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A latitudinal gradient in tree growth response to climate warming in the Siberian taiga

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Abstract

We investigated the climate response of three Siberian taiga species, *Larix cajanderi*, *Picea obovata*, and *Pinus sylvestris*, across a latitudinal gradient in central Siberia. We hypothesized that warming is more frequently associated with increased growth for evergreen conifers (*P. obovata* and *P. sylvestris*) than for *L. cajanderi*, and for northern than for southern sites; we also hypothesized that increased growth is associated with a positive trend in normalized difference vegetation index (NDVI). In mixed stands, growth of *L. cajanderi* and *P. obovata* increased over time, but the larger growth increases in *P. obovata* may presage a shift in competitive balance between these species. Climate response varied among and within populations of all species, and positive responses to temperature prevailed at northern sites, where trees grew faster in years with warm early summers. Negative responses to warming declined along the south to north latitudinal gradient. We observed considerable variability in climate response within populations which even exceeded that among species or sites. Tree response to climate was correlated with NDVI trends, indicating that patterns of tree-growth response to climate were indicative of a coherent landscape-scale response to warming. Our findings suggest that increased productivity with warming is likely only in the northern reaches of the Siberian taiga. An increased prevalence of evergreen conifers in areas currently dominated by deciduous *Larix* species also seems likely.

Keywords: boreal forest, climate change, dark taiga, dendrochronology, light taiga, NDVI, taiga

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Introduction

Feedbacks on climate that are likely to develop as the boreal forest responds to climate warming result from high variability within the boreal forest and between boreal forest and adjacent tundra or steppe ecosystems in characteristics that affect carbon cycling and energy exchange (Chapin *et al.*, 2000, 2005). Within the boreal forest, variation in attributes that influence energy-exchange processes arises in large part from differences between forest types, particularly evergreen and deciduous tree communities (e.g., Eugster *et al.*, 2000; Kharuk *et al.*, 2005; MacDonald *et al.*, 2008). This heterogeneity is perhaps most pronounced in the Eurasian taiga, where evergreen conifers (spruce, *Picea* spp. and pine, *Pinus* spp.) share dominance with deciduous conifers (larch, *Larix* spp.). Larch forests currently prevail in the coldest regions of Siberia, particularly in sites underlain by shallow permafrost, whereas evergreen spruce and pine forests dominate warmer regions. Larch forests have a relatively high albedo, much more similar to that of adjacent tundra ecosystems (MacDonald *et al.*, 2008); changes in the abundance of larch forests relative to more southerly evergreen species may thus produce strong feedbacks on climate (e.g., Eugster *et al.*, 2000).

Although the Siberian taiga occupies a huge area, it has been poorly studied, and significant uncertainty about future change remains. The most straightforward prediction is that a northward migration of species and forest types will accompany warming: larch will shift northward into tundra, evergreen spruce and pine species will expand northward into areas currently dominated by larch (Arctic Climate Impact Assessment, 2004; Soja *et al.*, 2007; Tchebakova *et al.*, 2009). This prediction is supported by recent observations of evergreen conifers expanding near timberline (Moiseev *et al.*, 2004) and into larch-dominated forests in central Siberia (Kharuk *et al.*, 2005, 2007, 2009). The scenario of a northward displacement of forest types is also supported by paleoecological data indicating that significant northward displacement of larch and more limited northward expansion of *Picea obovata* occurred during the Holocene thermal maximum (Pisaric *et al.*, 2001; MacDonald *et al.*, 2008).

This simple scenario of a progressive northward march by boreal forest species is complicated by two factors. First, the current distribution of species is

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influenced by permafrost, which may constrain future change: larch are much more tolerant of shallow permafrost than spruce and pines, and expansion of spruce and pines may thus be contingent upon thawing of permafrost-affected soils (Tchebakova *et al.*, 2009). Although permafrost is likely to retreat northward, the wholesale loss of permafrost from the continuous permafrost zone is extremely unlikely in the near term (Arctic Climate Impact Assessment, 2004). This may impose a significant time lag on the northward expansion of permafrost-limited species (Tchebakova *et al.*, 2009).

Second, the pattern of change in productivity and/or tree growth varies between boreal forest and tundra (Goetz *et al.*, 2005), among boreal forest species (Bunn *et al.*, 2007; Lloyd & Bunn, 2007), and even within single populations (Wilmking *et al.*, 2005). Both satellite-derived estimates of productivity (e.g., the normalized difference vegetation index, NDVI), and tree-ring data indicate that while larch-dominated forests of eastern Siberia have experienced widespread increases in growth and productivity (Kirdyanov *et al.*, 2003; Bunn *et al.*, 2007; Nikolaev *et al.*, 2009), productivity and growth in the spruce-dominated boreal forests of western Eurasia and North America have declined or remained stable (Briffa *et al.*, 1998; Lloyd & Fastie, 2002; D'Arrigo *et al.*, 2004; Goetz *et al.*, 2005; Wilmking *et al.*, 2005; Bunn & Goetz, 2006; Bunn *et al.*, 2007; Lloyd & Bunn, 2007; Wilson *et al.*, 2007; D'Arrigo *et al.*, 2008). A variety of hypotheses have been proposed to explain the failure of tree growth to respond positively to warming in some regions, and include both local (e.g., pollution) and regional to global (e.g., heat stress, drought stress, global dimming) factors (D'Arrigo *et al.*, 2008). Temperature-induced drought stress or direct heat stress seem the most likely explanations for the very widespread pattern of negative responses to warming (Lloyd & Bunn, 2007). According to these hypotheses, temperatures have exceeded key physiological thresholds, and tree growth is reduced in warm years either by direct heat stress or by drought stress caused by greater evaporative demands. Collectively, NDVI and tree-ring data suggest that warming has increased stress on even the northernmost spruce forests, and cast doubt on whether a widespread expansion of these populations is likely.

Two scenarios of change in the Siberian taiga over the coming decades thus seem plausible. More southerly spruce and pine species may continue to expand northward at the expense of larch, leading to a reduction in surface albedo and potentially to a positive feedback on warming. Alternatively, heat or drought stress, perhaps combined with constraints related to the presence of permafrost, may limit the northward expansion of more southerly spruce and pine species and thus reduce the importance of such amplifying feedbacks on climate. A comparison of differences in response to recent warming among species and along spatial gradients would contribute to an improved understanding of which scenario is more likely.

We used tree-ring data to explore the response of the Siberian taiga to recent climate warming, testing three hypotheses. (1) Recent warming favors more southern evergreen conifers (particularly spruce) over more northern deciduous conifers in the genus *Larix*. We predicted that recent warming would lead to greater growth enhancement for *P. obovata* (Ledb.) than *Larix cajanderi* (Mayr.) at sites where the two species co-occur. (2) Because evidence suggests that heat stress or temperature-induced drought stress may limit growth in southern sites (Lloyd & Bunn, 2007), we hypothesized that positive responses to warming would become more prevalent along a south to north latitudinal gradient. We predicted that the proportion of trees within a stand showing a positive response to warming (i.e., positive correlations between growth and monthly temperature) would increase along our sampled latitudinal gradient. (3) NDVI is directly related to population-level patterns of response to climate. We predicted that 'greening' of the landscape around each site (positive trends in NDVI between 1982 and 2005) would be significantly and positively correlated with the proportion of trees at a site showing a positive response to temperature.

Materials and methods

We sampled at seven sites along the Lena River in the Sakha Republic (formerly Yakutia, Fig. 1). All sites were low elevation (< 250 m), and most were located on the floodplain of the Lena River or a major tributary. Forests were dominated by a single species, except at the Indylyun River (IND) site, where *L. cajanderi* and *P. obovata* were co-dominant. To minimize impacts of human disturbance, we selected relatively old forests. The recruitment date of the oldest tree sampled at each site ranged from the early 1500s (site IND) to 1810 (site BAL). Our transect of sites extended from regions where *P. obovata* and *Pinus sylvestris* (Linn.) were relatively common to northern regions where they were relatively rare. We did not encounter any *P. sylvestris* forests in the sites north of the region around Yakutsk. We sampled three species overall: *L. cajanderi* ($n = 5$ sites: YUT, SYL, IND, LRB, and CSZ), *P. sylvestris* ($n = 1$ site: BAL), and *P. obovata* ($n = 2$ sites: IND and ZHF). At each site, we sampled the largest individuals of each species of canopy dominant conifer, for a total of 176 trees across all sites. Two increment cores were taken at breast height from each tree.

In the lab, each core was mounted in a wooden core mount and sanded until individual xylem cells could be resolved under a dissecting microscope. Cores were measured on a Velmex sliding-stage micrometer to a precision of 0.002 mm, and were visually crossdated with skeleton plots (Stokes & Smiley, 1968). Crossdated series were quality-checked using the program COFECHA (Holmes, 2000).

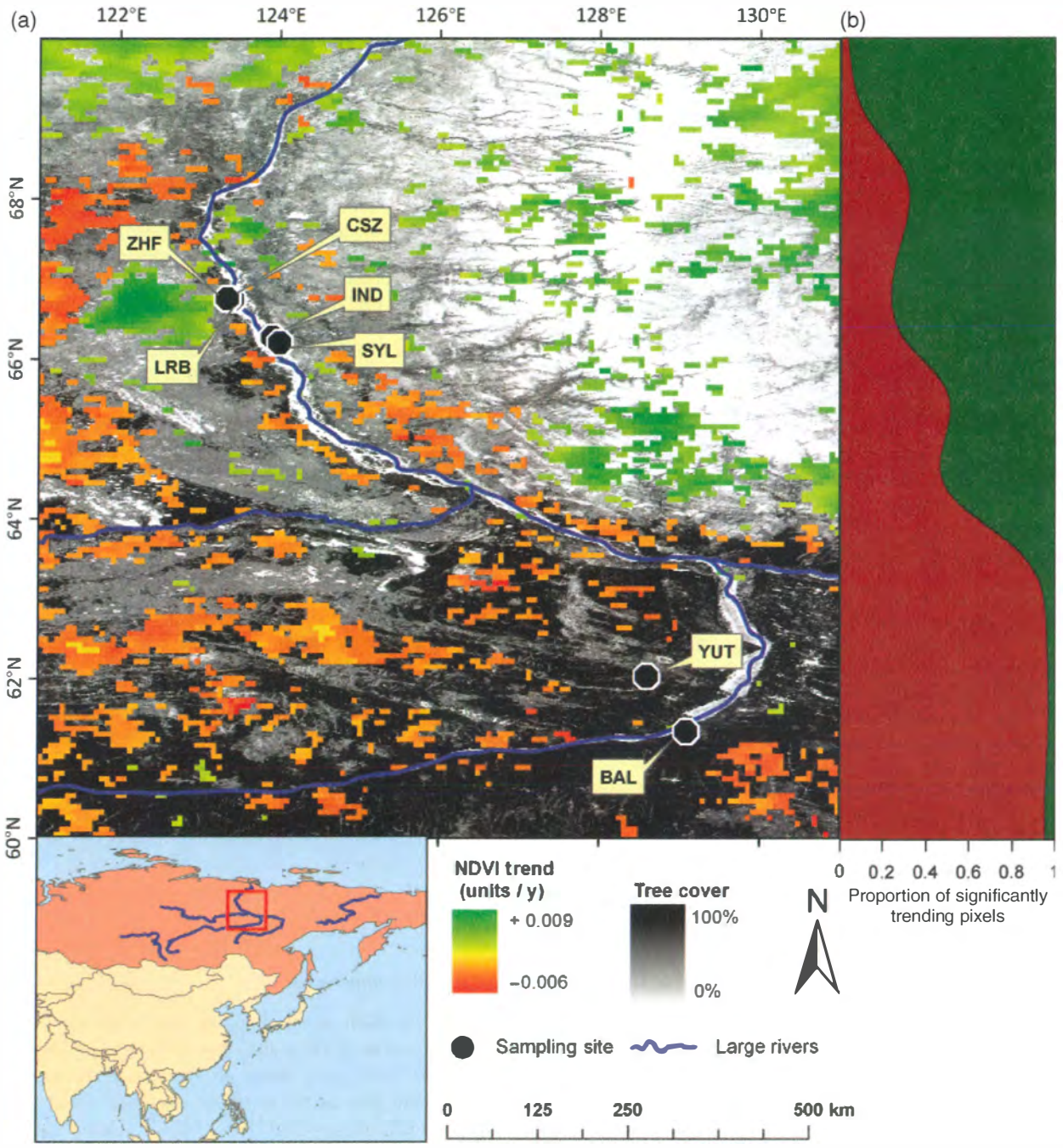

Fig. 1 (a) Location of study sites and trends in normalized difference vegetation index (NDVI) in the study region (identified by the red box on the inset map at lower left). Study site locations are indicated by black circles. The Lena River is the major river running through the study region. Significant trends in NDVI (see Materials and methods) are indicated by colored pixels (8 km × 8 km), with orange-red pixels indicating significant negative trends in NDVI and green pixels indicating significant positive trends in NDVI. The background tree canopy cover data are from Hansen *et al.* (2003). (b) Proportion of significant trending pixels which exhibited either positive (green) or negative (red) trends for each 0.07° (8 km) latitudinal band.

Growth rate comparisons (Hypothesis 1)

To compare differences in growth rates over time and between species, we calculated annual basal area increment (BAI) for *L. cajanderi* and *P. obovata* at the Indylyun River (site IND) and near Zhigansk (sites CSZ and ZHF). If the core did not contain the pith, distance to the pith was estimated by fitting a template of circles with known radii to the curve of the

innermost rings. Cores in which the innermost rings did not curve (and hence for which the radius of the innermost part of the core could not be estimated) were excluded from the analysis. The radius (mm) of the tree in each year was calculated from the measured raw ring widths, and converted into an annual estimate of basal area (mm^2) using the equation for the area of a circle. BAI was calculated by subtracting the basal area in year $t-1$ from that in year t. BAI values were averaged across the two cores to produce an estimate of BAI for the entire tree. Average annual BAI was calculated for each tree for four 50-year periods: 1808–1857, 1858–1907, 1908–1957, and 1958–2007.

BAI data were analyzed using repeated-measures ANOVA in SPSS (version 16.0.1), with time as the within-subjects factor and latitude and species as between-subjects factors. Data were log-transformed before analysis in order to meet the assumptions of ANOVA. Because the data violated the assumption of sphericity of the variance–covariance matrix (Mauchly's $W = 0.275$, $P < 0.0005$, df = 5), we used the Greenhouse–Geisser correction for the within-subjects tests.

Climate response (Hypothesis 2)

To quantify tree growth response to climate, crossdated ring-width series were detrended with a modified negative exponential curve, a line of negative slope, or a horizontal line to remove the geometric growth trend. Individual tree chronologies were constructed for all trees at each of the seven sites by averaging the two detrended ring-width series for each tree. Detrending was accomplished in R (R Development Core Team, 2009) using the package DPLR (Bunn, 2008).

We compared tree growth to climate data obtained from the CRU (Climate Research Unit) interpolated spatial data set (CRU TS 2.10), which is publicly available (http://www.cru.uea.ac.uk). The data set, which has a resolution of $0.5^\circ \times 0.5^\circ$ (latitude × longitude), is described in detail in Mitchell & Jones (2005). Lloyd & Bunn (2007) compared CRU data to Historical Climatology Network (HCN) data at a range of boreal sites, and found no evidence for systematic bias in the CRU data. We used a 17-month climate window, in which tree growth in year t was compared with monthly mean temperature and total monthly precipitation for a period extending from April of year $t-1$ to August of year t. Climate response was estimated for each individual tree in R (R Development Core Team, 2009) using the package BOOTRES (Zhang, 2009), based on DENDROCLIM2002 (Biondi & Waikul, 2004), which calculates bootstrapped correlation coefficients between growth and climate. Each tree's response to temperature was categorized into one of four response types: positive (>67% of significant correlations with temperature were positive), negative (<33% of significant correlations with temperature were positive), mixed (between 33% and 67% of significant correlations with temperature were positive), or none (no significant correlations with temperature). Trees were similarly categorized with respect to their pattern of response to precipitation. The proportion of trees exhibiting each response type was tallied for each species at each site. We used Pearson's product–moment correlation coefficients to identify significant relationships between the proportion of positive and negative responders at a site and the latitude of that site.

Comparison between tree climate response and NDVI trends (Hypothesis 3)

The NDVI trends presented here were derived by Bunn *et al.* (2007) using NDVI data from the NOAA Advanced Very High Resolution Radiometer (AVHRR) and processed as part of the NASA Global Inventory Modeling and Mapping Studies project (GIMMS, Tucker *et al.*, 2005). The trend analysis, covering the 1982–2005 period, was based on mean May through August NDVI and calculated at a nominal spatial resolution of 8 km × 8 km. The NDVI trend map was clipped to the region surrounding Yaktusk, Russia, using a $10^\circ \times 10^\circ$ box, extending from 121 to 131°E and from 60 to 70°N. The number of pixels that exhibited positive and negative trends was determined for each 8 km (0.07°) latitudinal band ($n = 143$ bands). The conditional density plot shows, for each latitudinal band, the proportion of significant trending pixels that exhibited either positive or negative trends (Fig. 1). The kernel density estimation used a default Gaussian smoothing kernel with bandwidth equal to the standard deviation of the smoothing kernel. To compare NDVI trends to population-level patterns of tree response to climate, we calculated the percentage of pixels exhibiting significant positive or negative trends within an 8×8 pixel neighborhood (64 km × 64 km) around each site. The percentage of pixels showing a significant positive trend was compared with the percentage of trees exhibiting positive responses to warming using a Pearson's product–moment correlation coefficient. All sites were included in this analysis. However, two sites (CSZ and ZHF) were so close together that they fell within the same NDVI buffer area, so the percent of trees exhibiting a positive response was averaged between the two sites.

Results

Growth rate comparisons

Growth rate (BAI, mm^2) of spruce and larch increased after 1907 across all three sites (Fig. 2; $F_{1.747,156} = 39.585$, $P < 0.0005$). Trees grew faster, on average, at the southern IND site than at the northern sites near Zhigansk (ZHF and CSZ; $F_{1,52} = 36.177$, $P < 0.0005$). There was no significant difference in growth rate between *P. obovata* and *L. cajanderi* overall ($F_{1,52} = 1.111$, $P = 0.297$), but there was a significant species-by-latitude interaction ($F_{1,52} = 10.175$, $P = 0.002$) and a significant interaction among species, latitude, and time ($F_{1.747,156} = 3.347$, $P = 0.047$). Averaged over all time periods, the growth rate of *L. cajanderi* exceeded that of *P. obovata* at the southern Indylyun River site. In contrast, *P. obovata* growth exceeded that of *L. cajanderi* at the northern sites near Zhigansk, largely due to rapid increases in *P. obovata* growth, relative to *L. cajanderi*, in the most

recent time period. Although growth of all trees increased over time, the pattern of increase differed between species and across sites. At both sites, *P. obovata* growth increased between the earliest time period (1808–1957) and the latest (1958–2007) by a factor of approximately 4. Growth of *L. cajanderi*, in contrast, increased more over time at the northern site (where growth increased by a factor of 6 between the earliest and latest time period) than at the southern (where growth increased only by a factor of 1.8).

Climate response

There were significant positive trends in spring and winter temperatures from 1902 to 2002 at all sites (Table 1). Trends in summer temperatures were always positive, but were not significant at any site. There was a significant positive trend in fall precipitation at three sites (BAL, YUT, and SYL) and a significant positive trend in winter precipitation at all of the more northern sites (SYL, IND, LRB, CSZ, and ZHF).

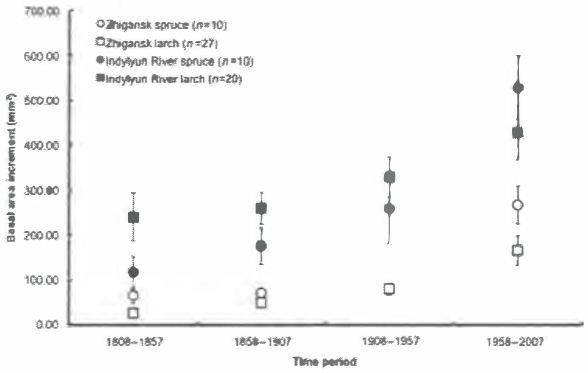

Fig. 2 Mean (± 1 SE) basal area increment (BAI), over 50-year time intervals, for *Picea obovata* and *Larix cajanderi* at a southern site (IND, Indylyun River, latitude 66.28°N) and for *Picea obovata* (site ZHF) and *Larix cajanderi* (site CSZ) at a more northern location outside the town of Zhigansk (latitude 66.76°N). Cores that did not reach sufficiently near the pith were eliminated from this analysis, thus reducing the sample size of larch at both sites.

Tree growth was significantly correlated with both current and previous year climate variables, a finding consistent with the significant first-order autocorrelation we found in all ring-width series from both deciduous (*L. cajanderi*) and evergreen (*P. sylvestris* and *P. obovata*) species. Average (across all series at a site) first-order autocorrelation ranged from a low of 0.731 (*L. cajanderi* at site IND) to a high of 0.832 (*P. obovata* at site IND).

We found substantial within-population variation in climate response at all sites, with at least two different response categories represented at each site (Fig. 3). Most *P. sylvestris* near Yakutsk (site BAL) responded positively to temperature, but there was a substantial minority (28%) in which growth was negatively correlated with temperature. *P. obovata* responses differed between sites: 33% of trees at the more southern site (IND) responded positively to warming, whereas 80% of the trees at the more northern site (ZHF) responded positively to warming. It should be noted that climate response was particularly variable for *P. obovata* at the IND site, as no more than one-third of the population fell in any one response category. The proportion of *L. cajanderi* at each site with a negative response to temperature was inversely correlated to latitude (Fig. 3a; $r = -0.895$, $P < 0.05$, df = 3). Although the proportion of *L. cajanderi* with a positive response to temperature increased slightly along the latitudinal gradient, the correlation was not significant ($r = 0.756$, $P > 0.05$, df = 3).

Positive correlations between *L. cajanderi* growth and temperature were concentrated in early spring and summer (April through June; Table 2a). A lagged response to the previous spring's temperatures was common. In all *L. cajanderi* populations, the modal number of correlations occurred in either May or June (of the current or previous year). Growth of negatively responding *L. cajanderi*, in contrast, was primarily

Table 1 Trends in temperature and precipitation from 1902 to 2002

	Temperature				Precipitation			
Site	Spring	Summer	Fall	Winter	Spring	Summer	Fall	Winter
BAL	0.0273	0.0033	0.0007	**0.0435**	0.0692	0.1110	**0.2786**	0.0512
YUT	**0.0274**	0.0031	0.0011	**0.0470**	0.0615	0.0631	**0.2361**	0.0475
SYL	**0.0153**	0.0023	−0.0050	**0.0284**	0.0018	0.0574	**0.1190**	**0.0665**
IND	**0.0162**	0.0030	−0.0050	**0.0286**	0.0055	0.0586	0.1131	**0.0668**
LRB	**0.0159**	0.0032	−0.0066	**0.0270**	0.0026	0.0597	0.0863	**0.0644**

Values are unstandardized regression coefficients. Bold font indicates a significant trend in that climate parameter over time ($P < 0.05$). The northernmost three sites (LRB, CSZ, and ZHF) occupy the same 0.5° × 0.5° CRU grid cell, so climate trends are only reported for one of the sites (LRB).

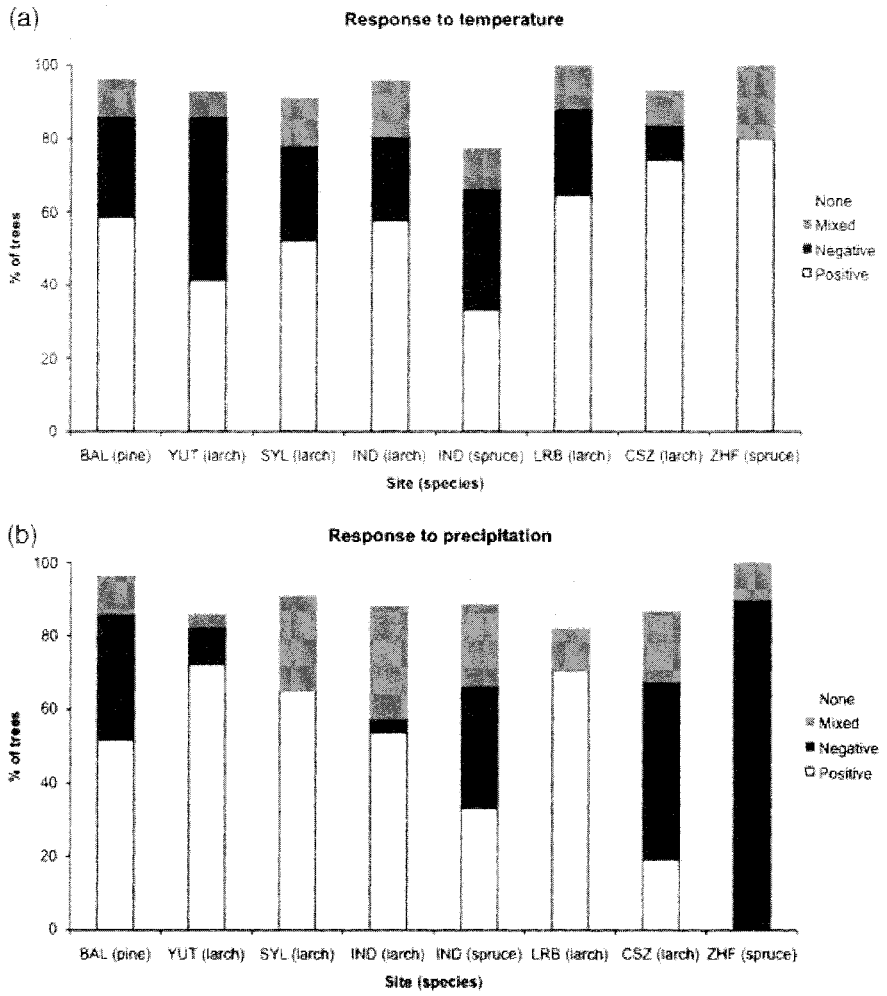

Fig. 3 Patterns of response to (a) temperature and (b) precipitation. Response categories are defined in the Materials and methods. Bars indicate the percent of trees at each site in each response category. Sites are arranged from southernmost (BAL) to northernmost (ZHF). Total number of trees varied among sites: $n_{BAL} = 29$, $n_{YUT} = 29$, $n_{SYL} = 23$, $n_{IND} = 26$ larch and nine spruce, $n_{LRB} = 17$, $n_{CSZ} = 31$, $n_{ZHF} = 10$.

correlated with July temperatures of the pervious year (sites YUT, SYL, IND) or with winter temperatures (sites LRB, CVZ). Growth of *P. sylvestris* responded to a broader window of climate conditions. Positive correlations with temperature were common in late winter, spring, and early summer months, of both the current and previous year. Negative correlations were spread throughout the year, but were most frequent in winter and early summer. Growth of positively responding *P. obovata* was correlated with late winter and spring temperatures. Growth of negatively responding *P. obovata*, in contrast, was correlated exclusively with late summer and autumn conditions of the previous year.

The majority of trees responded positively to precipitation, growing more in wetter years (Fig. 3b). The two *P. obovata* sites were an exception: only one-third of *Picea obovata* at the IND site, and none of the *P. obovata* near Zhigansk responded positively to precipitation. There was no significant correlation between latitude and the proportion of trees responding positively ($r = -0.443$, $P > 0.05$, $df = 3$) or negatively ($r = 0.131$, $P > 0.05$, $df = 3$) to precipitation. Positive correlations between growth and precipitation were most prevalent in summer (Table 2b). Negative correlations between growth and precipitation, in contrast, tended to occur in the late summer and winter months.

Comparison between tree/climate response and NDVI trends

The proportion of positively responding trees at a site was significantly correlated with the percentage of cells

Table 2 Patterns of correlation between tree growth and climate

	Positive correlations (%)			Negative correlations (%)		
Month	*Pinus sylvestris*	*Picea obovata*	*Larix cajanderi*	*Pinus sylvestris*	*Picea obovata*	*Larix cajanderi*
(a) Correlations with temperature						
Prior April	27.6	36.8	35.7	13.8	–	–
Prior May	27.6	42.1	30.2	3.4	–	0.8
Prior June	34.5	–	–	–	–	2.4
Prior July	3.4	–	–	–	15.8	**31.0**
Prior August	–	–	–	3.4	5.3	8.7
Prior September	3.4	–	1.6	–	10.5	1.6
Prior October	3.4	–	0.8	–	**31.6**	10.3
Prior November	10.3	–	0.8	–	5.3	7.1
Prior December	6.9	–	7.9	–	–	5.6
January	3.4	–	13.5	**31.0**	–	–
February	34.5	26.3	17.5	6.9	–	0.8
March	–	–	5.6	6.9	–	–
April	**44.8**	31.6	18.3	10.3	–	1.6
May	31.0	**57.9**	38.1	3.4	–	0.8
June	–	21.1	**42.9**	17.2	–	–
July	34.5	10.5	–	–	–	4.0
August	3.4	–	–	–	–	0.8
(b) Correlations with precipitation						
Prior April	–	–	2.5	6.9	42.1	12.7
Prior May	3.4	–	–	–	5.3	0.8
Prior June	20.7	10.5	22.2	20.7	–	–
Prior July	10.3	10.5	**52.4**	–	–	–
Prior August	3.4	10.5	19.8	–	36.8	0.8
Prior September	13.8	5.3	5.6	10.3	5.3	0.8
Prior October	–	–	4.8	10.3	10.5	13.5
Prior November	24.1	5.3	6.3	17.2	–	7.9
Prior December	3.4	5.3	2.4	–	–	19.8
January	–	–	2.4	**51.7**	–	6.3
February	13.8	**15.8**	10.3	3.4	5.3	1.6
March	3.4	–	–	–	10.5	3.2
April	3.4	–	1.6	–	15.8	4.0
May	–	**15.8**	–	–	–	3.2
June	**58.6**	–	1.6	6.9	5.3	–
July	3.4	–	5.6	–	10.5	2.4
August	3.4	5.3	7.9	6.9	**47.4**	7.9

Climate variables are listed in the first column; those designated "Prior" indicate correlations between growth in year t and monthly climate in year $t-1$. Analyses were conducted for each individual site, but to simplify presentation the results are presented here by species. Values represent the percentage of individual trees of that species that exhibited a significant correlation with (a) mean temperature or (b) total precipitation of that month (*Pinus sylvestris*: $n = 29$ trees at one site; *Picea obovata*: $n = 19$ trees at two sites; *Larix cajanderi*: $n = 126$ trees at five sites). The modal value is highlighted in bold font. Absence of any significant correlations in a month is indicated by '–'.

in the surrounding landscape exhibiting a positive trend in NDVI (Fig. 4; $r = 0.945$, $P < 0.01$, df = 4).

Discussion

Although a number of recent studies have shown that boreal spruce species have tended to respond negatively to recent warming (Wilson & Elling, 2004; Driscoll *et al.*, 2005; Wilmking *et al.*, 2005; Lloyd & Bunn, 2007; D'Arrigo *et al.*, 2008), our data confirmed our prediction that warming would favor *P. obovata* over the more northerly *L. cajanderi* in floodplain sites where the two species co-occur. At both mixed-species sites, spruce growth has grown more than larch in the period 1958–2007 relative to the period 1808–1957. This is consistent with previous studies, which have found increases in height growth (Lopatin, 2007), increased recruitment, and range expansions of *P. obovata* in Siberia (Moiseev

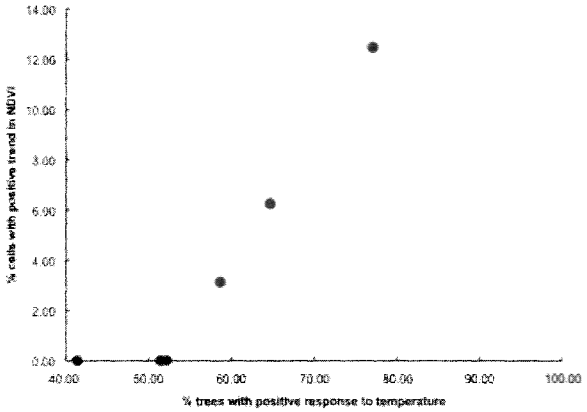

Fig. 4 Relationship between the proportion of trees at each site exhibiting a positive response to temperature and the percentage of cells in the surrounding landscape that exhibit a positive trend in normalized difference vegetation index (NDVI). Two sites (CSZ and ZHF) were so close together that they fell within the same NDVI buffer area, so the percent of trees exhibiting a positive response was averaged between the two sites, and they are represented by only a single data point. Trend in NDVI is reported as a percentage of all cells; the percentage of cells exhibiting a trend ranged from 0% to 22%.

et al., 2004; Kharuk *et al.*, 2005), and suggest that warming may favor more southerly dark taiga species, including *P. obovata*, over more northerly *Larix*. Greater growth of *P. obovata* compared with *L. cajanderi* in recent decades may reflect trade-offs between growth and cold-tolerance observed in other ecosystems (Loehle, 1998); in this case, shifts in the optimum leaf phenology are a likely underlying cause of those trade-offs. Extremely harsh winter conditions should favor deciduousness (Givnish, 2002), but milder winters (Table 1) may increase the competitive advantage of evergreen *Picea*, which are better able to take advantage of early growing season warmth (Givnish, 2002). Our findings, however, may not be easily extrapolated to nonfloodplain areas. The range of *P. obovata* is limited to areas where permafrost is either absent or quite deep (e.g., Tchebakova *et al.*, 2009), so its expansion beyond the relatively well-drained, warm floodplain soils along the Lena River is questionable.

Although we were unable to directly compare growth of *P. sylvestris* and *L. cajanderi* (as we did not sample any mixed stands of the two species), patterns of climate response hint at possible differences between the two species in response to recent warming. The *P. sylvestris* site (BAL) was dominated by positive responders, which made up 58% of the population. Negative responders, in contrast, made up only 28% of the population. At the most southern *L. cajanderi* site (YUT), which was also located in the vicinity of Yakutsk, positive responders (41% of the population) were less frequent than negative responders, which made up 44% of the population. These differences, although small, are consistent with previous findings that negative responses to warming are more frequent in sites in the southern part of a species range (Lloyd & Bunn, 2007), and with evidence that pines respond more favorably to warming than larch (Kharuk *et al.*, 2009).

The differences among sites in population-level responses to warming were consistent with our hypothesis that warming would have a more positive effect in more northern sites. Negative responses to warming became increasingly rare along the south–north latitudinal gradient, a pattern consistent with a previous study which found that negative responses to warming were more frequent in the southern half of a species' sampled range (Lloyd & Bunn, 2007). For positively responding trees, correlations with monthly climate highlighted the importance of early growing season conditions for larch growth. The timing of soil thaw seems particularly crucial for initiating physiological activity in *Larix* (Vaganov *et al.*, 1999; Kirdyanov *et al.*, 2003; Nikolaev 2003; Lopez *et al.*, 2007). Studies analyzing daily climate data have found that growth of *Larix* is most highly correlated with temperatures from early or mid-June through early to mid-July (Vaganov *et al.*, 1999; Kirdyanov *et al.*, 2003; Knorre *et al.*, 2006). Growth of individual *L. cajanderi* trees at our sites displayed a broad range of correlations with monthly temperatures from January through June, but correlations with early summer (May–June) temperatures were the most prevalent. Climate response of positively responding *P. obovata* was similar to that of *L. cajanderi*, emphasizing the importance of the early growing season for both species. *P. sylvestris* displayed a different pattern of response: winter and spring temperatures were more important than growing season temperatures.

The climate response of negatively responding *P. obovata* and *L. cajanderi* was quite different from that of the positive responders, even within a site. This suggests that the two response groups may be subject to different limiting factors (as opposed to having different responses to the same limiting factors), consistent with the hypothesis that within-population variation reflects microsite variability (e.g., Wilmking *et al.*, 2004). Within-population differences were particularly striking in *L. cajanderi*, given the uniformity of climate response previously reported for this species. Growth of negatively responding *L. cajanderi* was most frequently correlated with July temperature of the previous growing season, a finding surprising for two reasons. First, it suggests that the middle or end of the growing season, rather than its onset, may be more important for negatively responding trees. Such a pattern would be

expected if negative responders are limited by growing season moisture deficits, which in boreal regions are likely to become more pronounced as the growing season progresses and to be greater in years when mid and late summers are warm (Nikolaev, 2003). A prevalence of positive correlations with July precipitation in these same trees supports the hypothesis that moisture stress may contribute to the negative response to summer warmth observed here. The second surprising aspect of the climate response of negatively responding *L. cajanderi* is the 1-year lag in response. However, although deciduousness may reduce the effects of 1 year's growth on the next, there is some carryover of carbohydrates from 1 year to the next. Kagawa *et al.* (2006), in a pulse-labeling experiment on *Larix cajanderi*, found that 24–91% of carbohydrates produced in August were incorporated into the following year's ring. Poor conditions for photosynthesis at the end of the growing season in year $t-1$ might therefore plausibly be reflected in the ring produced in year t, a scenario supported by the existence of significant first order autocorrelation in our *L. cajanderi* ring-width data.

The role of temperature as a limiting factor thus changes over the latitudinal gradient, with warmer temperatures benefiting a larger percentage of trees in northern than southern populations. Our data suggest that the role of precipitation also changes along the latitudinal gradient. At least half of the trees in the more southern sites responded positively to precipitation, generally during the growing season. Negative correlations with precipitation, in contrast, were concentrated in the winter months and at the northernmost latitudes, and may reflect the influence of winter precipitation on growing season length: a delayed start to the growing season is likely in years with a heavy snowpack (Vaganov *et al.*, 1999; Kirdyanov *et al.*, 2003). The one exception to this pattern of negative responses to precipitation at northern sites was the LRB site, where a population of *L. cajanderi* is perched on a well-drained bluff above the Lena River. Trees there were likely particularly susceptible to moisture stress, possibly explaining the prevalence of positive correlations with precipitation.

Although the prevailing population-level response to climate thus changed along the sampled latitudinal gradient in a manner consistent with our hypothesis, the high within-population heterogeneity in climate response is notable. Multiple response types – to both temperature and precipitation – were identified at every site. The northernmost spruce population (site ZHF) was the most homogenous: 80% of the trees responded positively to temperature and 90% responded negatively to precipitation. The other populations (of all species) showed a consistent pattern of divergent responses within a single stand. A similar magnitude of within-population variability in climate response has been found in the Alaskan boreal forest (Wilmking *et al.*, 2004, 2005; Wilmking & Juday, 2005); within-population divergence may thus be a widespread feature of boreal ecosystems. The multiple response types within populations may reflect microsite variation (Wilmking *et al.*, 2005). Hummocky microtopography, widely observed at our sites, may create heterogeneity in soil thermal conditions over a small spatial scale. The importance of soil temperature for tree growth in this region has been well established (Kirdyanov *et al.*, 2003; Nikolaev 2003; Nikolaev *et al.*, 2009), and provides a plausible basis for intrapopulation variability in climate response. Within-population variability could also have a genetic basis. Such variation could be critical for evolutionary responses to climate change, and further investigation of the causes of within-population heterogeneity in climate response is warranted.

The population-level patterns of tree response to climate are mirrored in the NDVI data, suggesting that the prevalence of positive responders is part of a broader landscape-scale response to warming. Our data confirmed our hypothesis that 'greening' of the landscape around each site (measured by positive trends in NDVI between 1982 and 2005) would be significantly and positively correlated with the proportion of trees at a site showing a positive response to temperature. The relationship between NDVI and tree growth derives from a shared dependence on gross photosynthesis, and a correlation between the two has been documented at individual sites in other studies (D'Arrigo *et al.*, 2000; Lopatin *et al.*, 2006). However, Berner *et al.* (in press) found a relatively weak association between trends in NDVI and trends in tree growth across Siberia and Canada. They attribute the comparatively weak association in part to the relatively low forest cover at most sites: differences in climate response among functional groups (Knorre *et al.*, 2006) may weaken relationships between tree growth and NDVI trends. Our data, in which we compared trends in NDVI to the prevalence of a particular climate response rather than to the overall trend in tree growth, suggests that the 'greening' or 'browning' signal in the NDVI data does reflect the prevailing climate response within dominant tree populations, even in sites where forest cover is low. This suggests that the variability in NDVI trends identified in the Eurasian boreal forest by Bunn *et al.* (2007) is likely to reflect, in part, real differences among dominant forest types in the pattern of response to warming.

In summary, our results suggest that continued climate warming is likely to have pronounced effects on the Siberian taiga. Warming, particularly in the early

growing season, was associated with increased growth of both *L. cajanderi* and *P. obovata* at the northernmost latitudes sampled. Productivity of these forests thus seems likely to increase in the future – a pattern consistent with the recent upward trends in NDVI in the landscape surrounding those sites. However, the pattern of response was not uniform between species: our data suggest that *P. obovata* growth has increased in recent decades to a greater extent than has that of *L. cajanderi*. Continued warming may thus lead to changes in the competitive balance and, ultimately, the composition of these mixed-species forests. Such compositional changes are already underway in other sites (e.g., Kharuk *et al.*, 2007). Compositional changes are also possible in southern locations, where negative responses to warming were more common in *L. cajanderi* than in *P. sylvestris*. Finally, our study indicates that heterogeneity in species' responses to climate variation is substantial: we found that response to climate varied as much within populations as it did among species or sites. The causes of this variation, however, are unknown: to what extent does within-population variation in climate response reflect fine-scale environmental heterogeneity, and to what extent is it indicative of possibly adaptive genetic variation? That neighboring individuals of the same species could exhibit dichotomously opposed responses to climate is quite remarkable, and understanding the cause of that variation is crucial to efforts to predict the future of the boreal forest.

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