

Article

# Site- and Species-Specific Influences on Sub-Alpine Conifer Growth in Mt. Rainier National Park, USA

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**Abstract:** Identifying the factors that influence the climate sensitivity of treeline species is critical to understanding carbon sequestration, forest dynamics, and conservation in high elevation forest/meadow ecotones. Using tree cores from four sub-alpine conifer species collected from three sides of Mt. Rainier, WA, USA, we investigated the influences of species identity and sites with different local climates on radial growth–climate relationships. We created chronologies for each species at each site, determined influential plant-relevant annual and seasonal climatic variables influencing growth, and investigated how the strength of climate sensitivity varied across species and location. Overall, similar climate variables constrained growth on all three sides of the mountain for each of the four study species. Summer warmth positively influenced radial growth, whereas snow, spring warmth, previous summer warmth, and spring humidity negatively influenced growth. We discovered only a few subtle differences in the climate sensitivity of co-occurring species at the same site and between the same species at different sites in pairwise comparisons. A model including species by climate interactions provided the best balance between parsimony and fit, but did not lead to substantially greater predictive power relative to a model without site or species interactions. Our results imply that at treeline in moist temperate regions like Mt. Rainier, the same climatic variables drive annual variation in growth across species and locations, despite species differences in physiology and site differences in mean climates.

**Keywords:** high elevation conifers; climate sensitivity; tree rings; climatic context; Mt. Rainier National Park; Washington

## 1. Introduction

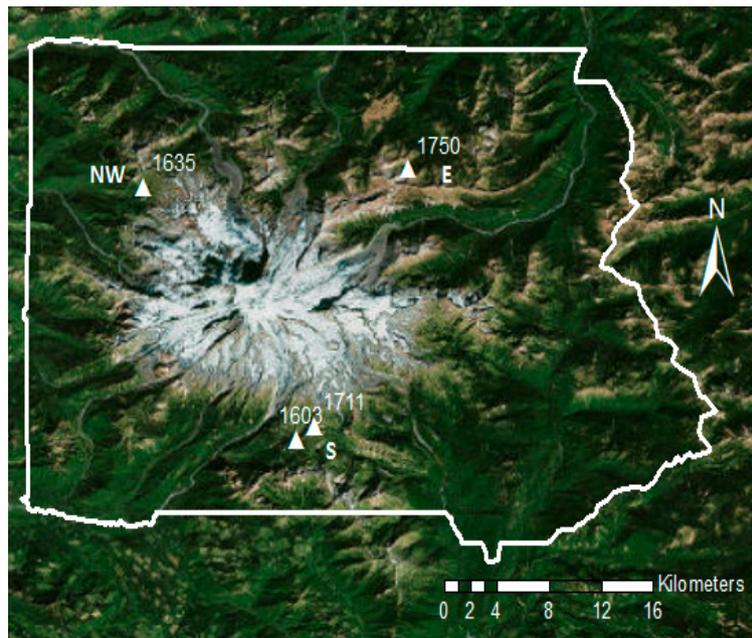
Climate change is expected to affect alpine and sub-alpine areas [1–4] and forecasting changes to these areas is critical for natural resource management and conservation. On a warming planet where multiple aspects of climate are changing [5], climate sensitivities that differ among sub-alpine tree species could result in differing growth responses. Since sub-alpine trees set the important forest/meadow ecotone at high elevations [4], the drivers of variability in climate–growth responses of sub-alpine tree species may therefore have particular significance for ecosystem function, resource management and conservation (e.g., the amount of carbon stored in trees, the upslope movement of treeline, conversion of alpine habitat to forests). For example, high mountain meadows are species rich (e.g., [6,7]), and—due to their isolation from each other, and the shape of mountains—are likely to decrease in area if sub-alpine tree growth increases greatly with climate warming. This may have negative consequences for the plants and animals associated with high mountain meadows.

Additionally, larger scale ecosystem functions may be strongly influenced by the position of treeline, especially in the Pacific Northwest, where forests hold large amounts of carbon [8]. Finally, high mountain meadows in parks receive high recreational visitation, thus, changes to the extent of and diversity in mountain meadows could have impacts on the experience of visitors to protected natural areas [9]. In short, understanding the factors that impact climate sensitivity of trees is critical in order to be prepared for future changes at the community or ecosystem level [10–13].

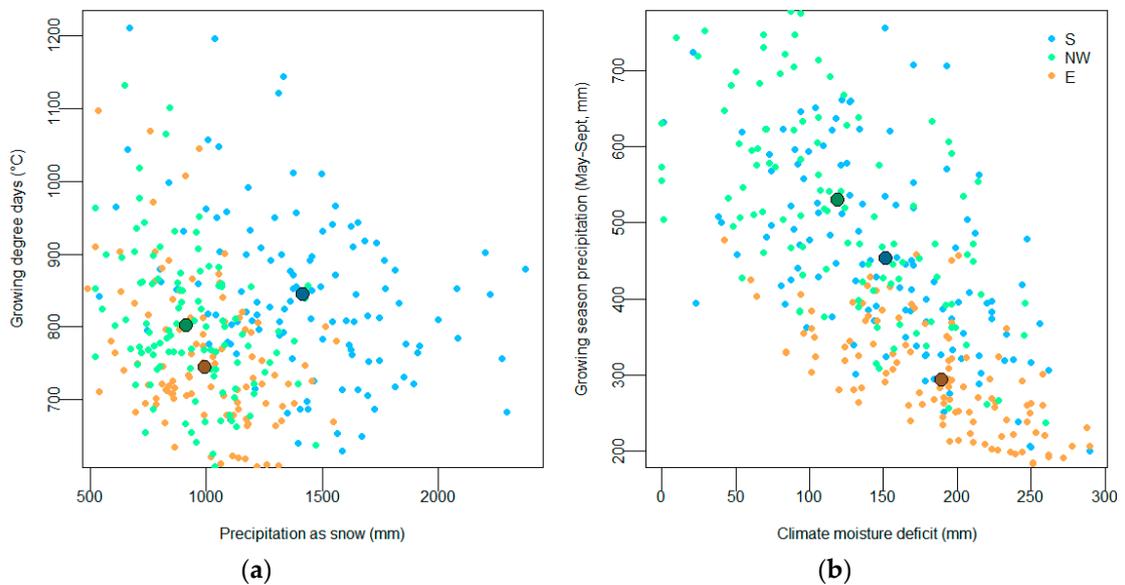
Ecologists have made a great deal of progress in understanding that sub-alpine trees are often strongly limited by climate, and thus, that treeline is likely to respond to warming [11,13,14]. However, much work remains to be done to understand how treeline responses might vary locally (i.e., different sides of a mountain) and across species [15], the scales at which conservation and resource management occur. Even though it is common for treeline to be dominated by more than one species, studies often focus on how climate sensitivity of an individual species varies across vast regions with different macroclimates [11,16–21]. Studies like these have shown synchrony within a climatic zone and significant differences in influential climate variables and climate sensitivity across climatic zones [11,16–24].

Fewer studies examine the radial growth climate sensitivity of multiple species at different locations. Most studies that explicitly compare species responses tend to focus on a single site [25–27] or species that don't directly co-occur [28]. Those studies that do consider species differences at multiple sites have found conflicting results. For two climatically different sub-alpine regions, Nakawatase and Peterson reported that tree growth in the wetter region was limited by growing degree days, whereas in the drier region soil moisture limited growth [29]. In contrast, Deck et al. found that co-occurring conifers across two regions responded to the same most influential variable [30]. Peterson and Peterson also reported consistency between the identities of the influential climate variables across locations with different aspect, and that species identity has a greater influence on climate sensitivity than site [31]. Conversely, Liang et al. concluded that topography had a greater effect on climate sensitivity than species identity [32]. They found that topography influenced the climate variables to which tree species responded, and concluded that species physiology influenced the strength of sensitivity to a particular climate variable [32]. In all, these studies demonstrate that climatic zones can generate different climate sensitivities, but do not tell us at what spatial scale these differences in radial growth sensitivity for a single species arise. Similarly, although it is clear species identity can influence climate sensitivity, it is not clear if species-driven differences in climate sensitivity become more or less pronounced under certain climatic conditions. Since managed forest areas (e.g., national parks) do not extend across continents (and therefore usually do not encompass large changes in climate), it is imperative to understand the factors that influence climate sensitivity at a local level.

In this study, we explored two potential drivers of variation in radial growth climate sensitivity of sub-alpine trees—site influences and species identity—at a local scale. We characterized site differences as the differences in long-term mean climate at the scale of our collection sites in Washington, USA. Specifically, we assessed (A) whether the identity of climate variables constraining growth and the strength of their effects differed by site; (B) whether the identity of climate variables constraining growth and the strength of their effects differed by species; and (C) whether there were site by species interactions in climate sensitivity. We did so by collecting tree cores from the four dominant conifer species forming treeline at three broad locations in Mt. Rainier National Park (Figure 1). Each of our sampling locations was on a different side of Mt. Rainier, and therefore experienced different mean climates (Figure 2). We hypothesized that all trees would be sensitive to similar climate variables, but that both species identity and location (site climatic context) would affect the magnitude of growth sensitivity to climate. Our results demonstrate that tree growth of our four focal high elevation conifers on all three sides of the mountain responded to similar climate variables, and that climate sensitivities for each climate variable—regardless of the species or site—were similar in magnitude, with a few minor exceptions. Our results imply that at treeline in moist temperate regions (like Mt. Rainier), neither species identity nor mean climatic conditions has a major influence on high elevation conifer climate sensitivity.



**Figure 1.** Tree core collection locations in Mt. Rainier National Park, Washington. The labels denote elevation in meters. White line shows the border of Mt. Rainier National Park.



**Figure 2.** Annual climate variability since 1901 (small points) and long-term mean climate (large points) for the three sub-alpine sampling locations on Mt. Rainier. Selected climate variables: precipitation as snow and growing degree days (a) and climate moisture deficit and growing season precipitation (b) for comparison among the three sites. Climate data obtained from ClimateWNA (Version 5.40, University of British Columbia, BC, Canada) spans from 1901 to 2015. Growing degree days, precipitation as snow, and climate moisture deficit are derived annual summaries of monthly variables calculated by ClimateWNA. The data for the south side is for the long-term forest demographic monitoring site on that side of the mountain (1603 m).

## 2. Materials and Methods

### 2.1. Study Site and Species

Tree cores were collected in Mt. Rainier National Park, WA, USA. The climate is temperate maritime with dry summers, and heavy winter precipitation. Mt. Rainier National Park is an ideal study system for examining climate–tree growth relationships. Since its establishment in 1899, the forests and alpine ecosystems have been relatively undisturbed by human influences. Additionally, the different sides of Mt. Rainier experience different local climates. The south side has the most snowfall, the northwest side receives the most growing season rainfall, and the east side of the mountain is the driest, according to 30 year PRISM (Parameter-elevation Regressions on Independent Slopes Model) climate averages [33] downscaled using the ClimateWNA downscaling algorithm [34] (Figure 2).

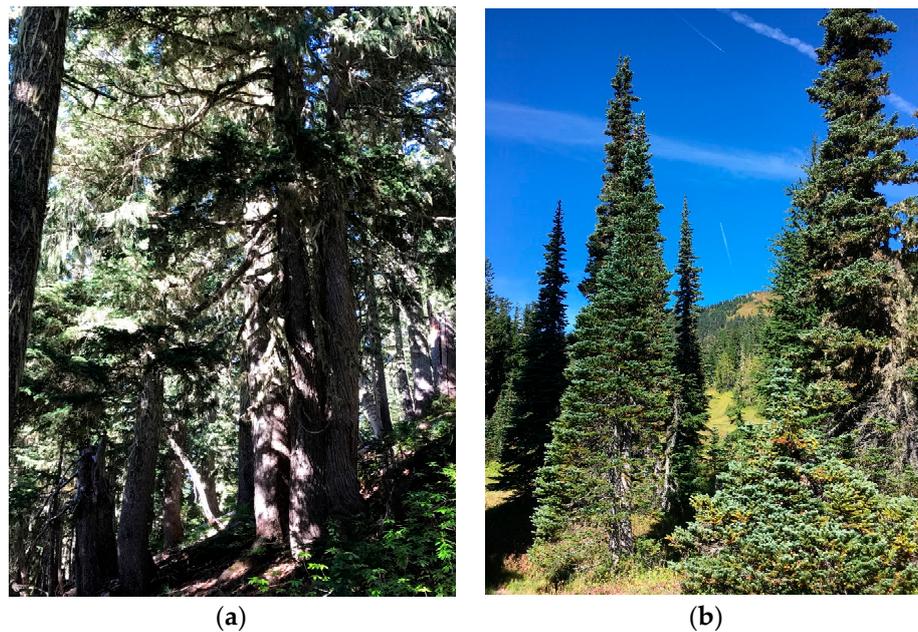
At high elevation treeline, dominant tree species are *Abies amabilis* Douglas ex J Forbes (Pacific silver fir), *Tsuga mertensiana* (Bong.) Carriere (mountain hemlock), *Callitropsis nootkatensis* (D. Don) Oerst. ex D.P. Little (Alaska yellow cedar), and *Abies lasiocarpa* (Hook.) Nutt. (sub-alpine fir). Tree cores were collected from all four dominant tree species at three high-elevation sites on the three climatically different sides of Mt. Rainier (Figure 1).

### 2.2. Tree Growth Data

Up to 20 mature, canopy dominant individuals of *A. amabilis*, *T. mertensiana* and *C. nootkatensis* were sampled from three high elevation locations that are the sites of long-term forest demographic monitoring [35]. Trees cores were collected within an approximately 1 hectare (100 m × 100 m) area, with individuals of the same species located at least 20 m apart from each other. These sites were established in 2010, and described in a recent publication on seedling recruitment [35]. One site was also described in two recent publications about growth–climate sensitivities [36,37]. These sites are located at elevations of 1603 m (south), 1635 m (northwest), and 1750 m a.s.l. (east) (Figure 1). The canopy density was similar across sites; all locations were mature, closed canopy forests (e.g., Figure 3a). The average size of trees cored was 60.54 cm diameter at breast height (range: 30.5–117 cm DBH). Cored trees were selected to capture the approximate size distribution of dominant, mature trees at the plot to obtain the mean growth response of a typical canopy tree, and were situated away from any detectible topographic features (e.g., drainages). These trees, which were cored during 2009–2013, were resampled in 2016 to extend the chronologies until 2015. This allowed us to include growth from the years with the latest (2011) and earliest (2015) snowmelt dates on record.

Sampling for *A. lasiocarpa* deviated slightly from that of the other species. *A. lasiocarpa*, unlike the other three species, is extremely shade-intolerant and only rarely grows in moderate to closed canopy forests in Mt. Rainier National Park (ML pers. obs.) [38]. Therefore, *A. lasiocarpa* was sampled in the open areas adjacent to the closed canopy forest site on the northwest side (Figure 3b) and sampled within and adjacent to the closed canopy forest site on the east side in 2016. *A. lasiocarpa* trees sampled at these two sites ranged from 39.0 cm to 86.3 cm diameter at breast height. On the south side, *A. lasiocarpa* was sampled at a site 1.3 km away from the permanent stand (1711 m a.s.l. elevation) (Figure 1) in 2012. These trees ranged from 28.2 cm to 41.5 cm diameter at breast height. Trees from all focal species cored are near the upper range limits of the study species. For all species, at least two cores per individual were collected from opposite sides of the tree perpendicular to the aspect. See Table A1 in Appendix A for number (*n*) of trees sampled for each species.

Increment cores were dried, mounted, sanded with progressively finer grits of sandpaper (according to standard protocol [39]), and scanned. The program Windendro (Version 2009b; WinDENDRO 2009, Regent Instruments Inc., Quebec, QC, Canada) was used to measure annual growth rings to 0.001 mm [40]. Visual crossdating was performed in Windendro, and COFECHA (Version 6.06P, Laboratory of Tree-Ring Research, Tucson, AZ, USA) [41] was used to verify and to determine the quality of the crossdating [42] for all rings formed after 1880.



**Figure 3.** Closed-canopy forest where *A. amabilis*, *T. mertensiana*, and *C. nootkatensis* co-occur (a) and open meadow where *A. lasiocarpa* has established (b) at the sampling locations on the northwest side of Mt. Rainier.

Once all cores were crossdated, a mean chronology was created for each tree by averaging the ring widths from all cores taken from the same tree using Windendro [40]. Before detrending, the chronologies were shortened to 1880 (the date up to which the chronologies had been crossdated). The chronologies were detrended with a 67-year spline (to reduce age and forest dynamics effects on growth—growth suppression or release patterns related to the competitive environment, not climatic fluctuations) and then pre-whitened using an AR1 autocorrelation model (to remove autocorrelation effects on growth) using dplR (Version 1.6.5, R Foundation for Statistical Computing, Vienna, Austria) [43]. Then, master chronologies for each species at each site were created from the tree chronologies using the Tukey’s biweight robust mean function in R (R. version 3.3.2, R Foundation for Statistical Computing: Vienna, Austria) [44]. Master chronologies were later shortened to the same length as the climate data available (1901 to year of most recent ring).

### 2.3. Climate Data

Our study required site-specific climate data, since climatic conditions in montane ecosystems can change substantially at scales of a few hundreds of meters in elevation [45,46]. In Mt. Rainier National Park, there is only one long-term high elevation weather station (the Paradise meteorological station, on the south side of the mountain). Fortunately, ClimateWNA can provide localized climate estimates using partial derivative functions of climatic change along elevational gradients, thereby providing high-resolution climate data for mountainous terrain [34]. ClimateWNA also provides biologically relevant climate variables using monthly climate data [34]. Monthly temperature and precipitation anomalies are used to adjust the interpolated baseline data obtained from PRISM [47] for a chosen location [34]. All downscaling algorithms are evaluated against the observations from 3353 weather stations across Western North America [34]. ClimateWNA provides monthly climate variables from the CRU TS 2.1 0.5 degree gridded historical dataset, interpolated using the PRISM 2.5 arcminute climate normal and a scale-free downscaling technique [34]. While ClimateWNA is a gridded product that may contain errors and biases, our hope was that the interpolation algorithm would serve as the ‘best guess’ for the climate of the specific site. We believe that this algorithm largely maintains similar interannual anomalies in temperature and precipitation across sites (once variables

were z-score standardized), and provides the best possible estimate for derived variables such as precipitation as snow and growing degree days that have nonlinear relationships with temperature and precipitation lapse rates. Both the absolute magnitude and interannual variability of precipitation and temperature variables from climateWNA compare favorably to station observations from the Paradise meteorological station, corrected to the location of the long-term forest demography site on the south side, which is the closest to the station (see Ettinger et al., 2011). This suggests that climateWNA, while not perfect, captures interannual climate variability without major biases (See Figure A1 in Appendix A).

Climate data were obtained for the mean latitude, longitude and elevation of each master chronology of a species at each site based on the coordinates of individual trees from ClimateWNA (Version 5.40, University of British Columbia, BC, Canada) [48]. For GPS coordinates where an elevation was not recorded, elevation was determined from latitude and longitude using Geoplaner (Version 2.7, München, Germany) (height accuracy of 6 m and horizontal resolution of 30 m) [49]. Therefore, every species at each site had its own time series of climate variables, although climate time series for trees at the same site were quite similar.

#### 2.4. Climate Variable Selection, Model Selection and Statistical Analyses

We first used simple univariate climate correlations with growth anomaly and our biological knowledge of the system to identify relevant climate variables for further analysis. The strongest univariate correlations with monthly variables given by ClimateWNA [48] using the response and correlation function analysis in the R program treeclim (Version 2.0.0, R Foundation for Statistical Computing, Vienna, Austria) [50] helped guide our choices of annual and seasonal variables for quantifying growth sensitivity of our focal species to climate. Variables were tested for the previous May to the current October. Previous studies have indicated that snow negatively impacts and warmth positively impacts the growth of high elevation conifers [17,18,31,36,37]. Rather than test only these climatic variables, our procedure enabled us to identify additional variables that might have unexpected yet significant influences on growth.

From the univariate correlations from treeclim [50], six main categories of annual and seasonal variables emerged as potential explanatory variables of tree growth: summer warmth (June–August), summer moisture/drought variables (June–August), spring warmth (March–May), snow (precipitation as snow = previous August–current July, winter precipitation = previous December–current February), spring humidity (March–May), and previous summer warmth (previous June–previous August). Rather than using general temperature and precipitation summaries (e.g., mean annual temperature, total precipitation) as explanatory variables, we chose to examine the effects of plant-relevant climate variables from each of these categories to more accurately model the complexities of climate responses [19]. Timeseries of these variables for our sampling sites were obtained from ClimateWNA [48]. We used our biological knowledge of the study system to pick one explanatory variable from a suite of potential explanatory variables that were highly correlated. From our univariate correlations, we found that spring and summer Hargreaves reference evaporation (a simple estimate of potential evapotranspiration [51]) and climate moisture deficit in the current growing season had a positive influence on growth. These drought stress metrics were highly correlated with temperature variables (e.g., 0.76 correlation between summer growing degree days and summer Hargreaves reference evaporation from east side *A. amabilis* climate dataset). We therefore assumed that these positive correlations between drought and growth (i.e., more growth in drier years) instead reflect effects of summer warmth on growth. Therefore, we selected growing degree days (degree days above 5 °C) to quantify summer warmth and did not include any additional summer moisture/drought variables in models to avoid including correlated explanatory variables. For spring warmth, we chose growing degree days (degree days above 5 °C) because they are more plant-relevant than freezing degree days (degree days below 0 °C). On Mt. Rainier, precipitation as snow is more biologically relevant than winter precipitation because, in the sub-alpine, snow falls in seasons other than winter.

Metrics for spring humidity and previous summer warmth were relative humidity and growing degree days, respectively. Because we had found no evidence of interactions among climate variables for three of our focal species (*A. amabilis*, *T. mertensiana*, *C. nootkatensis*) at the high elevation site on the south side of Mt. Rainier [36], we included only additive effects in our model of RWI (ring width indices).

Our final equation for testing climate sensitivity was:

$$\text{RWI} = \text{sm\_GDD} + \text{sp\_GDD} + \text{PAS} + \text{prev\_sm\_GDD} + \text{sp\_RH} \quad (1)$$

(sm = summer, sp = spring, prev = previous, GDD = growing degree days, PAS = precipitation as snow, RH = relative humidity). To avoid violating the assumption of independence, none of the explanatory variables we included in the final model were highly correlated ( $r < 0.55$ ).

We tested the relative importance of these five climate variables by fitting the above model and all possible nested models for each species at each site, ranking models by their AIC-weight and assessing the variable importance (proportion of top models including the variable) of each climate factor based on the top models that cumulatively accounted for 95% of the AIC-weight for every focal species at each site (Table 1). Nested models were fit and variable importances assessed using the MuMIn package (R Foundation for Statistical Computing: Vienna, Austria Version 1.15.6) in R [52].

**Table 1.** Importance factors (proportion of top models including the variable) for RWI/climate variable relationships for all species at each site. Importance factor values range from 0 to 1, 1 being the most important. (sm = summer, sp = spring, prev = previous, GDD = growing degree days, PAS = precipitation as snow, RH = relative humidity). Note: species codes in column 1 are the first two letters of the genus and the first two letters of the species epithet.

Species/Site	GDD_sm	GDD_sp	PAS	Prev_GDD_sm	RH_sp
ABAM/S	1.00	0.74	1.00	0.83	0.65
ABAM/NW	1.00	1.00	1.00	1.00	0.51
ABAM/E	1.00	1.00	1.00	1.00	0.56
ABLA/S	1.00	1.00	1.00	1.00	1.00
ABLA/NW	0.97	0.65	1.00	1.00	0.33
ABLA/E	1.00	1.00	1.00	1.00	0.72
TSME/S	1.00	0.23	1.00	0.58	0.24
TSME/NW	1.00	0.92	1.00	0.82	0.94
TSME/E	1.00	0.47	1.00	1.00	0.73
CANO/S	0.89	0.21	1.00	0.31	0.29
CANO/NW	1.00	0.36	1.00	0.50	0.83
CANO/E	0.86	0.33	1.00	0.62	0.43
<b>Average</b>	<b>0.98</b>	<b>0.66</b>	<b>1.00</b>	<b>0.81</b>	<b>0.60</b>

To quantify growth sensitivity to climate, we then fit Equation (1) to each species at every site. We standardized climate variables with the z-score standardization method for each species at a site, before including them as explanatory variables for RWI values. Thus, the slope value given by the regression for a particular climate variable is analogous to the coefficient of growth sensitivity for that species to that climate variable. Since climate data was standardized, the effects of different climate variables on tree growth can therefore be directly compared. These individual models for each species and site were used for computing the climate sensitivities and confidence intervals reported in the figures.

To test for significant differences in sensitivity between co-occurring species at each site, we modified Equation (1) to include interactions between climate variables and species identity, and fit three separate models, one per site. Specifically, we asked whether climate effects on growth for one species differed from those of all other species at the site (i.e., climate by species interactions—at  $\alpha = 0.05$ ). From our previous studies in this study system, *A. amabilis* has been shown to have the greatest sensitivity to snow out of all of our focal species [36,37]. Thus, we expected *A. amabilis* to be the most climate-sensitive species in

our analysis. Therefore, we set *A. amabilis* as the intercept for all site models, and used model contrasts (based on t-distributions) to test for significant differences between *A. amabilis* sensitivity and the climate sensitivity of the three other species. Our rationale was that if the most sensitive species did not show significant differences in climate sensitivity from the three other species, then it was unlikely that the other three species differed from each other.

We then modified Equation (1) to include a site interaction and fit the model to all data from each species (1 model for each of the four study species) to test whether climate sensitivity for all master chronologies of the same species varied by site. This allowed us to determine whether the same species experienced different sensitivities to climate depending on where it was growing on the mountain. Based on our previous research, we would expect to see the greatest differences between the snowiest site and the rest of the sites, because snow had a strong effect on growth in this study system [36,37]. Thus, using the same rationale as above, we set the south side site as our intercept for site comparisons, and tested for significant differences in site climate sensitivities using contrasts based on t-distributions. While this does not allow us to test all pairwise climate sensitivities between species and sites, we chose these contrasts to pick up the largest differences in sensitivity, which would be of most interest to forecasting and management. We also saw no evidence that additional post-hoc tests were warranted to detect differences between species/sites not included in the model contrasts given the overlap between the confidence intervals of climate sensitivity parameters for almost all species and sites and the results of the final analysis testing the overall importance of species identity and site (see below). Statistics for these comparisons are located in Table A2.

Finally, to determine the relative importance of site and species on overall climate sensitivity of treeline species at Mt. Rainier, four multiple linear regression models were fit to a combined dataset including all data from all species and all sites. The models were compared using AIC-based model selection. The following models were tested: a null model (Equation (2)), a climate-only null model (Equation (3)), a model with species influences (Equation (4)), a model with site influences (Equation (5)), and a model with both species and site influences (Equation (6)).

$$\text{RWI} = 1 \quad (2)$$

$$\text{RWI} = \text{sm\_GDD} + \text{sp\_GDD} + \text{PAS} + \text{prev\_sm\_GDD} + \text{sp\_RH} \quad (3)$$

$$\begin{aligned} \text{RWI} = & \text{sm\_GDD} * \text{species} + \text{sp\_GDD} * \text{species} + \text{PAS} * \text{species} + \text{prev\_sm\_GDD} * \text{species} \\ & + \text{sp\_RH} * \text{species} - \text{species} \end{aligned} \quad (4)$$

$$\text{RWI} = \text{sm\_GDD} * \text{site} + \text{sp\_GDD} * \text{site} + \text{PAS} * \text{site} + \text{prev\_sm\_GDD} * \text{site} + \text{sp\_RH} * \text{site} - \text{site} \quad (5)$$

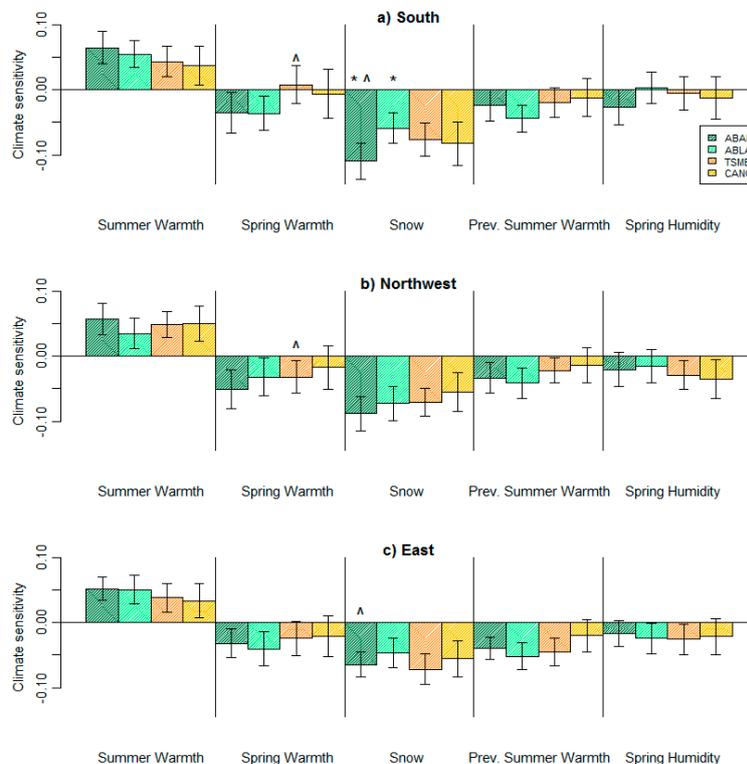
$$\begin{aligned} \text{RWI} = & \text{sm\_GDD} * \text{species} * \text{site} + \text{sp\_GDD} * \text{species} * \text{site} + \text{PAS} * \text{species} * \text{site} \\ & + \text{prev\_sm\_GDD} * \text{species} * \text{site} + \text{sp\_RH} * \text{species} * \text{site} - \text{species} - \text{site} - \text{species:site} \end{aligned} \quad (6)$$

### 3. Results

The identity of the climate variables that most strongly influenced radial growth (RWI) did not vary by side of the mountain (Table 1). For all species at all Mt. Rainier locations, tree growth was most strongly influenced by two climatic variables—summer warmth which had positive effects, and snow which had negative effects (Figure 4, Table 1). Sensitivity to spring humidity was small and not significantly different from zero for most species at most sites (Figure 4). Sensitivity to previous summer warmth was non-significant for *C. nootkatensis*, but the other three species generally responded negatively, with the exception of *A. amabilis* and *T. mertensiana* on the south side (Figure 4a). For each site, effects of all climate variables on species growth were in the same direction (i.e., all positive, or all negative), or were not significant (Figure 4).

Overall, the sensitivities of each species did not vary greatly across the three sides of the mountain, and all species at the same site were similarly affected by climatic variables. For example, *A. lasiocarpa* had a consistent sensitivity to summer warmth, spring warmth, snow, and previous summer warmth

at all three sites (Figure 4). Similarly, previous summer warmth did not significantly influence growth of *C. nootkatensis* (Figure 4), no matter what side of the mountain. On the northwest side and the east side of the mountain, all four species had similar sensitivities to summer warmth and snow (Figure 4b,c).



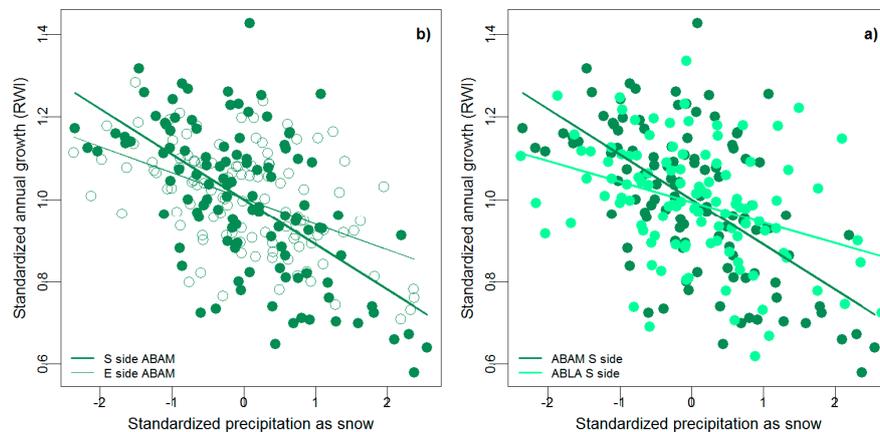
**Figure 4.** Climate sensitivity for all focal species across all three study sites at Mt. Rainier: (a) south side, (b) northwest side, (c) east side. The magnitude of climate sensitivity indicates the strength of sensitivity; the larger the bar, the more sensitive the group of trees is to that particular climate variable. A positive direction of climate sensitivity represents a positive growth response for an increase in the climate variable and vice versa. Error bars are  $1.96 \times$  standard error. \* s indicate significantly different climate sensitivities for two species at a site. ^ s indicate significantly different climate sensitivities for a single species across two sites.  $\alpha = 0.05$ .

We only identified two site-level differences in climate sensitivity within a species. *A. amabilis* was more sensitive to snow on the snowiest side of the mountain—the south side, than on the drier side—the east side ( $p = 0.0114$ ) (Figure 5a). The mean climates of these two sides are the most different from each other (Figure 2), due to the rain shadow effect. Additionally, *T. mertensiana* was more sensitive to spring warmth on the northwest side (the rainiest side) than on the snowiest side ( $p = 0.0403$ ) (Figure 4a,b).

With one exception, species were sensitive to the same climatic variables, and with similar climate sensitivities within each of the three sites. However, on the snowiest side, the south side, *A. amabilis* was significantly more sensitive to snow than *A. lasiocarpa* ( $p = 0.0114$ ) (Figure 5b), but not significantly more (or less) sensitive than the other two species (Figure 4a).

Species identity emerged as a slightly more important determinant of growth sensitivity to climate than site in our comparison of four multiple linear regression models with different combinations of species and site interactions fit to all data. Specifically, the best model according to AIC included RWI modeled as a function of climate with species interactions, and the second best model included climate with site interactions (Table 2). However, allowing climate sensitivity to vary by either species or site

only explained an additional 1–2% of the variability in RWI (Table 2). No species/site interactions were apparent in the interaction models that we tested.



**Figure 5.** Significant differences in climate sensitivity (a) for *A. amabilis* growing on different sides of the mountain ( $p = 0.0114$ ) and (b) between *A. amabilis* and *A. lasiocarpa* on the same side of the mountain ( $p = 0.0114$ ).

**Table 2.** Model selection for ring width indices as a function of climate, ring width as a function of climate with species interactions, with site interactions, and with both species and site interactions.  $\Delta$ AIC is relative to the climate-only null model. A negative  $\Delta$ AIC indicates that the model is better than the null.  $\diamond$  denotes the best model.

Model	df	$\Delta$ AIC	R <sup>2</sup>
rwi~1	2	572.80	0
rwi~climate	7	0	0.349
rwi~climate*site	17	−2.42	0.360
$\diamond$ rwi~climate*species	22	−8.20	0.367
rwi~climate*species*site	62	31.90	0.386

#### 4. Discussion

Overall, our results demonstrate that similar climate variables act as important constraints on tree growth (RWI) of four sub-alpine trees on all sides of Mt. Rainier, despite climatic differences between sites and differences in species traits. The radial growth–climate relationships reported here suggest that growth of high elevation conifer trees in our study was primarily constrained by the snow and increased by summer warmth, regardless of species or side of Mt. Rainier (Figure 4). This is consistent with previous studies at this site [36,37] and other sites for three of the four sub-alpine species in the Pacific Northwest [17,18,31]. Similarly, over a range of elevations at two different regions on the Kamchatka peninsula in Russia, two co-occurring conifer species tested had the same most influential climatic driver: summer (May–August) temperature [30].

We found that climate sensitivity did vary by species, but that differences were not great. For example, although *A. amabilis* was more sensitive to snow than *A. lasiocarpa* (Figure 5b) on the snowiest side of the mountain, both species were still negatively affected by high snowfall years. In addition, the relative sensitivity of *A. amabilis* compared to *A. lasiocarpa* for summer warmth, snow, and previous summer warmth was generally consistent across sites, with slight differences that were not significant (Figure 4). Differing from the two *Abies* species, *C. nootkatensis* and *T. mertensiana* were not significantly affected by spring warmth, and *C. nootkatensis* was uninfluenced by previous summer warmth (Figure 4). Models of climate–growth relationships fit across all species provide additional support that climate–growth sensitivity varies by species, but not in a dramatic fashion.

Specifically, a model including a climate by species interaction was the best fitting model to all tree ring data, but the species by climate interaction did not greatly improve the predictive power of the climate-only null model (Table 2). Previous research suggests climate sensitivity often differs between co-occurring species [31,53], which is why we were surprised not to see greater differences.

The slight difference in sensitivity to snow we found between *A. amabilis* and *A. lasiocarpa* on the south side of Mt. Rainier could in part be due to the different growth habits of these two species. In the Cascade Mountains, *A. lasiocarpa* is a shade-intolerant colonizing species [38], whereas *A. amabilis* is extremely shade-tolerant [54] and part of a secondary forest community [55]. Thus, tree growth of *A. amabilis* may have been more strongly constrained by climate than the growth of *A. lasiocarpa*, whose growth may be more strongly influenced by competitive dynamics. However, we did not see the same pattern on any of the other sides of the mountain (Figure 4b,c). Because these species were sampled 1.3 km away from each other on the south side, there could also have been edaphic, topographic, or microclimate differences that we did not measure, and therefore could not account for, that influenced this slightly significant difference in sensitivity, rather than true differences in species physiology.

We were surprised to find that climate sensitivity of our focal species varied only subtly by site (Table 2, Figures 4 and 5a), despite the fact that these three sites differ in climatic conditions (Figure 2). This is in contrast to the many studies that have found considerable differences in climate sensitivity within individual species across large-scale (i.e., latitudinal or continental) climate gradients. For instance, climate responses have been shown to depend on environmental conditions that vary by latitude and elevation [53], to differ by climatic regime [16,19,24] and to differ by latitude [56]. In all, this suggests that the climatic differences among the sides of Mt. Rainier were not large enough to result in substantially different sensitivities to climate. Indeed, although long-term (1901–2015) mean values of precipitation as snow, growing degree days, climate moisture deficit and May–September precipitation differed between sites, there was a large amount of overlap in the annual values when considering interannual variability (Figure 2). Perhaps we did not find the site-specific variation that we expected in part because we compared our chronologies to site-specific climate data, unlike previous studies, which have compared growth to regional climate records (e.g., [16,19,24]).

The subtle differences in climate sensitivity we did observe between species growing at different sites (e.g., *Abies amabilis* S- and E-side sites—Figure 5a) could be due to microsite differences [57–60], although we do not believe it very likely. Unfortunately, we did not have tree-specific microsite data to assess significant differences between the sites to test this idea. Topography is known to impact local climate (e.g., [32]), and both the aspect [57–59] and hydrological position [60] a tree is growing in have been shown to influence climate sensitivity of conifer species, and they may differ systematically between the three sites. However, unless these microsite differences were strong enough to significantly alter the annual variability in climates the trees experienced (as opposed to simply the mean climate), we do not expect such microsite differences to strongly influence the identity of climatic variables identified as important.

While our results indicate a consistent effect of snow and summer warmth on annual growth of all species growing at their upper range limits across Mt. Rainier, forecasting forest dynamics in a warming world will depend on additional factors not investigated in this study. For one, radial growth–climate sensitivity is only one component of tree demography that may be influenced by climate. Height growth, mortality or reproductive output could have different climate sensitivities by species and/or location (e.g., [35,61]). In addition, climate sensitivity can change over time, as has been reported for boreal northern regions which are temperature limited [62,63], and for one of our focal species (mountain hemlock) on the Western slopes of the Cascade range (where Mt. Rainier is located) [64]. Another important factor could be competitive dynamics. While our findings of consistent climate sensitivities across species and sites suggest consistent responses to climate change (and thus, minimal effects on forest composition) [37], more study is needed to determine whether

competitive interactions may change with warming. Finally, changes in disturbance could potentially alter sub-alpine community structure [37]. All of these factors are a critical direction for future research and must additionally be taken into account to provide accurate estimates of future treeline forests, and of the processes that depend on them (e.g., future carbon storage [62]).

## 5. Conclusions

In summary, we found that species identity and site differences in climate-growth sensitivities will likely not complicate extrapolation of tree growth responses to climate change on Mt. Rainier. Specifically, growing season temperature and snowpack size were consistently the most important drivers of tree growth across all four species and three climatically different sites, with only subtle differences in the strength of effects and effects of a few other climatic variables. Given that growing season temperatures are projected to increase while snowpack declines in the Pacific Northwest with future climate change, our results therefore suggest that we can expect tree encroachment and corresponding decreases in alpine meadows throughout Mt. Rainier National Park, regardless of compositional differences at treeline or differences in mean climates at different sites. More broadly, our results imply that at climate space at wet treeline (such as found throughout the Pacific Northwest), neither species identity nor site-specific differences have a major influence on high elevation conifer climate sensitivity. If these results are verified by other studies (in the Pacific Northwest and beyond), generalization of treeline responses may be possible.

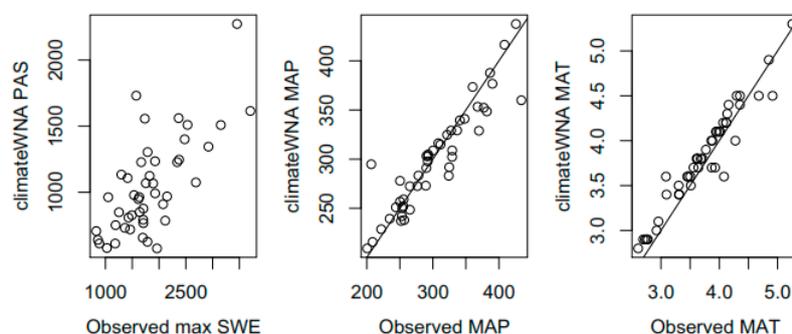
**Supplementary Materials:** The code used and data files produced in this study are available online at [www.mdpi.com/1999-4907/9/1/1/s1](http://www.mdpi.com/1999-4907/9/1/1/s1).

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**Conflicts of Interest:** The authors declare no conflict of interest.

## Appendix A



**Figure A1.** A comparison of climate variable observations taken at the Paradise meteorological station (located on the south side of Mt. Rainier) corrected to the permanent forest demography plot on the south side using PRISM normals (see Ettinger et al., 2011), vs. climateWNA for the same permanent forest demography plot for the years 1965–2007. PAS = precipitation as snow; SWE = snow-water equivalent; MAP = mean annual precipitation; MAT = mean annual temperature.

**Table A1.** Number of trees sampled from each species at each site included in analysis.

	South	Northwest	East
ABAM	20	19	21
ABLA	10	19	20
TSME	20	19	19
CANO	19	20	19

**Table A2.** Test statistics for the pairwise differences that revealed significantly different climate sensitivities, either between two species at a site, or two sites for the same species. *A. amabilis* was set as the intercept for comparisons between species at a site, and the south (snowiest) side was set as the intercept for comparisons between sites. PAS = precipitation as snow, DD5\_sp = spring growing degree days.

Species/Site	Comparison	F-Statistic	df	t-Value	p-Value
ABAM/SOUTH	siteEAST:PAS	20.14 on 15	323	2.544	0.01143
TSME/SOUTH	siteNORTHWEST:DD5_sp	16.29 on 15	324	−2.059	0.04031
ABAM/SOUTH	speciesABLA:PAS	14.67 on 20	428	2.542	0.01137

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