

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

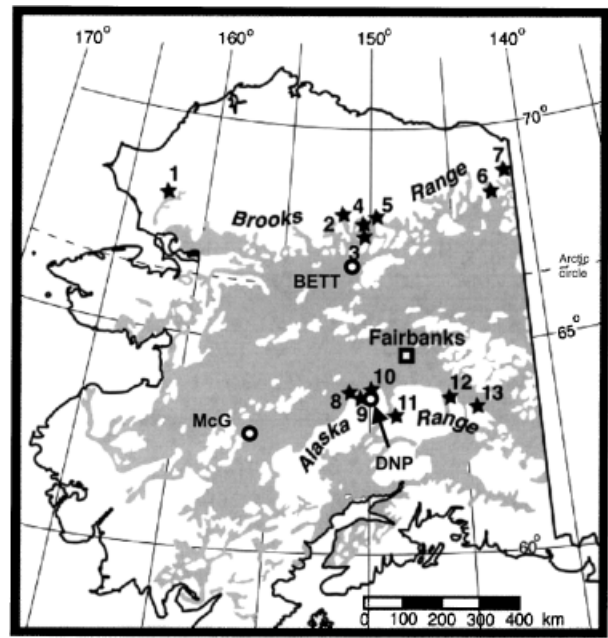


Fig. 1 Location of study sites in Brooks Range and Alaska Range in Alaska. Shaded area is extent of boreal forest. All sites are at or near treeline. Brooks Range sites: 1, BRKG (68.0°N, 161.5°W); 2, BRHF (67.8°N, 152.4°W); 3, BRCL (67.7°N, 150.5°W); 4, BRNF (67.9°N, 150.5°W); 5, BRNC (67.9°N, 149.8°W); 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

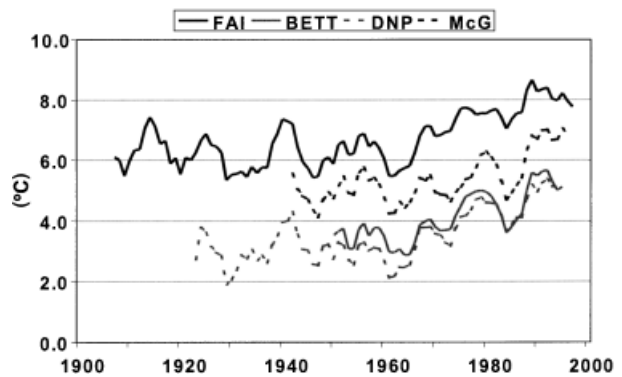


Fig. 2 Relationship of climate stations throughout Interior Alaska. Year-to-year variability of averaged March–August mean monthly temperatures (5 years smooth) is similar for four stations in Interior Alaska. FAI, Fairbanks; BETT, Bettles; DNP, Denali National Park; McG, McGrath. For location see Fig.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

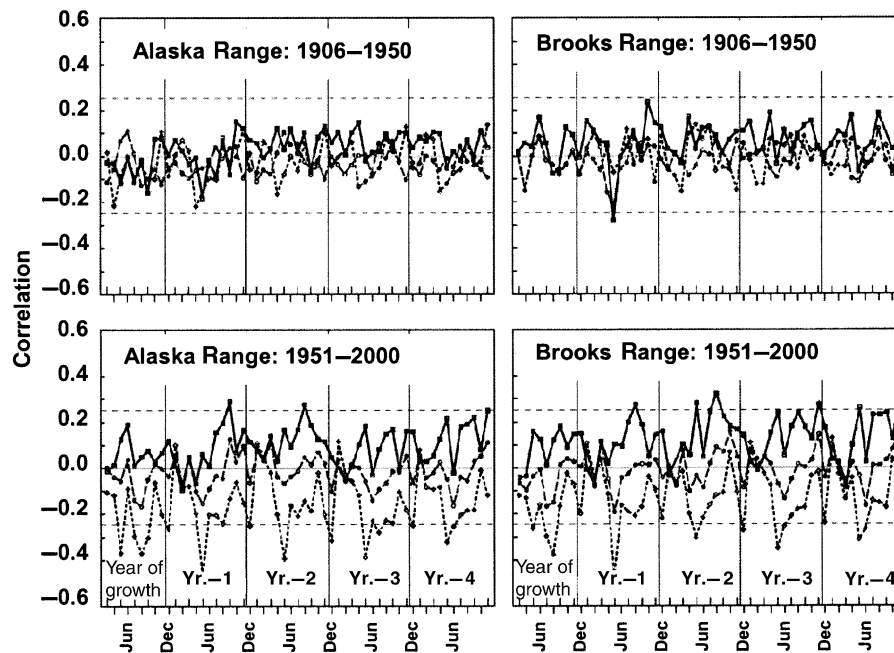


Fig. 3 Cluster analysis of climate–tree correlation scores. Correlation scores of detrended annual radial growth with Fairbanks mean monthly temperature over a 57-month period prior to the end of each yearly ring formation. The three lines depict the mean of the three most distinctive clusters developed 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

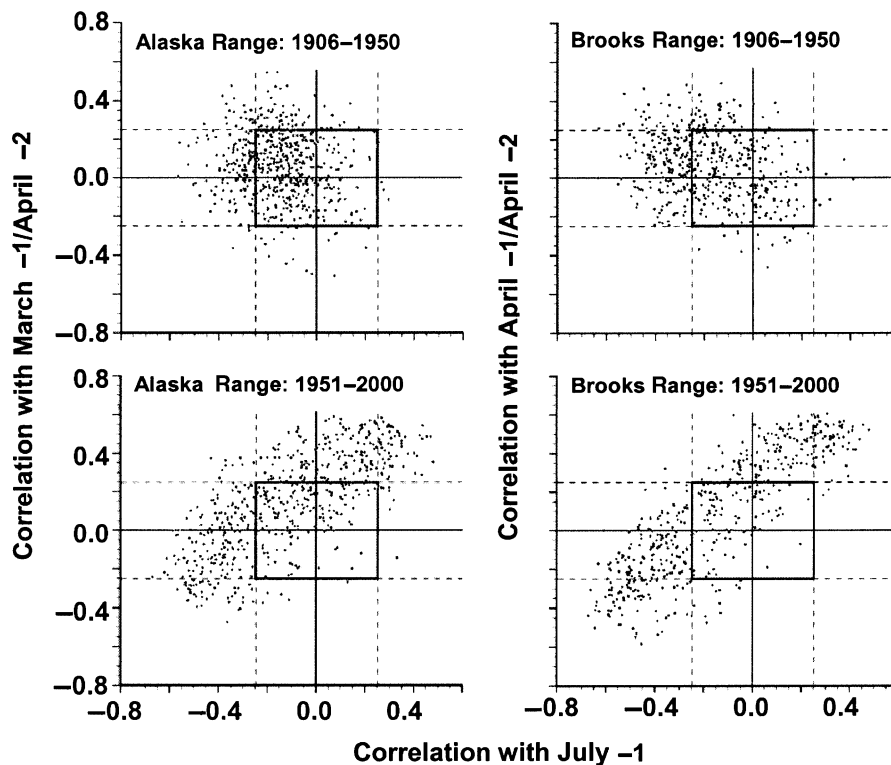


Fig. 4 Growth predictor indices before and after 1950. Scatter diagram of correlation scores of individual tree radial growth (MRWI) with previous July temperature (x -axis) and spring temperature index (y -axis) for Alaska Range ($n = 600$) and Brooks Range ($n = 555$) before 1950 and after 1950. This 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.

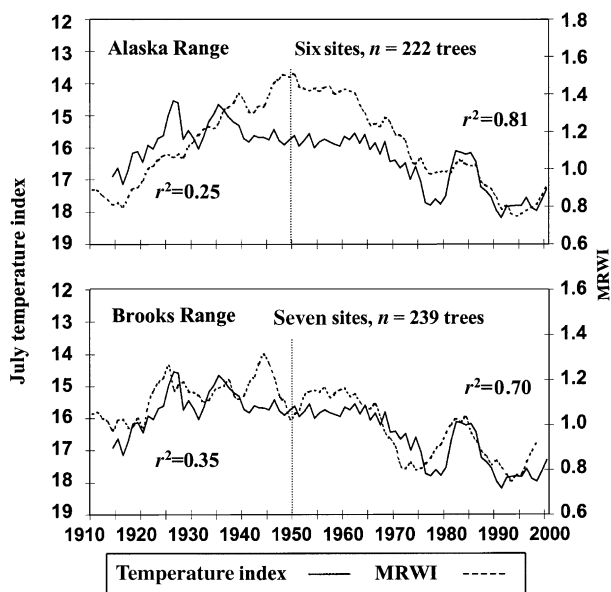


Fig. 5 Relationship between negative growth responders and July temperature index. Note the inverted scale on the left y -axis. Both data arrays have been smoothed (5-year running mean). Warmer Julys lead to less growth in the negative-responding population in both mountain ranges. After 1950, correlation scores increase, apparently reflecting the higher occurrence of the temperature threshold ($\sim 16^\circ\text{C}$).

be noted: (1) the relationship between predictor index (spring temperature) and radial growth is only apparent in the second half of the 20th century (Fig. 6) and it is weaker than the relationship of the negative responders to temperature. (2) Even though a consistent general trend can be observed, lag effects seem to be operating (e.g. inclines and declines in radial growth of the Alaska Range population seem to lag 8–10 years behind their predictor index). (3) The relationship between radial growth and spring temperature in the Brooks Range begins about 1975, whereas Alaska Range trees start to respond to variation in spring temperature already in the 1950s (Fig. 6).

Variability between and within sites

To test for site-specific responses, we examined the proportion of negative and positive responders at each site (Table 1). We checked for consistency of predictive power of the climate indices before and after 1950 by developing site-specific climate predictor indices that maximized the correlation scores of the mean of each positive and each negative population both before and after 1950 (Table 1).

Before 1950, a variety of months best predicted annual growth for positive- and negative-responding populations, but after 1950, the months contributing to

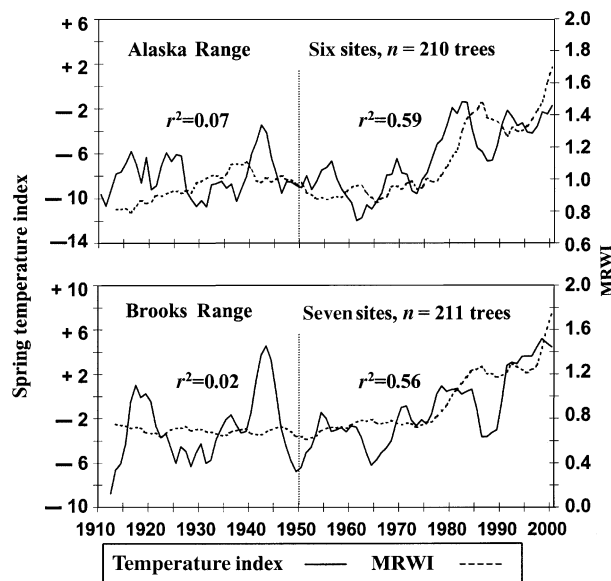


Fig. 6 Relationship between positive growth responders and spring temperature index. Before 1950, no relationship exists between the positive-responding population and the spring temperature index (here calculated as sum of March $-1/\text{April} -2$ in the Alaska Range, and mean of April $-1/-2$ in the Brooks Range). After 1950 however, spring temperatures indices have a statistically positive relationship to tree growth. White spruce growth in both mountain ranges displays a secular increase in the last decades of the 20th century, which occurred slightly after the rise in the temperature index.

the best predictor index were highly consistent among sites and identical to the two predictor indices derived from the overall population clustering procedure: previous July limits radial growth in negative-responding trees and warm springs increase growth in positive-responding trees. Correlation scores after 1950 are greater in magnitude than before 1950. Unlike previous studies (Garfinkel & Brubaker, 1980; Lloyd & Fastie, 2003), Fairbanks precipitation and cold season temperatures added no independent explanatory power to the climate–tree-growth relationship after 1950.

The smoothed values (5-year running mean) of our climate indices explain up to 81% of the variability in growth of the sampled trees after 1950 (Table 1). During the same period, 43% of the Brooks Range trees showed significant negative responses to climate, and 38% positive, while 37% of the Alaska Range trees were negative and 35% positive. The higher correlation of the individual tree-growth response to climate after 1950, demonstrated first by the cluster analysis, then the scatter of the two best predictor indices, is also consistent across all sites and site types in both mountain ranges (Table 1, Figs 5 and 6), suggesting widespread occurrence and unique processes after 1950.

Table 1 Correlation scores of radial growth with temperature index before and after 1950 by site for negative responders (upper portion) and positive responders (lower portion)

Site	<i>n</i> > 100 years at site	% sig.	After 1950	<i>r</i>	5 years smooth	Before 1950	<i>r</i>
ARBC	167	19.8	Jul -1	-0.63	-0.85	Aug	-0.41
ARCC	28	78.6	Jul -1	-0.50	-0.82	Jul 1/-3	-0.33
ARRC	121	38.0	Jul -1	-0.59	-0.86	Aug/Aug -1/Apr -3	-0.47
ARSC	15	33.3	Jul -1	-0.52	-0.80	Aug	-0.35
ARTK	146	35.6	Jul -1	-0.54	-0.85	Aug/Aug -1	-0.37
ARTL	123	52.8	Jul -1	-0.77	-0.81	Jul -1/Aug -1	-0.38
BRCL	68	38.2	Jul -1	-0.68	-0.86	Apr/Jul -1/Jul -3	+0.55
BRFR	59	67.8	Jul -1	-0.64	-0.90	Jul/Feb -1	+0.35
BRHF	73	42.5	Jul -1	-0.66	-0.83	Jun/May -2	+0.42
BRKG	67	8.9	Jul -1	-0.58	-0.75	Jan -1/Jul -1	+0.48
BRNC	109	46.8	Jul -1	-0.65	-0.87	Jul -1/Apr -4	-0.53
BRNF	79	51.9	Jul -1	-0.64	-0.88	Jul -1	-0.52
BRSJ	100	46.0	Jul -1	-0.66	-0.87	Jul -1/Apr -4	-0.41
ARBC	167	33.1	Mar -1/Apr -2	+0.53	+0.78	Mar/Jul -1	-0.41
ARCC	28	7.1	Mar -1/Apr -2	+0.56	+0.65	Aug/Aug -2	-0.36
ARRC	121	49.5	Mar -1/Apr -2	+0.60	+0.85	Mar/Jul -1	-0.44
ARSC	15	53.3	Apr -1/Apr -2	+0.61	+0.75	Aug	-0.40
ARTK	146	27.4	Mar -1/Apr -2	+0.60	+0.81	Aug -1/-2	-0.42
ARTL	123	36.5	Mar -1/Apr -2	+0.63	+0.84	Jul -1/Aug -1	-0.38
BRCL	68	51.5	Apr -1/-2/-3	+0.67	+0.77	Jun/Jan -2/-3	+0.50
BRFR	59	16.9	Jul/Apr -2	+0.70	+0.76	Aug/Feb -1/Aug -2	+0.50
BRHF	73	30.1	Apr -2/Feb -2/Jan -3	+0.54	+0.82	Jul/Aug -2	+0.43
BRKG	67	76.1	Apr -2/Jul -2/Dec -2	+0.55	+0.87	Aug -1/-2	+0.51
BRNC	109	43.1	Apr -1/-2	+0.62	+0.74	Jul -1/Apr -4	-0.47
BRNF	79	32.9	Apr -1/-2	+0.60	+0.70	Jan -3/-4	-0.30
BRSJ	100	20.0	Apr -1/-2	+0.58	+0.73	May -1/Dec -1	+0.37

ARBC is the site name (site locations: Fig. 1). At that site, 167 trees were older than 100 years, which were used in the analysis. Of these 167 trees 19.8% were negative responders and the best predictor index of annual radial growth after 1950 was the July temperature prior to growth (Jul -1) with an *r*-value of -0.63 (-0.85 for the 5-year smoothed correlation). Before 1950, August was the best predictor for growth (*r* = -0.41). We built positive- and negative-responding site chronologies by averaging detrended annual growth of either all negative- or positive-responding trees at that site. We then correlated annual values of the positive- or negative-responding population with each of the 57 mean monthly temperatures preceding the end of each ring formation. Combination of months with highest predictive power is shown. After 1950, the unifying month with highest explanatory power for negative responders is prior July (indicating drought stress) at each site. The smoothed (5-year running mean) values explain up to 81% of variation in growth at these sites. March and April temperatures 1 and 2 years prior to ring formation are the months with peak correlation for the positive responding populations at each site after 1950, consistent with the earlier onset of spring in this period.

To examine whether there was any obvious relationship between the relative proportion of negative and positive responders and site type, we calculated the amount of each responder group according to landscape position within a site (floodplains vs. high-density vs. low-density stands, Table 2). There seems to be no consistent relationship of growth response with landscape position or aspect at this scale. Even though differences in relative abundance of positive vs. negative responders between site types can be large (i.e. in some sites most positive responders can be found in low-density stands or floodplains), overall there seems to be no single-site type favouring either growth response.

Growth comparison over 200 years

In the first seven decades of the 19th century, mean radial growth of negative and positive responders were essentially equivalent in the Alaska Range, while in the Brooks Range, negative responders grew at a greater rate, although not significantly greater at the 95% level (Fig. 7). Sample depth declined with increasing age and this contributed to the overlapping confidence intervals of the growth rates of positive and negative responders.

For the next 10 decades (1870s–1960s), negative responders grew at a significantly greater rate in both mountain ranges than positive responders. In the decade of the 1970s, rates of growth were equivalent.

Table 2 Stand characteristics and relative distribution of positive and negative responding trees (>100 years old) by site type

	<i>n</i>	avg. height (m)	avg. dbh (cm)	avg. age	% neg	% pos	% ns
<i>ARBC, n = 167</i>							
LD	38	7.2	19.4	136	32	25	43
HD	71	13.4	22	176	14	26	60
FL	58	13.2	26.2	184	15	42	43
<i>ARCC, n = 28</i>							
LD	9	10	24.7	142	75	12	12.5
HD	19	11.5	31.4	131	79	5	16
FL							
<i>ARRC, n = 121</i>							
LD	47	9.4	20.8	140	34	48	18
HD	54	15	34.2	127	28	58	14
FL	20	21	47.5	158	56	32	12.5
<i>ARSC, n = 15</i>							
LD	7	10.5	32.6	125	43	28	29
HD							
FL	8	15.5	29.3	163	25	62	12.5
<i>ARTK, n = 146</i>							
LD	51	12.4	19.6	184	27	34	39
HD	33	11.5	14.9	206	21	49	30
FL	62	17.1	23.6	183	50	10	40
<i>ARTL, n = 123</i>							
LD	21	9.6	20.4	144	14	62	24
HD	40	14.4	22.5	133	50	43	7.5
FL	62	16.4	30.3	188	64	23	13
<i>BRCL, n = 68</i>							
LD	52	6.5	12.6	118	26	66	8
HD	16	11.8	22.9	151	53	26	21
FL							
<i>BRFR, n = 59</i>							
LD	26	7.6	15.7	133	46	32	22
HD	17	10.9	26.7	151	94	6	0
FL	16	8.7	19.9	176	100	0	0
<i>BRHF, n = 73</i>							
LD	25	10	16.4	147	33	15	52
HD	15	13.2	27.1	137	82	0	18
FL	33	12.8	22.8	159	32	55	13
<i>BRKG, n = 67</i>							
LD							
HD	67			175	9	76	15
FL							
<i>BRNC, n = 109</i>							
LD	45	7.5	13.6	131	44	44	13
HD	47	9.6	18.5	167	66	14	20
FL	17	11.1	22.3	136	16	53	31
<i>BRNF, n = 79</i>							
LD	35	8.4	17.4	130	39	33	28
HD	44	10.9	22.9	160	56	25	19
FL							
<i>BRSJ, n = 100</i>							
LD	11	5	9.5	134	16	44	40
HD	30	5.6	10.5	139	34	19	47
FL	59	10.8	13.8	126	43	17	40

LD, low-density upland sites; HD, high-density upland sites; FL, floodplain sites. Percentage of trees with significant correlation scores, either positive (pos) or negative (neg), are based upon correlation with best climate predictor index at that site (see Table 1); ns, no significant correlation with climate. White spruce trees in the Alaska Range are on average bigger than in the Brooks Range, reflecting latitudinal difference. That regional signal is modified at smaller scales, however, and can be highly variable (e.g. ARBC is comparable with sites in the Brooks Range). Trees at low-density sites appear to be smaller and younger, but this pattern is not consistent across sites. There is no consistent relationship between site type and growth response at this scale.

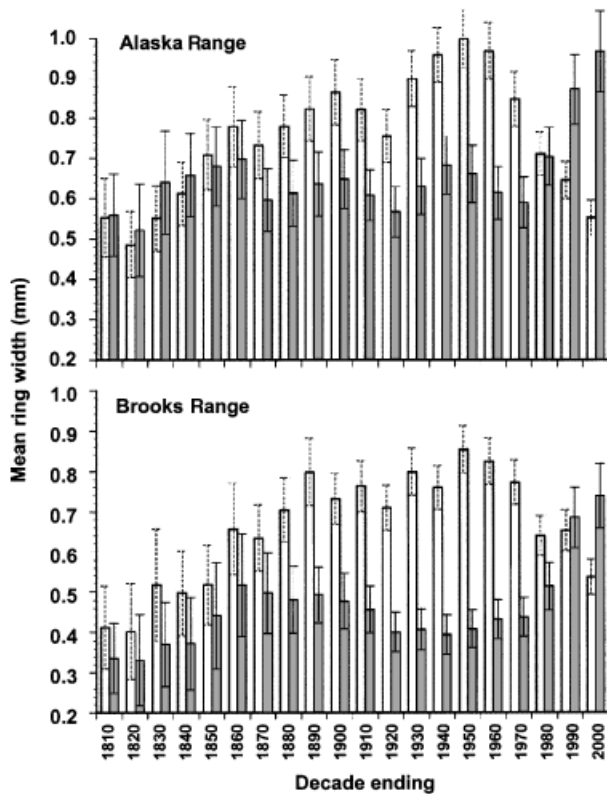


Fig. 7 Mean raw radial growth by decade of negative and positive responders. Negatively (white columns) and positively (grey columns) responding populations in the Alaska Range and Brooks Range. Note the reversal of historic relationship of growth in the last part of the 20th century, consistent with recent climate warming.

In the last two decades of the 20th century, positive responders grew at a rate equivalent to or greater than negative responders, and at their highest rate of growth during the 200-year period.

Temperature threshold effects

For negative responders, the colder portion of the range of July temperatures ($< \sim 16^\circ\text{C}$) has little predictive power for radial growth in both mountain ranges ($r^2 = 0.02$ and 0.05 , Fig. 8). July temperatures over $\sim 16^\circ\text{C}$, however, show a strong significantly negative relationship with growth (Alaska Range, $r^2 = 0.46$; Brooks Range, $r^2 = 0.42$). This apparent threshold operates at all sites. The relationship of July temperatures in Fairbanks to the actual temperatures at most sites remains unknown. However, at one site (ARRC), climate records exist from Denali National Park Headquarters. July temperatures at Denali Headquarters are on average (1923–1997) $\sim 4.5^\circ\text{C}$ lower than in Fairbanks. We calculated a similar offset (4 years overlap)

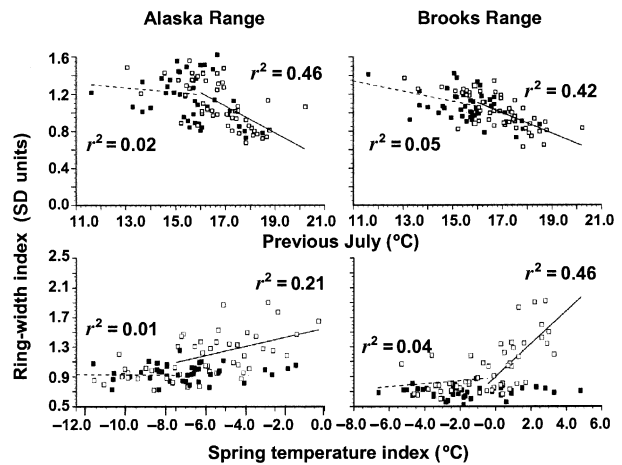


Fig. 8 Ring width controlled by temperature thresholds. Piecewise linear regression of annual correlation scores of detrended radial growth (standardized values) vs. temperature indices in the Alaska Range and Brooks Range before 1950 (solid squares) and after 1950 (hollow squares). Two regression lines are produced for each data set, maximizing the difference in slope to estimate 'breakpoint' or threshold. Dashed lines indicate regression line before threshold, solid lines after threshold. Correlation scores are calculated for the entire range of data for July (1906–2000), since the relationship did exist before 1950 (Fig. 6). July temperature ($^\circ\text{C}$) displays little predictive power for growth in both mountain ranges until an apparent $\sim 16^\circ\text{C}$ threshold. Correlation scores for positive responders are calculated for the period 1951–2000. Before 1950, detrended radial growth of positive-responding trees shows little response to temperature predictor index (mean March -1 /April -2 in the Alaska Range, and mean of April -1 / -2 in the Brooks Range). After 1950, growth responds positively to an increase in temperature index in the upper portion of the range of values (warm springs). The absolute values of the apparent spring temperature thresholds differ between the mountain ranges, because of the different months used in calculating each temperature index.

for one site in the Brooks Range (BRNC). Based on these offsets, we estimate the mean July temperature above which radial growth in the following year would be limited is about 11 – 12°C . An empirical study would be necessary to calibrate actual temperature differences more precisely.

The spring temperature index predictors also appear to be operating above certain thresholds (Fig. 8), but only after 1950. Correlation scores increased from $r^2 = 0.01$ before 1950 to $r^2 = 0.21$ above the predictive threshold in the Alaska Range and from $r^2 = 0.04$ to 0.46 in the Brooks Range. In the Alaska Range after 1950, the years of highest radial growth are associated with the warmest spring index values. There is a similar relationship in the Brooks Range, but the warmest seven springs were all in the 1990s. Therefore, we

cannot exclude the possibility that the apparent spring temperature threshold of growth acceleration is partly coincidental in the Brooks Range.

Discussion

The finding of highly significant negative relationships between July temperature and radial growth as the most common climate signal present at treeline and near treeline sites in Alaska is quite surprising, and apparently not consistent with much published literature in North America (Garfinkel & Brubaker, 1980; Jacoby & D'Arrigo, 1989; Jacoby *et al.*, 1996; Overpeck *et al.*, 1997; Lloyd & Fastie, 2003). Negative response of growth to July temperatures from drought stress is reported for white spruce in particular habitats: (1) It is the most common signal in upland white spruce in Interior Alaska (Barber *et al.*, 2000). (2) Single white spruce in some treeline areas also show negative growth response (Garfinkel & Brubaker, 1980; D'Arrigo & Jacoby, 1993; Lloyd & Fastie, 2002).

Here we report that the most frequent growth response to increasing temperatures is negative at the northern and altitudinal tree limit in Alaska. Not only single trees, but large populations of trees at every site show reduced growth with warming temperatures. In most of the previous studies in this environment (exception Lloyd & Fastie, 2002), the sampled trees were deliberately chosen in order to obtain a pure climate signal with positive response to temperature (e.g. for climatic reconstructions). Our sampling, in contrast, was based on landscape parameters and can be taken as representative of the population of trees in this environment.

Dendroclimatological research is often site specific and includes some subjective elements in the selection of the climatic parameters used in reconstruction. Our clustering approach applied a consistent criterion to all trees across all sites and only then proceeded to site-specific analysis. The consistency of white spruce growth response to climate across all sites and both mountain ranges, both negatively and positively, and the strengthening of this response in the post-1950 time period, suggests that a true climatic control is involved.

This strengthening of the climate-growth relationship after 1950, in our sample, contrasts with the hemisphere-wide decrease in positive sensitivity of northern tree growth to summer warmth (Briffa *et al.*, 1998). Possible explanations for the discrepancy include (a) we did not assume a coherent climatic signal at each site, but tested each tree explicitly for its growth response to climate and thus did not average opposite responses, (b) we exclusively examined white spruce and not a variety of species that may have included

opposite trends, (c) warm season temperature trends in the western North American Arctic have been the opposite of hemisphere-wide trends. Many subregions across the Arctic experienced a period of cooling following 1950 until the late 20th century (Overpeck *et al.*, 1997; Vaganov *et al.*, 2000). However, interior Alaska experienced steadily warming growing season temperatures since 1950 (Barber *et al.*, 2004; Juday *et al.*, 2003).

A large proportion of sampled negative-responding trees grows in higher-density upland forest stands, in tree islands or in floodplains. These are locally the most productive stands, with higher stem density than most of the treeline ecotone. Higher stem densities, physiological limitation on water transport due to low soil temperatures in these sites (Goldstein *et al.*, 1985) and increases in shrublayer (Sturm *et al.*, 2001) result in higher competition for below-ground resources such as water at these sites, and may ultimately lead to drought stress. Growth of boreal conifers is affected mostly by previous year temperatures (Jacoby & D'Arrigo, 1995; Jarvis & Linder, 2000). Thus the pattern in negative responders of maximized correlation scores with previous July temperature is consistent with a drought stress mechanism, as established for low-elevation white spruce stands in central Alaska (Barber *et al.*, 2000). Other factors could enhance a drought induced reduction in growth: (1) Higher stem density lead to lower snow depth at the ground level, which promotes greater conduction of cold into the soil layer. This would result in delayed initiation of thawing during spring, which if combined with higher temperatures could lead to extreme levels of moisture tension within the tree (Berg & Chapin, 1994). (2) Higher stem density stands have a lower albedo than low density stands and therefore experience higher leaf temperatures and higher transpiration rates. Boreal conifers are known to suspend the photosynthetic process in dry air, even though soil moisture is freely available (Brooks *et al.*, 1998).

Positively responding trees may be benefiting from lengthening of the growing season observed in high-latitude environments (Keeling *et al.*, 1996; Myneni *et al.*, 1997), leading to earlier onset of ring formation and increased CO₂ assimilation early in spring (Keeling *et al.*, 1996). Lengthening of the growing season may be due largely to the timing of snowmelt, which in turn may be strongly influenced by late winter/early spring temperatures (our predictor index). In the case of the spring temperature index in the Alaska Range, the mean of March and April temperatures at Denali National Park Headquarters is only about 2 °C lower than in Fairbanks, so that the upper half (above threshold) of spring temperature index values may

actually reflect the onset of snowmelt at the sites. Timing difference of these events between the Alaska and Brooks Range caused by latitudinal difference also support the hypothesis that threshold values for positive responders reflect onset of snowmelt. In the Alaska Range the positive correlation of growth with temperature is maximized earlier than in the Brooks Range (Fig. 3, Table 1), which is further north and experiences later snowmelt.

Boreal coniferous trees need soil water to reinitiate photosynthetic activity in spring (Jarvis & Linder, 2000). Liquid water can be available at the soil surface as soon as overlying snow starts to melt, even though mean air temperatures are below freezing (Jarvis & Linder, 2000). We infer that warmer spring temperatures produce earlier onset of snowmelt leading to the positive growth response of a subpopulation of white spruce. Although this explanation is consistent with our data, further work needs to be done to confirm this mechanism. On the other hand, the consistency of this positive response from individual trees to sites to entire mountain ranges suggests that a true threshold mechanism is involved.

The apparent lag effects in the positive growth response as a result of warmer spring temperatures points to a complex mechanism of cause and effect. For example, a long-term warming of spring temperatures could not only lead to earlier snowmelt, therefore longer snow-free season and warmer soils in the summer, but also to more overall heat transfer into the ground. Degradation of permafrost takes effect as soon as soils are warmed sufficiently (to 0 °C), but to warm a frozen soil up to that temperature would require considerable energy over a long period of time, thus possibly introducing lag effects.

Carbon sequestration in deciduous boreal ecosystems is positively related to early thaw (Black *et al.*, 2000; Jarvis & Linder, 2000; Barr *et al.*, 2002). We show that in coniferous forests also wood production, and therefore above-ground carbon uptake, can increase due to warm springs, but only in our positive-responding population. Some boreal systems switch from carbon sink to carbon source over periods of years, and net ecosystem productivity (NEP) in them is actually controlled by respiration (Valentini *et al.*, 2000). Carbon flux measurements, needed to calculate respiration and ultimately NEP, are not available for our sites.

The similarity of the percentages of positive and negative responders in both mountain ranges after 1950 could lead to the conclusion that in the short term there has been no net change in carbon uptake on a regional scale by trees in these environments. However, it appears that positive responders are more frequent in environments with lower stem density than negative responders. If low stem density is a necessary property

of a positive-responding population, than calculated per unit area, the carbon uptake potential of positive responders may be less than that of negative responders. Even more significantly, the majority of trees now responding positively, historically grew less than negative responders until the late 20th century (Fig. 7) and as a result are smaller (avg. dbh 16.0 cm, height 8.4 m) than negative responders (avg. dbh 23.0 cm, height 10.4 m). This earlier period generally experienced cooler summers. Negative responders have achieved significantly less growth than positive responders since the 1970s (Fig. 7), the timing of a major summer temperature regime shift characterized by the warmest and driest conditions of the last 200 years (Barber *et al.*, 2004).

Therefore, in these environments future climate warming might not be associated with a significant increase in carbon uptake and sequestration, but carbon uptake overall may actually decline. Surprisingly, in our results, age as an independent factor did not affect the correlation of trees to temperature as reported elsewhere (Szeicz & MacDonald, 1994; Lloyd & Fastie, 2002).

Conclusions

Recent climate warming has intensified the negative growth response of a large proportion of trees at locally productive sites near treeline in Alaska. Trees on less favourable sites may be benefiting from earlier thaw and are now outperforming productive sites, reversing the historical growth relationship (Fig. 7). Any assumption that white spruce growth at treeline will change uniformly in relation to climate appears unjustified, and this changing sensitivity to climate is an obvious contributor to the error term in ring-width-based reconstruction of past climate. Our results indicate that climate–tree-growth relationships of treeline white spruce in Alaska can be modelled successfully as two distinct responses across entire mountain ranges. For modelling applications at larger scales, the main question becomes the relative proportion of positive spring responders and negative summer drought responders in the area of interest. The consistency of the proportion of trees displaying these two responses at a regional scale in the Brooks Range and Alaska Range suggests that these ratios are applicable to similar areas of the boreal forest. Landscape and local scale influences on the distribution and abundance of each growth response on the other hand, are not consistent between and within sites.

Unprecedented levels of high temperatures in the last decades (Barber *et al.*, 2004) have led to nonlinear patterns of white spruce growth responses to warming

at Alaska's treelines and temperature thresholds appear to be operating. Drought stress may now also be affecting treelines at the cold margin of the boreal forest. In the longer term, intensification of warming could lead to the elimination of these negative-responding trees through stress-related mortality. Dynamic vegetation and biogeochemical models need to incorporate these divergent responses and apparent temperature thresholds to avoid overestimation of treeline advance, high-latitude carbon uptake and future above-ground carbon storage.

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References

- Barber VA, Juday GP, Finney BP (2000) Reduced growth of Alaskan white spruce in the twentieth century from temperature-induced drought stress. *Nature*, **405**, 668–673.
- Barber VA, Juday GP, Finney BP *et al.* (2004) Reconstruction of summer temperatures in interior Alaska from tree ring proxies: evidence for changing synoptic climate regimes. *Climatic Change*, **63**, 91–120.
- Barr AG, Griffis TJ, Black TA *et al.* (2002) Comparing the carbon budgets of boreal and temperate deciduous forest stands. *Canadian Journal of Forest Research*, **32**, 813–822.
- Berg EE, Chapin SF III (1994) Needle loss as a mechanism of winter drought avoidance in boreal conifers. *Canadian Journal of Forest Research*, **24**, 1144–1148.
- Black TA, Chen WJ, Barr AG *et al.* (2000) Increased carbon sequestration by a boreal deciduous forest in years with a warm spring. *Geophysical Research Letters*, **27**, 1271–1274.
- Bonan GB, Pollard D, Thompson SL (1992) Effects of boreal forest vegetation on global climate. *Nature*, **359**, 716–718.
- Briffa KR, Schweingruber FH, Jones PD *et al.* (1998) Reduced sensitivity of recent tree-growth to temperature at high northern latitudes. *Nature*, **391**, 678–682.
- Brooks GR, Flannagan LB, Ehrlinger JR (1998) Responses of Boreal conifers to climate fluctuations: indication from tree ring width and carbon isotope analysis. *Canadian Journal of Forest Research*, **28**, 524–533.
- Chapin FS III, McGuire AD, Randerson J *et al.* (2000) Arctic and boreal ecosystems of western North America as components of the climate system. *Global Change Biology*, **6** (Suppl. 1), 211–223.
- Cook E, Briffa K, Shiyatov S *et al.* (1992) Tree ring standardization and Growth-trend Estimation. In: *Methods of Dendrochronology: Applications in the Environmental Sciences* (eds Cook ER, Kairiukstis LA), pp. 104–123. Kluwer Academics, Dordrecht.
- D'Arrigo RD, Jacoby GC (1993) Secular trends in high northern latitude temperature reconstructions based on tree rings. *Climatic Change*, **25**, 163–177.
- Dixon RK, Brown S, Houghton RA *et al.* (1994) Carbon pools and flux of global forest ecosystems. *Science*, **263**, 185–190.
- Foley JA, Kutzbach JE, Coe MT *et al.* (1994) Feedback between climate and the boreal forest during the Holocene epoch. *Nature*, **371**, 52–54.
- Foley JA, Levis S, Costa MH *et al.* (2000) Incorporating dynamic vegetation cover within global climate models. *Ecological Applications*, **10**, 1620–1632.
- Garfinkel HL, Brubaker LB (1980) Modern climate–tree-growth relationships and climatic reconstructions in sub-Arctic Alaska. *Nature*, **286**, 872–874.
- Goldstein GH, Brubaker LB, Hinkle TM (1985) Water relations of white spruce (*Picea glauca* (Moench) Voss) at tree line in north central Alaska. *Canadian Journal of Forest Research*, **15**, 1080–1087.
- Jacoby GC, D'Arrigo RD (1989) Reconstructed northern hemisphere annual temperature since 1671 based on high latitude tree-ring data from North America. *Climatic Change*, **14**, 39–59.
- Jacoby GC, D'Arrigo RD (1995) Tree-ring width and density evidence of climatic and potential forest change in Alaska. *Global Biogeochemical Cycles*, **9**, 227–234.
- Jacoby GC, Wils G, D'Arrigo RD (1996) Alaskan dendroclimatic variations for the past 300 years along a north–south transect. In: *Tree Rings, Environment and Humanity. Proceedings of the International Conference, 17/21 May 1994 Tucson, Arizona* (eds Dean JS, Maco DM, Swetnam TW. *Radiocarbon* 235–248.
- Jarvis P, Linder S (2000) Constraints to growth of boreal forests. *Nature*, **405**, 904–905.
- Juday GP, Barber VA, Rupp TS *et al.* (2003) A 200-year perspective of climate variability and the response of white spruce in Interior Alaska. In: *Climate Variability and Ecosystem Response at Long-Term Ecological Research (LTER) Sites* (eds Greenland D, Goodin DG, Smith RC), pp. 226–250. Oxford University Press, New York.
- Keeling CD, Chin JFS, Whorf TP (1996) Increased activity of northern vegetation inferred from atmospheric CO₂ measurements. *Nature*, **382**, 146–149.
- Kittel TGF, Steffen WL, Chapin FS (2000) Global and regional modeling of Arctic-boreal vegetation distribution and its sensitivity to altered forcing. *Global Change Biology*, **6** (Suppl. 1), 1–18.
- Koerner C (2000) Biosphere responses to CO₂ enrichment. *Ecological Applications*, **10**, 1590–1619.
- Kullman L (1996) Recent cooling and recession of Norway spruce (*Picea abies* (L.) Karst.) in the forest-alpine tundra ecotone of the Swedish Scandes. *Journal of Biogeography*, **23**, 843–854.
- Kullman L (2001) 20th century climate warming and tree-limit rise in the southern Scandes of Sweden. *Ambio*, **30**, 72–80.
- Lloyd AH, Fastie CL (2002) Spatial and temporal variability in the growth and climate response of treeline trees in Alaska. *Climatic Change*, **52**, 418–509.

- Lloyd AH, Fastie CL (2003) Recent changes in treeline forest distribution and structure in interior Alaska. *Ecoscience*, **10**, 176–185.
- Luckman B, Kavanagh T (2000) Impact of climate fluctuations on mountain environments in the Canadian Rockies. *Ambio*, **29**, 371–380.
- Myneni RB, Keeling CD, Tucker CJ *et al.* (1997) Increased plant growth in the northern high latitudes from 1981–1991. *Nature*, **386**, 698–702.
- Overpeck JT, Hughen KA, Hardy D *et al.* (1997) Arctic environmental change of the last four centuries. *Science*, **278**, 1251–1256.
- Pilcher JR, Schweingruber FH, Kairiukstis L *et al.* (1992) Primary data. In: *Methods of Dendrochronology: Applications in the Environmental Sciences* (eds Cook ER, Kairiukstis LA), Kluwer Academic, Dordrecht.
- Rupp TS, Chapin FS, Starfield AM (2001) Modeling the influence of topographic barriers on treeline advance at the northern forest-tundra ecotone in northwestern Alaska. *Climatic Change*, **48**, 399–416.
- Schweingruber FH, Kairiukstis L, Shiyatov SG (1992) Sample selection. In: *Methods of Dendrochronology: Applications in the Environmental Sciences* (eds Cook ER, Kairiukstis LA), Kluwer Academic, Dordrecht.
- Sturm M, Racine C, Tape K (2001) Increasing shrub abundance in the Arctic. *Nature*, **411**, 546–547.
- Suarez F, Binkley D, Kaye MW (1999) Expansion of forest stands into tundra in the Noatak National Preserve, northwest Alaska. *Ecoscience*, **6**, 456–470.
- Szeicz JM, MacDonald GM (1994) Age-dependent tree-ring growth responses of subarctic white spruce to climate. *Canadian Journal of Forest Research*, **24**, 120–132.
- Vaganov EA, Briffa KR, Naurzbaev MM *et al.* (2000) Long-term climatic changes in the arctic region of the Northern Hemisphere. *Doklady Earth Sciences*, **375**, 1314–1317.
- Valentini R, Matteucci G, Dolman H *et al.* (2000) Respiration as the main determinant of carbon balance in European forests. *Nature*, **404**, 861–865.