Historical Tree Species Height Growth Pattern Associated With Climate Change in Western North America

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Abstract

Background

The climate variables effect on tree growth in boreal and temperate forests has received increased interest in the global context of climate change. However, most studies are geographically limited and involved few tree species. Here, sixteen tree species across western North America were used to investigate tree response to climate change at the species range scale.

Methods

Forest inventory data from 36,944 stands established between 1600 and 1968 throughout western Canada and USA were summarized. Height growth (total height at breast-height age of 50 years) of healthy dominant and co-dominant trees were related to annual and summer temperatures, annual and summer Palmer Drought Severity Index (PDSI, and tree establishment date (ED). Climate-induced height growth patterns were then tested to determine links to spatial environment (soil conditions and geographic locations), species range (coastal, interior, and both ranges) and species traits (shade tolerance and leaf form), using linear mixed model for the global height growth and general linear model to test the height growth patterns for each species.

Results

Increase of temperatures and PDSI had a positive effect on height growth for most of the study species, whereas Alaska yellow-cedar (*Chamaecyparis nootkatensis*, (D. Don) Spach) height growth declined with ED. All explaining variables and the interactions explained 59% of the total height growth variance. Although tree height growth response was species-specific, increased height growth during the 20th century was more pronounced for coastal ranged species, high shade tolerant species, and broadleaf species. Furthermore, height growth increase occurred mostly on rich soil, at the northernmost species range, and, unexpectedly, at lower elevations. A decline in height growth for some species further north and especially higher in elevation possibly related to increased cloudiness and precipitation. However, drought conditions remain in interior areas despite moving northward and upward that decrease height growth.

Conclusion

These results highlight the general trend (species characteristics and range) and the species-specific height patterns, indicating the spatio-temporal complexity of the growth response to recent global climate change.

Background

Understanding recent climate change effects on tree growth is needed to accurately forecast species and forest dynamics under future climate change scenarios (Brecka et al. 2018). Numerous studies highlight

the effect of recent global temperature increase on tree growth around the world, especially at higher latitudes and elevations where temperature limits growth (Wieser et al. 2009; Zhang et al. 2017; Holz et al. 2018; Schwab et al. 2018; Tei and Sugimoto 2018). In many studies, tree growth is positively associated with increasing temperature as a result of global climate change (Lloyd and Bunn 2007; Devi et al. 2008; Tchebakova et al. 2016; Cienciala et al. 2018); however, growth decline has been observed in water-stressed environments (Dietrich et al. 2016; Sangines de Carcer et al. 2018) with tree dieback becoming more obvious, in areas with severe drought (O'Brien et al. 2017).

Understanding how the magnitude of growth response to climate may differ with species growth habits and autecology is necessary to improve predictive modelling. In optimal environmental conditions, photosynthesis increases with increasing temperature (Pallardy and Kozlowski 2008). Thus, faster growing species (shade intolerant) may increase photosynthetic capacity, and consequently growth in response to increased temperature better than slower growing species (shade tolerant), which generally have lower light saturation points for photosynthesis (Pallardy and Kozlowski 2008). In boreal forests, the faster-growing genera *Betula* and *Populus* tend to have greater responses to increasing temperature than slower-growing genera *Pinus* and *Picea* (Woodward 1995). Similarly, Saxe *et al.* (Saxe *et al.* 2002) reported that broadleaved species such as trembling aspen (*Populustremuloides* Michx.) and paper birch (*Betulapapyrifera* Marsh.) exhibit a higher relative growth rate under higher temperatures than the conifer species tamarack (*Larix laricina* (Du Roi) K. Koch), black spruce (*Piceamariana* (Mill.) B. S. P.), and jack pine (*Pinus banksiana*) (Lamb.), suggesting a different growth pattern with leaf form. However, this trend is not unanimous. Woodward (1995) reported that in the same environmental conditions, Norway spruce (*Piceaabies* (L.) Karst), a coniferous species, had a better relative growth rate and height increment than the deciduous species European beech (*Fagus sylvatica* L.). These opposite findings may be related to the difference in shade tolerance between the deciduous species; trembling aspen and paper birch are shade intolerant, while European beech is very shade tolerant. Therefore, growth habits may also play a big role in a tree's response to climate change (Cahoon et al. 2018). A study on the effects of paleoenvironmental changes on the interspecific differences in life-history traits for tree species (Lacourse 2009) found that climate change during the cold period following deglaciation favored species with a 'fast' life-history strategy (e.g. high relative growth rate, short life span, and shade intolerance) such as lodgepole pine (*Pinuscontorta* Dougl. ex. Loud.). In contrast, the relative climatic stability of the last ca. 8000 yr favored species that exhibit a 'slow' life-history strategy such as western hemlock (*Tsugaheterophylla* (Raf.) Sarg.) (e.g., low relative growth rate, long life span, and high shade tolerance).

In forest ecosystems, tree growth is limited by energy (growing season length, degree-days, or temperatures) in some regions and by soil properties (moisture, nutrient regimes) in other regions (Littell et al. 2008; Gao et al. 2018). For instance, several studies reported a positive growth response to recently increased temperatures at higher latitudes or elevations where temperature is usually the limiting factor (Kremenetski et al. 1998). At lower latitudes or elevations, however, increased water deficits associated with temperature increases can lead to declining tree growth (Lopatin 2007; Babst et al. 2013; Martin-Benito et al. 2018). Similar declines were also observed in interior boreal forest of Alaska, in the prairies,

and in the southern interior of British Columbia with higher rates of tree mortality associated with a warmer climate (Barber et al. 2000; Hogg et al. 2002; Hogg et al. 2008; Hynes and Hamann 2020).

The pattern of increased or decreased growth with recent climate change is globally still unclear. In western North America, similar growth pattern regardless of the species have been reported (Hararuk et al. 2018), while others studies found species-specific growth response to climate change (Peterson and Peterson 1994; Messaoud and Chen 2011; Sullivan et al. 2017; Cahoon et al. 2018). These contradictory findings could be related to the scale of the study area and/or studied species. Most studies are conducted at smaller scales (except Messaoud and Chen (2011)) and a few species (except Hararuk et al. (2018)). Moreover, Miyamoto et al. (2010) raised that, although tree growth for subalpine fir, lodgepole pine (*Pinus contorta* Dougl. ex. Loud.), and white spruce (*Picea glauca*, Moench) Voss) was strongly temperature sensitive at a large scale of western North America, the response growth pattern with climate change was species-specific and site-specific, also corroborating with findings from European tree species (Babst et al. 2013). Thus, it is crucial to examine the historical tree growth at the whole species range to capture the whole pattern of historical tree growth response in order to increase the knowledge of future forest dynamic and species distribution (Lévesque et al. 2016).

In addition, spring snowpack accumulation appears to have a contrasting effect; indeed, Peterson and Peterson (1994) mentioned that spring snowpack accumulation affected negatively on tree growth for subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), and subalpine larch (*Larix lyallii* Parl.) at more temperature limits i.e. high elevations of the Cascade Mountains of western North America. In contrast, spring snowpack had a positive effect on tree growth in water limits i.e. pine forests in low latitudes and elevations (Gleason et al. 2020). In addition, Lévesque et al. (2016) pointed out the importance of soil moisture and nutrients on the tree growth pattern with climate change-induced. Indeed, they found that high soil nutrient and water availability promoted and magnified significantly tree growth pattern for most of the dominant tree species in central Europe. In conclusion, they argued that many studies related tree growth with climate variability did not include the effect of the soil properties.

Studies conducted mostly in the transition area between the forest and tundra zones show that other factors, for example, soil properties and disturbances (wind, fire, and grazing) may alter or mask the species response to climate change (Hofgaard et al. 2010; Sanders-DeMott et al. 2018). Several studies used stem radial increments to reconstruct growth and correlate it with recent climate change (Lloyd and Bunn 2007; Wang et al. 2019), while in comparison to radial growth, height growth is more strongly dependent on climate and soil properties and less affected by stand density (Monserud 1984; Chen et al. 1998; Nigh 2006; Ritchie et al. 2012), making it a complementary method to examine the response of tree species to climate change.

This study examines the long-term effect of global climate change (temperatures and soil moisture availability) on the height growth of 16 tree species of western North America. We hypothesize that (1) similar to recent findings of tree radial growth, there is also a positive height growth response to global

warming; (2) growth responses differ with species' growth habits (fast *versus* slow growth), and leaf form (needle leaves, deciduous needle leaves, deciduous broadleaves); (3) growth responses differ with spatial environment based on the resource limitation theory.

Materials And Methods

Study area

The study area covers western Canada and the western USA, ranging from 31°24' to 62°08'N latitude, 99°31' to 153°51'W longitude and at elevations from 5 to 3687 m above sea level (Table 1; Fig. 1). This western North America contains one of the most diverse ecoregions in the world (ftp://newftp.epa.gov/EPADDataCommons/ORD/Ecoregions/cec_na/NA_LEVEL_I.pdf).

Sampling design

The study uses forest inventory data provided by government agencies in Canada and the USA (FIA). For Canada, dataset originated from SIBEC project (Site Index Biogeoclimatic Ecosystem Classification). This project reflects the average growth potential of tree species in forested site in British Columbia. Data from Yukon and Alberta originated from permanent sample plots. In total, 36,944 sample stands were selected and spanned from Alaska to southern California (Fig. 1). The forest inventory database was realized since the 1930s. All selected stands were naturally established after a wildfire, unmanaged, and without visible damage or disturbance. These stands are of variable ages, and for a given period of growth (the first 50 years) at breast height, stands experienced a wide range of historical growing conditions of temperature associated with climate change. In each stand, a plot size ranged from 0.01 to 0.5 ha in Canada and 0.017 ha in the USA (<https://www.fia.fs.fed.us/library/database-documentation/index.php>). For each plot, retrieved data include geographic locations (latitude, longitude, and elevation), stand condition (i.e. visible natural or anthropic disturbance, treatment, plantation or natural establishment), year of measurement (1937-2018), and selected trees for site index (top tree height, diameter at the breast height, breast height age, total age, and site index).

Tree height and site index

Within a plot, dominant and co-dominant (largest trees) living trees for each species were aged by counting tree rings from an increment core sample extracted at the breast height of a tree where the diameter is measured at root collar for each species. These trees are free from suppression above breast height, had no visible damage, and had a full crown. Only trees with total age ≥ 50 years were selected. Then, we averaged the height (measured with a clinometer or other approved instrument from the ground to the top of the tree) and age for each species within each plot. Site index (SI) is defined as the height of dominant and co-dominant trees at a reference age, usually 50 years at breast height and is a strong predictor for forest stand productivity. SI was calculated using top tree height of dominant and co-dominant sample trees at a reference age of 50 at the breast height and for each tree of each species

using the software Site Tools 4.1 Beta developed by the Forest Analysis & Inventory Branch, British Columbia Ministry of Forests (<https://www2.gov.bc.ca/gov/content/industry/forestry/managing-our-forest-resources/forest-inventory/field-forms-and-software/software-download#tipsy>). This modelling software is a growth and yield program allowing to calculate the site index for each tree according to the height-age model equation developed for each species using the top height and total age of the sample tree. The establishment date was estimated by subtracting the year of measurement and total tree age. The establishment date of all species was site specific but ranged between 1600 and 1968 CE.

Study species

Sixteen tree species were used in the analysis, including conifers and broadleaves with different ecology, shade tolerance, and geographic ranges (Fig. 1; Table S1). The description of the studied species is given by Burns and Honkala (1990) and (Klinka et al. 2000). These species together account for more than 60 percent of the total tall and medium size, and wide range tree species (taller than 9 m in height) in western North America (Viereck and Little 2007).

Alaska yellow-cedar (*Chamaecyparis nootkatensis* (D. Don) Spach), Amabilis fir (*Abies amabilis* Dougl. ex Loud. Forbes), Sitka spruce (*Picea sitchensis* (Bong.) Carr.) and red alder (*Alnus rubra* Bong.) are restricted to the Pacific coast and coastal mountains (i.e. Cascade) range (Fig. 1). Conversely, Engelmann spruce (*Picea engelmannii* Parry ex Engelmann) and subalpine fir (*Abies lasiocarpa* Hook Nutt.) are located and associated with each other throughout interior Rocky Mountain mostly at high elevations (Fig. 1). Western larch (*Larix occidentalis* Nutt) is also located in the interior range restricted to the Rockies.

Six species have two distinct ranges; along the Pacific coast and coastal mountains and through Rocky Mountain. Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) ranged from central British Columbia south to central California but the interior range extends further south to central Mexico. Although, mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.), western hemlock (*Tsuga heterophylla* Raf. Sarg.) and western redcedar (*Thuja plicata* Donn ex D. Don Spach) extend their range further north to Alaska, the interior range is smaller and restricted to high elevation in the Rocky Mountains. Grand fir (*Abies grandis* Dougl. ex D. Don Lindl.) has small coastal and interior ranges, while western white pine (*Pinus monticola* Dougl. ex D. Don) is more commonly located in mountainous areas.

Three species have a continuous range from the Pacific coast to the Rocky Mountains. These are lodgepole pine (*Pinus contorta* Dougl. ex Loud.), ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) and black cottonwood (*Populus trichocarpa* Torr. & Gray). Lodgepole pine is one of the widest species range in western North America. It grows throughout the Rocky Mountain and Pacific coast regions from Yukon territory and the Pacific coast of Alaska south to about latitude 31° N in California and Colorado. Ponderosa pine extends from southern Canada into Mexico and spreads towards the Pacific coast. The main range of black cottonwood extends along with coastal Alaska through the forested areas of

Washington and Oregon to northern California. The species is also found inland, generally in the Rocky Mountains of British Columbia, western Alberta to northern Idaho.

Soil properties

Slope was extracted from a Digital Elevation Model (DEM) of North America. The slope was classified as low ($< 4\%$), moderate ($4\% \geq$ to $< 16\%$), and steep ($\geq 16\%$) according to the landform slope class developed by the government of Canada (Anonymous 2010). Slope was used as a proxy to estimate soil moisture because the increase of slope percentage implies increased drainage (MacMillan et al. 2005). The rate of the organic matter carbon decomposition (C/N) was extracted by a raster provided by the Food Agriculture Organization (FAO) world map with a 5 x 5 arc minutes (<http://www.fao.org/geonetwork/srv/en/main.home?uuid=73aef710-b773-11db-8df6-000d939bc5d8>).

Climate variables

The climate data were obtained from the National Oceanic and Atmospheric Administration (<https://www.ncdc.noaa.gov/paleo-search/study/24230>). Reconstructed anomaly of annual (AN_T_a) and summer mean temperature (June-August; JJA_T_a) represents deviations from the annual mean (1961-1990) for the northern hemisphere surface temperatures over a period of 998 years (1000-1998) and 1400 years (600-2002 AD) for respectively annual and summer mean temperature derived from the global climate proxy network (Shi et al. 2013; Guillet et al. 2017). Then, we extracted the real annual (AN_T) and summer mean temperature (June-August; JJA_T) for each plot by using climate simulation software at $0.5^\circ \times 0.5^\circ$ resolution as the source of data ClimateWNA (Wang et al. 2016). This software extrapolates climate variables from the nearest weather stations for the period 1901-2018. For the period before 1901, we previously used this software to extract the annual and summer mean temperature for the period 1961-1990 corresponding to the base of the anomaly. Then, we were able to estimate the real temperature for each plot by adding the anomaly with the real mean temperature for the period between 1961-1990. We also extracted annual and June-August Palmer Drought Severity Index (PDSI; Dai et al. 2004) for the global surface temperatures over a period between 0-2000 years derived from the global climate proxy network gridded at $\sim 2^\circ \times 2^\circ$ resolution (Steiger et al. 2018). PDSI uses annual (PDSI_AN) and June-August (PDSI_JJA) rainfall to obtain a measure of drought to estimate the soil water budget for the period 0-2000 years. PDSI shows long-term dry (negative values) and wet (positive values) weather conditions. All plots in the same grid have the same PDSI. Averages that are greater than 0 represent a warmer/moister climate.

For each plot, these data were averaged for the period of tree growth under consideration (i.e., from the year of establishment to the year it reached breast height age 50 years). Then, we related establishment date to the averaged climate values.

Statistical analyses

Global and species-specific models were assessed to examine the relationship between site index and the independent environmental variables. Since species are nested inside the species range groups and characteristics, linear mixed model was used to assess the influence of the environmental variables and species traits on the tree height growth. This model included soil characteristics (slope and soil fertility), species range (group I = coastal, group II = interior, and group III = both), species characteristics (shade tolerance and leaf form), geographic locations (latitude, longitude, and elevation), climate (PDSI_JJA), and the interaction between climate-other independent variables as the fixed effect. Species and establishment date (ED) were used as a random effect. These two effects were related to site index. Then, generalized linear model was used at the species scale and excluded, groups, shade tolerance, and leaf form. ED was chosen for the base of the interactions to examine the historical pattern of height growth with climate change. The variance components were estimated through the method of restricted maximum likelihood (REML). Since the correlation between AN_T and JJA_T as well as between PDSI_AN and PDSI_JJA were highly correlated (multi-collinearity; Table S2), we selected only AN_T and PDSI_AN because AN_T had the highest correlation value with the total SI than JJA_T and PDSI_AN was the most correlation frequency with site index than PDSI_JJA. Prior to analyses, a plot of the residuals was realized and confirmed that the relationship is linear. To test the first and second hypothesis, we developed respectively two models as follows:

Global model:

$$Y = \sum_{i=1}^n \beta_1 \text{Latitude}_i + \beta_2 \text{Longitude}_i + \beta_3 S_i + \beta_4 [C/N]_i + \beta_5 \text{AN_T}_i + \beta_6 \text{PDSI_AN}_i + \beta_7 \text{Gp}_i \\ + \beta_8 \text{ST}_i + \beta_9 \text{LF}_i + \beta_{10} + \beta_{11} S_i * \text{ED}_i + \beta_{12} [C/N]_i * \text{ED}_i + \beta_{13} \text{Gp}_i * \text{ED}_i + \beta_{14} \text{ST}_i \\ * \text{ED}_i + \beta_{15} \text{LF}_i * \text{ED}_i + \beta_{16} (1|SP_i) + \beta_{17} (1|\text{ED}_i) + \beta_0$$

Where Y is site index, S and C/N represent respectively slope classes and organic matter decomposition rate, ED = establishment date, Gp = species groups, ST = shade tolerance, LF = leaf form, SP = species, and n represents the number of species.

Species-specific model:

$$Y_i = \beta_1 \text{Latitude}_i + \beta_2 \text{Longitude}_i + \beta_3 \text{Elevation}_i + \beta_4 S + \beta_5 \frac{C}{N} + \beta_6 \text{AN_T} + \beta_7 \text{PDSI_AN} + \beta_8 \text{ED} \\ + \beta_9 \text{Latitude} * \text{ED} + \beta_{10} \text{Longitude} * \text{ED} + \beta_{11} \text{Elevation} * \text{ED} + \beta_{12} S * \text{ED} \\ + \beta_{13} \frac{C}{N} * \text{ED} + \beta_0$$

Species that have two distinct geographic ranges such as Douglas-fir, grand fir, mountain hemlock, western hemlock, and redcedar, and western white pine were divided into coastal (Douglas-fir_C, grand fir_C,

mountain hemlock_c, western hemlock_c, western redcedar_c, western white pine_c) and interior (Douglas-fir_i, grand fir_i, mountain hemlock_i, western hemlock_i, and western redcedar_i, western white pine_i) populations. All analyses were performed with the R statistical software ([Team 2018](#)).

Results

Tree site index and climate

Except for red alder, Site index (SI) for all species was correlated at least to one of the climate variables (AN_T, JJA_T, PDSI_AN, PDSI_JJA) or establishment date (ED; Table 2). AN_T and JJA_T had the most frequent significant relationship with site index ($p = 0.508$ and 0.342 respectively). SI for coastal western white pine was not correlated with AN_T, while SI for interior grand fir was not correlated with JJA_T, but AN_T had globally the highest correlation values than any other climate variables or ED ($p = 0.071, 0.084$, and 0.235 for respectively PDSI_AN, PDSI_JJA, and ED).

SI for 7 species and populations was related to all climate variables or ED, while SI for coastal grand fir and coastal western white pine was only related to respectively ED and JJA_T (Table 2). Among the climate variables, SI for Engelmann spruce, coastal and interior western hemlock, western larch, and the interior western white pine was related to only temperature variables. However, no species SI were only related to PDSI variables. Among the significant relationships, AN_T had a negative relationship with only SI for coastal Douglas-fir, while JJA_T had a negative relationship with SI for coastal Douglas-fir and ponderosa pine. The negative effect of PDSI_AN on the tree SI was observed for amabilis fir, subalpine fir, and the two populations of western redcedar, while the negative effect of PDSI_JJA occurred for coastal mountain hemlock, Sitka spruce, and coastal western redcedar. In addition, only SI for Alaska yellow-cedar was negatively correlated with ED.

Since 1880, JJA_T was globally higher than the average and influenced differently on the species SI (Fig. 2a). The estimated values represent the magnitude of the slope regression trend between SI and ED (Fig. 2). Positive and negative values indicate respectively in increase or decrease of SI through the study period. Except for Alaska yellow-cedar, all estimated values were positive indicating an increase of SI within this period of time. The magnitude being the greatest for interior western white pine and least for ponderosa pine (Fig. 2).

Global growth pattern

The global model explained 56 % of the variation in total tree SI (Table 1). All explanatory variables had a significant influence on tree SI ($p < 0.05$). However, the significance level was the strongest for AN_T and the weakest for leaf form.

All interactions between ED and other explanatory variables had a significant effect on tree SI with the strongest influence from the interaction between shade tolerance and ED and the weakest from the interaction between leaf form and ED (Table 1). The increase was the greatest for coastal species range

(group I) and the least for both species' ranges (group III; Fig. 2b). High shade tolerant species demonstrated the greatest height increase (Fig. 2c). SI increased most for broadleaf species and was not significant with needle leaf species (Fig. 2d).

Species-scale growth patterns

The species-specific model showed that the range of the variability of SI explained by the model varied between 22.1 % for Alaska-cedar to 61.3 % for ponderosa pine (Table 3). We note that this model explained more than half of the SI variability for two species (amabilis fir and ponderosa pine) and more than the third for 13 species and populations. Nevertheless, SI for 6 species was not significantly influenced by any interactions between variables.

The interaction between ED and soil properties demonstrated that best SI occurred on low and moderate slopes for interior Douglas-fir and coastal mountain hemlock (Fig. 4). SI for interior Grand fir, lodgepole pine, red alder, and coastal western hemlock did not significantly differ with slope classes, although higher SI value was observed on the steep slope for interior Grand fir and red alder. With the fertility gradient, the largest significant increase of SI occurred on rich soil for black cottonwood, coastal and interior Douglas-fir, and lodgepole pine, whereas it was greater on poor soil for ponderosa pine (Fig. 4). Only black cottonwood and interior Douglas-fir showed a decline of SI on poor soil.

The SI-ED induced pattern demonstrated that all species had a greater increase at higher latitudes compared to lower latitudes except for Sitka spruce, coastal western hemlock, and coastal western redcedar, where it was greater at lower latitudes (Fig. 5). Only coastal western redcedar demonstrated a slow decline of SI at the higher latitudes. In contrast, 5 species demonstrated a decline of SI at low latitudes. With longitudes, all significant interactions showed that the largest increase occurred westward, except for coastal western hemlock and redcedar, where it increased eastward. All significant interactions between SI and ED at different elevations showed that all species demonstrated higher SI at lower elevations. Further, a decline of SI occurred at higher elevations for coastal and interior Douglas-fir, coastal mountain hemlock, ponderosa pine, Sitka spruce, and coastal western hemlock.

Anomaly of species site index and climate change

The anomaly of SI, representing the deviation from the mean of the total species SI of the study area, differed with species, establishment date, and geographic locations (Fig. 6). Negative and positive anomalies indicate that species SI was below or above that mean. The threshold of 20% of the variation of the mean SI was chosen to highlight where and when significant higher or lower SI values occurred. During the warmth period (1880 and afterward), Alaska yellow-cedar was the only species having the highest and the least frequency of plots where anomaly was below and above the threshold (42.86 and 11.90% respectively). The plots of Alaskan yellow-cedar with a site index anomaly below the threshold occurred mostly since the middle of the 18th century and at the northernmost species range. Most species

that had plots with positive site index anomaly greatly overwhelming the threshold, especially during the warmth period. However, interior Douglas-fir, Engelmann spruce, interior grand fir, and ponderosa pine had a slightly more plots having negative values (Fig. 6). In addition, plots with negative values, below the threshold, occurred mostly in the southernmost species range, while plots with positive values, above the threshold, occurred mostly in the center or in the northernmost species ranges. Conversely, plots with positive values above the threshold occurred mostly in the southernmost species range for Sitka spruce, coastal western hemlock and redcedar and at the lesser extent coastal mountain hemlock.

Discussion

Relationship between height growth and temporal variables

Except for Alaska yellow-cedar, all study species that established during the 20th century showed higher SI values than those established before that period. Increases in temperature and precipitation of 0.8°C and 14%, respectively, during the 20th century in the Pacific Northwest of North America (Mote 2003; Abatzoglou et al. 2014; Mildrexler et al. 2016) likely contribute to the height growth increase (Fig. 2 and 3). An explanation for this trend is that longer growing seasons since 1880 (Fig. 3a) can promote earlier plant growth (Lyu et al. 2017). Temperature variables and ED were better for predicting height growth at both the global and species levels for species in western North America compared to the two PDSI variables similar to previous studies (Nigh et al. 2004; Miyamoto et al. 2010; Sharma and Parton 2018). Further, Hayes et al. (1999) noted that PDSI could be less suited for predicting growth in mountainous areas with frequent climatic extremes and more variation of precipitation and soil moisture.

As predicted, increased temperature generally had a positive effect on tree height growth when water availability was not limiting (Adams 2007; Cortini et al. 2011; Sharma and Parton 2018; Zhou et al. 2019). In non-water limiting areas, heat promotes photosynthesis and carbohydrate allocation to the stem (Pallardy and Kozlowski 2008). The exception being height growth for coastal Douglas-fir and ponderosa pine was negatively related to both temperature variables, especially to JJA_T (Table 2), which may be explained by water limitations. Ponderosa pine occurs in dry climate and on sandy soils (Burns and Honkala 1990; Klinka et al. 2000). Consequently, an increase in JJA_T could put trees in a higher water stress situation (Erickson and Waring 2014). Coastal Douglas-fir occurs mostly in the region characterized by a Mediterranean climate with a high amount of winter precipitation but hot and dry summers (Finlayson 2010). Thus, an increase in JJA_T may exacerbate evaporation and water stress sensitivity during the summer growing season (Beedlow et al. 2013). Nevertheless, the absence of height growth decline during the 20th century indicates that these two species globally overcame their growth limitations perhaps by using water that condensates from fog which arises from contacts between the warm air above the coast and cooler water of the Pacific, especially for coastal Douglas-fir (Fig. 2; Williams et al. 2008).

The negative effect of PDSI_AN and PDSI_JJA on tree height growth for 4 and 3 species, respectively, and populations appears to have two major causes. First, soil water surplus could decreased root activity due

to asphyxia and photosynthetic activity and thus reduced growth (Deal 2006; Pallardy and Kozlowski 2008; Cortini et al. 2012). Second, the cooler summer temperatures and snowpack accumulation in mountainous areas can negatively affect tree height growth. Indeed, Appleton and St. George (2018) found that the growth of mountain hemlock, growing in the central Pacific coast, was negatively related to the cool-season precipitation, corroborating with our findings. The increase of PDSI_AN could be also related to an increase in snow cover during the winter at higher elevations. A deep snowpack, not measured in the study, decreases soil temperature and growing season at the local scale and long-lasting snowpack serve to limit the growth for high interior elevation species and populations (Gustafson et al. 2017). Kajimoto et al. (2018) found that heavy snow accumulation was responsible for tree damage and thus reduced growth.

Only Alaska yellow-cedar demonstrated a negative correlation with ED and had the strongest decline in height growth during the 20th century (Table 2; Fig. 2). Unexpected but not surprisingly, this may be explained by other factors not included in our study. Beier et al., (2008) also found a decline in radial growth for Alaska yellow-cedar during the 20th century likely related to warmer winters resulting in less snowpack and therefore less protection of surface roots from freeze-thaw events leading to root injury (Hennon et al. 2012). Schaberg et al. (2011) added that the roots of Alaska yellow-cedar were the highest vulnerability to freezing compared to Sitka spruce, western and mountain hemlock, and western redcedar.

Global height growth pattern

The global model explained more than 56% of the total tree height growth variability (Table 3), corroborating the tenet that tree height growth is mostly influenced by climate, soil conditions, and species characteristics (Messaoud and Chen 2011; Yener and Altun 2018). However, the historical height growth relationship with ED differed in magnitude with different geographic locations, species characteristics, and soil properties, in line with our expectation. This confirms that historical tree height growth pattern was not uniform for all studied species and for the whole study area as mentioned in the work of Hararuk (2018). However, our findings corroborated the findings in Messaoud and Chen (2011), Sullivan et al. (2017), and Cahoon et al. (2018) suggesting the trends found here represented the general trend in western North America.

Coastal species (group I) demonstrated a higher increase in height growth with ED than other species groups and benefited more from climate change in the 20th century (Fig. 2). Species in group II had the second highest increase of height growth being the most sensitive to warmth because they are located mostly in the elevated Rocky Mountains and thus are more temperature-driven, whereas the coastal Pacific region is a temperate rainforest and benefits from a mild temperature with a high water availability i.e. rain and/or fog (Adams 2007; Bailey 2014; Sedmáková et al. 2019). This temperate rainforest is the largest and one of the most productive in the world (Orians and Schoen 2017), which may explain the best benefit of climate warming to the species in this area.

The hypothesis that fast-growing species benefit more from climate change than slower growing species (Karnosky et al. 2003; Lambers et al. 2008) is not corroborated by our study since the increase of height growth with ED was higher for high shade tolerant (slowest growing) species than mid and low shade tolerant (faster growing) species. A similar increase of height growth between mid and low shade tolerant species appears to have two explanations. First, species located in the coastal temperate forest benefitted the most from the recent climate change, which masks the effect of the shade tolerance. Second, some mid-shade tolerant species, such as interior western white pine, exhibited the greatest increase of height growth with ED.

The other hypothesis that deciduous broadleaf species exhibit greater climate growth response than coniferous species (Woodward 1995) is supported by our findings. High leaf photosynthetic capacity i.e. broadleaf, can achieve their growth and acquire resources rapidly in order to maintain high growth rates under environmental change such as recent climate change (Weemstra et al. 2013), while needle leaf species allocate their resources not only for their growth but also for leaf protection during the winter period.

Species-specific growth pattern

Tree height growth was mainly greater on higher than lower slope values and on high soil fertility sites (Fig. 3 and 4), which are considered to have good soil quality for growth (mesic soil; Lévesque et al. 2016; Eckhart et al. 2019). Leonelli (2008) found that historical increase in height growth for trembling aspen in British Columbia was greater on rich soil. We found increased height growth of ponderosa pine on low soil fertility contrary to the norm. This could be explained by these sites having higher organic matter known as higher water holding capacity (Machmuller et al. 2015; Bhadha et al. 2017), which is crucial for species growth in dry climates. Furthermore, Lévesque et al. (2016) found that, in contrast with other tree species growing in central Europe, recent tree growth for Scots pine and oak species was relatively good on poor and dry soil. They explained that these two dry climate adapted species have competitive advantage over water- and nutrient-demanding species on poor and dry soils.

Several studies have reported different tree-growth patterns with geographic locations, with increases at higher latitudes and elevations, and a decline at lower latitudes and elevations due to drought conditions (Sedmáková et al. 2019), which was corroborated by our findings only for high latitudes (Fig. 5). At higher latitudes, an increase in temperature at more limiting environments has a stronger and more beneficial effect on tree height growth than at low latitudes (Gao et al. 2018). Higher increases in growth for most species at westernmost and lower elevation of ranges indicate that close to the Pacific coast benefited from a longer growing season and increased precipitation. A decline of height growth at southward and eastward sites demonstrated the possible drought occurrence at the eastern edge of the species ranges because increase of temperature brought trees under water deficit stress (Venegas-González et al. 2018). In fact, an obvious southward decline of height growth response for coastal Douglas-fir corresponds to the coastal areas of California characterized by summer drought Mediterranean climate conditions (Peel et al. 2007) and to drier conditions occurred in interior southwestern USA for other species. Indeed,

western North America is known for its peculiarity, high latitudes correspond mostly to low elevations and vice versa (Table S2; Fries et al. 2000). As well, an unexpected decline of height growth for many tree species at higher elevations appears to be related to increase of cloudiness or water stress in interior dry conditions, impeding the positive effect of recent increase of temperature (Babst et al. 2013).

In contrast, we observed slower growth for a few coastal species and decline for coastal western redcedar at the leading range and upward corresponding to the coastal and mountainous areas of the Pacific region, respectively, where they reach their northernmost limit (Viereck and Little 2007). Further, increased precipitation in the 20th century likely increased cloud cover which at regions corresponding to limiting temperatures can reduce summer temperatures and photosynthesis (Rodríguez-Ramírez et al. 2018).

Spatio-temporal variation of species tree growth

The anomaly of site index gives additional information on the amplitude of species height growth variation. Most species increased their height growth by at least 20% (threshold) of the species mean SI on many plots, especially during the warmth period (1880 and afterward Fig. 6), supporting the previous findings that a warmer climate positively affects species height growth. Only 5 species had a higher percentage of plots with anomaly values below the threshold, with the greatest values for Alaska yellow-cedar (42.86%). For the latter species, the trend indicated that few plots had a positive anomaly of SI supporting the negative effect of warming on the species height growth. The plots with the negative values below the threshold were mostly located at the northernmost species range, supporting the decline of Alaska yellow-cedar in southernmost of Alaska (Beier et al. 2008; Hennon et al. 2012). For the remaining 4 species, we found many plots with high positive anomalies compensated for the higher proportion of plots with negative anomalies (Fig. 6).

Geographically, most plots with height growth anomalies over the threshold were located at the northernmost species range, supporting the previous findings. In addition, Sitka spruce, coastal western hemlock and redcedar magnified their height growth mostly at their southernmost ranges, corroborating globally with our previous findings. In contrast, only few species show an opposite trend; interior grand fir and ponderosa pine, which had their height growth anomaly over the threshold throughout the west toward the Pacific area, avoiding the drought condition in the interior part of the study area (Ganey and Vojta 2011; Anderegg et al. 2013; Restaino et al. 2019). Negative height growth anomaly below the threshold was also found for ponderosa pine in the northernmost of the species range corresponding to the southeastern part of the British Columbia. This area represents the ponderosa pine zone known as the driest of the forested zones in the province (Ministry of Forests 1988).

Conclusion

In western North America, the relationship between historical tree height growth and climate change demonstrated that the temperatures were the best predictors for growth dynamics. The 20th century warmth was beneficial for all study species, except for Alaska yellow cedar. Only historical height growth

for red alder was related neither to the independent variables, nor to the interactions. Furthermore, red alder was also the only species, which had the same proportion of plots having height growth below and above the 20% of the mean SI. Thus, our results pointed out the complexity of growth response with climate change-induced at the subcontinental scale where both global trend and species-specific height growth occurred simultaneously and differed geographically and on different soil qualities. Climate-change induced growth patterns could be used as a proxy to highlight the potential interspecific growth competition and thus detects the possible spatio-temporal shift of species distribution, especially at the species leading and tailing range. However, performance under future climate change scenarios could be more complex than expected by simulated predictions because of the complexity of tree response with climate change where species ecological amplitudes and traits play a stronger role at a larger scale.

Declarations

Availability of data

The data that support the findings of this study are available for USA but under licence agreement for those from Canada and are thus not publicly available. The data are, however, available upon reasonable request and with permission from the different government (Canada).

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Authors' contributions

YM conceived the original study idea, designed the methodology, led the analysis of the data and the writing of the manuscript. AR revised and did the English editing. NT and AH contributed critically to the drafts and gave final approval for publication. FM contributed to data extraction and revised the drafts.

Ethics approval and consent to participate

Not applicable.

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Competing interests

There is no conflict of interest.

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Tables

Table 1. Characteristics of the study plots showing ranges in latitude, longitude, elevation, establishment date (ED), and site index at age 50 (SI).

Species	N	Latitude	Longitude (W)	Elevation (m)	ED	SI (m)
Alaska-cedar	445	44°24'-58°50'	121°30'-136°23'	8-1781	1601-1940	2.78-29.5
Amabilis fir	791	42°56'-55°49'	120°37'-130°21'	1-1920	1604-1968	2.02-48.52
Black cottonwood	99	43°33'-61°19'	109°05'-153°51'	30-2048	1783-1965	8.83-41.60
Douglas-fir	13987	31°24'-55°02'	104°19'-127°26'	5-3477	1600-1966	2.44-53.34
Engelmann spruce	3899	32°42'-56°59'	104°56'-128°23'	610-3687	1634-1964	2.85-32.24
Grand fir	1345	39°06'-50°14'	113°47'-125°24'	25-2103	1739-1966	6.10-59.89
Lodgepole pine	6784	34°07'-62°08'	104°58'-136°14'	11-3612	1604-1966	2.13-32.92
Mountain hemlock	1825	37°09'-61°06'	114°36'-150°36'	7-3150	1600-1960	2.01-27.01
Ponderosa pine	6838	31°47'-51°12'	99°31'-124°03'	91-3036	1625-1967	4.07-49.53
Red alder	135	40°45'-57°59'	121°09'-135°28'	5-1072	1781-1963	14.54-42.31
Sitka spruce	922	40°34'-61°07'	121°47'-153°11'	1-1255	1603-1962	2.31-57.91
Subalpine fir	5296	33°36'-61°12'	105°06'-133°04'	100-3627	1624-1967	1.82-40.39
Western hemlock	3479	37°55'-61°04'	114°29'-148°04'	1-2896	1601-1967	2.33-43.28
Western larch	1006	44°18'-50°50'	112°51'-121°16'	455-2286	1617-1964	7.2-34.14
Western redcedar	1424	43°35'-58°20'	113°44'-135°06'	1-1783	1601-1962	3.52-36.86
Western white pine	165	36°18'-52°13'	113°50'-124°28'	91-3018	1659-1963	5.57-36.58
Total	48440	31°24'-62°08'	99°31'-153°51'	1-3687	1600-1968	1.82-59.89

Table 2. Pearson correlation values between site index, climate variables, and the establishment date (ED). In bold significant level ($0.01 < \alpha < 0.05$, * $0.001 > \alpha < 0.01$, ** $\alpha < 0.001$. In italic, $0.05 < \alpha < 0.06$. AN_T =

annual mean temperature (°C), JJA_T = June-August mean temperature (°C), annual PDSI_AN and June-August PDSI_JJA (Palmer Drought Severity Index). Subscript 'c' and 'i' indicate respectively coastal and interior ranges.

Species	AN_T (°C)	JJA_T (°C)	PDSI_AN	PDSI_JJA	ED
Alaska-cedar	0.195**	0.266**	0.296**	0.164*	-0.255**
Amabilis fir	0.554**	0.552**	-0.115*	-0.020	0.478**
Black cottonwood	0.366**	0.299*	0.309*	0.286*	0.274*
Douglas fir _c	-0.044**	-0.239**	0.183**	0.143**	0.182**
Douglas fir _i	0.307**	0.225**	0.086**	0.108**	0.175**
Engelmann spruce	0.459**	0.452**	-0.026	0.006	0.157**
Grand fir _c	0.052	0.085	0.138	0.120	0.214*
Grand fir _i	0.172**	-0.011	0.084*	0.090*	0.040
Lodgepole pine	0.375**	0.376**	0.047**	0.042**	0.336**
Mountain hemlock _c	0.121**	0.186**	0.056	-0.142**	0.254**
Mountain hemlock _i	0.401**	0.401**	0.118	0.164	0.323**
Ponderosa pine	0.207**	-0.145**	0.099**	0.094**	0.008
Red alder	0.062	-0.057	0.048	0.022	0.161
Sitka spruce	0.437**	0.417**	-0.030	-0.105*	0.433**
Subalpine fir	0.394**	0.336**	-0.044*	5 x 10 ⁻⁴	0.306**
Western larch	0.270**	0.231**	0.049	0.040	0.203**
Western hemlock _c	0.528**	0.450**	-0.038	0.025	0.487**
Western hemlock _i	0.271**	0.272**	-0.010	0.077	0.390**
Western redcedar _c	0.308**	0.423**	-0.191**	-0.070	0.463**
Western redcedar _i	0.103*	0.127*	-0.104*	-0.073	0.286**
Western white pine _c	0.195	0.224	0.171	0.173	0.135
Western white pine _i	0.210	0.255	-0.029	-0.029	0.313*
Total	0.508**	0.342**	0.071**	0.084**	0.235**

Table 3. Summary of linear mixed model between site index (m), independent variables and their interactions. C/N = organic matter decomposition rate, AN_T = mean annual temperature, PDSI_AN = annual palmer drought severity index.

Fixed effects	F-value	P-value	Random effects	Variance	SD	Total effects
<i>R² = 0.410</i>						<i>R² = 0.560</i>
AN_T	2704.29	<0.001	ED	0.07	0.27	
Longitude (°W)	1481.85	<0.001	Species	12.30	3.51	
Latitude (°N)	372.54	<0.001				
C/N	225.43	<0.001				
PDSI_AN	106.14	<0.001				
Slope	76.23	<0.001				
ED	58.47	<0.001				
Shade tolerance	52.60	<0.001				
Groups	24.03	<0.001				
Leaf form	3.41	0.033				
Shade tolerance*ED	46.69	<0.001				
Groups*ED	22.77	<0.001				
Leaf form*ED	2.84	0.059				

Table 4. F-values of the general linear model between species site index and the independent variables. Only the interactions of the model are shown in the table. Lat. = latitude, Lon. = longitude, ele. = elevation. In bold significant level ($0.01 < \alpha \leq 0.05$, * $0.001 > \alpha < 0.01$, ** $\alpha < 0.001$). In italic, $0.05 < \alpha < 0.06$.

Species	Lat.*ED	Lon.*ED	Ele.*ED	Slope*ED	C/N*ED	R ²
Alaska-cedar	1.14	1.61	0.05	0.83	0.57	0.221
Amabilis fir	2.47	10.23*	34.04**	1.11	0.35	0.606
Black cottonwood	2.35	0.27	3×10^{-3}	0.36	8.70*	0.495
Douglas fir _c	103.15**	3.20	5.84	0.52	10.80*	0.335
Douglas fir _i	356.44**	119.94**	31.82**	4.71*	21.20**	0.466
Engelmann spruce	29.42**	1.19	29.17**	2.44	0.06	0.378
Grand fir _c	1.49	1.84	0.03	0.68	0.01	0.235
Grand fir _i	1.79	3.66	2.37	3.91	0.13	0.449
Lodgepole pine	204.74**	104.44**	3.23	10.14**	8.23*	0.403
Mountain hemlock _c	30.85**	21.26**	19.84**	3.61	1.24	0.355
Mountain hemlock _i	0.61	0.41	0.87	0.46	0.19	0.239
Ponderosa pine	26.61**	8.10*	65.24**	0.39	29.29**	0.613
Red alder	0.64	0.40	2.15	3.13	4×10^{-3}	0.223
Sitka spruce	10.12*	0.10	13.13**	0.08	0.08	0.379
Subalpine fir	87.52**	42.98**	0.30	1.74	0.02	0.352
Western larch	25.81**	1.12	0.27	1.52	1.36	0.243
Western hemlock _c	8.12*	13.83**	133.63**	5.48*	0.41	0.446
Western hemlock _i	1.64	6.89*	8.67*	1.05	0.35	0.267
Western redcedar _c	32.41**	4.48	2.59	0.04	0.37	0.352
Western redcedar _i	0.03	0.02	1.60	1.40	0.06	0.242
Western white pine _c	3.23	1.47	0.44	0.46	2.72	0.309
Western white pine _i	0.02	0.62	0.47	0.05	0.60	0.317

Figures

Figure 1

Distribution of sample plots of the sixteen study species in Western North America. Each map also indicates species geographic range (in green).

Figure 2

Estimated parameters of the simple regression trend between species site index (SI) and establishment date (ED). White bars indicate the non-significant relationship between SI and ED. The small panels indicate the evolution of the average June-August temperature (JJA_T) anomaly from the Northern Hemisphere mean temperature 1961-1990 in light red and the best fitted regression line in dark red (a), the estimated parameters between SI and ED according to the species range groups (b), shade tolerance

(c: HG = high, MD = medium, LW = low), and leaf form (d: NL = needle leaf, DNL = deciduous needle leaf, and BL = broadleaf). The letter above each bar indicates significant (different letters) or no significant (same letters) differences between the groups, shade tolerance and leaf form.

Figure 3

Estimate parameters of simple regression between SI and ED at different slope classes. The letter above each bar indicates significant (different letters) or no significant (same letters) differences between the

slope classes.

Figure 4

Relationship between species SI and ED according to the soil fertility (gradient of the soil decomposition rate; C/N).

Figure 5

Relationship between species SI and ED at different geographic locations. Also inset maps indicate species geographic range.

Figure 6

Graphs show the evolution of the anomaly of species SI on each plot according to ED. The anomaly represents the deviation from the mean SI of each species within the whole study area (Table S3). The long-dashed lines indicate the threshold of 20% of the mean SI value and maps show the distribution of the plots with the anomaly values below (negative = red circles) or above (positive = green circles) this

threshold. The percentages indicate the proportion of these plots among those established during the warmth period (1880 and afterward; see fig. 3a).

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