

Recent climate warming forces contrasting growth responses of white spruce at treeline in Alaska through temperature thresholds

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Abstract

Northern and high-latitude alpine treelines are generally thought to be limited by available warmth. Most studies of tree-growth–climate interaction at treeline as well as climate reconstructions using dendrochronology report positive growth response of treeline trees to warmer temperatures. However, population-wide responses of treeline trees to climate remain largely unexamined. We systematically sampled 1558 white spruce at 13 treeline sites in the Brooks Range and Alaska Range. Our findings of both positive and negative growth responses to climate warming at treeline challenge the widespread assumption that arctic treeline trees grow better with warming climate. High mean temperatures in July decreased the growth of 40% of white spruce at treeline areas in Alaska, whereas warm springs enhance growth of additional 36% of trees and 24% show no significant correlation with climate. Even though these opposing growth responses are present in all sampled sites, their relative proportion varies between sites and there is no overall clear relationship between growth response and landscape position within a site. Growth increases and decreases appear in our sample above specific temperature index values (temperature thresholds), which occurred more frequently in the late 20th century. Contrary to previous findings, temperature explained more variability in radial growth after 1950. Without accounting for these opposite responses and temperature thresholds, climate reconstructions based on ring width will miscalibrate past climate, and biogeochemical and dynamic vegetation models will overestimate carbon uptake and treeline advance under future warming scenarios.

Keywords: Alaska, carbon uptake, climate change, cluster analysis, dendrochronology, threshold effects, treeline, white spruce

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Introduction

High-latitude forests provide important feedbacks to global climate: on the one hand, they contain 49% of the carbon stored in forested ecosystems (Dixon *et al.*, 1994). Increases in growth, as well as forest expansion (treeline advance) due to warming could enhance CO₂ uptake (Koerner, 2000), therefore acting as a negative feedback to warming. On the other hand, however, replacement of tundra by evergreen conifers (treeline advance) decreases albedo, which acts as positive feedback and enhances warming (Bonan *et al.*, 1992; Foley *et al.*, 1994, 2000).

Treelines as the edge of the boreal forest have been investigated for a long time, since trees at treeline are believed to be free from tree-to-tree competition and record a pure climatic signal (Schweingruber *et al.*, 1992). Dendrochronological studies and climate reconstructions of the boreal forest focus on the positive growth response of treeline trees to warmth (Garfinkel & Brubaker, 1980; D'Arrigo & Jacoby, 1993; Briffa *et al.*, 1998), from limited samples on sensitive sites (Pilcher *et al.*, 1990). Their results confirms the intuitive understanding that treeline trees in these cold environments are temperature limited, warming would lead to more growth, better survival of individuals and ultimately expansion of trees into tundra. Likewise, cooling of temperature would lead to recession of treelines (Kullman, 1996). Using these parameters, vegetation models

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produce upward and northward expansion of boreal forest under warming climate (Chapin *et al.*, 2000; Kittel *et al.*, 2000; Rupp *et al.*, 2001), supported by some site studies (Suarez *et al.*, 1999; Luckman & Kavanagh, 2000; Kullman, 2001).

However, positive sensitivity of northern high-latitude trees to temperature has recently declined (Briffa *et al.*, 1998), and temperature-induced drought stress can limit white spruce radial growth within the boreal forest (Barber *et al.*, 2000) and of some individual trees at treeline (Lloyd & Fastie, 2002). In other words, annual radial growth in individual trees is negatively correlated to temperature. However, population-wide responses of treeline trees to climate in Alaska remain largely unexamined.

Our study identifies opposing population-wide growth responses (enhanced and decreased growth with warming climate) in two mountain ranges in Alaska, quantifies the relative abundance of each growth response at three scales (regional, by site and by site type) and provides a plausible mechanism, through which climate is forcing these opposing growth responses.

Materials and methods

We collected tree ring samples from 1558 white spruce (*Picea glauca* (Moench (Voss)) in the Brooks Range and Alaska Range of Alaska (Fig. 1). Where possible (eight out of 13 sites), we sampled three site types: floodplain, high-density upland stands (north- and south-facing forest) and low-density upland stands (north- and south-facing tree limit). Low-density upland stands are usually higher in absolute elevation on a given slope than high-density upland stands; however, we made an effort to sample high-density trees across their elevational distribution (i.e. some stands were just 30–50 m lower in elevation than the low-density stands on that slope). Low-density stand were assumed to be free of tree-to-tree competition (except tree islands), high-density stands could include tree-to-tree competition.

We collected nearly exclusively penetrating cores, so that two radial measurements were available for each year. Ring width was measured (Velmex sliding stage, resolution: 0.001 mm) and both annual ring width measurements were then averaged. This analysis is based on the 1155 trees older than 100 years. The 403 younger trees showed nearly identical results, but were excluded to maintain stable sample size throughout the common period of analysis. Tree growth was compared with the Fairbanks record (1906–2000) of mean monthly temperatures and total monthly precipitation. Fairbanks is centrally located between the two mountain ranges and is highly representative of temperature

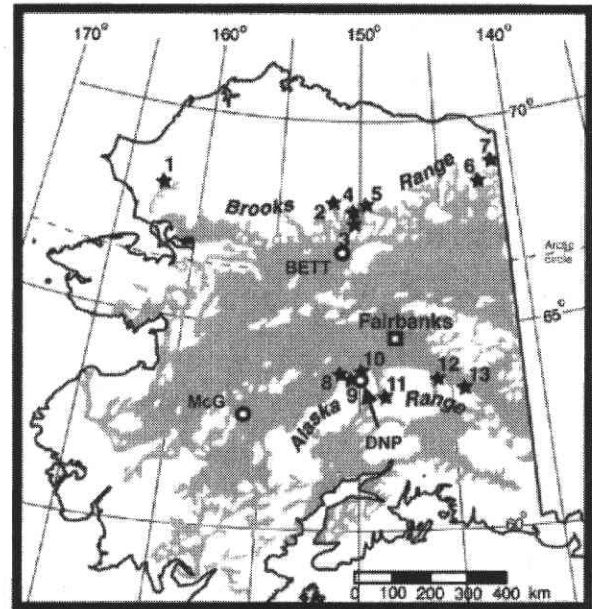


Fig. 1 Location of study sites in Brooks Range and Alaska Range in Alaska. Shaded area is extent of boreal forest. All sites are at or near treeline. Brooks Range sites: 1, BRKG (68.0°N, 161.5°W); 2, BRHF (67.8°N, 152.4°W); 3, BRCL (67.7°N, 150.5°W); 4, BRNF (67.9°N, 150.5°W); 5, BRNC (67.9°N, 149.8°W); 6, BRSJ (68.5°N, 143.8°W); 7, BRFR (68.6°N, 141.6°W). Alaska Range sites: 8, ARCC (63.6°N, 150.0°W); 9, ARTL (63.4°N, 149.2°W); 10, ARRC (63.7°N, 149.0°W); 11, ARSC (63.5°N, 148.8°W); 12, ARBC (63.4°N, 146.4°W); 13, ARTK (63.3°N, 143.3°W). Location of climate stations used in Fig. 2. BETT, Bettles; DNP, Denali National Park; McG, McGrath and Fairbanks.

trends in the boreal forest region of Alaska and has therefore been frequently used to model treeline growth in Brooks Range, Alaska Range and other mountain ranges (Garfinkel & Brubaker, 1980; Jacoby & D'Arrigo, 1995; Barber *et al.*, 2000; Lloyd & Fastie, 2002, 2003). In a previous dendrochronological study (Barber *et al.*, 2000), the Fairbanks temperature record was found to be strongly and consistently correlated with ring width of 20 white spruce stands across central Alaska and with $\delta^{13}\text{C}$ and maximum late-wood density at one and three stands, respectively.

The Fairbanks record we used is a composite of University Experiment Station (1906–1947) and Fairbanks International Airport (1948–2000). During the period of overlap between the two stations (1948–1996), there was no significant difference in the summer mean monthly temperatures. Fairbanks is the only climate station in Interior Alaska with a record extending back to the first decade of the 20th century. Other available station records we evaluated included: Denali National Park Headquarters (1923–2000), McGrath (1942–2000),

and Bettles (1949–2000). Most of these data sets were affected by missing data, and relocation effects to a greater degree than Fairbanks. The relationship of mean March–August temperature at those four stations revealed the same pattern of year-to-year variability (Fig. 2).

Thus, both the station data themselves and the tree-growth responses across Interior Alaska indicate that Fairbanks climate data are indeed a valid indicator of year-to-year variability in climate as it affects the growth of white spruce.

Tree ring series were cross-dated on the basis of prominent and well-known marker ring series. Accuracy of dating was checked using COFECHA runs for each site. Dating errors were limited to 1 or 2 years and corrected for subsequent analysis. Individual tree ring series were detrended by ARSTAN (detrending removes the age effect, Cook *et al.*, 1992) using the first detrending option (negative exponential or straight line fit). We correlated each tree's record of detrended annual radial growth (1906–2000 overlapped with the climatic record) with the 57 mean monthly temperatures and precipitation preceding the end of ring formation. Results from nondetrended tree ring series exhibited similar results, suggesting that age did not have a significant influence on the tree-growth–climate relationship. The resulting matrix included about 8 million correlation scores for temperature alone.

To search for common pattern of correlation scores, we used these matrices as input into a cluster analysis (STATISTICA). Our objective was to simplify the task of identifying significant correlation scores for each tree (which is a usual procedure in dendroclimatology) as well as search for overall population-wide response types.

We used 'joining' (tree diagram, complete linkage) in the cluster module and then refined the clusters using the 'k-means' clustering procedure, where the program calculates a user-specified number of clusters. We increased the number of clusters in each step (starting from two) to maximize the difference between clusters. By visually inspecting the means of each clustering run, we were able to stop the procedure as soon as the new run did not produce new clustering pattern (significantly different mean), but merely created a new cluster emulating an existing pattern. We did not remove the serial autocorrelation, because our goal was to establish a relationship between growth and some combination of months and not reconstruct or predict one parameter (growth) with the other (mean temperature of the 1 month with highest correlation score).

Once we had identified the two dominant climate signals (July and spring temperature indices, precipitation was not significantly correlated), we calculated the

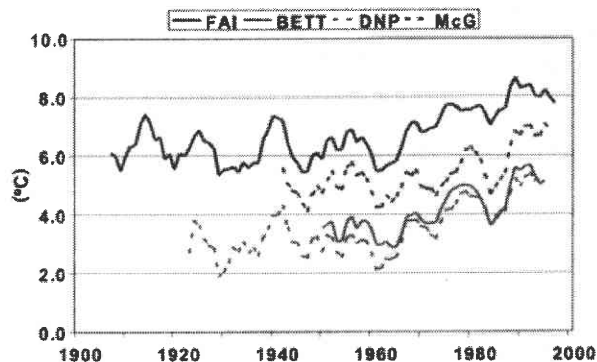


Fig. 2 Relationship of climate stations throughout Interior Alaska. Year-to-year variability of averaged March–August mean monthly temperatures (5 years smooth) is similar for four stations in Interior Alaska. FAI, Fairbanks; BETT, Bettles; DNP, Denali National Park; McG, McGrath. For location see Fig. 1.

correlation score of each individual tree's detrended radial growth with these two climatic predictors. We then grouped the trees according to the following criteria: first, negative responders were defined by a correlation score of ≤ -0.25 (threshold of significance, $P = 0.01$) of detrended growth with the July prior temperatures after 1950. Positive responders were all remaining trees with a correlation score ≥ 0.25 of growth vs. the spring temperature index (after 1950).

To examine the consistency of the growth responses throughout the last 200 years, we calculated the mean raw ring width (decadal average) of trees belonging to the two clusters that were significantly correlated with temperature in both mountain ranges. Because the number of trees contributing rings in each decade varied (because of different dates of origin during the 19th century), we calculated the 95% confidence interval in differences of the means of radial growth by decade for the two clusters. To examine the consistency of growth responses by site through time, we identified the temperature factors that produced the highest correlation scores for each site's average of radial growth index by responder type, both before and after 1950. Selection of the highest correlation score was based upon annual values. To provide additional insights into the strength of the relationship, we used a 5-year smoothing algorithm removing some of the effects of short-term variability. We chose a 5-year smoothing term, because there is a 8–9 and 16.7–18 years periodicity in both white spruce growth and summer temperatures in Interior Alaska (Juday *et al.*, 2004), and therefore we decided to use a period that would extend over at least half of the short cycle. A smoothing term of approximately half of the cycle length will enhance the expression of the medium-term

trends in the data, without dampening the cycles that are present.

We then developed a regression of the two climatic predictors vs. the mean of detrended radial growth of the two significant groups of trees (negative and positive responders). Piecewise linear regression in STATISTICA was used to test, whether a single regression was equally predictive across the entire range of data. The program calculates two linear regressions for a data array. The breakpoint or 'threshold' of these regressions is chosen where the difference in slope of the two models is maximized. We tested the significance of these differences by comparing the slope and *P*-values of the two resulting equations.

Results

Pattern of growth response to temperature

Based on the relationship between annual radial growth and Fairbanks mean monthly temperature, the initial clustering 'tree' diagram over the entire period (1906–2000) of climate record revealed a major division

between trees with generally positive vs. negative correlations with temperature. The 'k-means' clustering procedure produced three distinctive clusters, revealing three populations of (1) consistently negative, (2) consistently positive and (3) nonsignificant correlation of growth with temperatures (Fig. 3). It is particularly noteworthy that this pattern repeated itself at each of the 13 sites in both mountain ranges. More trees belonged to the cluster defined by negative growth responses to warm temperatures at these cold sites (40.1%) than to the cluster with positive growth responses (36.3%). While all 57 monthly correlations define membership in a cluster, statistically significant or near-significant scores are concentrated in only a few specific months (Fig. 3). Serial autocorrelation leads to a similar pattern of correlation each year for a period of years prior to ring formation.

Recent findings identify a difference in tree-growth/ climate relationships at treeline between the periods pre- and post-1950 (Briffa *et al.*, 1998; Lloyd & Fastie, 2002). Even though this division is arbitrary, we adopted it to (1) compare our results to other studies and (2) obtain two time periods of about equal length in

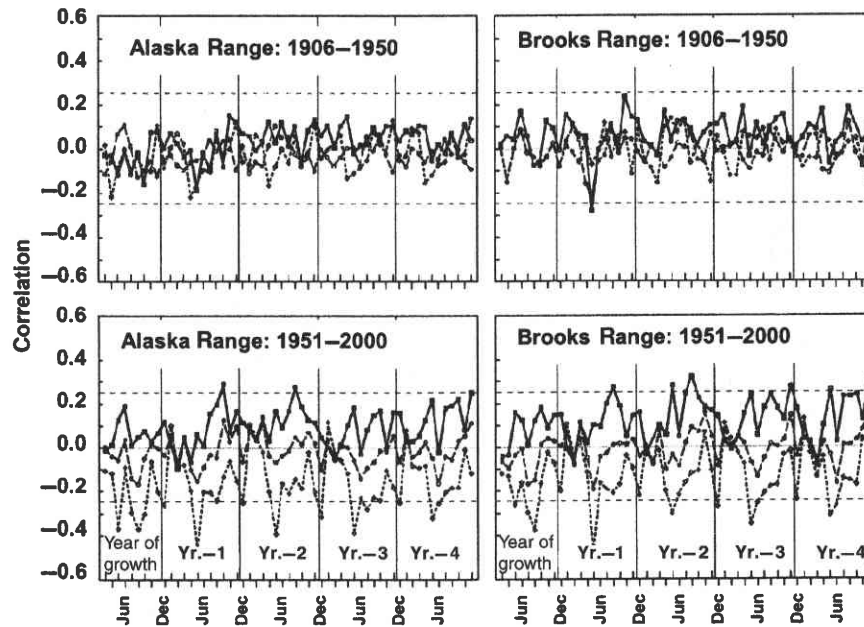


Fig. 3 Cluster analysis of climate–tree correlation scores. Correlation scores of detrended annual radial growth with Fairbanks mean monthly temperature over a 57-month period prior to the end of each yearly ring formation. The three lines depict the mean of the three most distinctive clusters developed using 'k-means' clustering. Solid lines represent the mean correlation scores of all trees included in the cluster with positive radial growth responses to monthly temperatures, dotted lines represent the cluster defined by negative responses, and dashed line represents clusters defined by trees with no consistent growth response. Level of statistical significance ($P \sim 0.01$) indicated by horizontal dashed lines. Note intensification of growth response after 1950 and the maximization of correlation scores in the July prior to ring formation for negative responders in both mountain ranges and in the spring (March and/or April) for the positive-responding population. Because of a high degree of serial autocorrelation most explanatory power is concentrated in the maximum correlation scores of the 2 years prior to ring formation.

our data set. Clustering runs from our sample restricted to the pre- and post-1950 periods also show distinct differences across this time boundary (Fig. 3). The absolute value of the mean correlation scores of our population-wide clusters in both mountain ranges changed from almost uniformly nonsignificant pre-1950 ($P > 0.01$, Fig. 3) to a pattern after 1950 in which correlation scores of several months were statistically significant (Fig. 3). All further references to statistical significance are based on $P < 0.01$.

At each of the 13 sites, as well as the combination of data in each mountain range (Fig. 3), the three most distinct clusters in the post-1950 data displayed essentially the same pattern of correlation scores: Cluster 1, a highly significant negative response to previous July temperature; Cluster 2, a highly significant positive response to spring temperatures (March 1 year and April temperatures 2 years prior in the Alaska Range, and April 1 and 2 years prior in the Brooks Range), and Cluster 3, no significant responses. This pattern persisted even at one site where only 15 trees met our age criterion. These July and spring tempera-

tures serve as our climatic predictor indices for positively and negatively responding trees.

Before 1950 the individual tree mean ring width index (MRWI) correlation scores with the two climatic predictor indices were distributed normally (Fig. 4) on each axis with the modal class centred near the significance level ($r = \pm 0.25$). However, after 1950, distributions of individual tree correlation scores in both mountain ranges have become either strongly positive or strongly negative (Fig. 4). This diverging opposite response was especially distinct, and underscores the nonoverlap of the two significant climate responses. The distinctiveness of the clusters therefore was not the result of a few trees with unique growth patterns, rather trees generally responded either negatively or positively to warming.

Annual radial growth (composite mean of all trees in each mountain range) in the negative-responding population tracks its predictor index (mean monthly temperature in Fairbanks of the July prior to growth) very well, especially after 1950 (Fig. 5). In the positive-responding populations, however, three things need to

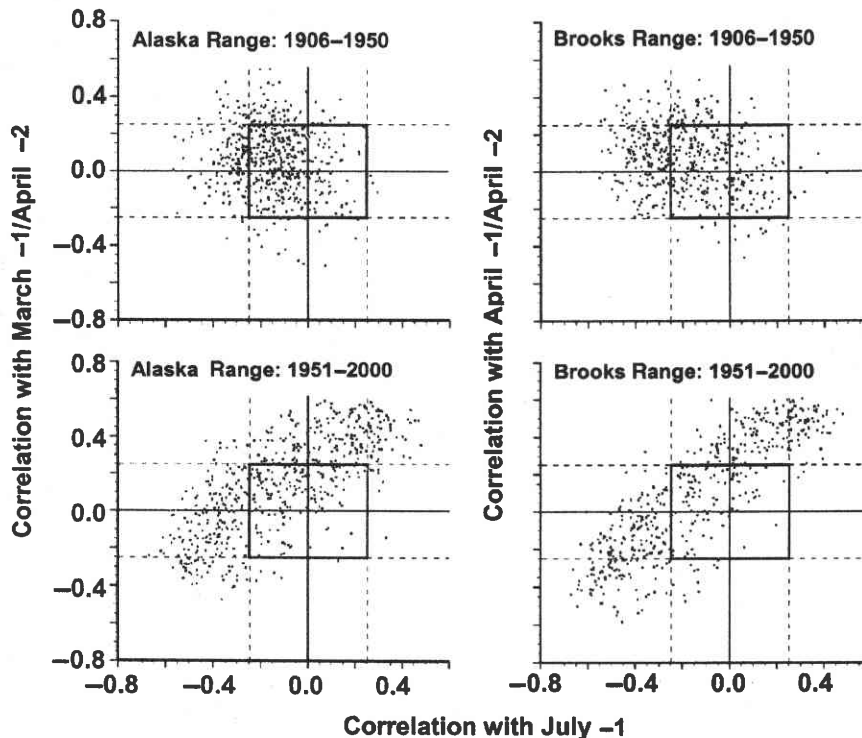


Fig. 4 Growth predictor indices before and after 1950. Scatter diagram of correlation scores of individual tree radial growth (MRWI) with previous July temperature (x -axis) and spring temperature index (y -axis) for Alaska Range ($n = 600$) and Brooks Range ($n = 555$) before 1950 and after 1950. This figure displays, how responsive each individual tree in the sample is to the climate factors that best predict growth of positive (y -axis) and negative responders (x -axis). Level of statistical significance indicated by dashed lines. The values inside the box are nonsignificant. Note the scatter before 1950 indicating normal distribution along both axes. After 1950 the distribution shifts in the direction of strong positive and strong negative correlations. Note that the majority of trees display either negative or positive correlation with predictor indices, rather than both responses simultaneously.