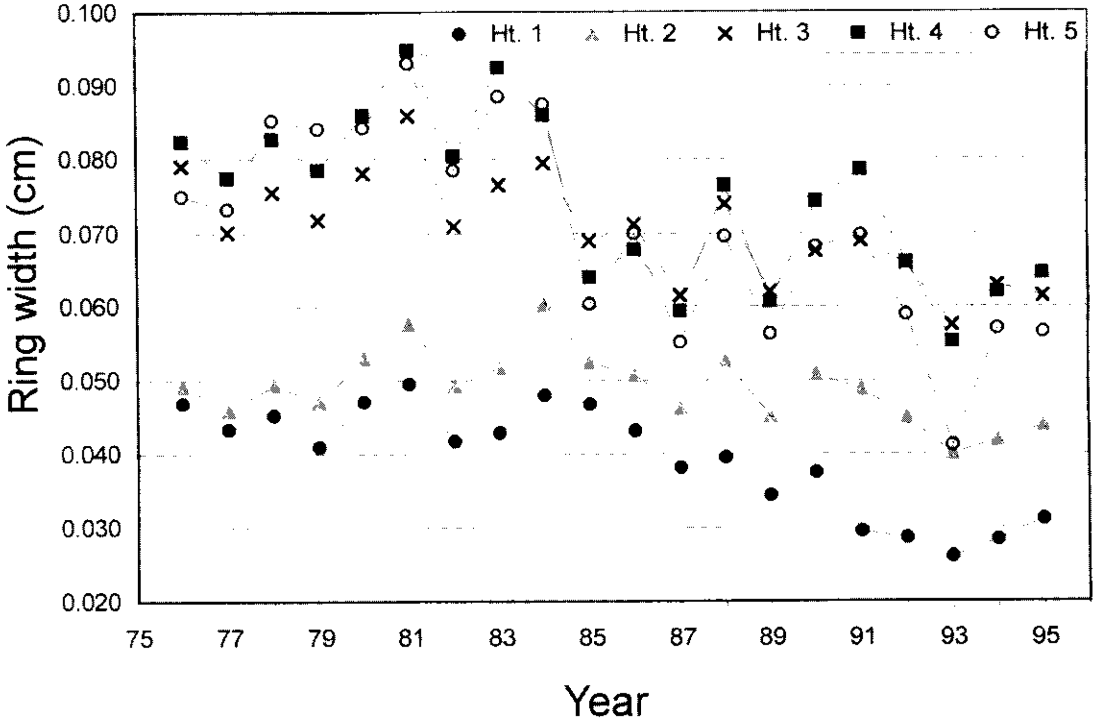

Figure 3. Biweight means for each height class of western hemlock for a 20-year increment record. Data are not transformed and represent actual ring increment widths.

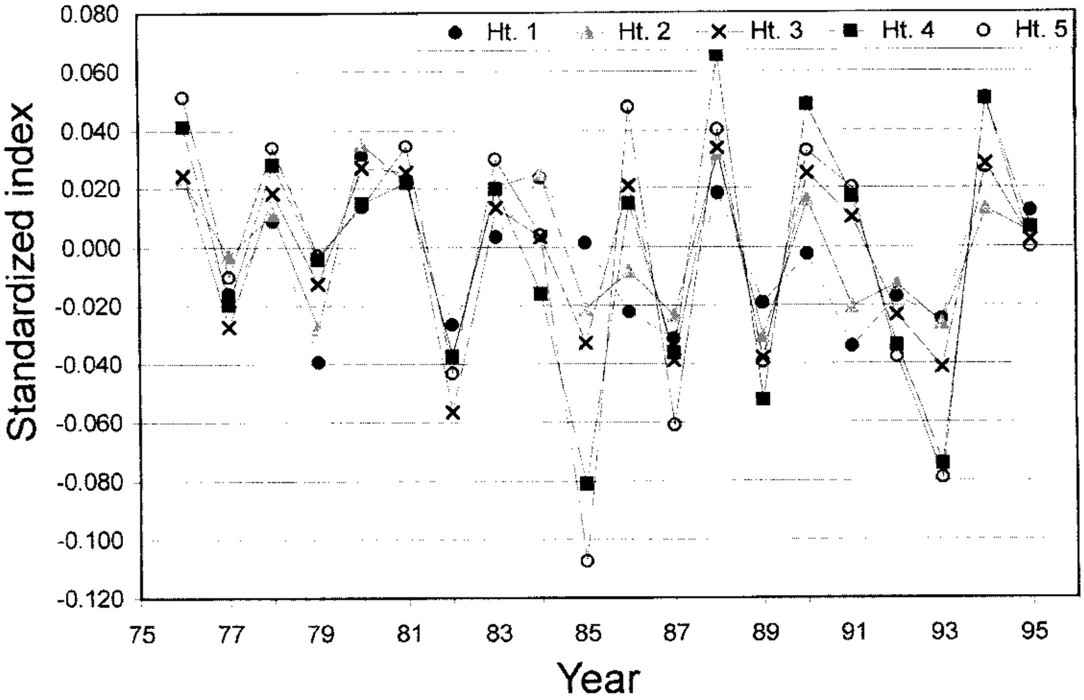

Figure 4. Chronologies for five height classes of western hemlock for a 20 year record. Data are transformed using the standardization technique of "differencing."

TABLE 2. Climatic variables chosen for analysis with height class growth data.

Variable	Description	Rationale
PT9-11	Mean temperature and precipitation September, October and November. Means of parameters were multiplied	These two variables were combined to reveal any interactive effects that may not be revealed in multiple regression techniques. Other combinations of temperature and corresponding precipitation were also investigated, but failed to produce a result of at least intermediate strength ($\|R\| > 0.4$ in any height class).
T9-11	Mean temperature September, October and November	Warmer temperatures during this period may serve to extend the growing season, especially when combined with the termination of the summer droughty season. An extension of favorable conditions for growth should translate into continued photosynthetic activity and cambial expansion.
P9-11	Mean precipitation of September, October and November	The summer dry climate of the Pacific Northwest results in low soil moisture in late summer and reaches its extreme in August. While preliminary investigation revealed poor correlation between summer (July through September) precipitation and growth, the later precipitation during September through November did correlate with growth. Improved soil water status late in the growing season may act to extend the growing season and continue cambial activity and growth.
T7-9	Mean temperature of July, August, and September	Warmer temperatures accelerate cambial cell division and cell expansion is sensitive to warmer than average temperatures during the period of cambial activity. Warm temperatures during this period should enhance the radial increment by increasing rates of cambial activity, cell expansion and photosynthesis (Brubaker et al.1992).
T2-4	Mean temperature of February, March and April	Photosynthetic rates increase in response to rising air and soil temperatures in the spring. Early spring temperature should combine the direct effects of air temperature on photosynthesis as well as the indirect effects of snow melt on the physiological activity of trees (Brubaker et al.1992).
T4	April temperature	See "T2-4".
AT	Mean annual temperature	This variable was retained to provide a baseline of comparison to the aforementioned variables and because of its own significance over the 20 year period
AP	Mean annual precipitation	This variable was retained to provide a baseline of comparison to the aforementioned variables and because of its own significance over the 20-year period.
AS	Mean annual depth of snow	Depth of snow is known to negatively effect growth rates of trees in the Cascade Mountains (Brubaker et. al. 1992; Ettl and Peterson 1995). Deep and lingering snows can delay the onset of cambial activity and hence reduce the growing season.
P-PT9-11	Previous year mean temperature and precipitation September, October and November. Means of parameters were multiplied.	Since it is usually assumed that biological processes cause growth in one year to influence growth in subsequent years, a lag effect from an increased growing season should positively effect the shoot and cambial predeterminism of the subsequent year (Fritts 1976; Hughes et al.1982; Kramer and Kozlowski 1979). Increased photosynthesis late in the growing period may not prolong cambial activity but may instead be stored as simple carbon for the following season. Lag effects for all variables were investigated while "P-PT9-11" was best correlated to tree growth variability.

dardization upon the height class robust means. All regressions and correlations were done using these transformed chronologies.

The choices for the climatic variables (Table 2) are a combination of pre-defined models and correlation analysis. Pre-defined models or variables that have demonstrated effects on growth in past studies restricted the variables entering the analysis to biologically relevant variables that are expected to affect growth (Brubaker et al. 1992). The minimum daily temperature, maximum daily temperature, average daily precipitation and average daily snowfall were obtained for cooperative station #451160 Carson Fish Hatchery (45.54^0 N -121.51^0 W Elev. 345m) and cooperative station #459342 Wind River (45.48^0 N -121.56^0 W Elev. 351m). The data from the Carson Fish Hatchery covered 1977-1996 and data from the Wind River station covered 1975-1976. To fill data gaps of one or two days, we used averages of previous and following days. We filled larger data gaps (whole months) with regression outputs based on regional climatic data. Less than 1% of the climatic data was estimated. We constructed climatic variables by sorting month(s) and parameter(s) of interest and averaging over 20 years. To investigate lag effects of the growth-climate we correlated growth in year *t* with climatic variables from year *t*-1.

The relative correlation strengths of chronology to each climatic variable were determined using Pearson's correlation analysis. Absolute values of correlations to each climatic variable were averaged to obtain a mean correlation for each height class. Moving averages were applied to the climatic variables and used to examine longer wavelengths or lag effects in tree growth-climate relations (Douglas 1936, Fritts 1976). The 3-year moving average removes trends shorter than three years and is used to determine which climatic variables have a long-term influence upon the growth rate differences. Used in a similar fashion, the 5-year moving average affords a longer perspective on the chronology-climate relationships. Pearson's correlation analysis was performed between chronologies and each climatic variable after application of the three and 5-year moving averages.

Multiple linear regression analysis was conducted using SAS and the best final regression models were chosen using two procedures (SAS Institute 1989). The "all possible regressions" procedure was used to choose the best model for growth prediction. The best model or "goodness of fit" was determined with the adjusted coefficient of determination (adj. r^2), and a model bias estimate based on the total mean squared error (Mallow's Cp) (Neter et al. 1996). Stepwise regression, with an entry/exit threshold of P=0.15, was the second technique for choosing the best model. Friedman's test was used to determine whether the correlations for all climatic variables were equal across height classes. Since correlation data for height classes three, four and five failed the Shapiro-Wilks' W test for normality (P=0.008, 0.005, and 0.018, respectively), a non-parametric test was used (StatSoft, Inc 1998). The Wilcoxon matched pair signed rank test was used to investigate significant differences in correlation of growth rate to climatic variables between all pairs of height classes (StatSoft, Inc 1998).

Results

Results of the statistical analysis are separately described in order of Pearson correlation temporal scales followed by regression models selection and nonparametric tests. Chronology correlations without application of a moving average is strongest in the 40-50m height class with a mean correlation of $|R|$ =0.37, and reaches its lowest mean correlation of $|R|$ =0.13 in the 10-20m height class (Table 3). Correlation to "AS" reveals negative correlation for all height classes with the highest correlations from the 50-60m height class (Figure 5a). Height class one shows no correlation ($|R| < 0.2$) to temperature variables (T9-11, T7-9, T4, T2-4, AT) and weak correlation ($0.2 > |R| < 0.4$) to the remaining precipitation variables. While the sign of the Pearson correlations are evaluated,

TABLE 3. Absolute value means of all Pearson correlations ($|R|$) between climatic variables and western hemlock chronologies by height class.2

Height Class	10–20m	20–30m	30–40m	40–50m	50–60m
Mean correlation	0.13	0.23	0.27	0.37	0.34
Mean correlation of 3-year averages	0.44	0.35	0.14	0.29	0.21
Mean correlation of 5-year averages	0.62	0.46	0.25	0.35	0.22

its strengths are considered as absolute values. The 20-30m and the 30-40m height classes are most similar in their correlation response to climatic variables resulting in similar means (0.23 and 0.27 respectively) (Figure 5a). Height class five (50-60m) is moderately correlated ($0.4 > |R| < 0.6$) to variables PT9-11, AT, and AS.

The application of the 3-year moving average dramatically increases correlation strengths for height class 10-20m well into the moderate range ($0.4 > |R| < 0.6$) for all climatic variables except AS and P-PT9-11 (Figure 5b). The negative correlation response by both the 10-20m and the 20-30m height classes are similar for all temperature variables. For remaining height classes three, four, and five, correlation strengths decline for nearly all other comparisons of climate and growth. Means of the 3-year average climatic correlations indicate that those for the 10-20m height class are strongest and those for the 30-40m height class are weakest (Table 3).

The correlations from the 5-year moving average are strong ($0.6 > |R| < 0.8$) for the 10-20m height class for all climatic variables except PT9-11, T2-4, and P-PT9-11 (Figure 5c). Similar to the 3-year moving average the 10-20m and 20-30m height classes are negatively correlated to all temperature variables and have positive correlations to precipitation variables. Strong correlations to AS are found for all height classes except at 40-50m, which was of moderate strength. AS is the only climatic variable which all height classes are compatible in correlation sign and strength (Figure 5c).

Multiple linear regression models indicate the 10-20m height class is least correlated to climate for both model selection procedures (Table 4). The 40-50m height class has the highest coeffi-

TABLE 4. Coefficient of determination (r^2) for each multiple regression modeling approach by height class. "Stepwise" is an automated approach in SAS (SAS institute 1997), "Adjusted r^2/Cp" is selecting the model with the combined most favorable output total. The "Full model" is the output with all ten climatic variables included.

Height Class	10–20m	20–30m	30–40m	40–50m	50–60m
Stepwise	0.19	0.29	0.27	0.38	0.45
Adjusted r^2&Cp	0.16 / 0.06*	0.22 / 0.13*	0.21 / 0.12*	0.38 / 0.31*	0.37 / 0.30*
Full model	0.25	0.35	0.36	0.51	0.46

* Adjusted r^2 of regression model.

TABLE 5. The climatic variables included for two approaches to multiple regression modeling, stepwise selection and an integrated Adjusted r^2 and Cp approach, are given for each height class of western hemlock. Climatic variable definitions can be found in Table 2.

	Height Class									
Climatic	10–20m		20–30m		30–40m		40–50m		50–60m	
variable	Stepwise	Adj. r^2/Cp	Stepwise	Adj. r^2/Cp	Stepwise	Adj. r^2/Cp	Stepwise	Adj. r^2/Cp	Stepwise	Adj. r^2/Cp
PT9-11			X	X			X	X	X	
T9-11					X	X			X	
P9-11	X	X			X	X				
T7-9							X	X		
T4	X		X	X						
T2-4										
AT			X				X	X		
AP										
AS			X	X					X	X
P-PT9-11	X	X			X				X	X

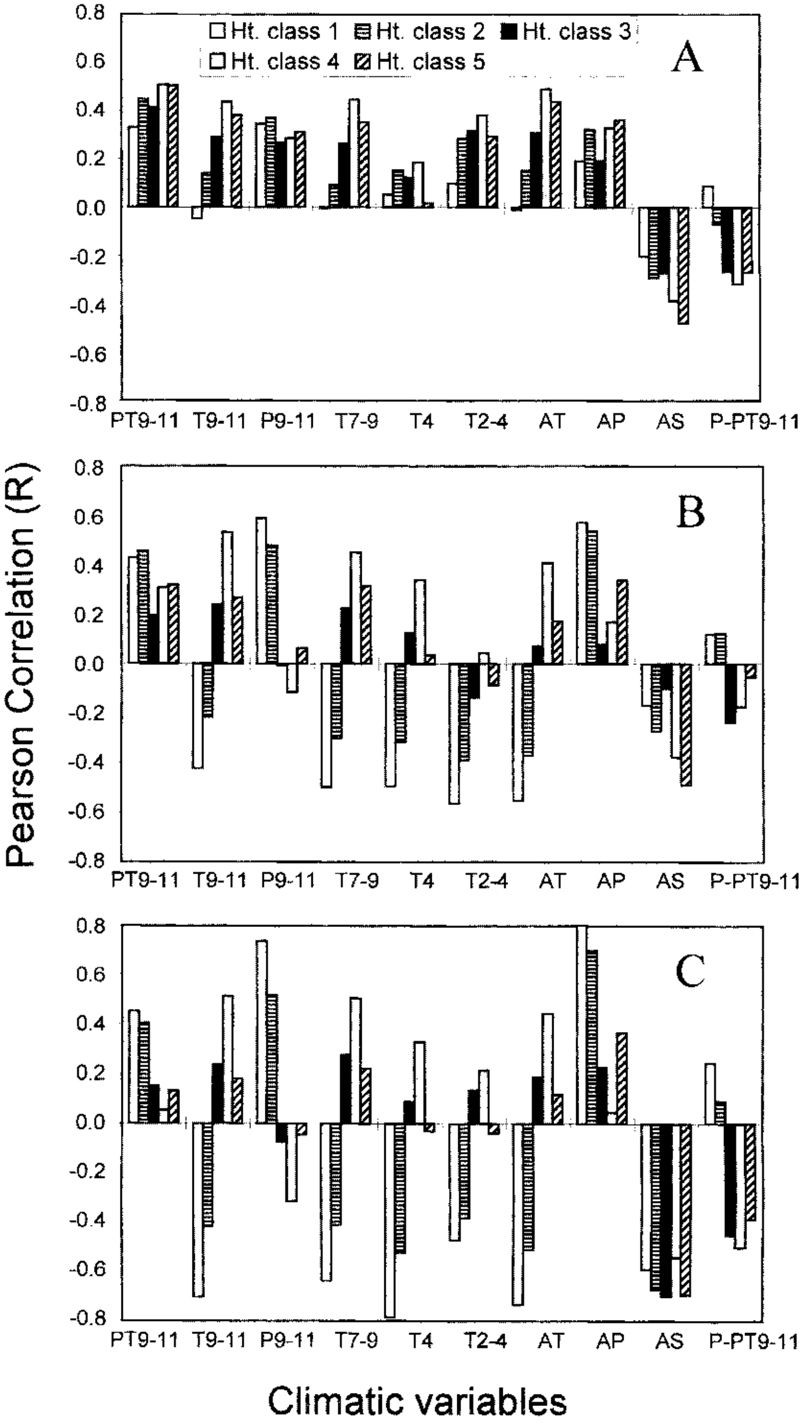

Figure 5. Pearson correlations (R) between climatic variables and western hemlock chronologies by height class. Correlations without an applied moving average (A). Correlations after application of a 3-year moving average (B). Correlations after the application of a 5-year moving average (C).

TABLE 6. Wilcoxon signed rank test significant difference (P-value) for each pairing of height classes. Test if height class pairing correlations to climate are unique.

Height class	Height class 10–20m	20–30m	30–40m	40–50m
20–30m	0.06			
30–40m	0.28	0.98		
40–50m	0.14	0.28	0.05	
50–60m	0.28	0.58	0.45	0.06

cient of determination with the adj. r^2 & C_p selection procedure while the 50-60m height class has the best model using the stepwise procedure (Table 4). The two selection procedures selected most of same climatic variables for the best models (Table 5). No single climatic variable was chosen for all height classes, regardless of selection procedure, although temperature or precipitation variables during the autumn months (PT9-11, T9-11, P9-11, P-PT9-11) are present in all height classes.

The correlations between chronologies and climate are significantly different (Friedman's nonparametric test, $P = 0.0003$) among the five height classes. The Wilcoxon signed rank test comparing all possible pairs of chronologies for differences in correlation to climate indicate a few pairs are significantly different (Table 6). The Wilcoxon test comparing the 20-30m and 30-40m height classes indicate they are the least different ($P = 0.98$) in their correlation to the ten climatic variables.

Inspection of raw data statistics shows that the 40-50m height class contains the greatest mean ring increment, maximum ring increment, standard deviation, and variance (Table 7). Smallest mean ring widths, standard deviations, and variances were all found in the lowest two height classes.

Discussion and Conclusion

Our results show the growth rates of western hemlock trees present in each height class have a different response to climate. The Wilcoxon test revealed that adjacent height classes, with the exception of height classes two and three, were significantly different in their correlation to climatic variables. Significant differences in adjacent height class correlations support the notion that each has a unique relationship with climate and represents a separate ecological gradient. The Pearson correlations reveal the relative differences in correlation strength to each climatic variable while the regression models determine which combination of climatic variables best predict a change in growth. Strengths of the climatic growth correlations to canopy dominants in this study were similar to those reported by others in the region (Brubaker 1980, Brubaker et al. 1992, Peterson and Peterson 1994, Ettl and Peterson 1995). The raw data show differences of growth rates between height classes and are consistent with the notion that understory trees have reduced growth rates (Figure 3) (Table 7).

To understand the relationship of growth to climate we can view the results by height class, variable season (spring, summer etc.), variable type (temperature and precipitation), temporal scale (3-year and 5-year moving averages) or combinations of the above. For the suppressed trees in height class one, the striking result of the mov-

TABLE 7. Summary statistics for raw ring widths (mm) of western hemlock, by height class.

Parameter	Height Class 10–20m	20–30m	30–40m	40–50m	50–60m
N of rings	3500	2480	2220	3280	1180
Mean (cm)	0.066	0.075	0.108	0.120	0.105
Median (cm)	0.049	0.063	0.091	0.104	0.099
Minimum (cm)	0.004	0.001	0.006	0.006	0.016
Maximum (cm)	0.447	0.303	0.584	0.848	0.714
Sample variance	0.0031	0.0025	0.0059	0.0067	0.0034
Standard deviation	0.0558	0.0496	0.0769	0.0820	0.0582

ing average indicates that these trees were most affected by longer term trends in the climate (Figure 5c) (Table 3). The presence of T4 in only the first two height class regression models indicates that spring temperatures are important but the strong negative relationship of growth to temperature was only revealed with longer time scale analysis. The canopy dominants were most affected by short term climatic trends; correlation strength decreased as the time scale of analysis increased (Table 3). The notable exception to this short-term correlation trend for height class five was the climatic variable AS to which ring widths were moderately or strongly correlated for all time scales (Figure 5). The annual depth of snow affects growth for all height classes at the 5-year time scale showed that consecutive years of deep snow have a negative impact upon all western hemlock productivity. The presence of autumnal climatic variables in the regression models (PT9-11, T9-11, P9-11, P-PT9-11) of all height classes suggests these climatic conditions also influence productivity across the entire stand.

It appears that as tolerant trees such as western hemlock pass through structural levels in the canopy they experience different relationships to climate. Hence, the resulting ring series have widths with a complicated history of causation. Current dendrochronological practices avoid stands and trees that experienced suppression or treat the relationships to climate uniformly along a tree ring series. Understanding what climatic variables have the most effect upon growth at a given height class has the potential to reveal past climatic conditions recorded in large old-growth trees and aid in the understanding of recruitment dynamics.

Future studies might include similar analysis of other species in the same stand to provide insight into their ecology and better illustrate the complete stand dynamic. Finally, this study illustrates the need to preserve the remaining old-growth because there is still much unknown about the dynamics and complexity of these systems.

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