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LETTER

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Do limiting factors at Alaskan treelines shift with climatic regimes?

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Abstract

Trees at Alaskan treelines are assumed to be limited by temperature and to expand upslope and/or to higher latitudes with global warming. However, recent studies describe negative temperature responses and drought stress of Alaskan treeline trees in recent decades. In this study, we have analyzed the responses of treeline white spruce to temperature and precipitation according to different climatic regimes in Alaska, described as negative (cool) and positive (warm) phases of the Pacific Decadal Oscillation (PDO). We found that in three consecutive phases (positive from 1925–46, negative from 1947–76, and positive again from 1977–98), the growth responses to temperature and precipitation differed markedly. Before 1947, in a phase of warm winters and with summer temperatures being close to the century mean, the trees at most sites responded positively to summer temperature, as one would expect from treeline trees at northern high latitudes. Between 1947 and 1976, a phase of cold winters and average summers, the trees showed similar responses, but a new pattern of negative responses to the summer temperature of the year prior to growth coupled with positive responses to the precipitation in the same year emerged at some sites. As the precipitation was relatively low at those sites, we assume that drought stress might have played a role. However, the climate responses were not uniform but were modified by regional gradients (trees at northern sites responded more often to temperature than trees at southern sites) and local site conditions (forest trees responded more often to precipitation than treeline trees), possibly reflecting differences in energy and water balance across regions and sites, respectively. However, since the shift in the PDO in 1976 from a negative to a positive phase, the trees' climate–growth responses are much less pronounced and climate seems to have lost its importance as a limiting factor for the growth of treeline white spruce. If predictions of continued warming and precipitation increase at northern high latitudes hold true, the growth of Alaskan treeline trees will likely depend on the ratio of temperature and precipitation increase more than on their absolute values, as well as on the interaction of periodic regime shifts with the global warming trend. Once a climatic limitation is lifted, other factors, such as insect outbreaks or interspecific competition, might become limiting to tree growth.

Keywords: Alaska, climate regime, dendroecology, global warming, treeline, site factors, white spruce

1. Introduction

Tree growth in most cases is limited by one of the following factors: temperature, water availability, light and/or nutrient

supply, and often further affected by intra- and interspecies competition. Trees at northern high latitudes, especially at treelines, i.e. at the forest–tundra ecotone, are assumed to be limited primarily by temperature (Körner 2007). This is why their annual growth rings are often used to reconstruct temperature beyond historical records (Cook and Kairiukstis 1990). As the climate is warming, especially at

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northern high latitudes (IPCC 2007) and well observed in Alaska (Juday *et al* 2005), these temperature limited trees are expected to respond to increasing temperatures with increased growth (Holtmeier and Broll 2005). Furthermore, warm temperatures facilitate successful germination, enhance seedling and sapling growth rates and reduce the risk of seedling mortality (Hobbie and Chapin 1998, Danby and Hik 2007). Provided that reproduction rates are stable, this should lead to an advancement of trees to higher elevations and/or higher latitudes. Trees invading tundra will alter the carbon storage capacity and albedo, which could lead to major changes in northern high-latitude ecosystems (Suarez *et al* 1999).

However, recent studies point to deviations from this pattern. Historically temperature sensitive trees seem to have become insensitive to temperature in the later part of the 20th century. This phenomenon has become known as the 'divergence problem' (D'Arrigo *et al* 2008). Explanations vary from methodological objections related to detrending (i.e. standardization of age related growth trends) and data processing (Briffa *et al* 1998, Esper and Frank 2009) to ecological explanations (e.g. Wilmking and Singh 2008). Often, high temperatures are suggested as a cause for the divergence (Biondi 2000, Lloyd and Fastie 2002, Büntgen *et al* 2006, Zhang *et al* 2009), as they lead to increased evapotranspiration and therefore can cause a water deficit. This seems to be the case in some parts of Alaska, where precipitation does not keep up with temperature increase, causing drought stress in treeline trees (Wilmking *et al* 2004, Wilmking and Juday 2005). In studies of white spruce (*Picea glauca* (Moench [Voss])) in interior Alaska, Barber *et al* (2000) highlight that high temperature limits the trees' growth, due to temperature-induced drought stress during the growing season. Wilmking *et al* (2004) found white spruce, which is also the typical tree species at Alaskan treelines, to either respond positively or negatively to warmer temperatures, especially since the 1950s. The proportion of positive and negative responding trees at each site depends on the site's position along the Alaskan west–east precipitation gradient (Wilmking and Juday 2005). However, summer temperature in most of Alaska was not rising significantly until about 1975; rather, in some areas precipitation has decreased since then, giving rise to the presumption that during certain climatic conditions trees at northern treelines might be limited directly by precipitation.

Moreover, temperature gradients within one site can also lead to diverging climate–growth relationships. Zhang and Wilmking (2010) examined the influence of elevation on the climate–growth relationships of Qinghai spruce in China and found large differences between trees' responses at the upper treeline as opposed to trees right below. Elevation-dependent climate–growth relationships were found by Lloyd and Fastie (2002) for white spruce in Alaska, for mountain hemlock in Oregon (Peterson and Peterson 2001), and for Douglas-fir in Washington and Montana (Littell *et al* 2008), to mention just a few.

Viewed more from a stand perspective, Wilmking and Juday (2005) found that trees growing in low density

stands at the upper treeline tended to respond positively to temperature whereas trees growing in high density stands below the upper treeline tended to respond negatively. A corresponding response to precipitation which could be related to drought stress was not reported. However, the dependence of climate–growth responses on stand density has not been intensively studied until now.

Most studies in Alaska are based on a comparison of the trees' climate responses before and after 1950 (Lloyd and Fastie 2002, Driscoll *et al* 2005, Wilmking *et al* 2004, Wilmking and Juday 2005). However, the climate in Alaska in large part corresponds to the Pacific Decadal Oscillation (PDO), which has been varying with 20–30 yr intervals. The most important shifts in PDO values occurred around 1925, 1947 and 1977, demarcating a warm, a cool, and again a warm phase (Mantua and Hare 2002). The PDO is an index derived from changes in North Pacific monthly sea surface temperature north of 20°N. Positive values are associated with a strong Aleutian Low, inducing cool conditions in the west Pacific, while the east Pacific warms. Hence, warm air flows toward Alaska, though mainly from the south. As the Alaska Range functions as a barrier to precipitation, this results in anomalously warm and dry conditions in interior Alaska (Mantua and Hare 2002). During negative/cool phases, the opposite applies. Although the PDO mainly describes winter atmospheric conditions, its importance for the climatic regime and the ecosystems of Alaska has repeatedly been discussed (Mantua *et al* 1997, Hartmann and Wendler 2005) and long-term changes in the PDO are detectable in corals (Gedalof *et al* 2002) as well as in tree rings (D'Arrigo *et al* 2001, Gedalof *et al* 2002, Wiles *et al* 2004, Wilson *et al* 2007). Generally, over the last hundred years summers have become warmer and the number of growing degree days has increased by 21% (Wendler and Shulski 2009). Such a change in formerly limiting climatic factors can substantially alter the responses of tree growth to climate. According to Liebig's law of the minimum (Mitscherlich 1909) a factor can change to an amount such that it is no longer limiting, i.e. growth rates of temperature sensitive trees will increase with climate warming until some other factor(s) become limiting.

Considering the shifts in the climate regime, i.e. in temperature and precipitation, in Alaska over past decades, we assume that the trees' responses to temperature and precipitation vary accordingly over time, but are confounded by site specific factors, such as the trees' position at the upper treeline or in open canopy forest right below the upper treeline. More specifically, we analyze when and where temperature is the limiting factor for white spruce growth at Alaskan treelines, when and where precipitation is the limiting factor for the trees' growth, and in which cases neither of the two factors is important for the trees' growth. We hypothesize that (i) in cold phases the trees respond more positively to temperature than in warm phases, (ii) in dry phases the trees respond more positively to precipitation than in wet phases, (iii) the responses are conditioned by each site's location within the north–south temperature and the west–east precipitation gradient, and (iv) the responses are conditioned by the individual tree's position at the upper treeline or in open

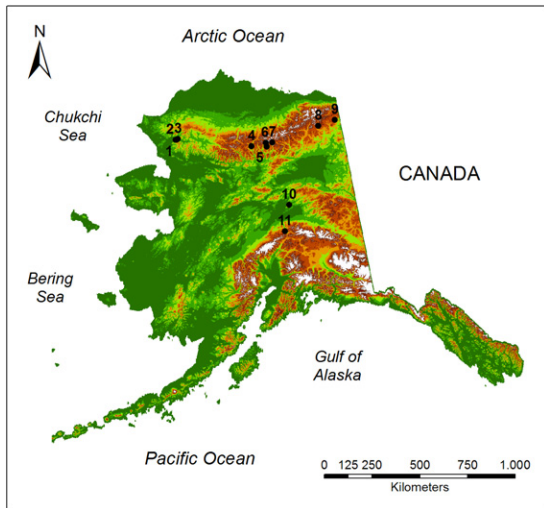


Figure 1. Location of the study sites in Alaska along the Brooks Range in the north and toward the Alaska Range in the south. 1—NOF; 2—NOC; 3—KG; 4—HF; 5—CL; 6—NF; 7—BRN; 8—SJ; 9—FR; 10—MUD and 11—ROC. The colors indicate approximate elevation; for exact geographical and elevational position of the sites see table 1.

canopy forest, i.e. treeline trees will respond more strongly to temperature whereas forest trees will respond more strongly to precipitation.

2. Methods

2.1. Tree-ring data

We sampled 11 treeline sites across Alaska (figure 1), following the west–east precipitation gradient and the north–south temperature gradient (table 1). We took cores from 747 mature white spruce trees in total. Data from six sites have been published before (Wilmking *et al* 2004). Here we updated some of these chronologies, added five new sites to the network and analyzed them in a different way. For the new samples, the growth rings were absolutely dated and ring widths were measured using a LINTAB 5 measuring stage and TSAP-Win tree-ring analysis software (Rinn 2003).

Crossdating of half-cores was carried out visually and with the help of COFECHA (Grissino-Mayer 2001). Afterward the two half-cores of each tree were averaged to obtain one tree-ring series per tree. As *Picea glauca* is primarily (at the north-western sites exclusively) growing on south facing slopes and in order to keep this factor consistent, only trees from south facing slopes were analyzed. At all sites except KG and SJ cores were taken both from the treeline, i.e. low density stands at the upper tree margin, where trees are standing far apart, free from tree-to-tree competition (termed ‘treeline trees’), and from open canopy forest, i.e. higher density stands right below the upper treeline, where tree crowns are not necessarily touching, but tree-to-tree competition is assumed to be present (termed ‘forest trees’). Series of trees younger than 50 yr were excluded, leading to a sample size of 487 trees for subsequent analyses.

Tree-ring series showing a common age related growth trend (i.e. decreasing ring width with increased tree age) were detrended by fitting a negative exponential curve (56% of all samples). Standardization was achieved by dividing each series by the estimated growth trend in order to obtain a dimensionless ring-width index. This conservative method was applied because it removes the overall biological growth trend, stabilizes high variances in the first years of growth and keeps more long-term variability (low-frequency) than, for example, spline approaches (Helama *et al* 2004). In cases where a negative exponential curve could not be fitted (e.g. trees with constant or increasing ring width with increased tree age), a straight line with negative or no slope was fitted (44% of all samples).

For each site, two chronologies were built, one from the ring-width indices of the treeline trees, the other one from the ring-width indices of the forest trees. Chronologies were calculated using a biweight robust mean, which down-weights outliers. Where treeline and forest were not sampled independently (KG and SJ) a site chronology from all ring-width indices of that site was built, which is a common practice in tree-ring research (Fritts 1976, Cook and Kairiukstis 1990). Standardization and chronology building were carried out using dplR (Dendrochronology Program Library in R, Bunn 2008). Standard chronologies were used for further analyses.

Table 1. Site characteristics. All climate data represent century means (1901–2008), with mean *T*—annual mean temperature; max *T*—mean temperature of the warmest month; min *T*—mean temperature of the coldest month; annual *P*—annual precipitation sum; and growth *P*—precipitation sum for the growing season (May–August). For KG and SJ elevation was not recorded.

Site	Lat (°N)	Long (°W)	Elevation (m)	Mean <i>T</i> (°C)	Max <i>T</i> (°C)	Min <i>T</i> (°C)	Annual <i>P</i> (mm)	Growth <i>P</i> (mm)
1 NOF	67.9	161.7	150	−7.40	14.24	−25.7	424.50	173.55
2 NOC	68.0	161.6	113	−7.36	14.29	−25.6	402.29	165.48
3 KG	68.0	161.5	N/A	−7.39	14.32	−25.8	387.45	162.45
4 HF	67.8	152.4	507	−8.35	12.66	−26.7	304.91	144.57
5 CL	67.8	150.5	760	−9.58	10.53	−26.3	387.78	195.53
6 NF	68.0	150.6	770	−10.53	9.38	−26.2	361.16	184.42
7 BRN	67.9	149.8	848	−9.53	10.52	−25.4	312.51	154.55
8 SJ	68.5	143.8	N/A	−9.57	10.94	−25.3	321.40	177.41
9 FR	68.6	141.6	715	−7.73	12.35	−24.8	275.01	155.57
10 MUD	64.9	148.3	725	−2.00	14.85	−18.6	508.89	296.70
11 ROC	63.7	149.0	856	−3.76	11.31	−17.6	447.07	249.92

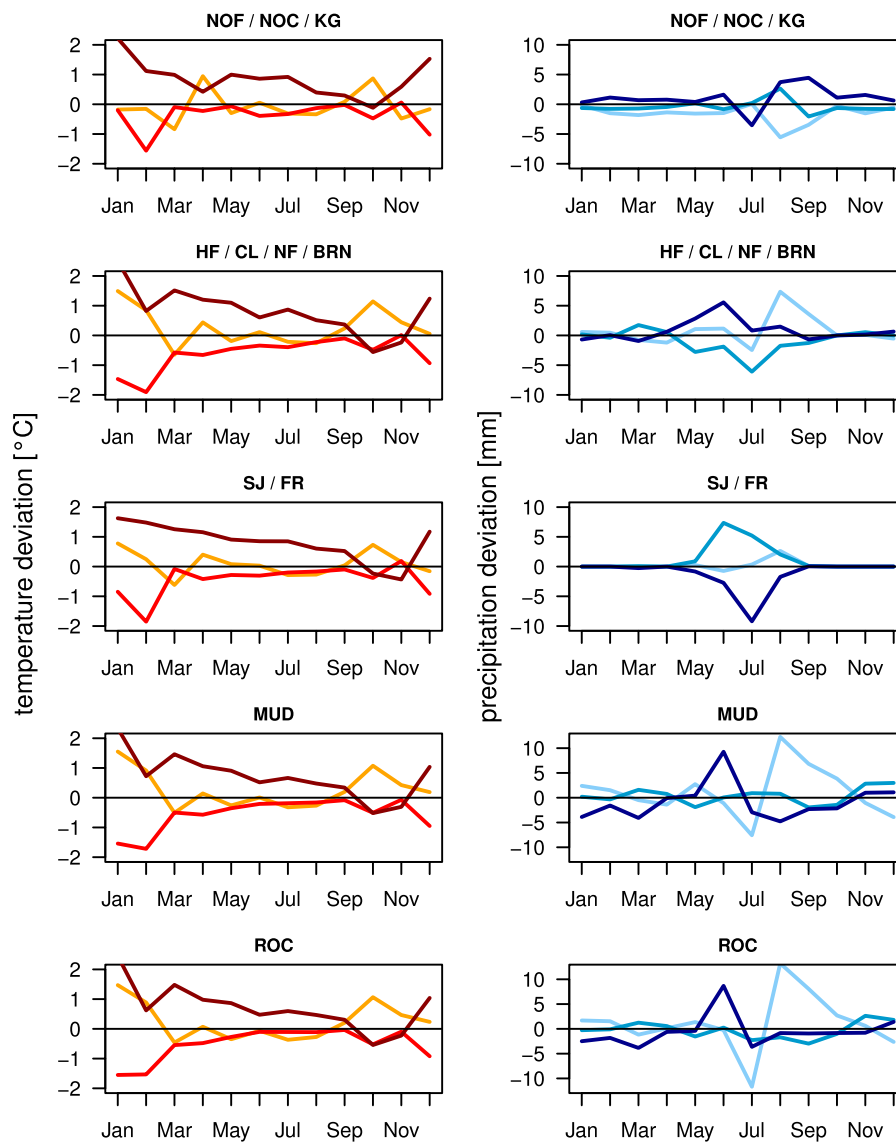


Figure 2. Deviations of mean monthly temperature (left panels) and monthly precipitation sums (right panels) with respect to the long-term mean (1901–2008 and 1901–2006, for temperature and precipitation, respectively). The three time periods for which anomalies were calculated are indicated by light color (1925–46), medium color (1947–76) and dark color (1977–98). Sites are grouped according to geographical position (see also figure 1); there were no differences visible in seasonal climate patterns between sites of one group.

2.2. Climate data

For analyses of tree–climate relationships we used climate data of mean monthly temperature and monthly precipitation sums. Previous studies of tree–climate relationships most often used climate data from Fairbanks, interior Alaska (Garfinkel and Brubaker 1980, Jacoby and D’Arrigo 1995, Barber *et al* 2000, Lloyd and Fastie 2002, Wilmking *et al* 2004, Wilmking and Juday 2005) as this station is the one with the longest record (starting in 1906), and with temperature values correlating well with other stations in the state of Alaska, while being more reliable (Wilmking and Juday 2005). However, here we aimed at detecting regional differences in the trees’ responses to climate and therefore based our correlations on gridded climate data. We used data provided by SNAP (Scenarios Network for Alaska Planning 2010), which are based on CRU gridded data (CRU TS

2.1 5° grid, Mitchell and Jones 2005) interpolated with a PRISM approach (Daly *et al* 1997) and are downscaled to a 2 km resolution. According to the shifts in climate regimes we calculated mean monthly temperature and precipitation anomalies for three periods (1925–46, 1947–76, 1977–98) as deviations from the century mean (figure 2). After the 1946 shift in the PDO from a positive to a negative phase, temperature decreased at all sites, especially in winter. Summer precipitation increased at some sites (north-west, north-east), and decreased at others (north-central, south), while being distributed more evenly in the growing season at most sites. Although often only the winter index of the PDO is used (Mantua and Hare 2002) we found the summer index to have the same sign and almost the same magnitude as the winter index (table 2). Hence, we still assume an influence on tree growth in Alaska, which mainly is driven by summer climate. After the regime shift in 1976, i.e. back to a positive

Table 2. Mean values of the Pacific Decadal Oscillation index according to the three phases used in this study, with annual means, winter half-year means (October–March) and summer half-year means (April–September).

PDO phase	Annual	Winter	Summer
1925–46	0.44	0.42	0.46
1947–76	−0.62	−0.71	−0.53
1977–98	0.60	0.42	0.78

phase, winter and summer temperatures generally increased all over Alaska, while precipitation increased at all but the north-eastern sites (FR, SJ). However, at six sites the months of peak precipitation were different from those in the earlier warm phase (north-central and southern sites, June instead of August).

2.3. Climate–growth relationship analyses

Climate–growth relationships were analyzed by correlating each tree-ring chronology with mean monthly temperature and monthly precipitation sums of both the year prior to growth (March–December) and the year of growth (January–August). Correlation values were calculated as bootstrapped correlation functions using the package *bootRes* (Zang 2009). Bootstrapped correlation functions were first introduced to dendrochronology by Biondi and Waikul (2004) and have been widely applied since. Correlation values were calculated for each of the three time periods. The three time slices, shorter than in previous studies and matching the climate regime shifts, were chosen to specifically determine the effects of climate regime shifts on the climate–growth relationships of white spruce.

3. Results

3.1. Temperature–growth relationships in year of growth

Correlations of annual tree-ring width with current year spring and summer temperatures (figure 3) varied in time and space. Generally, the responses were strongest in the first and mid time periods and weakened markedly in the last time period. However, the monthly correlations differed across sites and between treeline and forest plots. In detail, in the first period the trees responded significantly positively to June temperature (7 of 11 sites). In four cases this response was stronger at the treeline than in the forest. At three sites (but only in the forest) significant negative responses to March and April temperatures were found. In the second period, the trees responded positively to July temperature, i.e. later in summer (8 of 11 sites). Similarly, the negative response to spring temperatures occurred later, i.e. now in April and May (4 of 11 sites). In the third period the responses to current year spring and summer temperature weakened at almost all sites. Significant responses were only found for June at five sites (positive, north-west and north-east, predominantly at treeline) and for March/April/May at four other sites (negative, north-central and south, predominantly forest).

3.2. Precipitation–growth relationships in year of growth

Correlations of annual tree-ring width with current year spring and summer precipitation were generally less significant than correlations with temperature (figure 4). However, the responses of forest trees to precipitation were more pronounced than the responses of treeline trees. In the first period four sites (mostly forest) responded positively to precipitation, either to March, May or July. In the second period most of these sites (again mostly forest) still responded positively, although mainly to April precipitation. In the third period the most marked trends were two sites (but only treeline) responding negatively to July precipitation and two sites (only forest) responding positively to June/July precipitation.

3.3. Climate–growth relationships in year prior to growth

Correlations of annual tree-ring width with spring and summer temperature and precipitation of the year prior to growth differed greatly from correlations with climate of the year of growth (see figures 5 and 6 for details). Most noticeable were the generally negative responses to June and July temperatures in the second and last periods and the generally positive responses to spring temperatures (April/May), especially in the last period. Correlation values with previous year precipitation are much more diverse and go from negative in the first period to positive in the second period (both north-central sites) to completely mixed responses in the last period.

4. Discussion

4.1. Growth responses depend on climate regime

White spruce growth responses to temperature and precipitation in Alaska vary more than assumed over time, and depend in large parts on the respective climate regime. If summer temperatures are close to the century mean, as in the first and second time periods, the trees at Alaskan treelines respond strongly positively to temperature. If temperature is increasing, as is the case in the third period (after 1976), the trees' responses to temperature are much weaker or nonsignificant. Such a general decrease in sensitivity is in line with previous findings (D'Arrigo *et al* 2004, Davi *et al* 2003), which show a decline in temperature sensitivity of trees after 1970 in north-west and south-east Alaska, respectively. The respective authors partly attribute this decreased sensitivity to large scale changes, such as increases in UV-B radiation, global dimming and air pollution (see D'Arrigo *et al* 2008 for a comprehensive review). Although we cannot preclude these factors as potential causes, we assume that their influence is not sufficient to alter the climate–growth relationships of trees in Alaska to the extent seen in our results. Also, poor quality of the climate data can be excluded as a reason in this case, as data quality has become much better during recent decades. Rather, high summer temperatures, as they have emerged with global warming since the mid-1970s, may

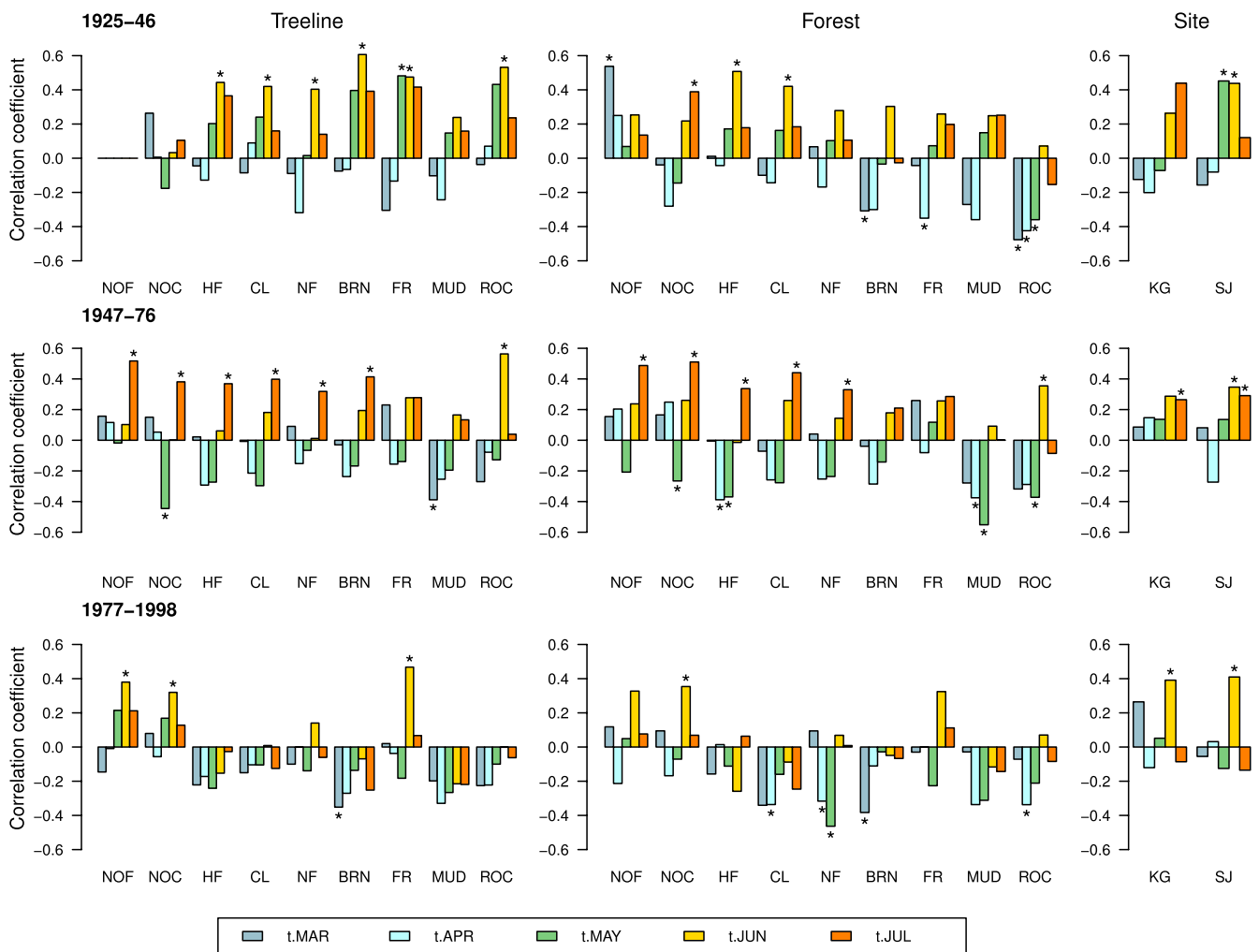


Figure 3. Correlation values of ring-width indices for each site with spring and summer temperatures of the year of growth. Left: treeline trees; center: forest trees; and right: sites without separate treeline and forest plot. Top: 1925–46; center: 1947–76; and bottom: 1977–98. For the locations of sites see figure 1. Stars indicate significance at $p < 0.05$.

cause a threshold related decrease in sensitivity (Solberg *et al* 2002), indicating that temperature has changed to a degree that decouples tree growth from temperature (Fritts 1971). This finding confirms our hypothesis (i) that in (relatively) cool periods trees respond more positively to temperature than in warm periods. However, the strong decline of the importance of summer temperature for tree growth since 1976 with its subsequent warming was not expected to that extent.

Tree growth responses to precipitation vary similarly over time, depending partly on the climatic regime and partly on the site’s location. During the second period, when low precipitation values occurred, for example, in north-central Alaska (HF, CL, NF, BRN), precipitation seems to be a limiting factor only at HF, indicated by a significant positive response to June precipitation (i.e. any increase in precipitation in that month leads to better tree growth in that year). Also surprisingly, in the third period, when precipitation was relatively high in north-central Alaska, there were still some sites responding positively to precipitation, indicating that access to water was still limited. However, the

pattern in precipitation responses is much more diverse than hypothesized (ii), and differences in precipitation–growth responses seem to depend on smaller temporal scales, e.g. a change in peak months of precipitation.

Also, spatial differences on a local scale may influence climate–growth relationships. The reasons for these differences may be non-climatic factors, such as slope, i.e. drainage patterns, and soil properties, which define site specific water capacity and play an important role for the trees’ water supply (Linderholm 2001), and hence obscure the interpretation of precipitation sums. For example, trees at NOF, a site in the wet north-west with a flat relief and insufficient drainage, respond negatively to July precipitation in the second and third periods, possibly because during these time periods summers (especially July) were rainier than in the first period, leading to waterlogged soil. This result supports a theory that relates high precipitation, especially at high-latitude sites, to reduced ring-width growth (Fritts 1971). Accordingly, at NOC, which lies in the same climatic area but has a steep slope and thus more efficient drainage, the trees do

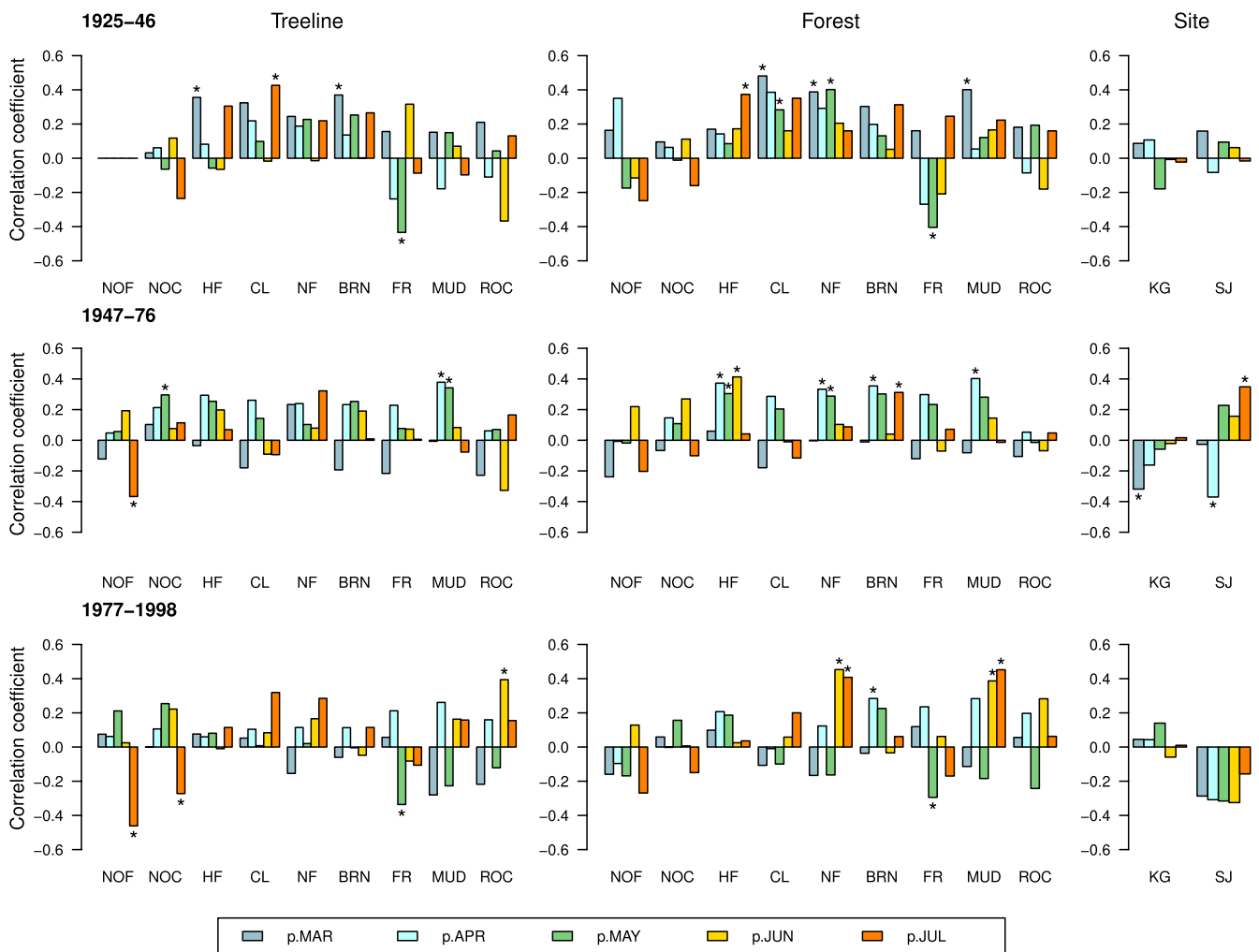


Figure 4. Correlation values of ring-width indices for each site with spring and summer precipitation of the year of growth. Left: treeline trees; center: forest trees; and right: sites without separate treeline and forest plot. Top: 1925–46; center: 1947–76; and bottom: 1977–98. For the locations of sites see figure 1. Stars indicate significance at $p < 0.05$.

not respond as negatively to summer precipitation, pointing to the importance of slope as a factor that significantly influences climate–growth relationships. This is in line with predictions of vegetation change at high latitudes derived from bioclimatic models, which have been shown to be much more precise if they include local abiotic site conditions, such as aspect or slope (Sormunen *et al* 2011).

A preliminary test of the effect of various non-climatic factors on tree growth revealed that at NOC shrub cover was the most important factor influencing single trees’ growth trends after 1976. Trees growing within a dense shrub cover (3 m radius around each tree) increased in radial growth after 1976, whereas trees within less shrub cover slightly decreased in growth. This suggests that on steep slopes snow accumulation by shrubs in winter (Sturm *et al* 2001, Liston *et al* 2002), leading to higher moisture supply in spring, i.e. at the beginning of the growing season (Sturm *et al* 2001), might favor tree growth. Accumulated snow also provides for higher insolation and higher soil temperatures in winter, as well as for increased winter decomposition and nutrient release (Sturm

et al 2001, Schimel *et al* 2004). In summer, shrubs may reduce surface run-off and erosion through fine-root mass. These positive effects of shrubs on tree growth could even outweigh interspecific competition. Tree–shrub interactions are increasingly important as shrubs have started invading tundra and influencing snow accumulation patterns at the forest–tundra ecotone (Sturm *et al* 2001).

Although limited by both temperature and precipitation at some time, the same trees can be uncorrelated with climate at other times, as is the case in the third climatic period in this study. Both factors, formerly limiting tree growth, became seemingly unimportant after the shift of the climatic regime in 1976. One hypothesis might be that the interaction of abiotic and biotic factors (e.g. droughts and insect outbreaks) is affecting climate–growth relationships at Alaskan treelines. In Alaska and Canada the area experiencing drought has almost doubled between 1959 and 1999, with the strongest increase in droughts since about 1975 (Xiao and Zhuang 2007). This could weaken trees and, in combination with insect outbreaks, explain parts of the decrease in climate

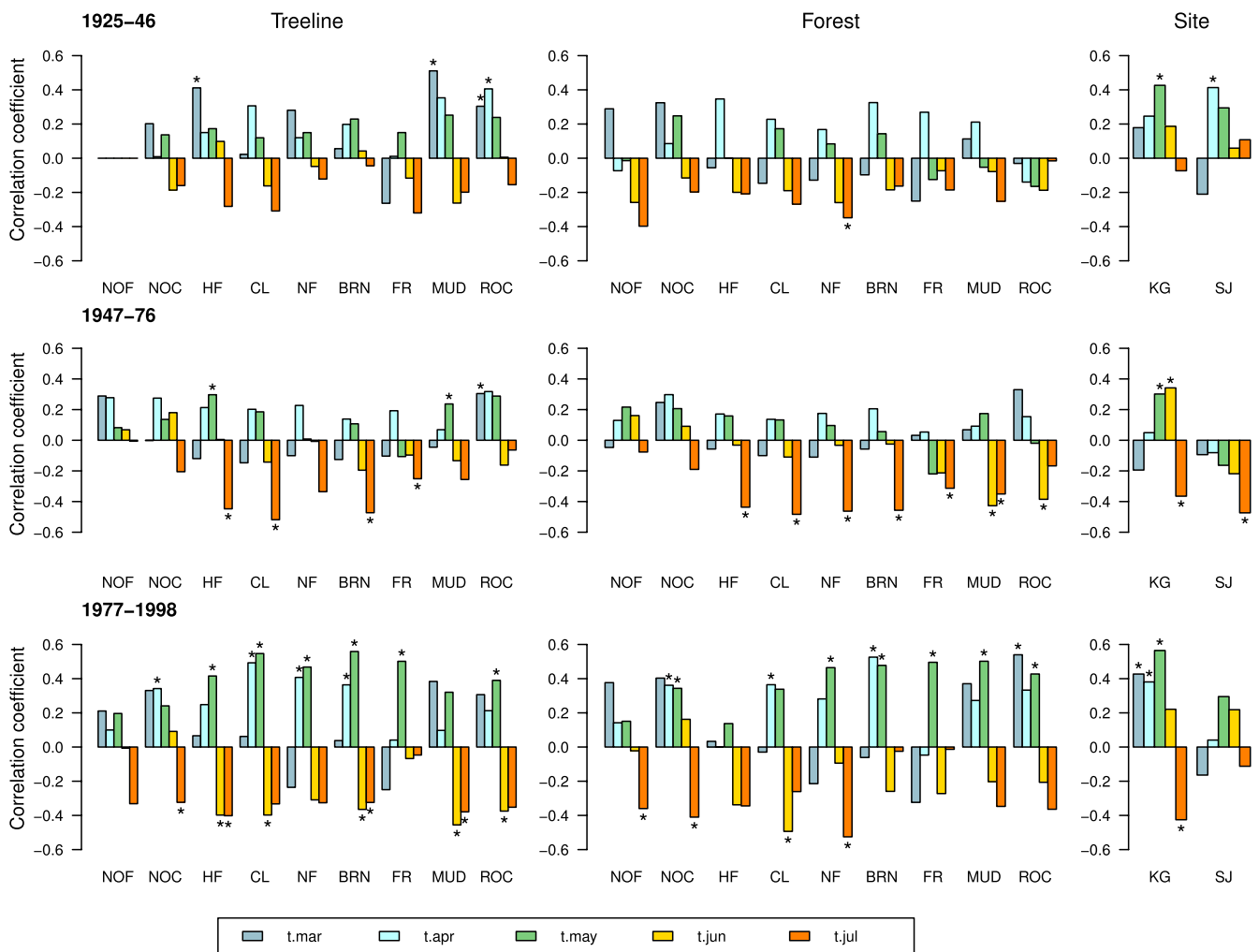


Figure 5. Correlation values of ring-width indices for each site with spring and summer temperatures of the year prior to growth. Left: treeline trees; center: forest trees; and right: sites without separate treeline and forest plot. Top: 1925–46; center: 1947–76; and bottom: 1977–98. For the locations of sites see figure 1. Stars indicate significance at $p < 0.05$.

sensitivity in the third time period. However, droughts are generally most pronounced in the interior of Alaska and thus do not affect the majority of our study sites. Insect outbreaks, in this case spruce budworm, did not have their first peak in interior Alaska until the mid-1990s and again in 2004 (USDA 2008) and have only recently been observed at the northern sites (Juday 2009 and our own observations). Other disturbances or extreme events possibly influencing climate–growth responses of white spruce are still to be investigated.

One also needs to consider that climatic thresholds might have been exceeded in different places at different times. Exact relationships are still largely unknown, and further research on threshold related growth responses as well as on the lag effect of previous year growing conditions on next year tree growth would provide necessary insights into the ecophysiology of boreal conifer trees. This could help to improve models of boreal ecosystem dynamics under climate change, which are needed to assess carbon storage capacity,

changes in habitat and climate feedback mechanisms, such as albedo, snow accumulation, etc (Malanson *et al* 2007).

4.2. Contradictory responses to climate of year prior to growth

Surprisingly, correlation results of tree growth with temperature and precipitation of the year prior to growth are partially contradictory to the ones with climate of the year of growth. This is best seen in the second time period, when trees, especially at the north-central sites, respond strongly negatively particularly to July temperatures. These inverse responses to summer temperature of the year prior to growth are in line with previous findings (Lloyd and Fastie 2002, Wilmking *et al* 2004) and seem to be common in the genus *Picea*, especially *Picea glauca* (Lloyd and Bunn 2007). Not stated in other studies to this degree was the strong positive response of these trees to July precipitation of the year prior to growth. As the negative temperature response and the positive precipitation response occur during the same time

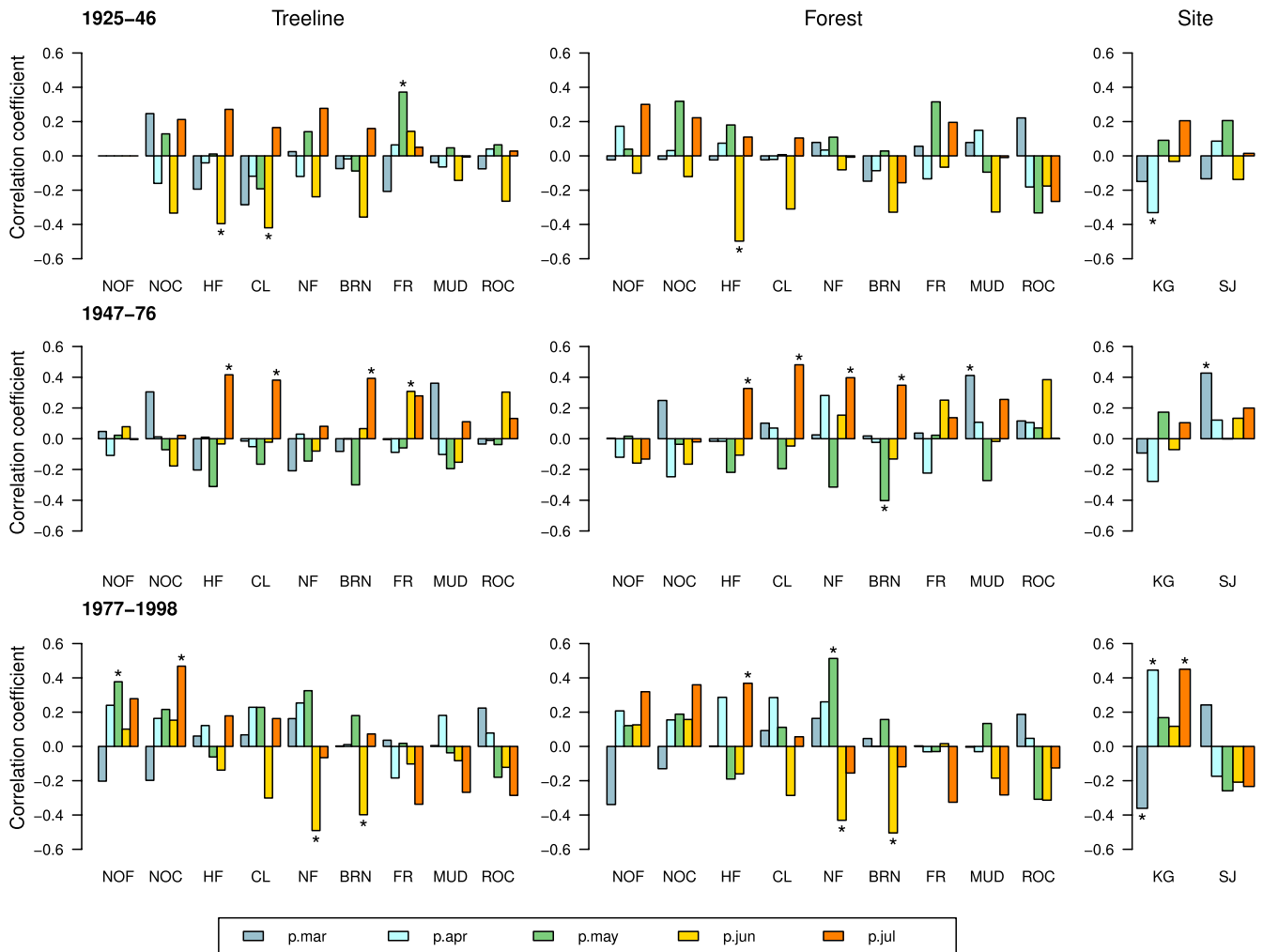


Figure 6. Correlation values of ring-width indices for each site with spring and summer precipitation of the year prior to growth. Left: treeline trees; center: forest trees; and right: sites without separate treeline and forest plot. Top: 1925–46; center: 1947–76; and bottom: 1977–98. For the locations of sites see figure 1. Stars indicate significance at $p < 0.05$.

period and at the same sites, it becomes evident that even in a ‘cool’ phase of the PDO trees might respond negatively to temperature (most likely due to drought stress), depending on the distribution of precipitation particularly during summer, i.e. early or late within the growing season.

From an ecophysiological point of view, the opposing responses to climate of the year of growth and the year prior to growth are not necessarily conflicting. Several conifers growing at arid sites correlate significantly with the climate preceding the growth period (Fritts 1971, Peterson and Peterson 2001, Littell *et al* 2008). Douglas-fir growth for instance was reported to correlate significantly with late summer precipitation of the year prior to growth (Littell *et al* 2008). This could also be true for northern high-latitude treeline trees during dry climatic conditions, as was the case in the second period in the central Brooks Range (hypothesis (ii)). One explanation can be found in a study on mountain hemlock, whose growth was also negatively correlated with previous year summer temperature, but positively with precipitation (Peterson and Peterson 2001). The authors attribute this response to cone production: if

in one year July temperature is high and a cone crop is developed, fewer resources will remain to support next year’s radial growth. However, to induce seed crops in white spruce in Alaska a complex succession of events (high radial growth, warm/dry spring, and low snow/wind damage in year 1; enough growing degree days, few rainy days and low seed predator population in year 2) is necessary (Juday *et al* 2003), and cone crops usually occur with an average frequency of 7–12 yr only (Coates *et al* 1994, Zasada and Viereck 1970). Such a rare cone production is unlikely to cause the strong negative responses to previous year July temperature over an entire climatic period, as was found in this study. Last but not least, low soil moisture in late summer of the year prior to growth (be it due to low precipitation or to high temperature) may impair next year’s bud and needle development and hence foliage expansion (Littell *et al* 2008), and thus provoke negative responses to July temperature of the year prior to growth. On the contrary, high summer temperatures in the year of growth may favor tree-ring development in that year and provoke positive responses to July temperature in the

same year. Nevertheless, one needs to consider that trees would likely optimize this trade-off.

4.3. Regional gradients and local site conditions modify climate response

In addition to temporal changes in sensitivity to climate we found regional site conditions mediating the trees' growth responses. As temperature generally decreases from south to north, we expected sensitivity to temperature to increase in the same direction (hypothesis (iii)). This assumption was supported by our results, both for the trees' responses to temperature of the year of growth as well as of the year prior to growth. The hypothesized gradient in sensitivity to precipitation, increasing from west to east, was not evident from our data, which is in agreement with previous findings that some climate responses are independent of the species distributional range (Lloyd and Bunn 2007). We have already discussed site specific water availability as one factor confounding state wide gradients in sensitivity to precipitation. Another confounding factor may be water use efficiency, which decreases with increasing age of the tree and impairs nutrient transport ability (Szeicz and Macdonald 1994). The trees in this study tend to be older in south-eastern sites than in north-western sites, yet they are not more sensitive to precipitation.

Our hypothesis (iv) was also that treeline trees are more sensitive to temperature, whereas forest trees are more sensitive to precipitation. Regarding the latter this was true for all three time periods and is most likely due to a higher tree-to-tree competition for water in higher density stands, a higher evapotranspiration rate (caused by lower albedo) and/or less snow accumulation in winter and hence moisture supply in spring, leading to higher sensitivity to precipitation. Therefore, the variability in sensitivity to precipitation is higher on a local than on a regional scale. Regarding sensitivity to temperature, the responses were generally more pronounced at the treeline, where the temperature is generally lower than in the lower elevation forest. Fritts (1971) even describes how only near the treeline (within about 100 m of the upper climatic limit) is the temperature sufficiently limiting to tree growth to override other growth controlling factors, such as competition. Similarly, for tree establishment at a treeline ecotone of the Alaska Range, recent investigations have shown that the biotic factor, in that case proximity to the 1953 treeline, was the overriding factor until a distance of 1000 m. Only beyond do abiotic factors such as sun exposure and wetness potential become relevant (Stueve *et al* 2011). Research using tree rings from Alaskan treelines should consider these small scale differences in sensitivity. At advancing treelines, older trees might have been 'treeline' trees once (*sensu* upper treeline), recording temperature, yet now be 'forest' trees (*sensu* lower treeline), recording precipitation. This poses a challenge especially for dendroclimatology, which aims at long climatic records from old trees.

A high portion of the trees responded significantly to spring temperatures. Unexpectedly, these responses were both

positive, as described in earlier studies (Wilmking *et al* 2004), and also negative. Especially in the second period trees from forested sites responded strongly negatively to spring temperatures. One reason could be that winters were relatively cold during that time period, causing deeply frozen soil. Yet, evapotranspiration might start in spring before the ground has thawed, leading to drought stress in boreal conifers (Berg and Chapin 1994). This problem is more pronounced in high density (i.e. forest) stands, which have a lower albedo and thus a higher evapotranspiration rate, possibly leading to drought related negative responses to temperature. In the third period, when winter temperatures are far higher (see figure 2), this effect disappears at most sites. Unfortunately we do not have appropriate data to analyze winter snow pack and its effect on root temperature and moisture supply in spring (but see Euskirchen *et al* 2006). Most studies examining climate-growth relationships of treeline trees use annual or seasonal data, or concentrate only on single summer months. However, single months' temperatures can have significant influences on the distribution of a species, as was shown for April/May temperatures in a species distribution model of white spruce (Ohse *et al* 2009). Detailed ecophysiological analyses of the influence of these climate parameters on tree growth would be necessary to better understand the climate-growth mechanisms of white spruce and to precisely predict the long-term treeline dynamics, particularly with regard to the strong warming trend of winter *and* summer temperatures in recent times (Serreze *et al* 2000).

5. Conclusion and outlook

The results of this study show that white spruce trees at Alaskan treelines are neither temperature nor precipitation limited at all times. Rather, the trees' sensitivity to temperature and precipitation varies markedly over time. This variation is most likely due to periodic shifts in the PDO index and thus in the climatic regime of Alaska. Additional climate warming in recent decades coupled with an increase in precipitation has already caused a significant decrease in sensitivity to both temperature and precipitation. Further warming and projected increases in precipitation might strengthen this trend until the climate is no longer limiting. This would possibly contradict previous studies, which assume either low temperatures or drought stress caused by high temperatures to limit tree growth at Alaskan treelines. Despite all this, trees do not necessarily respond uniformly to either periodic or long-term climatic changes, but tree-climate responses depend strongly on the trees' position within the treeline-forest ecotone as well as on other non-climatic factors, such as intra- and interspecific competition. Detailed studies of other potential limiting factors for white spruce growth during climatically favorable periods are necessary to accurately project treeline position and boreal forest dynamics in Alaska.

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