Autumn Snowfall Controls the Annual Radial Growth of Centenarian Whitebark Pine (Pinus albicaulis) in the Southern Coast Mountains, British Columbia, Canada

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ABSTRACT

Whitebark pine (*Pinus albicaulis*), an endangered keystone alpine tree species, faces multiple threats across its western North American range. Little is known of whitebark pine in the southern Coast Mountains of British Columbia relative to well-studied Rocky Mountain populations, especially with regard to the effects of climate on annual radial growth. Our results indicate centenarian whitebark pine annual radial growth is negatively influenced by the onset of snowfall in the prior autumn. This unusual growth limitation likely stems from the truncation of the prior year growing season and reduced physiological preparedness for growth in the following year. Autumn snowfall is moderated by temperature and the Pacific Decadal Oscillation (PDO), which controls large-scale weather patterns in the study region. Our results are distinct from studies of mature whitebark pine trees in continental populations where growth is typically limited by summer temperature, or occasionally by winter snowfall due to a reliance on snow meltwater during spring/summer. We suggest that predicted warmer and wetter climate and reduced snowpacks in the southern Coast Mountains may benefit the growth of the young population of maritime whitebark pine over the next few decades.

INTRODUCTION

Whitebark pine (*Pinus albicaulis* Engelm.) is an early successional tree species that grows in high-elevation, cold, windy, and snowy areas with weakly developed soils. This species has a large and well-studied continental distribution in the Rocky Mountains from Alberta south to Wyoming, and a lesser-studied maritime band of distribution in the Coast Mountains of British Columbia (B.C.), the Cascade Range of Washington and Oregon, and the Sierra Nevada Range of northern Nevada and California (Arno and Hoff, 1989). It is often the only tree species able to grow in these high-elevation conditions and is therefore considered a keystone species due to its importance as a source of food and shelter

for wildlife species, including grizzly bears (*Ursus arctos horriblilis* Ord; Mattson and Reinhart, 1997), Clark's nutcrackers (*Nucifraga columbiana* Wilson), and other small birds and mammals (Hutchins and Lanner, 1982; Tomback, 1982). At high elevations, whitebark pine is often the first tree species to colonize open treeless areas (Arno and Hoff, 1989). Once established, whitebark pine may mitigate microclimate through lowered radiation, wind speed, and soil temperature extremes so that less tolerant species including subalpine fir (*Abies lasiocarpa* [Hooker] Nuttall), limber pine (*Pinus flexilis* E. James), Douglas fir (*Pseudotsuga menziesii* [Mirb.] Franco), and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) can establish on their leeward sides forming "tree islands," as has been shown in some treeline sites in the Rocky Mountains

(Resler et al., 2014; Pyatt et al., 2016). Due to its high abundance in treeline habitats, whitebark pine plays a key role in facilitating treeline community development (Callaway, 1998; Pyatt et al., 2016).

Climate plays a very important role in tree growth, typically through the interaction of available energy and water (Stephenson, 1990, 1998). Trees limited by factors related to available energy (i.e., temperature and growing season length) are said to be primarily energy limited, while trees limited by factors related to water availability and evaporative demand (i.e., precipitation and evapotranspiration) are said to be primarily water limited (Albright and Peterson, 2013). Trees that grow at high elevations, along coasts, or in northerly latitudes are typically energy limited (Stephenson, 1990), usually by the influence of summer temperature and occasionally by the soil-cooling and growth-inhibiting influence of spring or autumn snow (Albright and Peterson, 2013; Franklin and Dyrness, 1988; Graumlich and Brubaker, 1986; Peterson and Peterson, 1994, 2001; Ettl and Peterson, 1995; Peterson et al., 2002).

Dendroclimatological studies in the U.S. Pacific Northwest and adjacent areas in Canada have shown that the energy-limiting influence of summer temperature and total annual snowpack depth primarily control the radial growth of alpine trees (Ettl and Peterson, 1995; Peterson et al., 2002; Koch et al., 2004; Youngblut and Luckman, 2013; Coulthard et al., 2016). Dendroclimatological investigations in the interior Canadian Cordilleras (Luckman et al., 1997; Youngblut and Luckman, 2013), central Coast Mountains of B.C. (Larocque and Smith, 2005), and U.S. Northern Rocky Mountains (Kipfmueller, 2008), suggest that annual radial ring width and density parameters of whitebark pine are generally limited by variations in summer temperature. One Idaho study documented moisture limitation relating to the influence of snowmelt quantities on soil moisture availability in spring and summer (Perkins and Swetnam, 1996). Studies of maritime alpine populations are especially limited, and the specific climate factors controlling whitebark pine growth and distribution in the southern Coast Mountains remain unknown.

Whitebark pine is currently facing a number of threats across its range, including climate change (Hamann and Wang, 2006; Wang et al., 2012a), white pine blister rust infections (*Cronartium ribicola* J. C. Fisch.; Campbell and Antos, 2000; Zeglen, 2002), mountain pine beetle outbreaks (*Dendroctonus ponderosae* Hopkins; Meddens et al., 2012), and fire exclusion and suppression (Murray et al., 2000; Campbell and Antos, 2003). Due to these threats, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) assessed and designated whitebark pine as Endangered in 2010. As the rapid decline of the tree became evident across its range over the past two decades, studies of whitebark pine increased, though maritime whitebark pine communities remain largely unstudied (Larson and Kipfmueller, 2012). We ask the following question: What climate parameters limit the annual radial growth of whitebark pine in the distinctive maritime band of distribution contained within the southern Coast Mountains? This research is vital to our understanding of the basic climate factors influencing the growth of an endangered species in the southern Coast Mountains of B.C. Before we can understand the ability of whitebark pine populations to respond to future climate change and the other threats facing the species, we must first understand the climate controls that shape populations in this setting, and how or if they differ from those of well-studied continental populations.

STUDY AREA

Field work was conducted near the western boundary of whitebark pine's range in the southern Coast Mountains of B.C. (Fig. 1) during July and August of 2011 and 2012. The study area covers the transition from the coastal maritime to interior continental climate. The western end of the study area, Pemberton, B.C. (50.317°N, 122.797°W), receives an annual average precipitation of 955 mm. Lillooet (50.686°N, 121.936°W), at the drier, eastern end of the study area, receives an annual average precipitation of 330 mm (Environment Canada, 2012).

To create a whitebark pine chronology representative of regional-scale growth variability, we collected tree rings at four study site locations: Blowdown Pass, Downton Creek, McGillivray Pass, and Texas Creek (Fig. 1). The study sites were chosen based on the presence of healthy, mature stands of upright whitebark pine, as well as the expectation that trees growing near their altitudinal limits exhibit maximum climate sensitivity (Cook and Kairiukstis, 1990). All stands were mixed species (whitebark pine with other alpine species: subalpine fir and occasionally Engelmann spruce), open-canopy patches growing above continuous treeline at approximately 2000–2100 m elevation on steep, southerly aspects (Table 1). Whitebark pine is generally a minor component of stands in the wetter Coast Mountains and is typically found in large numbers only on southerly aspects (Arno and Hoff, 1989). Trees were young (generally less than 120 years at diameter at breast height [dbh]) and understory vegetation was dominated by herbaceous species including *Phlox diffusa* Benth., *Arenaria capillaris* Poir., and *Artemisia norvegica* Fr.
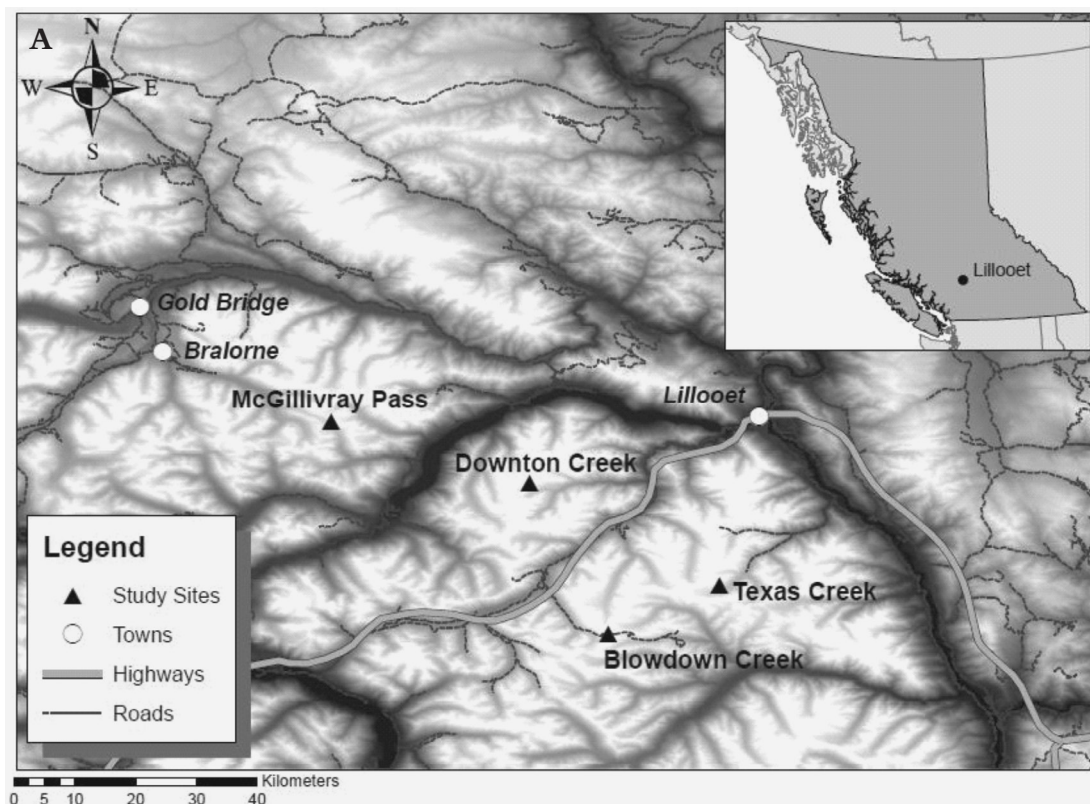
FIGURE 1. (A) Location of the four study sites in the southern Coast Mountains of British Columbia. Lighter areas are mountain tops and darker areas are rivers and valley bottoms. Inset map shows the location of Lillooet (50.686°N, 121.936°W) in British Columbia. Detailed locations of all sites are found in Table 1. (B) Photograph of whitebark pine at Texas Creek. Each site shared similar open-canopy and herbaceous groundcover characteristics.

METHODS

Tree-Ring Data

Tree core samples were extracted from whitebark pine trees throughout each stand during July and August 2012. Mature upright trees with no visible signs of disease or damage were selected for sampling. One core was taken per tree at breast height using a 5.2 mm increment borer. A total of 20–23 cores were collected per site based on stand size and mature whitebark pine availability, for a total of 85 cores. Cores were stored in plastic drinking straws and dried before being processed in the lab (Stokes and Smiley, 1964).

Dried cores were mounted on slotted boards and progressively sanded to a 600-grit finish using a belt sander.

TABLE 1

Study site locations and characteristics. Mean annual precipitation (MAP), mean annual temperature (MAT), and precipitation-as-snow (PAS) come from the ClimateWNA 1961–1990 climate normals.

Site	Location	MAP (mm)	MAT (°C)	PAS (mm)	Elevation (m)	Aspect (°)	Slope (%)
Blowdown Pass	50.3656°N, 122.1591°W	1055	−0.9	795	2105	202	70
Downton Creek	50.5881°N, 122.2749°W	1169	−0.9	857	2104	194	50
McGillivray Pass	50.6796°N, 122.5681°W	1249	−0.2	880	1963	200	75
Texas Creek	50.4358°N, 121.9950°W	905	−0.9	665	2115	158	60

Ring widths were measured to 0.01 mm using a Velmex measuring system and MeasureJ2X software (v4.2, 2010). Tree-ring measurement series (measurements from one tree core) were cross-dated visually (list method; Yamaguchi, 1991) and verified statistically using the program COFECHA 3.0 (Holmes et al., 1986; Grissino-Mayer, 2001). Interseries correlations (r) were calculated over 30-year intervals with a 15-year overlap and are statistically significant at the 0.01 level (Grissino-Mayer, 2001). Tree-ring records were cross-dated—or pattern matched—at the site level, and then across sites. Twenty-four series that could not be cross-dated were omitted from the analysis, for a remaining total of 61 series. The removed samples had nonuniform tracheid orientation along the length of the tree core due to sample twisting, making ring boundaries too indistinct for confident cross-dating.

A regional whitebark pine chronology was developed from tree-ring width data collected at the four study sites using the R package dplR (R Development Core Team, 2011; Bunn, 2008). Radial tree-growth data are often characterized by an age-related growth trend that obscures climate-related growth variability (Cook and Kairiukstis, 1990). To remove this trend, a 60-year cubic smoothing spline was applied to each measurement series, producing dimensionless ring-width indices. Analysis of the autocorrelation function indicated that growth in the current year is significantly influenced by conditions in previous years. Because this persistence is most likely related to biological growth processes rather than climate influences persisting for multiple years, an autoregressive (AR) model was fit to each series to estimate and remove autocorrelation. The resulting residual chronology maximizes the climate-related tree-ring variability of interest in this study (Cook and Kairiukstis, 1990). The AR model order was defined by minimizing the Akaike Information Criterion (AIC; Cook and Kairiukstis, 1990). Series were combined by a bi-weight robust mean estimation that minimizes the influence of outliers (Mosteller and Tukey, 1977). The hypothetical growth signal is an estimate of the extent that a tree-ring chronology compiled from a finite number of trees represents a hypothetically perfect tree-ring chronology compiled from an infinite number of trees (Wigley et al., 1984). The expressed population signal (EPS) provides a measure of the adequacy of the sample size (tree-ring series) for capturing the hypothetical population growth signal (Wigley et al., 1984). We calculated EPS with a 30-year window length and 15-year window overlap and truncated the chronology where EPS fell below a threshold value of 0.80 (Wigley et al., 1984; Fig. 2).

Climate Data

To evaluate growth-limiting climate factors, we acquired total monthly precipitation-as-snow (PAS), total monthly precipitation, and mean monthly temperature data that we estimated on the coordinates of each study site using the program ClimateWNA (Wang et al., 2012b) and regionalized by averaging all four sites for the period 1901–2011 (Blasing et al., 1981). ClimateWNA downscales PRISM monthly climate data (Daly et al., 2002) and integrates historical climate data for the period 1901–2011 for a point location based on latitude, longitude, and elevation (Wang et al., 2012b). The software provides a resolution of 1 km², so each of our sites has its own data set. We used ClimateWNA data because data sets may be estimated on a specific study site and are often more accurate than nonadjacent station data in topographically complex environments (Wang et al., 2012b).

We also obtained data for climate teleconnection patterns known to affect the climate of the U.S. Pacific Northwest and adjacent Canada. The Pacific Decadal Oscillation (PDO) is a long-term climate pattern varying at decadal scales that influences patterns of winter snowfall in the U.S. Pacific Northwest and adjacent Canada (Mantua and Hare, 2002). Negative values of the PDO are associated with cooler winter temperatures, higher precipitation, and greater snowpack accumulations. Monthly mean records for the PDO were accessed from the Joint Institute for the Study of the Atmosphere and Ocean (JISAO, 2012) website. The El Niño Southern Oscillation (ENSO) affects climate in the Pacific Northwest
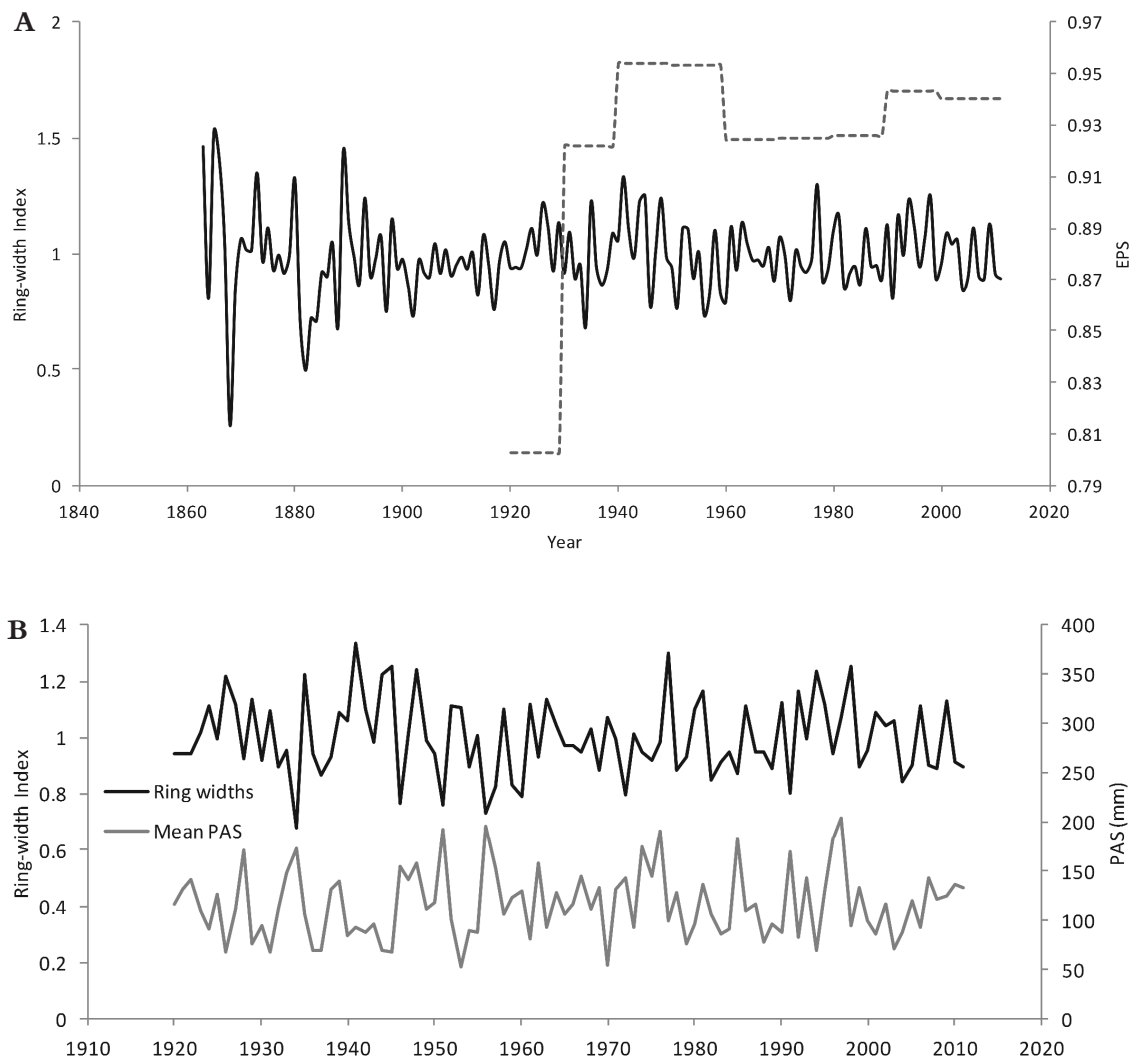
FIGURE 2. **(A) Time series plot of the regional ring-width index (*n* = 61) showing that the expressed population signal (EPS) falls below 0.80 at 1920. (B) Time series of EPS-truncated regional ring widths and mean autumn (previous October through previous December) precipitation–as–snow (PAS).**

and adjacent Canada at interannual scales. Cool phases of ENSO (La Niña) are characterized by cool, wet winters in the Pacific Northwest and adjacent Canada, and warm phases of ENSO (El Niño) are generally warmer and drier (Shabbar et al., 1997). The strength of El Niño and La Niña years was based on NOAA Multivariate ENSO Index ranks (http://www.esrl.noaa.gov/psd/enso/mei/). Modes of climatic variability described by the PDO and ENSO are strongest during the winter months, affecting snowfall patterns in the study area (Kiffney et al., 2002).

Assessment of Tree-Ring–Climate Relationships

Pearson's correlations were used to test relationships between various tree-ring and climate time series in

this study for the period 1920–2011. Where necessary, effective sample sizes were used to adjust for autocorrelation in testing correlations for significance (Dawdy and Matalas, 1964). Correlations and partial correlations were used to evaluate association of tree-ring widths with monthly and seasonalized PAS, mean temperature, and total precipitation data, in current and previous years, using the program Seascorr (Meko et al., 2011). Seascorr estimates the significance of sample correlations and partial correlations by a Monte Carlo method (Meko et al., 2011). Correlations were tested for 112 distinct months/seasons of climate data. 1-, 3-, 6-, and 12-month periods were used, ending in each month of the 14-month period bound by August of the year prior to current year ring formation and September of the current year of growth. This 14-month period was se-

TABLE 2

Regional whitebark pine chronology statistics. EPS is the expressed population signal.

Number of cores	Number of years	Period	Interseries correlation	Mean Sensitivity	Unfiltered Auto-correlation[a]	Filtered Auto-correlation[b]	EPS[c]
61	149	1863–2011	0.469	0.249	0.740	−0.010	1920

[a]Autocorrelation coefficient prior to detrending.
[b]Autocorrelation coefficient after detrending.
[c]Point where the EPS falls below 0.8 and the chronology is truncated.

lected to include a full water year and prior and current summer months. This allowed us to evaluate both traditional water-season and energy-season growth responses (Fritts, 1976). A difference-of-correlations test that employs a Fisher's Z transformation of correlations (Snedecor and Cochran, 1989) was used to assess the temporal stability of tree-ring–climate relationships in nonoverlapping subperiods of the data ("early" and "late" subperiods, partitioned in halves). This test was important because growth-limiting climate relationships should theoretically hold true over the long term (Cook and Kairiukstis, 1990). Trends in all tree-ring and climate data were tested using a *t*-test of the slope of a regression of the time series over time. Because PAS = 0 in June through August, relationships of tree growth to snow in those months, and seasons including those months, were not evaluated. The strongest monthly or seasonal correlation with PAS as determined with Seascorr was used to create a seasonal PAS variable for subsequent analyses.

We used two methods to evaluate relationships between the tree-ring width and seasonal PAS record, and relevant climate teleconnection patterns for the period 1920–2011. A chi-square test of proportions was used to determine whether the proportion of years with below-median or above-median (1) ring widths, and (2) seasonal PAS during strong El Niño/La Niña years equals the proportion of years with below-median or above-median (1) ring widths, and (2) seasonal PAS during weak or non–El Niño/La Niña years. The previously described difference-of-correlations test was used to test for differences in the strength and direction of the correlations of the tree ring and seasonal PAS records with winter PDO (October–March) during the cool (1951–1976) versus warm (1977–1998) phases of the most recent clearly detected PDO shift in western Canada (Whitfield et al., 2010).

RESULTS

The first-order autocorrelation coefficients in Table 2 indicate the detrending procedure effectively reduced persistence in the tree-ring data sets. Coefficients in the raw measurement series are variable, suggesting persistence is related to biological growth processes such as needle retention and energy storage, rather than climate (Cook and Kairiukstis, 1990). Tree-ring width measurement series across the four sample sites showed an average intercorrelation level for whitebark pine in North America (mean series *r* = 0.469), justifying the development of the regional whitebark pine chronology (Table 2; number of series = 61, number of trees = 61, average mean sensitivity = 0.25, chronology interval = 1920–2011). Of the climate variables that were tested, whitebark pine annual radial growth in the study region is most strongly correlated with PAS in the October through December season of the year prior to growth ($r = -0.50$, $p = 0.01$, Figs. 2–4). Relationships with PAS weaken after December, and partial correlations suggest temperature has no significant impact on growth that is independent from the PAS influence during the prior autumn (Fig. 4). Radial growth is also significantly correlated with PAS in those three single months, and in no other single month ($p = 0.01$, Fig. 4). The October through December PAS data were therefore summed to generate a "prior-autumn PAS" data set for further testing. Tree-ring widths are also more weakly negatively associated with seasonalized precipitation throughout the year, but single-month correlations occur only in the autumn prior to growth (October and November, both $r = -0.28$, $p = 0.01$).

Radial growth exhibits secondary sensitivity to prior autumn and winter mean temperatures when total precipitation is controlled for in a partial correlation test, for example most strongly in September through February ($r_{T.P} = 0.47$, $p < 0.01$). The influence of temperature is much weaker when PAS is controlled for (Fig. 4). Notably, no strong relationships exist with growing season climate variables, including temperature (Fig. 4). The maximum seasonal or monthly summer temperature partial correlation is $r = 0.23$, $p = 0.01$, and seasonal temperature correlation values diminish as summer months are incorporated over time (Fig. 4). Difference-of-correlations tests showed that all significant monthly and seasonal correlations among tree-ring and climate data were tempo-
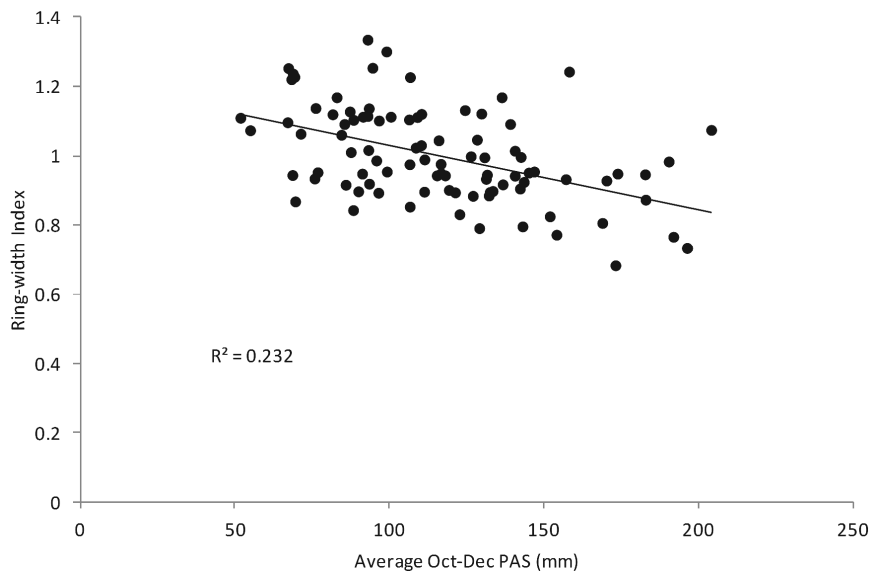
FIGURE 3. Scatterplot of the negative correlation between regional annual ring widths and autumn (previous October through December) PAS.
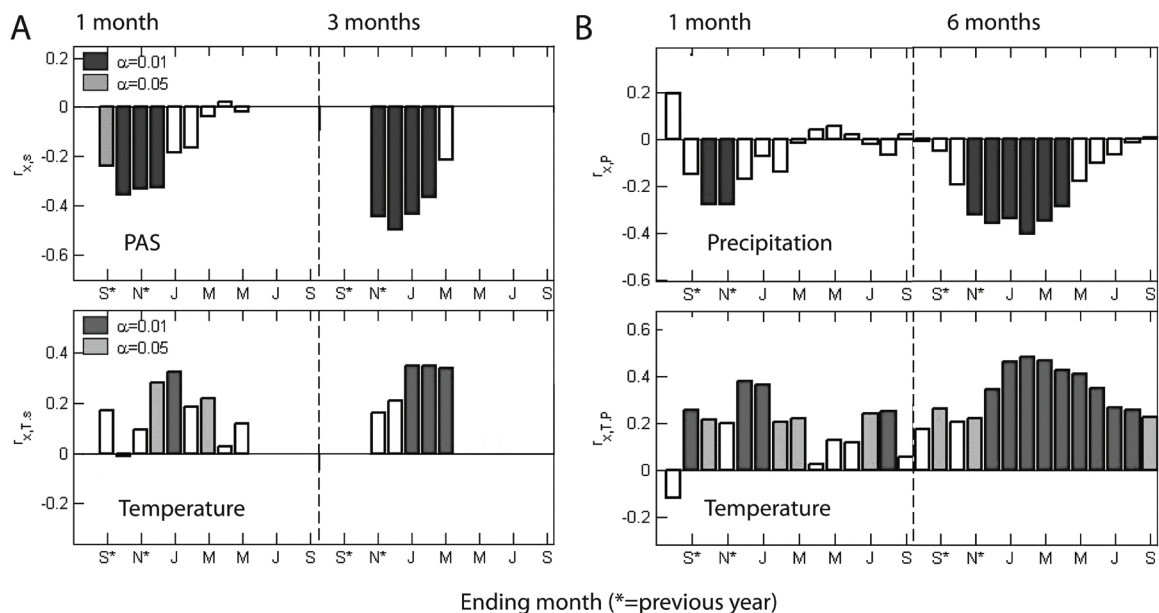

FIGURE 4. Single-month and strongest seasonal correlations (top) and partial correlations (bottom) of the whitebark pine chronology with total PAS, mean temperature, and total precipitation data (1920–2011). Note that the *y*-axes have different scales. (A) Correlations with PAS (top) and partial correlations with mean temperature that are independent from the influence of PAS (bottom). Months and seasons that are not plotted could not be evaluated due to a lack of data. The strongest correlation with PAS is during prior October through December, and the strongest partial correlation with temperature is during December through February. (B) Correlations with precipitation (top) and partial correlations with mean temperature that are independent from the influence of precipitation (bottom). The strongest correlation with PAS is during prior October through December and the strongest partial correlation with temperature is during December through February. Note the overall absence of temperature sensitivity during the growing season, with the strongest single or seasonal summer correlation being $r = 0.23$ ($p < 0.01$).

rally stable across early and late subperiods (for October through December PAS: early period $r = 0.62$, late period $r = –0.35$, $N_1 = 45$, $N_2 = 45$, $p = 0.10$).

The proportions of above- or below-median tree-ring widths or winter PAS were not significantly dif-ferent during strong El Niño years relative to weak and non–El Niño years. This was also the case for strong La Niña years relative to weak and non–La Niña years (Table 3). In general, narrow rings were associated with lower ENSO ranks (La Niña), and wider rings were as-

sociated with higher ENSO ranks (El Niño; Fig. 5). The narrowest ring of the chronology was associated with a strong La Niña event; however, many of the other narrowest rings were not (Fig. 5). The widest ring of the chronology was not associated with an El Niño event, though many of the other widest rings were (Fig. 5). Both tree-ring widths and winter PAS were significantly influenced by winter PDO conditions, positively and negatively, respectively (Table 4). Analysis of subperiods suggests that this influence is stronger during cool phases of the oscillation, although the difference-of-correlations test between subperiods was only significant for the winter PAS data.

Discussion

We present evidence that snowfall antecedent to the growing season negatively impacts whitebark pine growth in the maritime band of the species' distribution, a climate-growth response that has not been observed in studies conducted on older trees in other parts of the species' range. Specifically, in B.C.'s Coast Mountains, whitebark pine growth is most strongly influenced by PAS in the autumn prior to growth, is sensitive to total precipitation only in the prior autumn when it likely falls as snow, and is uncorrelated with monthly PAS or precipitation during winter, spring, or summer (Fig. 4). Prior autumn- and winter-season temperature influences growth, but this influence is only significant when PAS-temperature interactions are not accounted for (Fig. 4). The sensitivity of whitebark pine growth to autumn and winter temperature is therefore likely an artefact of the role of temperature in determining whether precipitation falls as rain or snow, and by extension, in determining snowpack dynamics. There was no indication that moisture from spring snowmelt promotes annual growth of whitebark pine in the Coast Mountains, and positive correlations with the summer climate variables that typically govern radial growth were weak and inconsistent. Taken together, we interpret these results to suggest that previous autumn snowfall is the primary determinant of whitebark pine annual radial growth in the study region. This climate-growth relationship has been temporally consistent over 91 years (1920–2011).

In the southern Coast Mountains regional snowpack depths are moderated by temperature and storm patterns, influenced at interannual and decadal scales by large-scale climate patterns, including the PDO and ENSO. The relationships we observed between PDO, tree rings, and PAS are consistent with antecedent snowfall-related limitation of whitebark pine growth. Cool phases of the PDO are associated with greater

TABLE 3

Test of proportions assessing the association of whitebark pine ring widths and October–December PAS with strongest El Niño and La Niña events over the period 1950–1990. Test calculated using function prop.test in R. Proportions of years in each ring width or PAS category are in parentheses. For all tests, the null hypothesis that groups have the same true proportions could not be rejected, *p*-values ranged from 0.51 to 0.92.

| Ring-width category	# El Niño years	# weak and non-El Niño years
Below median	10 (52.6%)	22 (51.2%)
Above median	9 (47.4 %)	21 (48.8%)
Total	19 (100%)	43 (100%)
	# La Niña years	# weak and non-La Niña years
Below median	11 (57.9%)	21 (48.8%)
Above median	8 (42.1%)	22 (51.2%)
Total	19 (100%)	43 (100%)
PAS category	# El Niño years	# weak and non-El Niño years
Below median	10 (52.6%)	21 (48.8%)
Above median	9 (47.4%)	22 (51.2%)
Total	19 (100%)	43 (100%)
	# La Niña years	# weak and non-La Niña years
Below median	9 (47.4%)	22 (51.2%)
Above median	10 (52.6%)	21 (48.8%)
Total	19 (100%)	43 (100%)
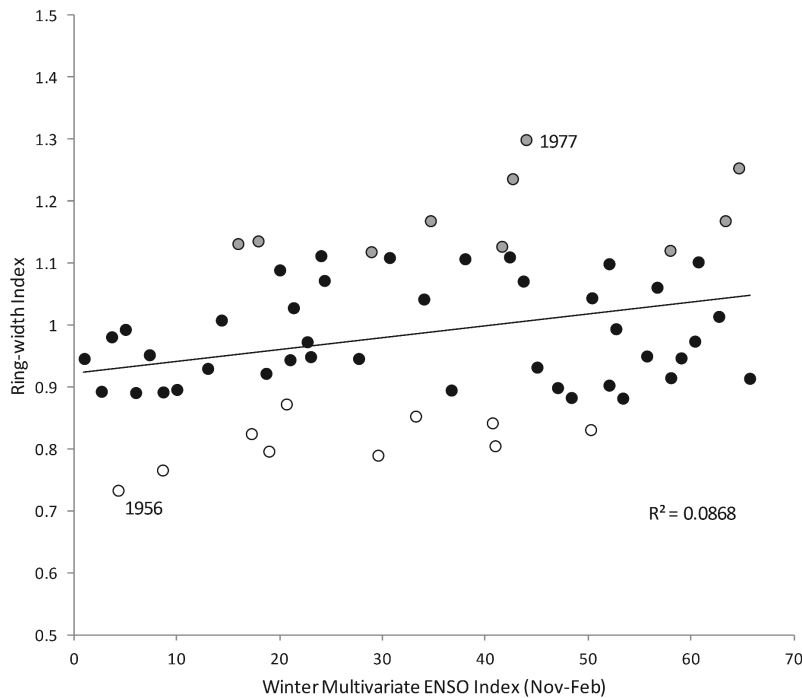
FIGURE 5. Scatterplot showing the relationship between tree-ring widths and winter (previous November through current February) multivariate El Niño Southern Oscillation (ENSO) index. Low values (1–13) of the ENSO index represent strong to moderate La Niña events, with the lowest value corresponding to the strongest La Niña. High values (54–66) of the index represent moderate to strong El Niño events, with the highest value corresponding to the strongest El Niño. The 10 narrowest rings from the chronology are shown in white, and the 10 widest rings are shown in gray. All other rings are shown in black. The overall narrowest ring and widest ring of the chronology are denoted by the year in which growth occurred.

snowfall, shorter growing season lengths, and reduced radial growth in various alpine conifers throughout the U.S. Pacific Northwest and adjacent Canada (Mantua and Hare, 2002; Koch et al., 2004; Starheim et al., 2013). Although snowpack depths are typically greater during La Niña years (Shabbar et al., 1997), we found no statistically significant influence of ENSO on either tree-ring widths or PAS. This may have been due to the short chronology length (91 years).

In Pacific maritime climates, deep or early snowfall often results in a dependence of high-elevation conifer growth on the length of the snow-free season, which is in turn a function of total annual snow depth and winter-through-summer air temperatures (Graumlich, 1993; Peterson and Peterson, 1994, 2001; Ettl and Peterson, 1995; Peterson et al., 2002; Coulthard et al., 2016). While the timing of tree-growth sensitivity to snow in

the prior autumn is unusual, the influence of conditions in the preceding autumn and winter on growing-season radial growth is well established in temperate alpine conifers (Peterson and Peterson, 1994, 2001; Ettl and Peterson, 1995; Gedalof and Smith, 2001; Peterson et al., 2002; Koch et al., 2004; Coulthard and Smith, 2015). We suggest prior autumn snowfall may negatively influence whitebark pine growth by truncating the prior growing season and inhibiting physiological preparedness for growth in the following year. While alpine conifers have a limited growth period—typically June through September (Fritts, 1966)—radial growth in most pines can be maintained well into autumn (Dougherty et al., 1994), and various physiological growth processes may be affected by environmental conditions at that time (Dougherty et al., 1994). In this case, the termination of the prior growing season by early snowfall and soil

TABLE 4

Associations of whitebark pine ring widths and October–December PAS with instrumental winter Pacific Decadal Oscillation (PDO) variability.

	Full period	Cool phase	Warm phase	N_1, N_2[a]	p[b]
Whitebark pine chronology	$r = 0.45$ ($p < 0.05$)	$r = 0.58$ ($p < 0.05$)	$r = 0.24$ ($p < 0.05$)	26, 22	0.18
PAS	$r = -0.48$ ($p < 0.0$)	$r = -0.72$ ($p < 0.05$)	$r = -0.25$ ($p < 0.05$)	26, 22	0.04

[a]Effective sample sizes for early and late periods.
[b]p-value for a test of the null hypothesis that the population sample correlations for the cool and warm phases are the same. Significant where $p < 0.05$.
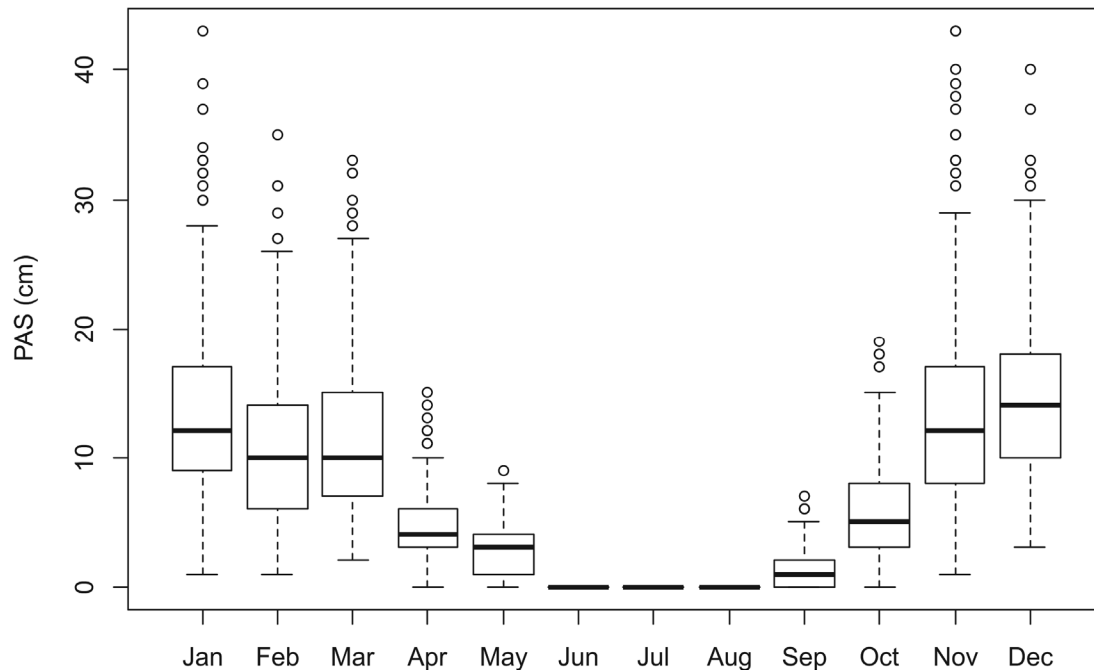
FIGURE 6. Box and whiskers plot of regionalized average monthly precipitation–as–snow (PAS). PAS data is from ClimateWNA for the period 1901–2011.

cooling likely reduces photosynthate storage for the following year (Fritts, 1976). The onset of winter conditions may also reduce mycorrhizal activity (Peterson and Peterson, 1994) and prevent proper maturation of leaf tissue and the cuticle leading to greater transpiration (Sowell et al., 1982). Comparable results were found in a study of treeline pine species at three varied latitudes (Mexico, Switzerland, and northern Sweden), where falling autumn temperatures inhibited the transfer of carbon into radial growth and subsequent storage of carbon for the following year, and cool soils limited the processes involved in tissue formation (Hoch and Körner, 2003).

A second possible explanation is that snowfall in the autumn months plays a disproportionate role in determining overall annual snow depth, the timing of snowmelt and soil warming in the following spring, and the length of the subsequent growing season. Although a substantial portion of annual snowfall occurs during autumn (an average of 81 cm falls between September and May and an average of 35 cm falls during October through December; Fig. 6), we consider this mechanism less likely given the absence of correlations with total annual or maximum spring PAS.

It is not known whether sensitivity to prior autumn snowfall is related to the younger ages of the trees growing in the Coast Mountains. Whitebark pine sampled from more interior locations were much older than the cen-

tenarian trees we sampled (Perkins and Swetnam, 1996; Larocque and Smith, 2005; Kipfmueller, 2008; Youngblut and Luckman, 2013). In general, young trees have lower carbohydrate storage capacity than mature trees (Dougherty et al., 1994), which could make them more susceptible to unfavorable conditions and shorter growing seasons. The sensitivity to prior autumn snow could also be due to earlier timing or greater autumn snowfall quantities in the Coast Mountains relative to interior sites.

Three different General Circulation Models (GCMs) applied to western North America predict warmer and wetter conditions in the coming decades, and drastically reduced snowpack is projected in the southern Coast Mountains by the 2080s (Wang et al., 2012b). Our results suggest that, at least initially, warmer temperatures may benefit whitebark pine in the study region by stalling soil cooling during autumn and/or reducing spring snow depths. Wetter conditions in the Coast Mountains could have negative consequences for whitebark pine populations if they promote early autumn snowfall, but it is more likely that warming temperatures will cause autumn precipitation to fall as rain (Wang et al., 2012b).

Too little snowpack may eventually limit tree growth through the loss of protection from freezing and wind scouring during the winter (Pederson et al., 2004; McLane and Aitken, 2012). With predicted warmer temperatures and reduced snowpack, whitebark pine

in the southern Coast Mountains could also shift from being negatively impacted by snow to becoming water limited (Littell et al., 2010; Marcinkowski et al., 2015), such that coastal populations may more closely resemble continental populations in the future. It is important to note that the impact of disease, pests, and increased competition (as less-tolerant species become established or species from lower elevations migrate upward) on whitebark pine might lead to reduced annual growth in parts of its range, even if climate becomes more favorable (Kipfmueller and Salzer, 2010; Littell et al. 2010).

Conclusions

Our results suggest that the annual radial growth of whitebark pine trees in the southern Coast Mountains of B.C. has been limited by the negative influence of snowfall in autumn of the year prior to the growing season over the past nine decades. Whitebark pine tree-ring width records developed for this study are most strongly negatively correlated with autumn PAS data in the year prior to growth, and other significant tree-growth–climate correlations and connections with the PDO are also consistent with conditions that promote enhanced snowfall. The growth-climate relationship likely arises from truncation of the prior growing season by early snowfall and soil cooling, which impedes physiological preparedness for growth in the following year. Our findings emphasize a difference between the growth characteristics of relatively young whitebark pine in a maritime alpine area and widely studied continental populations where energy limitation related to summer temperature fluctuations, and moisture limitation related to spring/summer snow meltwater availability, are documented. It is unknown whether the dissimilarity of this climatic response is because of unique snowpack depth and timing characteristics in the Coast Mountains, the young ages of the Coast Mountain whitebark pine trees, or some other factor. The dissimilar climate response of the trees analyzed in this study may suggest that maritime trees will be affected differently by a shifting climate in coming decades. More local-scale studies should be used in place of general species-wide approaches when developing management and restoration plans for whitebark pine in different parts of its range.

Acknowledgments

References Cited

Albright, W. L., and Peterson, D. L., 2013: Tree growth and climate in the Pacific Northwest, North America: a broad-scale analysis of changing growth environments. *Journal of Biogeography*, 40: 2119–2133.

Arno, S. F., and Hoff, R. J., 1989: *The Silvics of Whitebark Pine* (Pinus albicaulis). USDA Forest Service General Technical Report INT-253.

Blasing, T. J., Duvick, D. N., and West, D. C., 1981: Dendroclimatic calibration and verification using regionally averaged and single station precipitation data. *Tree-Ring Bulletin*, 41: 37–43, http://hdl.handle.net/10150/261056.

Bunn, A. G., 2008: A dendrochronology program library in R (dplR). *Dendrochronologia*, 26: 115–124.

Callaway, R. M., 1998: Competition and facilitation on elevation gradients in subalpine forests of the Northern Rocky Mountains, U.S.A. *Oikos*, 82: 561–573.

Campbell, E. M., and Antos, J. A., 2000: Distribution and severity of white pine blister rust and mountain pine beetle on whitebark pine in British Columbia. *Canadian Journal of Forest Research*, 30: 1051–1059.

Campbell, E. M., and Antos, J. A., 2003: Postfire succession in *Pinus albicaulis–Abies lasiocarpa* forests of southern British Columbia. *Canadian Journal of Botany*, 81: 383–397.

Cook, E. R., and Kairiukstis, L. A., 1990: *Methods of Dendrochronology: Applications in the Environmental Sciences*. Dordrecht: Kluwer Academic Publishers, 394 pp.

COSEWIC, 2010: Assessment and Status Report on the whitebark pine (*Pinus albicaulis*) in Canada. Committee on the Status of Endangered Wildlife in Canada, http://www.sararegistry.gc.ca/virtual_sara/files/cosewic/sr_Whitebark%20Pine_0810_e.pdf, accessed 13 May 2013.

Coulthard, B., and Smith, D. J., 2015: A 477-year dendrohydrological assessment of drought severity for Tsable River, Vancouver Island, British Columbia, Canada. *Hydrological Processes*, doi: http://dx.doi.org/10.1002/hyp.10726.

Coulthard, B., Smith, D. J., and Meko, D. M., 2016: Is worst-case scenario streamflow drought underestimated in British Columbia? A multi-century perspective for the south coast, derived from tree-rings. *Journal of Hydrology*, 534: 205–218.

Daly, C., Gibson, W. P., Taylor, G. H., Johnson, G. L., and Pasteris, P., 2002: A knowledge-based approach to the statistical mapping of climate. *Climate Research*, 22: 99–113.

Dawdy, D. R., and Matalas, N. C., 1964: Statistical and probability analysis of hydrologic data, part III: analysis of variance, covariance and time series. *In* Chow, V. T. (ed.), *Handbook of Applied Hydrology: a Compendium of Water-Resources Technology*. New York: McGraw-Hill Book Company, 8.69–8.90.

Dougherty, P. M., Whitehead, D., and Vose, J. M., 1994: Environmental influences on the phenology of pine. *Ecological Bulletins*, 43: 64–75.

Environment Canada, 2012: National Climate Data and Information Archive. Environment Canada, http://climate.weatheroffice.gc.ca/Welcome_e.html, accessed 18 January 2012.

Ettl, G. J., and Peterson, D. L., 1995: Growth response of subalpine fir (*Abies lasiocarpa*) to climate in the Olympic Mountains, Washington, USA. *Global Change Biology*, 1: 213–230.

Franklin, J. F., and Dyrness, C. T., 1988: *Natural Vegetation of Oregon and Washington*. Corvallis, Oregon: Oregon State University Press, 464 pp.

Fritts, H. C., 1966: Growth-rings of trees: their correlation with climate. *Science*, 154: 973–979.

Fritts, H. C., 1976: *Tree Rings and Climate*. London: Academic Press Inc., 567 pp.

Gedalof, Z., and Smith, D. J., 2001: Dendroclimatic response of mountain hemlock (*Tsuga mertensiana*) in Pacific North America. *Canadian Journal of Forest Research*, 31: 322–332.

Graumlich, L. J., 1993: A 1000-year record of temperature and precipitation in the Sierra Nevada. *Quaternary Research*, 39: 249–255.

Graumlich, L. J., and Brubaker, L. B, 1986: Reconstruction of annual temperature (1590–1979) for Longmire, Washington, derived from tree rings. *Quaternary Research*, 25: 223–234.

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

Hamann, A., and Wang, T., 2006: Potential effects of climate change on ecosystem and tree species distribution in British Columbia. *Ecology*, 87: 2773–2786.

Hoch, G., and Körner, C., 2003: The carbon charging of pines at the climatic treeline: a global comparison. *Oecologia*, 135: 10–21.

Holmes, R. L., Adams, R. K., and Fritts, H. C., 1986: *Tree-Ring Chronologies of Western North America: California, Eastern Oregon and Northern Great Basin, with Procedures Used in the Chronology Development Work, Including User Manuals for Computer Programs COFECHA and ARSTAN*. Tucson, Arizona: University of Arizona, Laboratory of Tree-Ring Research, Chronology Series VI.

Hutchins, H. E., and Lanner, R. M., 1982: The central role of Clark's nutcracker in the dispersal and establishment of whitebark pine. *Oecologia*, 55: 192–201.

JISAO [Joint Institute for the Study of the Atmosphere and Ocean], 2012: Climate Data Archive. http://jisao.washington.edu/pdo/PDO.latest, accessed 18 January 2012.

Kiffney, P. M., Bull, J. P., and Feller, M. C., 2002: Climatic and hydrologic variability in a coastal watershed of southwestern British Columbia. *Journal of the American Water Resources Association*, 38: 1437–1451.

Kipfmueller, K. F., 2008: Reconstructed summer temperature in the Northern Rocky Mountains wilderness, USA. *Quaternary Research*, 70: 173–187.

Kipfmueller, K. F., and Salzer, M. W., 2010: Linear trend and climate response of five-needle pines in the western United States related to treeline proximity. *Canadian Journal of Forest Research*, 40: 134–142.

Koch, J., Menounos, B., Clague, J. J., and Osborn, G. D., 2004: Environmental change in Garibaldi Provincial Park, southern Coast Mountains, British Columbia. *Geoscience Canada*, 31: 127–135.

Larocque, S. J., and Smith, D. J., 2005: A dendroclimatological reconstruction of climate since AD 1700 in the Mt. Waddington area, British Columbia Coast Mountains, Canada. *Dendrochronologia*, 22: 93–106.

Larson, E. R., and Kipfmueller, K. F., 2012: Ecological disaster or the limits of observation? Reconciling modern declines with the long-term dynamics of whitebark pine communities. *Geography Compass*, 6(4): 189–214.

Littell, J. S., Oneil, E. E., McKenzie, D., Hicke, J. A., Lutz, J. A., Norheim, R. A., and Elsner, M. M., 2010: Forest ecosystems, disturbance, and climatic change in Washington State, USA. *Climatic Change*, 102: 129–158.

Luckman, B. H., Briffa, K. R., Jones, P. D., and Schweingruber, F. H., 1997: Tree-ring based reconstruction of summer temperatures at the Columbia Icefield, Alberta, Canada, AD 1073–1983. *The Holocene*, 7: 375–389.

Mantua, N. J., and Hare, S. R., 2002: The Pacific Decadal Oscillation. *Journal of Oceanography*, 58: 35–44.

Marcinkowski, K., Peterson, D. L., and Ettl, G. J., 2015: Nonstationary temporal response of mountain hemlock growth to climatic variability in the North Cascade Range, Washington, USA. *Canadian Journal of Forest Research*, 45: 676–688.

Mattson, D. J., and Reinhart, D. P., 1997: Excavation of red squirrel middens by grizzly bears in the whitebark pine zone. *Journal of Applied Ecology*, 34: 926–940.

McLane, S. C., and Aitken, S. N., 2012: Whitebark pine (*Pinus albicaulis*) assisted migration potential: testing establishment north of the species range. *Ecological Applications*, 22: 142–153.

Meddens, A. J. H., Hicke, J. A., and Ferguson, C. A., 2012: Spatiotemporal patterns of observed bark beetle-caused tree mortality in British Columbia and the western United States. *Ecological Applications*, 22: 1876–1891.

Meko, D. M., Touchan, R., and Anchukaitis, K. J., 2011: Seascorr: A MATLAB program for identifying the seasonal climate signal in an annual tree-ring time series. *Computers & Geosciences*, 37: 1234–1241.

Mosteller, F., and Tukey, J. W., 1977: *Data Analysis and Regression: a Second Course in Statistics*. Reading, Massachusetts: Addison-Wesley Series in Behavioral Science, Quantitative Methods, 588 pp.

Murray, M. P., Bunting, S. C., and Morgan, P., 2000: Landscape trends (1753–1993) of whitebark pine forests in the West Big Hole Range of Idaho/Montana, U.S.A. *Arctic, Antarctic, and Alpine Research*, 32: 412–418.

Pederson, N., Cook, E. R., Jacoby, G. C., Peteet, D. M., and Griffin, K. L., 2004: The influence of winter temperatures on the annual radial growth of six northern range margin tree species. *Dendrochronologia*, 22: 7–29.

Perkins, D. L., and Swetnam, T. W., 1996: A dendroecological assessment of whitebark pine in the Sawtooth-Salmon River region, Idaho. *Canadian Journal of Forest Research*, 26: 2123–2133.

Peterson, D. W., and Peterson, D. L., 1994: Effects of climate on radial growth of subalpine conifers in the North Cascade Mountains. *Canadian Journal of Forest Research*, 24: 1921–1932.

Peterson, D. W., and Peterson, D. L., 2001: Mountain hemlock growth responds to climatic variability at annual and decadal time scales. *Ecology*, 82: 3330–3345.

Peterson, D. W., Peterson, D. L., and Ettl, G. J., 2002: Growth responses of subalpine fir to climatic variability in the Pacific Northwest. *Canadian Journal of Forest Research*, 32: 1503–1517.

Pyatt, J. C., Tomback, D. F., Blakeslee, S. C., Wunder, M. B., Resler, L. M., Boggs, L. A., and Bevency, H. D., 2016: The importance of conifers for facilitation at treeline: comparing biophysical characteristics of leeward microsites in whitebark pine communities. *Arctic, Antarctic, and Alpine Research*, 48: 427–444.

R Development Core Team, 2011: *R: a Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing, http://www.R-project.org/.

Resler, L. M., Shao, Y., Tomback, D. F., and Malanson, G. P., 2014: Predicting functional role and occurrence of whitebark pine (*Pinus albicaulis*) at alpine treelines: model accuracy and variable importance. *Annals of the Association of American Geographers*, 104: 703–722.

Shabbar, A., Bonsal, B., and Khandekar, M., 1997: Canadian precipitation patterns associated with the Southern Oscillation. *Journal of Climate*, 10: 3016–3027.

Snedecor, G. W., and Cochran, W. G., 1989: *Statistical Methods*. 8th edition. Ames, Iowa: Iowa State University Press, 503 pp.

Sowell, J. B., Koutnik, D. L., and Lansing, A. J., 1982: Cuticular transpiration of whitebark pine (*Pinus albicaulis*) within a Sierra Nevadan timberline ecotone, U.S.A. *Arctic and Alpine Research*, 14: 97–103.

Starheim, C. C. A., Smith, D. J., and Prowse, T. D., 2013: Multi-century reconstructions of Pacific salmon abundance from climate-sensitive tree rings in west central British Columbia, Canada. *Ecohydrology*, 6: 228–240.

Stephenson, N. L., 1990: Climatic control of vegetation distribution: the role of the water balance. *American Naturalist*, 135: 649–670.

Stephenson, N. L., 1998: Actual evapotranspiration and deficit: biologically meaningful correlates of vegetation distribution across spatial scales. *Journal of Biogeography*, 25: 855–870.

Stokes, M. A., and Smiley, T. L., 1964. *An Introduction to Tree-Ring Dating*. Chicago: University of Chicago Press, 73 pp.

Tomback, D. F., 1982: Dispersal of whitebark pine seeds by Clark's nutcracker: a mutualism hypothesis. *Journal of Animal Ecology*, 51: 451–467.

Wang, T., Campbell, E. M., O'Neill, G. A., and Aitken, S. N., 2012a: Projecting future distributions of ecosystem climate niches: uncertainties and management implications. *Forest Ecology and Management*, 279: 128–140.

Wang, T., Hamman, A., Spittlehouse, D. L., and Murdock, T. Q., 2012b: ClimateWNA—High resolution spatial climate data for western North America. *Journal of Applied Meteorology and Climatology*, 51: 16–29.

Whitfield, P. H., Moore, R. D., Fleming, S. W., and Zawadzki, A., 2010: Pacific Decadal Oscillation and the hydroclimatology of western Canada—Review and prospects. *Canadian Water Resources Journal*, 35: 1–28.

Wigley, T. M. L., Briffa, K. R., and Jones, P. D., 1984: On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. *Journal of Climate and Applied Meteorology*, 23: 201–213.

Yamaguchi, D. K., 1991: A simple method for cross-dating increment cores from living trees. *Canadian Journal of Forest Research*, 21: 414–416.

Youngblut, D. K., and Luckman, B. H., 2013: Evaluating the temperature sensitivity of radial growth patterns from whitebark pine in the western Canadian Cordillera. *Dendrochronologia*, 31: 16–28.

Zeglen, S., 2002: Whitebark pine and white pine blister rust in British Columbia, Canada. *Canadian Journal of Forest Research*, 32: 1265–1274.