Dendroclimatic response of mountain hemlock (*Tsuga mertensiana*) in Pacific North America

Ze'ev Gedalof and Dan J. Smith

Abstract: In this paper we review the ecology and physiology of mountain hemlock (*Tsuga mertensiana* (Bong.) Carrière) in the context of a dendroclimatological analysis. To better understand the relationship between mountain hemlock growth and climate variability throughout its range we have analyzed chronologies from 10 coastal sites, located along a transect extending from northern California to southern Alaska. The chronologies exhibit significant large-scale cross-correlations, with two distinct growth regions implied: chronologies from the northern Cascades in California, to the Queen Charlotte Islands, British Columbia, are correlated with each other but are distinct from Alaskan chronologies. While intervals of coherent reduced growth along the entire transect occur episodically throughout the record, intervals of coherent enhanced growth are less common. Response function analyses indicate that summer temperature is the most influential factor limiting growth throughout the study region, while winter precipitation is an additional limiting factor south of Alaska. Warm summer temperatures are associated with enhanced growth in the current year but with reduced growth in the following year. This response is believed to be a reflection of the energy required to mature cones initiated in the preceding year. The association with winter precipitation may reflect the role of deep, persistent snowpacks in regulating the duration of the growing season.

Résumé : Dans cet article, les auteurs réexaminent l'écologie et la physiologie de la pruche subalpine (*Tsuga mertensiana* (Bong.) Carrière) dans le cadre d'une analyse dendroclimatologique. Afin de mieux comprendre la relation entre la croissance de la pruche subalpine et les variations climatiques à travers son aire de répartition, les auteurs ont analysé les chronologies de 10 sites côtiers situés le long d'un transect allant du nord de la Californie jusqu'au sud de l'Alaska. À grande échelle, les chronologies mettent en évidence des corrélations croisées significatives qui supposent l'existence de deux zones de croissance distinctes : les chronologies du nord des Cascades en Californie jusqu'aux îles de la Reine-Charlotte en Colombie-Britannique sont corrélées les unes avec les autres mais sont différentes de celles de l'Alaska. Alors que les intervalles de réduction cohérente de croissance surviennent épisodiquement tout au long du transect pour toute la période étudiée, les intervalles d'augmentation cohérente de croissance sont moins fréquents. Les analyses d'une fonction de réponse montrent que la température estivale est le plus important facteur limitatif pour la croissance dans l'ensemble de la région étudiée, alors que la précipitation hivernale constitue un facteur additionnel au sud de l'Alaska. Des températures estivales chaudes sont associées à une augmentation de croissance dans l'année en cours mais avec une réduction de croissance l'année suivante. Cette réponse refléterait l'énergie requise pour amener à maturité les cônes formés l'année précédente. L'association avec la précipitation hivernale pourrait être le reflet du rôle que jouent les couverts de neige épais et persistants dans la régulation de la durée de la saison de croissance.

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Introduction

Climate plays an important role in limiting tree growth in Pacific North America (Brubaker 1986; Peterson and Peterson 1994; Rochefort et al. 1994; Wiles et al. 1996; Smith and Laroque 1998; Laroque and Smith 1999). Analyses of proxy data (Biondi et al. 1998; Wiles et al. 1998; D'Arrigo et al. 1999; Kadonaga et al. 1999) and instrumental records (Roden 1989; Ware 1995; Mantua et al. 1997; Zhang et al. 1997) have shown that the climate of this region is not static at any frequency of variability. Furthermore, many general circulation models predict not only future increases in temperature and precipitation but also changes in their seasonal distributions (Boer et al. 1992; Leung and Ghan 1999). It is, therefore, imperative that management strategies consider the potential consequences of these impending climatic changes on forest productivity. Important insights into the magnitude of the tree growth responses to climate change can be gained from species-specific dendroclimatic investigations over large geographical areas (Wiles et al. 1996; Hofgaard et al. 1999; Mäkinen et al. 2000).

In Pacific North America, mountain hemlock (*Tsuga mertensiana* (Bong.) Carrière) trees have a wide latitudinal distribution (Krajina 1969; Means 1990). The species primarily inhabits a narrow coastal band extending from Turnagain Pass on the Kenai Peninsula, Alaska (60°49′N), (Wiles et al. 1998) to Sequoia National Park in California (36°38′N) (Parsons 1972). Disjunct interior populations persist at scattered sites in the Bitterroot Mountains of Montana and Idaho (Habeck 1967) and within the Columbia Moun-

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tains of British Columbia (Parish and Thomson 1994). Mountain hemlock is a major component of the Mountain Hemlock biogeoclimatic zone of British Columbia (Brooke et al. 1970; Klinka et al. 1991) and is the main pioneer species within the timberline parkland subzone (Fonda and Bliss 1969; Brooke et al. 1970). Previous research has shown that 20th century climate changes were sufficient to initiate a period of enhanced radial growth (Heikkinen 1985; Graumlich and Brubaker 1986) and to instigate episodes of subalpine meadow invasion by mountain hemlock trees in the Washington and Oregon Cascade Mountains (Brink 1964; Franklin et al. 1971; Agee and Smith 1984).

Mountain hemlock has been shown to be sensitive to variations in climate and to have considerable dendroclimatological utility (Brubaker 1980; Heikkinen 1984, 1985; Graumlich and Brubaker 1986; Graumlich et al. 1989; Wiles et al. 1996, 1998; Smith and Laroque 1998). While various researchers have undertaken regional analyses of the associations between climate variables and radial growth of mountain hemlock (Blasing and Fritts 1976; Briffa et al. 1992; Wiles et al. 1998), no attempt had been made to assess spatial and (or) temporal variations in these associations over its entire range. The aim of this paper is to analyse the growth–climate associations for mountain hemlock ring-width chronologies located throughout Pacific North America. We interpret the climate–growth associations in the context of the ecology and physiology of mountain hemlock.

Research background

The Mountain Hemlock zone is normally divided into a forest subzone and a parkland subzone (Brooke et al. 1970; Klinka et al. 1991; Pojar and MacKinnon 1994). The forest subzone is an area of relatively continuous forest, with greater than 75% canopy cover (Means 1990). The parkland subzone typically occurs at higher elevations and is typified by scattered islands of trees growing on hummocks of relatively well-developed soil. Both subzones are characterized by cool moist climates, persistent snowpacks, and poor soils (Brooke et al. 1970). Mountain hemlock will occasionally grow in the alpine as a prostrate, matlike krummholtz shrub (Means 1990; Viereck et al. 1992). It may also occur well below its usual altitudinal limits on very poorly drained sites, where other species offer little competition (Dahms and Franklin 1965).

Mountain hemlock grows in a wide range of associations, depending most critically on precipitation, drainage, and soil temperature (Krajina 1965; Fonda and Bliss 1969; Brooke et al. 1970; Franklin and Dyrness 1973; Yarie 1980). At the southernmost extent of its distribution, mountain hemlock is restricted to cooler, north-facing slopes and canyons above 2700 m a.s.l. (Parsons 1972). At these latitudes the most common associates are lodgepole pine (*Pinus contorta* var. *murrayana* Dougl. ex Loud.), western white pine (*Pinus monticola* Dougl. ex D. Don in Lamb), foxtail pine (*Pinus balfouriana* Grev. & Balf. in A. Murr.), or red fir (*Abies magnifica* A. Murr.), depending on locale (Rundel et al. 1977). Mountain hemlock is most competitive at mesic and hydric sites but is often competitively excluded from better drained or more xeric locations (Taylor 1995).

In Washington and British Columbia, mountain hemlock is commonly associated with subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), lodgepole pine (*Pinus contorta* var. *contorta* Dougl. ex Loud.), Pacific silver fir (*Abies amabilis* Dougl. ex Forbes), and yellow-cedar (*Chamaecyparis nootkatensis* (D. Don) Spach) (Fonda and Bliss 1969; Franklin and Dyrness 1973; Laroque and Smith 1999). Subalpine fir tends to replace mountain hemlock at colder, drier sites, while Pacific silver fir is most competitive at warmer, wetter sites (Ettl and Peterson 1995; Woodward 1998). At lower elevations, mountain hemlock is most commonly replaced by western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) or Pacific silver fir (Krajina 1969; Brooke et al. 1970). Mountain hemlock is unable to survive at locations where soils seasonally freeze and is usually replaced by subalpine fir or Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) (Brooke et al. 1970; Means 1990).

At the northern extent of its range, in northern British Columbia and Alaska, mountain hemlock occurs from tree line down to sea level. At these latitudes it will often occur in pure stands but is also commonly associated with Sitka spruce (*Picea sitchensis* (Bong.) Carrière). At lower elevations it may be associated with western hemlock or western redcedar (*Thuja plicata* Donn ex D. Don), where it is confined to frost pockets or steep, north facing slopes (Viereck et al. 1992).

Methods

The approach used in this study was to identify a series of tree-ring sites located along a latitudinal transect extending from Alaska to California (Fig. 1). South of Alaska, mountain hemlock occurs as a tree line species, and most of the chronologies used were sampled from tree line or near tree line stands. This strategy allowed us to target trees growing at the limit of their environmental tolerance, thus maximizing the potential climate signal in the ring-width series (Fritts 1976). The pool of potential chronologies included those archived in the International Tree-Ring Data Bank (ITRDB) (Grissino-Mayer and Fritts 1997) provided by Greg Wiles and David Frank (see Wiles et al. 1996; Frank 1998) and held by the University of Victoria tree-ring laboratory (Smith and Laroque 1998). Since insufficient sites existed in coastal British Columbia, tree-ring samples (20 trees per site) were collected using an increment borer at locations in the Queen Charlotte Islands and near Bella Coola. Both of these sites were characterized by a continuous forest composed of mixed-age mountain hemlock trees, with yellow-cedar occurring as a secondary species. The trees sampled were located within approximately 200 m of the upper elevation tree line. The cores were cross-dated using standard dendrochronological techniques (Stokes and Smiley 1968) and measured to the nearest 0.001 mm. In the case of the archived tree ring series, we selected only cross-dated ring-width series that fell along our latitudinal transect.

All of the ring-width series were transformed into stationary, dimensionless indices to remove trends in growth related to tree-age and stand dynamics (Cook 1987). This transformation was undertaken in two steps using the computer program ARSTAN (Cook and Holmes 1986). First, a negative exponential curve or linear trend was fitted to each series, and each observed ring width in the series was divided by this “expected” value. Next, each series was detrended a second time by fitting a cubic smoothing spline with a 50% frequency cutoff of 95 years (Cook and Peters 1981). Double detrending is necessary in series where the smoothing spline that is most appropriate for the mature portion of the ring-width series is

Fig. 1. Location of the mountain hemlock sample sites used in this analysis.

not flexible enough to fit the sharp transition from juvenile to mature growth rates but where unwanted low-frequency variability remains in the mature growth portion of the series (Cook et al. 1990). Each ring-width-index series was then prewhitened using autoregressive and moving average (ARMA) models, to remove any autocorrelation effects (Biondi and Swetnam 1987; Cook 1987). Individual core series from each site were then combined into a site chronology using a robust mean (Mosteller and Tukey 1977).

Several descriptive statistics were calculated to describe the site chronologies. Mean first-order autocorrelation is a measure of the degree to which a given year's growth is correlated with the preceding year's growth, with high values indicating that a significant portion of the observed ring width is a function of the preceding year's growth rather than exogenous factors. Mean sensitivity is a measure of the relative difference in width between consecutive rings (Fritts 1976). Possible values range from 0 (indicating no change in ring width from one year to the next) to 2 (indicating a missing ring), with high mean sensitivity measurements interpreted as an indication that the ring-width series may have dendroclimatological utility (Fritts 1976). Mean series correlation is a measurement of the degree of commonality in the individual series contributing to the site chronology. It is calculated as the mean correlation coefficient between each core ring-width series and the mean site chronology. High mean series correlation values suggest that the trees at a site are responding in a similar manner to external influences and will likely contain a strong climate signal. Percent common signal (PCS) is a measure of the chronology signal strength and is an estimate of the degree to which the tree-ring sample expresses the true population signal (Cropper 1982).

Response function analysis (PRECONK, version 5.17; Fritts et al. 1971; Fritts 1976) was used to identify climate variables that have significant associations with annual radial growth of mountain hemlock. This method of analysis uses multivariate statistics and eigenvector techniques to identify associations. The significance of these associations was tested using a bootstrap method (Guiot 1991).

The meteorological data used in the response function analysis consisted of records extracted from the United States Historical Climatology Network (USHCN), the United States Divisional Climate Data, the Canadian Atmosphere Environment Service (AES), the Global Historical Climatology Network (GHCN), and the Alaska Historical Climatology Network (AHCN). The divisional climate data represent area-averaged records over regions that are ostensibly climatically homogeneous (Guttman and Quayle 1996). While many dendroclimatic studies have suggested that these data are more appropriate than individual station data (e.g., Fritts 1976; Brubaker 1980; Blasing et al. 1981; Ettl and Peterson 1995), in the western United States the divisions are often based on drainage boundaries or crop reporting districts rather than on climatic conditions (Guttman and Quayle 1996). For this reason, we chose to use single-station climate data wherever possible. Stations were selected on the basis of proximity, length, and presumed representativeness. In the case of the Lassen Peak, for instance, the nearest reporting station in the USHCN was located in Susanville, deep in the rainshadow of the Cascade Mountains. Since no climate station could be found for the California Cascades region we chose to use the divisional data for this region instead. In all cases, the data used consisted of mean monthly temperature and total monthly precipitation values.

Results

Ten sites between Lassen Peak, California, and Ellsworth Glacier, Alaska, were included in our analyses. We used tree-ring chronologies from 297 trees ranging in age from 198 to 645 years (Table 1). Significant first-order autocorrelation was present in every series analyzed. At most sites an ARMA(1,0) or ARMA(2,0) model was sufficient to remove the autocorrelation, although Bella Coola required an ARMA(3,0) model. Prior to autoregressive modelling the mean sensitivity values were slightly lower than those reported for other subalpine species in the Pacific Northwest but, following prewhitening, were comparable with those reported by Peterson and Peterson (1994) and Ettl and Peterson (1995). The mean series correlation values, after ARMA modelling, ranged from 0.27 to 0.58, suggesting that there is a moderately strong common signal among the individual chronologies at each of the study sites. Autoregressive modelling reduced the mean series correlation at Bella Coola and Hemlock Knob but improved it at all other sites. Nonetheless, the ARMA modelled series were retained at these two sites because of the spurious correlations, which can be introduced by serial autocorrelation (Katz 1988).

Correlation analyses of the 10 site chronologies shows two regional zones of growth patterns (Table 2). There is a significant correlation between all sites south of Alaska, and between the Alaskan sites. From Strathcona Park to Hemlock Knob, the correlations are variable, suggesting a zone of transition between the relatively distinct Alaskan chronologies and the southern chronologies. These regional correlation values are comparable in magnitude to others reported in the Pacific Northwest (e.g., Peterson and Peterson 1994; Ettl and

Table 1. Site characteristics and chronology statistics.

Site name	Source	Latitude (°N)	Longitude (°W)	Elevation (m)	Series mean first-order autocorrelation^a	Series mean sensitivity^b	Mean series correlation^b	Percent common signal^b	Total series length
Eyak Mountain, Alaska	G. Wiles	60.60	145.67	430	0.643	0.305	0.584	0.918	1365–1992
Ellsworth Glacier, Alaska	G. Wiles	60.08	148.96	480	0.561	0.252	0.444	0.897	1543–1991
Hemlock Knob, Alaska	D. Frank	59.48	139.13	30	0.695	0.211	0.516	0.936	1599–1995
Queen Charlotte Island, B.C.	UVTRL	53.00	132.10	615	0.428	0.239	0.290	0.824	1585–1998
Bella Coola, B.C.	UVTRL	52.30	126.40	1100	0.462	0.192	0.269	0.568	1668–1997
Strathcona Park, B.C.	UVTRL	49.50	125.50	1500	0.230	0.198	0.389	0.790	1412–1995
Mount Baker, Wash.	ITRDB	48.50	120.39	1330	0.489	0.18	0.376	0.884	1331–1976
Granite Mountain, Wash.	ITRDB	47.41	121.45	1530	0.538	0.171	0.377	0.865	1778–1976
Mount Hood, Oreg.	ITRDB	45.33	121.70	1600	0.359	0.248	0.493	0.893	1706–1983
Lassen Peak, Calif.	ITRDB	40.27	121.31	2550	0.185	0.179	0.458	0.899	1525–1983

[a] Autocorrelation calculated prior to ARMA modeling.

[b] Mean sensitivity, mean series correlation, and percent common signal were calculated after ARMA modelling.

Table 2. Pearson's *r* correlation values, showing the associations of the 10 site chronologies.

	Lassen Peak	Mount Hood	Granite Mountain	Mount Baker	Strathcona Park	Bella Coola	Queen Charlotte Islands	Hemlock Knob	Ellsworth Glacier	Eyak Mountain
Lassen Peak	—	0.33*	0.24*	0.28*	0.22*	0.27*	0.20*	0.01	–0.06	–0.09
Mount Hood	<0.001	—	0.42*	0.37*	0.42*	0.26*	0.32*	0.12	–0.02	0.02
Granite Mountain	0.001	<0.001	—	0.43*	0.43*	0.37*	0.27*	0.14*	0.07	0.14*
Mount Baker	<0.001	<0.001	<0.001	—	0.62*	0.29*	0.45*	0.22*	0.18*	0.04
Strathcona Park	0.002	<0.001	<0.001	<0.001	—	0.37*	0.61*	0.17*	0.18*	0.15*
Bella Coola	<0.001	<0.001	<0.001	<0.001	<0.001	—	0.39*	0.09*	–0.10	0.05
Queen Charlotte Islands	0.005	<0.001	<0.001	<0.001	<0.001	<0.001	—	0.22*	0.27*	0.33*
Hemlock Knob	0.864	0.103	0.045	0.002	0.014	0.194	0.001	—	0.39*	0.47*
Ellsworth Glacier	0.420	0.742	0.323	0.012	0.012	0.144	<0.001	<0.001	—	0.68*
Eyak Mountain	0.215	0.736	0.048	0.591	0.037	0.494	<0.001	<0.001	<0.001	—

Note: Pearson correlation coefficients are given above the diagonal, and *p* values are given below the diagonal. Correlations are calculated over the interval 1778 to 1976. *, Significant at the 95% confidence level.

Peterson 1995; Smith and Laroque 1998). The correlation coefficients between these chronologies remain significant across remarkable distances, albeit weakly. For instance, Lassen Peak and the Queen Charlotte Islands are separated by a distance of nearly 2000 km (r = 0.20, p = 0.005).

Intervals of coherent radial growth along the transect, and within the two growth zones, can be seen graphically when the chronologies are smoothed and plotted together on a time–latitude diagram (Fig. 2). Intervals of above average growth along the entire transect occur at ca. 1635, 1780, 1805, and from 1830 to 1840. Intervals of spatially consistent below average radial growth are more common, occurring at ca. 1620, 1730, 1745, 1815, 1850, and 1895. A number of intervals are seen where the northern and southern portions of the transect show a similar regional growth response, but are out of phase with each other. Examples of this mode of variability occur at ca. 1630, 1655, 1905, 1955, and 1985. In these examples, the transition occurs in the region of the Queen Charlotte Islands. There are also some instances, however, where this transition occurs in Washington state (e.g., 1750, 1895, 1935).

Response function analyses

The associations between annual radial growth and mean monthly climate conditions were explored using response function analyses. At every site, 40 years or longer of meteorological data were used to calibrate the response functions (Table 3). An inherent limitation of this study was the short duration of the common interval over which all of the sites being analyzed have both climate and tree-ring data available. Instead of using only the 32 years that were common to all sites, we opted to use all of the available data to calibrate the response functions. This strategy also ensured that each calibration interval included at least one full positive and negative phase of the Pacific decadal oscillation (PDO; Mantua et al. 1997), as well as at least one very strong and several strong El Niño – Southern Oscillation events. The possibility that differences in the observed response functions resulted from temporal differences in the climate experienced at the sample sites was minimized by using the bootstrap function to test the significance of the observed correlations. The bootstrap method uses Monte Carlo simulations to construct pseudodata sets from the original data by sampling with replacement (Guiot 1990). Regression analysis is undertaken on each of these pseudodata sets, and the mean and standard deviation of the estimated coefficients can be used to assess the significance of the identified associations. Instabilities in a response will be re-

Fig. 2. A time–latitude diagram of ring-width index at the 10 mountain hemlock sample sites, for the interval 1600–1900. The ring-width index series were smoothed using a 5-year digital filter along the *x* axis and interpolated between sites along the *y* axis. This axis has also been scaled so that each ring-width series represents an equal of range *y* values.

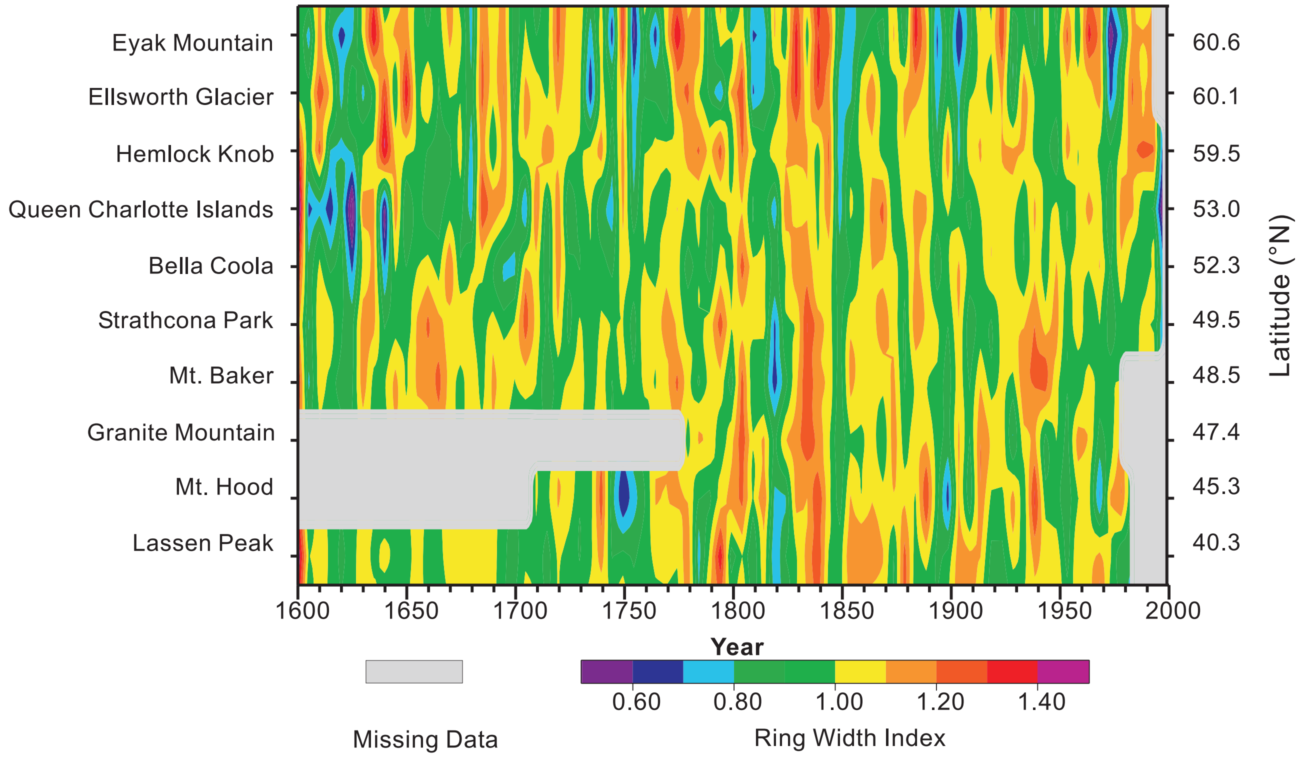


Table 3. Meteorological data used in the response function analyses.

Tree-ring site	Climate station	Climate data source	Latitude (°N)	Longitude (°W)	Elevation (m)	Calibration interval
Eyak Mountain	Seward, Alaska	AHCN	60.1	149.45	35	1908–1990
Ellsworth Glacier	Seward, Alaska	AHCN	60.12	149.45	35	1908–1990
Hemlock Knob	Yakutat, Alaska	AHCN	59.5	139.67	28	1917–1990
Queen Charlotte Islands	Sandspit, B.C.	GHCN	53.3	131.82	5	1945–1990
Bella Coola	Bella Coola, B.C.	AES	52.4	126.68	18	1907–1990
Strathcona Park	Comox, B.C.	AES	52.2	126.38	20	1945–1991
Mount Baker	Longmire, Wash.	USHCN	46.8	121.82	842	1909–1976
Granite Mountain	Longmire, Wash.	USHCN	46.8	121.82	842	1909–1976
Mount Hood	Crater Lake, Oreg.	USHCN	42.9	122.13	1974	1919–1983
Lassen Peak	Sacramento Drainage, Calif.	Divisional	na[a]	na	na	1896–1983

[a] na, not applicable.

vealed as a high standard deviation in the estimated regression coefficient and, consequently, will not be identified as significant. Five hundred bootstraps were used to test significance, and an association was considered to be significant at the $p \leq 0.05$ level if its mean regression coefficient was more than twice its standard deviation (Guiot 1991).

The percentage of variation in radial growth explained by the climate response functions ranged from 38% at Mount Baker to 68% at Strathcona Park (Table 4). The particularly weak association at Mount Baker may be a consequence of the substantial local variability in climate at Mount Baker and the lack of a representative meteorological station nearby (Heikkinen 1985). With the exception of Hemlock Knob, all of the sites show a negative response to summer temperature in the year preceding growth. In the year of growth there is a positive association to at least one month of spring or summer temperature at all sites except Hemlock Knob and Mount Hood. South of the Queen Charlotte Islands, four of the six sites exhibit a negative response to winter precipitation in the season preceding growth. While Hemlock Knob also exhibits a negative association with preceding November precipitation, the remaining Alaskan sites exhibit a positive response to precipitation in spring of the growth year.

Discussion

Growth–climate relationships

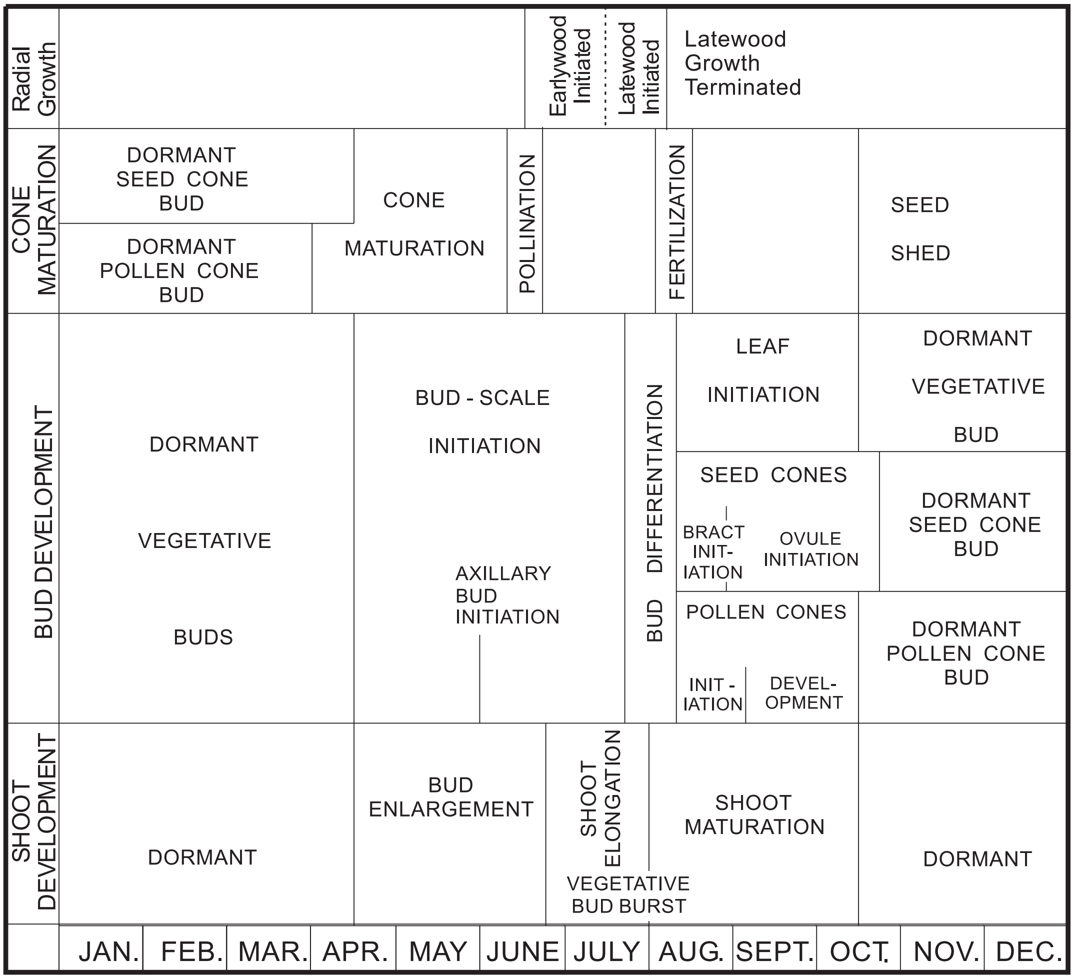
Four general radial growth–climate associations were observed in the response functions of the mountain hemlock chronologies: (*i*) a positive response to temperature in spring

Table 4. Significant standardized regression coefficients identified in the response function analyses.

		Year preceding growth							Year of growth							
	r^2	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.
Temperature associations																
Eyak Mountain	46	–0.166	–0.201										0.229	0.241	0.229	
Ellsworth Glacier	57		–0.296										0.259			
Hemlock Knob	50									0.224						
Queen Charlotte Islands	38		–0.295												0.273	
Bella Coola	71		–0.204												0.237	
Strathcona Park	53		–0.226											0.233	0.283	
Mount Baker	56		–0.177								0.199					
Granite Mountain	62		–0.308	–0.198									0.160			
Mount Hood	62			–0.266												
Lassen Peak	57			–0.181									0.250			
Precipitation associations																
Eyak Mountain											0.173					
Ellsworth Glacier											0.207					
Hemlock Knob							–0.196									
Queen Charlotte Islands																
Bella Coola									–0.200							
Strathcona Park							–0.266		–0.213							
Mount Baker																
Granite Mountain																
Mount Hood									–0.232							
Lassen Peak								–0.289								

Note: The r^2 values are the total percent variance in ring-width explained by both temperature and precipitation climate variables. Coefficients shown are significant at $p \le 0.05$.

Fig. 3. The yearly growth cycle of mountain hemlock growing at high elevations on Vancouver Island (adapted from Owens and Molder 1975; Owens 1984*a*, 1984*b*; Owens and Molder 1984; C. Laroque, personal communication).



or summer of the growth year; (*ii*) a negative response to summer temperature in the year preceding ring formation; (*iii*) a tendency for a negative response to precipitation in the winter preceding growth (south of the Queen Charlotte Islands); and (*iv*) a positive response to spring precipitation (southeastern Alaska).

The most consistent of these radial growth – climate relationships is the tendency for good growth to correspond to warm spring or summer temperatures. This relationship probably reflects the importance of air temperature during the growing season in regulating soil temperatures, rates of respiration and photosynthesis, metabolic processes, and consequent carbohydrate production of subalpine conifers in western North America (Krajina 1969; Brooke et al. 1970; Owens and Blake 1985). Radial growth in conifers is especially sensitive to variation in growing season temperature (Owens 1984*b*; Coleman et al. 1992; Kozlowski et al. 1997), since it is not initiated until after root growth and bud flushing are complete (Fig. 3). Consequently, if climate is not conducive to metabolic activity, these primary growth functions may be retarded and radial growth may not be initiated until later in the growing season, leaving less time for cambium production.

The tendency for warm summer conditions to be associated with enhanced growth during the current year but decreased growth in the following year may be due to a complex interaction of several physiological responses related to the cost of cone production and the antecedant conditions that initiate cone production. Woodward et al. (1994) studied the relationship between radial growth of mountain hemlock, climate conditions, and cone production. They observed that, while relatively larger cone crops in mountain hemlock occur at irregular intervals of approximately 3 years, the actual size of this crop appears to be modulated by weather conditions in the years preceding growth. In particular, they identified an association between warm summer conditions in the year preceding cone maturation with large cone crops and poor radial growth in the year of cone maturation. Reproductive buds are differentiated from vegetative buds in the year preceding cone maturation (Fig. 3; see also Owens and Molder 1975), with an increased proportion of reproductive buds associated with warm summer conditions (Owens 1984*b*). The subsequent energy cost of cone maturation in the following year is believed to result in decreased radial growth (Woodward et al. 1994). Woodward et al. also observed an association between cool wet winters in the season preceding cone production and increased cone crops. Therefore, the relationship between increased cone production and poor radial growth may be a consequence of a complex interaction of multiple factors; the climate that favours increased cone production results in poor radial growth, but the production cost of the cones themselves may also reduce radial growth (Woodward et al. 1994).

The inverse relationship to winter precipitation observed at most sites south of the Queen Charlotte Islands may be caused, in part, by the tendency for large cone crops to follow cool, wet winters. Equally important, however, may be the influence of winter snow accumulation on physiological processes. Several studies have identified the snow-free period as the most important factor limiting the radial growth of mountain hemlock (Brooke et al. 1970; Graumlich and Brubaker 1986; Taylor 1995; Smith and Laroque 1998). The duration of this interval is determined in part by spring and summer temperatures, but also by total winter snow accumulation. Deep, persistent, snowpacks keep soil temperatures low and tend to delay the initiation and rates of metabolic processes in subalpine conifers (Fig. 3; see also Brooke et al. 1970; Evans and Fonda 1990). The finding that winter precipitation is more influential at lower latitudes may be a consequence of the seasonal patterns of precipitation throughout mountain hemlock's distribution. While there is no trend in either mean annual temperature or total annual precipitation within the mountain hemlock zone, there is a trend in the portion of precipitation that falls as snow. In Alaska, on average only 14% of precipitation in the mountain hemlock zone falls as snow, whereas in northern California, 88% of precipitation typically falls as snow (Table 1, Means 1990). These factors will result in a typically smaller winter snow accumulation in the northern portion of mountain hemlock's range. A comparison of the climate records at Crater Lake, Oregon and Seward, Alaska, for the period 1930–1990 illustrates this finding. At Crater Lake, 67% of precipitation typically occurs during months when the mean temperature is below zero. At Seward, by contrast, even though temperatures are below zero for an average of 1 month more per year, only 43% of precipitation falls during months when the mean temperature is below zero. Mean total annual precipitation is not significantly different between the two sites.

It is not clear from the current analyses why this association to winter precipitation was observed at some, but not all, of the southern sample sites. Two possible explanations are that (*i*) winter snow accumulation is a significant limiting factor at these sites, but the meteorological data used in the response function analyses are influenced by local noise and are not representative of the sample site, and (*ii*) distinct site conditions determine the extent to which snow accumulation limits growth. Of these explanations, the first is possible but unlikely; experimentation using other, potentially more representative climate records and the divisional climate data did not produce substantially different response functions. Under the second scenario, possible candidate explanations include (*i*) the role of canopy structure in modulating snow accumulation and snowmelt (Golding 1986; Hudson 2000); (*ii*) the nonlinear association which has been observed between annual radial growth of mountain hemlock, summer temperature, and winter snow accumulation (Graumlich and Brubaker 1986; Smith and Laroque 1998); or (*iii*) the influence of topography and prevailing winds on snowdrift at tree line locations (Minnich 1984). Our analysis does not favour any of these interpretations, and clearly future research needs to address this response.

The positive relationship to March precipitation observed at the two northernmost sites may represent a response to rain-on-snow events. An examination of total March precipitation and mean March temperatures at Seward, Alaska, shows that there is a tendency for the wettest months to also be the warmest. A warm wet March would ripen and melt the winter snowpack, raise soil temperatures and may result in an earlier initiation of growth and faster metabolic activity among conifers (Peterson and Peterson 1994).

The two significant growth–climate associations observed at Hemlock Knob are unique to this site, a finding which warrants some discussion. If these associations represent true relationships than they are difficult to explain in physiological terms. The negative association with November precipitation may be a response to mechanical damage from freezing rain or rain-on-snow events. The normal daily minimum and maximum November temperatures at Yakutat, Alaska, are –3.8 and 2.9°C, respectively, suggesting that fluctuations around the freezing mark may be common. These events can damage the upper shoots of trees, resulting in decreased radial growth in the following season due to lost photosynthetic resources and a greater need for carbohydrate allocation in the damaged shoots (Grier 1988). The positive association with February temperatures may indicate reduced dormancy levels or wintertime photosynthesis (Waring and Franklin 1979). This explanation seems improbable, however, given the lack of a significant association with any other temperature variables. A more likely explanation for these associations is that the associations observed at Hemlock Knob are spurious and do not reflect actual relationships. Given the large number of regression coefficients that were estimated in this analysis it is not improbable that some spurious associations will be identified. The fact that the associations identified at Hemlock Knob both occur outside the growing season and neither is replicated at any other site suggests that they should be regarded with extreme scepticism, at best.

Spatial patterns

There was no obvious spatial trend in the response of mountain hemlock to temperature in either the year of growth or in the year preceding growth. The tendency for poor radial growth to follow years of high summer temperature throughout the transect suggests that the proposed relationship between antecedent climate conditions, cone production, and radial growth is consistent throughout the range of mountain hemlock. The response to winter precipitation exhibited a latitudinal trend, with sites south of Alaska tending to show a negative association to precipitation in one winter month. The two northernmost sites exhibited a positive response to march precipitation. These patterns may be a response to latitudinal trends in precipitation in the mountain hemlock zone.

Intervals of coherent growth along the transect may be a response to large-scale forcing from the Aleutian Low atmospheric pressure system. Years when the Aleutian Low is intensified are associated with consistent patterns of sea surface temperature and sea level pressure, generally termed the Pacific North America Pattern (Wallace and Gutzler 1981). When the Aleutian Low is enhanced, there is a tendency for wintertime cyclonic circulation to direct storm tracks into Alaska (Wilson and Overland 1987). Increased meridianal transport brings anomalously warm coastal waters and warm, dry weather to the Pacific Northwest (Emery and Hamilton 1985). In response to this pattern, winter snow accumulation is normally substantially decreased throughout the Pacific Northwest (Moore 1996; Moore and McKendry 1996). Spring and summer temperatures are increased throughout coastal western North America (Ware 1995; Mantua et al. 1997). Our analyses suggest that these conditions would enhance the radial growth of mountain hemlock throughout coastal western North America. Years with a weakened Aleutian Low are associated with enhanced zonal flow; cold, wet winters; and cool springtime conditions throughout the Pacific Northwest (Leathers et al. 1991; Moore and McKendry 1996). These conditions would normally reduce radial growth of mountain hemlock, particularly south of Alaska where mountain hemlock is sensitive to winter snow accumulation.

Interdecadal variability in the North Pacific ocean–atmosphere system has recently been identified and is generally termed the PDO (Hare 1996; Mantua et al. 1997). The PDO is characterized by decades-long regimes of an on average enhanced or diminished Aleutian Low, and corresponding patterns of sea surface temperature, punctuated by abrupt shifts between these states. The interval of reduced growth at all sites south of Alaska, which occurs at approximately 1955, for instance, corresponds to an extreme negative anomaly in the mean winter PDO index (Mantua et al. 1997). Similarly, the above-average growth that occurred south of Ellsworth Glacier in the mid-1930s corresponds to a large positive anomaly in the mean winter PDO index. These observations suggest that a carefully selected set of mountain hemlock chronologies could be used to develop a proxy record of interdecadal North Pacific ocean–atmosphere variability.

Conclusions

The dendrochronological and dendroclimatological characteristics of mountain hemlock were explored throughout the subalpine Mountain Hemlock zone in Pacific North America. The 10 chronologies analyzed showed significant correlations throughout the Pacific Northwest and Gulf of Alaska regions, with a transition between these two regions occurring at approximately the Queen Charlotte Islands. Intervals of below-average growth along the transect are not uncommon, but intervals of above-average growth are more rare. Response function analyses of the chronologies identified summer temperature, in both the year preceding growth and in the year of ring formation, as the dominant climate factors influencing radial growth of mountain hemlock. There is evidence that prior winter precipitation exerts a negative influence on radial growth at lower latitudes but not at the northernmost sites.

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