ECOSYSTEMS

Effects of Climate, Site Conditions, and Seed Quality on Recent Treeline Dynamics in NW Russia: Permafrost and Lack of Reproductive Success Hamper Treeline Advance?

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ABSTRACT

Treeline advance alters albedo and carbon storage and is an important feedback mechanism to the global climate system. Establishment of trees north of the treeline requires favorable climate, suitable microsites, and viable seeds. Here we studied the influence of climate and microsite conditions on tree and seedling growth at four transects from forest through woodland to tundra in NW Russia, and tested the viability of seeds from the region. General growth patterns and establishment periods of the treeline species *Picea obovata* are similar across the study sites suggesting a regional driver (for example, climate). Individuals established as early as the 1640s, but mainly between 1850 and 1880, and during a major and continental scale establishment wave in the 1950s and 1960s. No establishment occurred after 1982. Older trees mainly showed significant and stable positive relationships to growing year summer temperatures and significant stable negative correlations to previous year summer temperatures in nearly all plots. Trees from the last establishment wave showed more mixed responses, but current year summer temperature positively affected growth. Active layer depth was similar in all plots with trees but decreased sharply in treeless tundra. A major role for the lack of recent establishment seems to be very low seed viability, possibly combined with early strong fall frosts, which might have severely limited successful recruitment in the last decades of the twentieth century. For a successful establishment of *P. obovata* in tundra areas of NW Russia, permafrost degradation and (generally) warmer winters might be a prerequisite.

Key words: dendroecology; *Picea obovata*; recruitment; tree rings; seed viability; climate warming.

INTRODUCTION

Treeline dynamics provide important feedback mechanisms to the global climate system by altering albedo and carbon storage at high latitudes. The replacement of tundra vegetation by more productive boreal forests is often assumed to increase aboveground carbon storage (ACIA 2005) and to decrease albedo (Chapin and others 2005). Climate induced permafrost degradation might lead to treeline advance (Lloyd and others 2002) and successive gains in aboveground carbon, but these gains can be more than offset due to the respiration of old (soil) carbon resulting in significantly reduced ecosystem carbon storage (Wilmking and others 2006; Steltzer 2004). It is thus still unclear if treeline advance is a dampening or amplifying feedback mechanism to global warming. In general, the spatial pattern and speed of treeline advance at temperature limited sites and retreat at moisture limited sites following climate change will affect the extent of such feedbacks in the future (Tchebakova and others 2009; Lloyd and Fastie 2002).

At large spatial and temporal scales, temperature conditions are believed to be the main factor controlling the ultimate occurrence of trees at high latitudes and thus the position of the northern treeline (for example, Holtmeier and Broll 2007; MacDonald and others 2000; 2008). With rising temperatures, the northern treeline is expected to shift northwards and boreal tree species are likely to invade tundra ecosystems (French 2007; Lloyd and others 2002), as they have done during the Holocene warm period (for example, Bryson 1965). There is evidence that the twentieth century warming trend at high latitudes has already caused an expansion of northern treeline tree species into contiguous tundra ecosystems at some locations (Grace and others 2002; Harsch and others 2009; Lloyd and Fastie 2002; Lloyd and others 2003; Serreze and others 2000; Suarez and others 1999; Virtanen and others 2004). In other locations growth performance of existing treeline trees seems to decline due to increasing drought stress (Wilmking and others 2004; Wilmking and Juday 2005; Driscoll and others 2005). In general, the rate and direction of this expansion and these distribution shifts are difficult to determine and might be gradual until certain thresholds are surpassed (Thompson and others 2004).

At smaller spatial and shorter temporal scales, the expansion of trees at their distributional limit is not only dependent on the regional climatic conditions (climate driver), but also on other factors. For example, an increasing fire regime might on the one hand shift the balance from coniferous to more deciduous trees (Landhäusser and Wein 1993; Johnstone and others 2011), or on the other hand provide potential seedbed and suitable microsites for tree establishment at small scales (Kullmann 2010). Tundra vegetation and microtopography can hinder or favor the establishment of new trees (Sullivan and Sveinbjoernson 2010). Low nutrient supply rate (Hobbie and Chapin 1998), or the occurrence of permafrost (Lloyd and others 2003) might be detrimental to tree establishment. Permafrost will react to rising temperatures and projected increases in the severity and recurrence of fires (Johnstone and others 2010), with future increases in regional temperatures expected to lead to a widespread decrease in permafrost thickness (from both top and bottom) and an increase in the depth of the annually melting and refreezing upper soil portion, the active layer (2005; Anisimov and Reneva 2006; French 2007; Oberman and Mazhitova 2001; Osterkamp and Romanovsky 1999; Serreze and others 2000). In areas with discontinuous permafrost, the permafrost could disappear (French 2007). Thus, changes in both climate and microsite drivers are most likely to have strong effects on the tundra-taiga ecotone, especially where tree growth is limited by permafrost (Virtanen and others 2004).

Northwest Russia is singular in continental Europe by being covered by extensive lowland permafrost. This is discontinuous or ''warm'' permafrost which is sensitive to warming (French 2007; Mazhitova and others 2004). The treeline is nearly exclusively formed by *Picea obovata* (Ledeb.). In general, this is a wind-pollinated species, in which years with cone crops are infrequent at treeline and show a periodicity of three to six years between productive (high-yield) years (Koshkina and others 2008). Germination success shows large variations depending on the source tree (Popov 1980) and is highest on bare mineral soils (Sannikov 1970). *Picea obovata* has a high shade tolerance, but does not grow well on permafrost-influenced soils (Virtanen and others 2004) and probably succeeds in this region only by occupying permafrost-free sites, mainly located along the river banks. For the last 20–30 years, summers have warmed, and radial and height growth of conifers in the boreal region of northwest Russia has been increasing, as has the depth of the active layer (Lopatin and others 2007; Oberman and Mazhitova 2001). Because other pressures that can affect treeline dynamics, such as fire, browsing of seedlings, or other human influences are relatively light here (Gromtsev 2002; Virtanen and others 2004), a climatically driven northward migration of
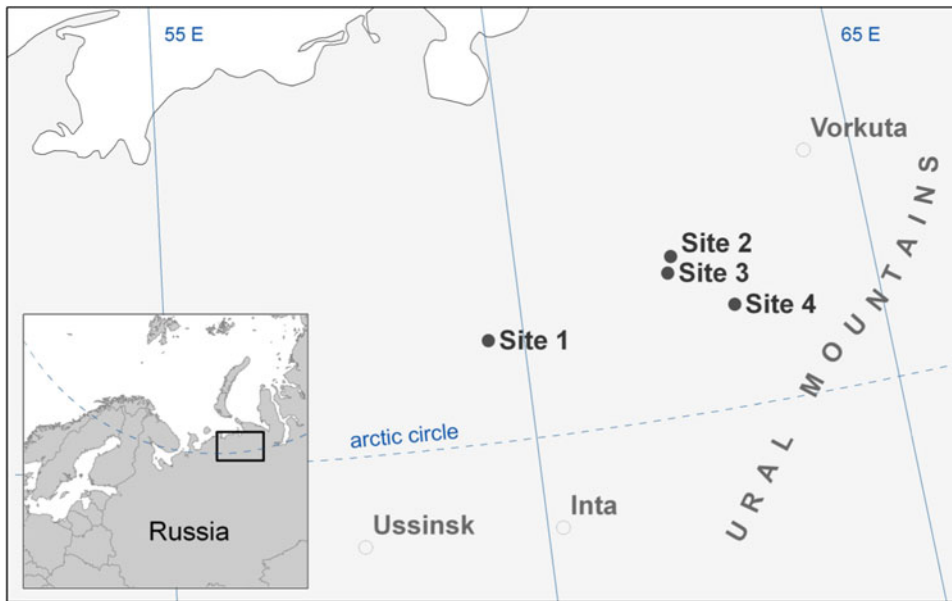
Figure 1. Location of study sites in NW Russia: Site 1 (Khoseda), site 2 (upper Rogovaya river), site 3 (lower Rogovaya river), and site 4 (Seida).

spruce at the northern treeline in northwest Russia seems likely.

In this paper, we examine whether environmental changes in northwest Russia during the last decades have already led to treeline advance or if recent changes are likely to lead to treeline advance in the near future. Our study is a nested approach at three spatial scales: (1) Regional scale: we examined relationships between radial growth of established trees and temperature and precipitation at four treeline sites located over an approximately 120 km transect from west to east (test for a climate drivers); (2) Local scale: we examined the age structure, radial growth performance and climate sensitivity of trees and seedlings extending from current tree islands at treeline (predominantly permafrost-free soils) into permafrost-influenced soils in the adjacent tundra (microsite driver) along short (<1 km) south-north transects; (3) Individual scale: we examined the germination rates of seeds and survival rates of seedlings in a controlled laboratory experiment.

METHODS

Field Sites

Four field sites were located at the northern treeline in NW Russia, spanning a regional west to east transect of approximately 120 km: (1) Site 1 (Khoseda), 67.0°N, 59.5°E, 127 masl; (2) Site 2 (upper Rogovaya River), 67.2°N, 62.1°E, 75 masl; (3) Site 3 (lower Rogovaya River), 67.1°N, 62.1°E, 73 masl; and site 4 (close to the village of Seida), 67.4°N, 62.3°E, 85 masl (Figure 1). At each site, a site transect (<1 km) was established on even terrain from forest tree islands with established trees on generally well-drained soil with permafrost pockets, through woodland with single widely spaced trees, to treeless tundra underlain by permafrost (Figure 1). These site transects represented conceptual transects of local permafrost degradation.

Field Sampling

In general, our measurements along each site transect were concentrated in three plots (15 × 15 m): (1) Forest, (2) woodland, (3) tundra. At site 1 we added a plot upslope of the forest plot (upland dense woodland), at site 3 we added a plot 20 m outside the forest (dense woodland). We measured depth of the active layer in July 2007 with a permafrost probe (length 1.2 m) in a grid of 5 × 5 m in each 15 × 15 m plot, resulting in 16 depth measurements per plot (no measurements in site 4). In each plot we also collected radial penetrating tree cores or cross-sections (at or very close to root collar level) from all *Picea obovata* trees and seedlings in July 2007. At site 3 we recorded the position of individuals at a micro-scale level (growing on hummocks, intermediate areas or in hollows).

Tree ring Analysis

Tree ring samples were prepared according to dendro-chronological standards (Fritts 1976). Age of samples was determined by ring counts if cross-

sections at root collar level were available (in case of seedlings and small trees). In the case of cores (which were collected at a certain height of the stem), we adjusted the ages to account for sampling height by using a linear regression of height versus age of all sampled and absolutely dated trees (derived average annual height growth was 3.05 cm/year). This procedure will introduce a level of uncertainty in the absolute ages; we do believe, however, that associated errors will generally fall within a decade, and usually are smaller. Tree ring width was measured in all samples using a LINTAB 5 measuring bench and microscope, precision 1/1,000 mm (Rinntech, Germany). Measurements were made on cores and cross-sections (disks) from all sample plots and, in addition, from other well-established trees close by. Samples were crossdated visually and using COFECHA (Grissino-Mayer 2001). We used the program ARSTAN (negative exponential, straight line fits, seldom Huggershoff spline functions, residuals calculated by division) to standardize the tree-ring series, remove the biological age trend, to calculate the tree-ring index and to build site chronologies (standard and residual) where applicable. To highlight possible differences in the climate–growth relationships between older trees, which established before the main establishment wave in the middle of the twentieth century, and the trees which initiated growth during this wave, we built two separate chronologies per plot, from the trees older and younger than 70 years old.

To calculate relationships between radial tree growth and climate parameters, we used the program DENDROCLIM2002, which utilizes 1,000 bootstrapped samples to compute response and correlation coefficients, and to test their significance at the 0.05 level (Biondi and Waikul 2004). We used mean monthly temperature and precipitation data (1901–2002) from the closest grid point of the gridded CRUTS 2.1-data set (Mitchell and Jones 2005) as climate input, because the CRU temperature record provided a century of data, and correlated very well with the closest station record (Khoseda Hard, $r > 0.98$) and other stations of the area (Pecora, $r > 0.90$, and Nar Jan Mar, $r > 0.87$). We used the residual chronologies (first-order autocorrelation removed) obtained by AR-STAN as tree-ring input.

Seedling Germination

Cones ($n = 40$) of *Picea obovata* Ledeb were collected at the end of the 2006 growing season at field site 4

from tree tops. Only about 50 seeds could be extracted, which were dried and sent to Great Britain for first germination trials. They were stored at 4°C for 6 weeks to simulate snow cover and subsequently warmed to room temperature. The seeds were brought out on de-ionized water agar at 17°C. None of the seeds germinated and a second batch of 200 seeds was provided by the Russian Institute for Forest Research which was collected in 2003 (a mast year, pers. comm. V. Pommarov, compare Koshkina and others 2008), 2004 and 2005 in northern Komi Republic, then air-dried and stored frozen. Before germination seeds were defrosted in the fridge (ca. 7 days). Seeds were then slowly warmed to growth chamber temperature and germinated by placing them on de-ionized water agar at 17°C under a 12 h light (photosynthetic photon fluence rate (PPFR) of 50–200 μmol m^{-2} s^{-1})/12-h dark cycle. A baseline for seasonal temperature changes was obtained during previous years growing season using in situ data loggers. This temperature regime was mimicked closely over the period of the germination and later growth trial. As a control on our handling of the seeds, we subjected commercial seed from the more southern boreal zone to the same treatment and handling.

RESULTS

Age Structure and Establishment Pattern

The main establishment wave at all plots occurred during the middle of the twentieth century, whereas the period between 1850s and 1880s is characterized by the first-regional establishment wave in our sample (Figure 2; Table 1). The oldest two trees sampled in the study area established in 1643 and 1647 in the forest area of site 3 and 4,
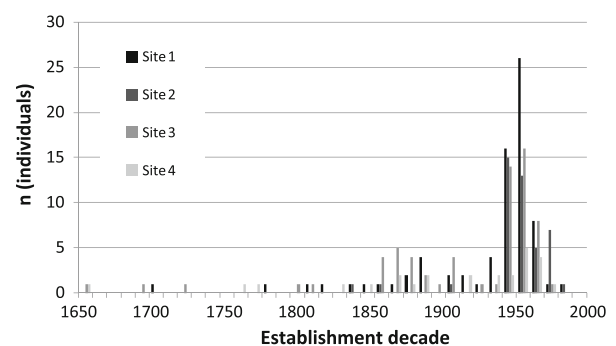

Figure 2. Establishment date of *Picea obovata* individuals at all sites by decade. Note distinct peak between 1940 and 1960.

Table 1. Chronology and Stand Characteristics

	n (trees > 70 y)	EPS > 0.85 since	Oldest tree	n (trees < 70 y)	Youngest tree	Density trees (>2 m)/ha	Density saplings (0.1–2 m)/ha
Site 1							
F	13	~1850	1699	32	1974	667	400
WL (lowland)	2		1885	16	1982	178	667
WL (upland)	20	~1880	1837	19	1964	622	133
Site 2							
F	12	~1890	1777	35	1981	1333	178
WL (lowland)	/		1950	11	1980	222	267
Site 3							
F	43	~1880	1647	21	1970	400	933
F edge (lowland)	/		1944	8	1973	178	222
WL (lowland)	3		1809	7	1963	89	400
Site 4							
F	7	~1900	1643	4	1949	444	0
WL (lowland)	1		1887	11	1975	133	400

F forest, WL woodland, EPS expressed population signal.

respectively. The oldest sampled tree in site 1 forest established in 1699 and in the forest at site 2 in 1777. Establishment in the woodland plots started later, 1809 in site 3, 1837 in the upland woodland of site 1, and 1885 and 1887 in the lowland woodland of site 1 and site 4, respectively. The first tree in site 2 woodland established in 1950. The last *Picea obovata* individuals established around 1963/64 in the lowland and upland woodland of site 1 and the woodland of site 3; between 1970 and 1975 in site 1 and 3 forest, and in site 4 woodland, and between 1980 and 1982 in site 1 forest and site 2 forest and woodland. No individual established after 1982 in any of our survey plots.

Long-term Radial Growth Trends

All chronologies constructed for trees older than 70 years old showed similar absolute radial growth values and radial growth patterns over time, both at low frequency (long-term trend) and high frequency (annual variation) (Figure 3A, B). A period of relatively high radial growth until around the 1780s was followed by a period of reduced radial growth with minimum values around 1825. These were the lowest recorded values in our chronologies. A slow increase with a local maximum around 1875 was followed by a subsequent reduction with a minimum in the 1890s and a strong increase at the beginning of the twentieth century with overall maximum radial growth rates from 1925 to 1950, depending on the sampling site. After 1950, annual radial growth decreased to a minimum around 1975
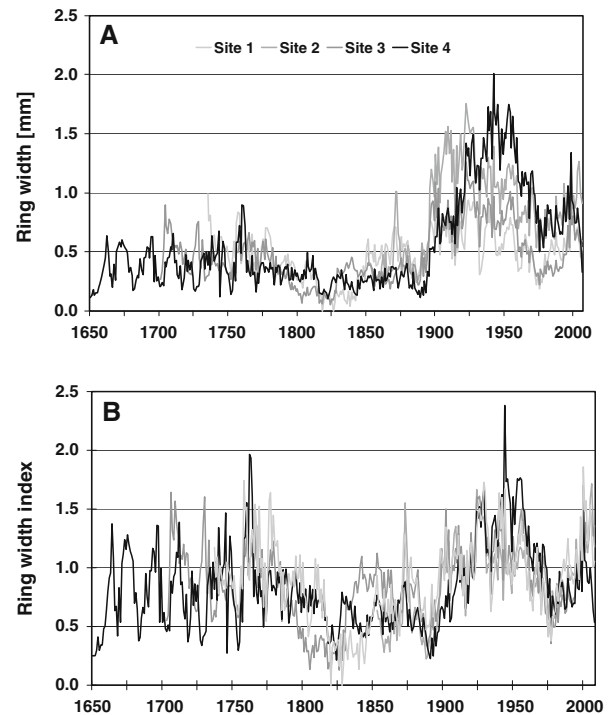

Figure 3. Raw (**A**) and standardized (**B**) chronologies showing a common pattern among sites, suggesting a regional driver of tree growth performance, for example, climate.

at all sites. After 1975, radial growth rates increased, but did not reach the maximum absolute values that were achieved in the middle of the twentieth century.

Annual radial growth trends of the chronologies from young trees (<70 years) in all plots also
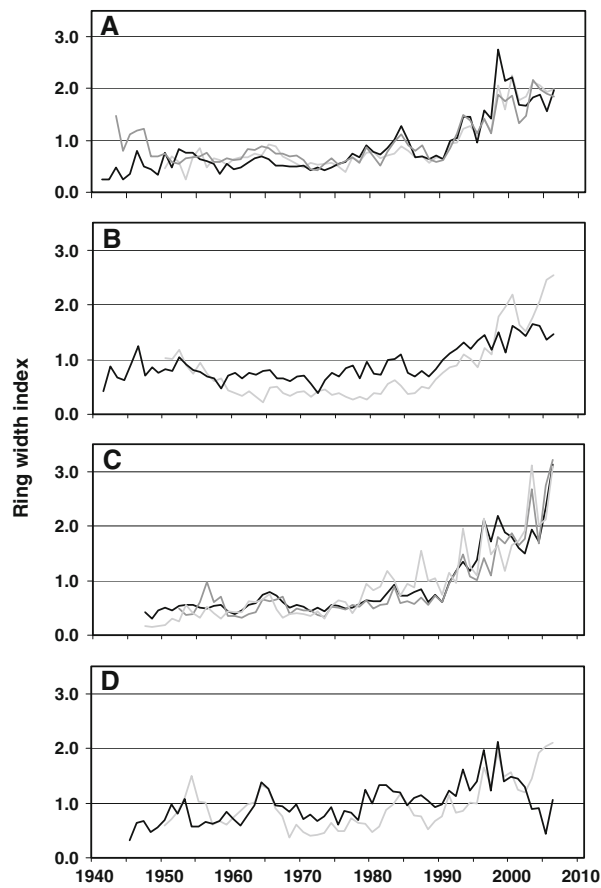
Figure 4. Standard chronologies from younger trees show a similar growth pattern across and within the four sites (**A** site 1, **B** site 2, **C** site 3, **D** site 4; *black line* forest plot, *gray lines* woodland plot(s)). Slow growth until about 1990 is generally followed by radial growth increases.

showed a regionally similar growth pattern (Figure 4A–D). Low absolute radial growth values until around 1990 were followed by an increase of radial growth in young woodland as well as young forest chronologies until the sampling year in 2007. However, the young forest chronology at site 4 showed reduced radial growth rates from around the year 2000, whereas the young forest chronology at site 1 also showed some initial reduction from around the year 2000, which levelled off soon after (Figure 4). Absolute growth values [mm/year] were similar for all sampling sites (0.1–2 mm/year) with the exception of the young forest chronology at site 4 (last decade). Within our sampling sites, trees in woodland plots were generally outperforming those in forest plots in absolute annual radial growth for the last decade (data not shown).

Climate–Growth Relationships

Climate–growth relationships for chronologies constructed from the older trees were very similar in all four sampling sites with significant negative correlations between annual radial growth and July, August and December mean monthly temperatures (MMTs) for the year prior to ring formation, and positive correlations (mostly significant) with June and July MMTs for the year of growth (Figure 5). These correlations were stable over time at all sites (data not shown). Significant correlations also existed which were not synchronous across all sites, with the possible exception of a significant positive correlation between previous May total monthly precipitation (TMP) and annual radial growth.

Climate–growth relationships evident in chronologies from the younger trees were also broadly similar in all four sampling sites with positive correlations (mostly significant) between annual radial growth and growing season temperatures for the year of growth. Other significant correlations existed, but were not synchronous across all sites (Figure 5).

Microsite Conditions

The active layer depth was generally notably shallower in the tundra plots compared to woodland and forest plots, which showed similar thaw depths (Figure 6), often exceeding the depth of the probe. Although forest plots were generally well-drained, woodland and especially tundra plots were often waterlogged. In general, most trees and seedlings grew on slightly elevated features (such as hummocks, 67%), followed by hollows (low areas), and intermediate areas (each 16.5%).

Germination Experiment

The germination and/or survival rate of the 50 seeds sampled at the field sites was nil. The germination rate of the 200 seeds sampled during 2003–2005 was less than 1%. Germination of the control seeds from the more southern boreal zone was 80%.

DISCUSSION

Treeline advance is generally a complex process. At temperature limited sites, the general prerequisite is an amelioration of climatic conditions for an extended period of time to allow build-up of growth reserves necessary for the production of cones and viable seeds (Juday and others 2003).
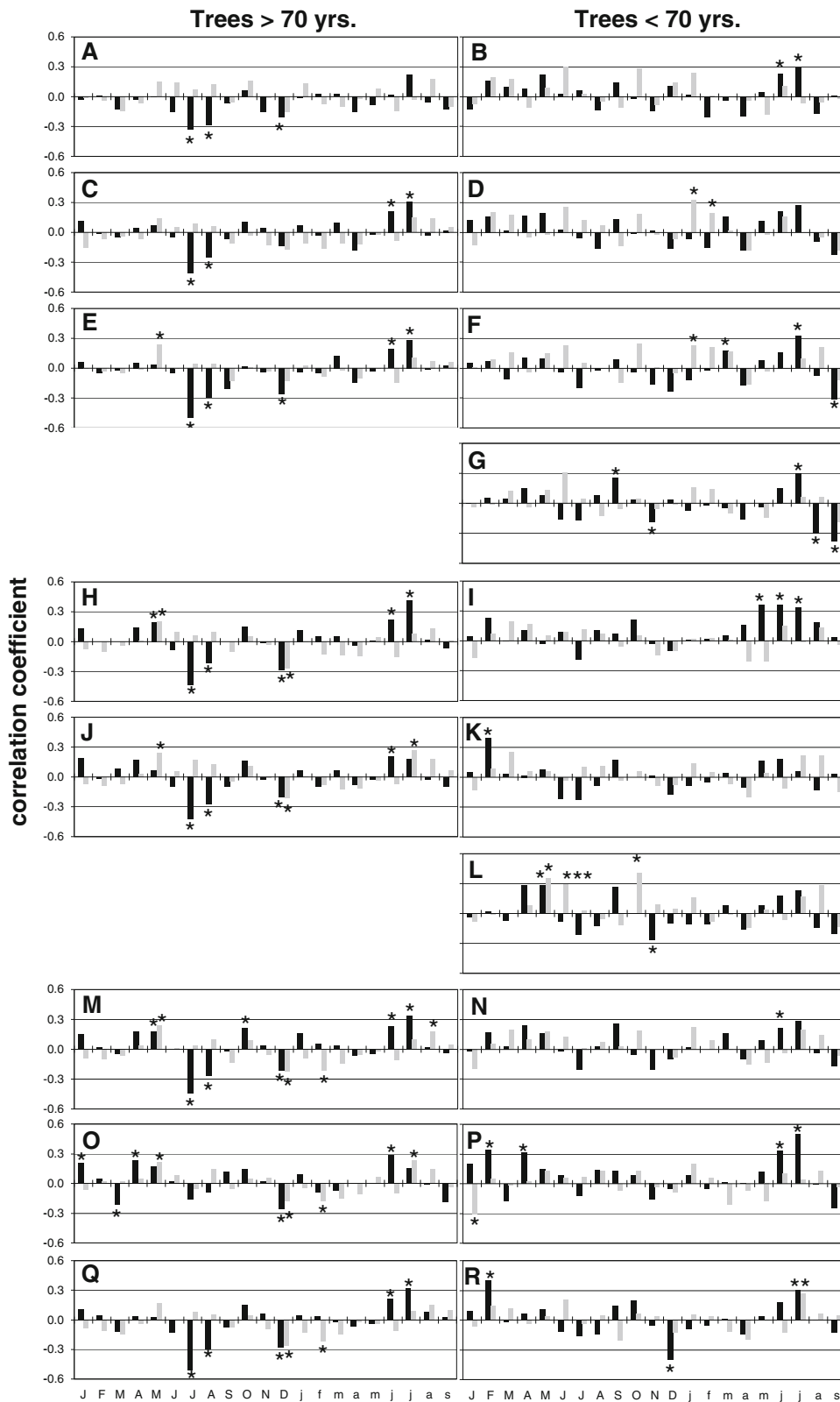
Figure 5. Climate–growth correlation of chronologies from trees older (*left column*) and younger than 70 years old (*right column*). Significant correlations (*P* = 0.05) obtained by bootstrapping marked by *asterisk*. Site 1 lowland woodland (**A**, **B**), forest (**C**, **D**), upland woodland (**E**, **F**); site 2 woodland (**G**), forest (**H**, **I**); site 3 woodland (**J**, **K**), dense woodland (**L**), forest (**M**, **N**); site 4 woodland (**O**, **P**), forest (**Q**, **R**). *Capitalized letters* refer to MMT of the year prior to growth, *small letters* to year of growth.

Once viable seeds are available, they need to germinate, establish and survive in tundra areas beyond the current treeline, and thus, need both favorable climatic conditions and suitable micro-sites (Lloyd and others 2003). However, successful recruitment is also a function of mortality and it is
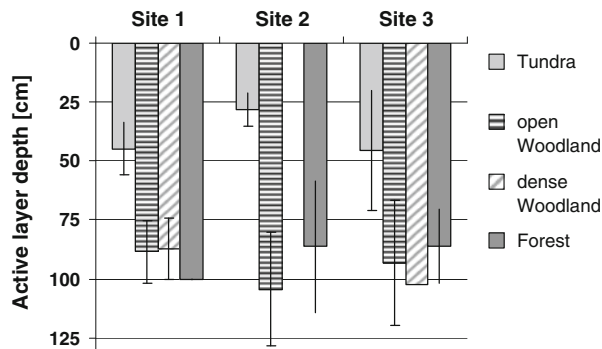
Figure 6. Minimum active layer depth (in cm on *y* axis) across the forest-tundra site transects, *error bars* are standard deviation. No values are available for site 4. Active layer depth in un-forested tundra sites is notably shallower than in woodland or forest sites.

difficult to determine whether populations establish because of high germination or low mortality rates (MacDonald and others 2008).

Climate-driven Growth and Recruitment Pattern

In northwest Russia, radial growth of established trees in our study sites shows a synchronous pattern over large areas, and similar relationships with climate (summer temperatures), suggesting a regional driver (for example, climate) over a disturbance driven system. Mainly positive correlations with current year summer temperatures are in line with the ecological theory of a thermal limit to the tree line in this area (MacDonald and others 2008), and in general agreement with a study about 150 km north of our site 1, where June and July temperatures showed significant correlations with ring width (Holzkämper and others 2008). Negative correlations of annual radial growth of older trees with previous summer temperatures suggest an operating drought stress mechanism in very warm years, as has been reported from Alaska (for example, Wilmking and others 2004; Ohse and others 2012). Here, it does not seem to hinder tree line advance as young (but cone bearing) trees seem not to be affected.

Periods of recruitment in all sample sites (Figure 2) have mostly mirrored periods of enhanced radial growth performance of parent trees (Figure 3) with a small recruitment wave between 1860 and 1880, concurrent with a local maximum in annual radial growth, and a large recruitment wave between 1940 and 1960, concurrent with a maximum of annual radial growth in all four sites. The recruitment wave in the middle of the twentieth century also coincides with or briefly lags a
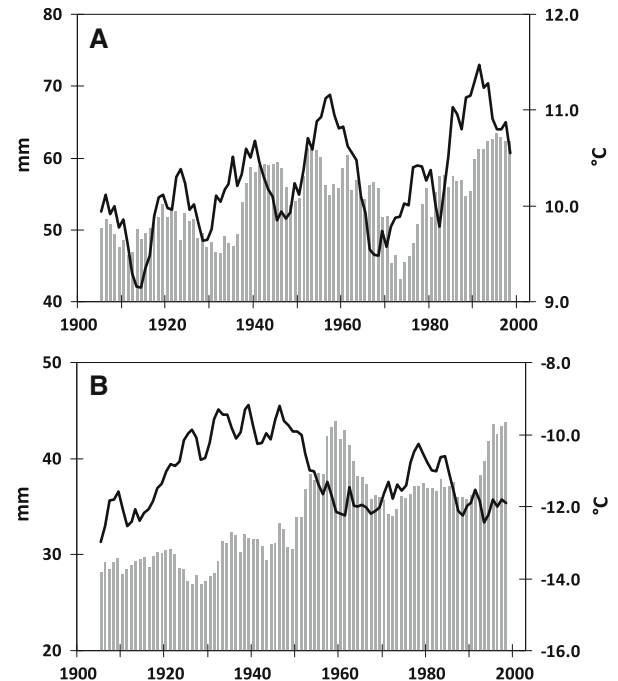

Figure 7. Climatic conditions of the study area based on CRUTs2.1 data. Averaged summer (JJA) (**A**) and early winter (OND) (**B**) mean monthly temperatures (*black lines*) and total monthly precipitation (*gray bars*) smoothed over 10 years show warm and wet summer conditions in the middle and end of the twentieth century, with dryer and cooler conditions from 1900 to 1930 and in the 1970s. Although summer temperatures are generally showing a warming trend in the last 20 years, this trend is absent in the early winter data.

period of generally warmer temperatures and higher precipitation levels during summer and relatively warm early winters (Figure 7), corroborating the general positive influence of temperature on tree establishment at this northern tree line; and seems to be part of a continental scale recruitment in northern Eurasia with similar germination periods noted on the Kola Peninsula (Gervais and MacDonald 2000), northern Sweden (Zackrisson and others 1995), and northern Siberia (Esper and Schweingruber 2004). Following the last establishment wave, temperatures decreased from 1960 to 1975 in our study area and subsequently, annual radial growth and recruitment decreased as well.

Decoupling of Climate, Radial Growth, and Recruitment at the End of the Twentieth Century?

Summer temperatures have again been rising since about 1970 and have been reaching or exceeding values similar to those during the mid twentieth century since about 1988. Radial growth of older

established trees and young trees which germinated during the main establishment wave between 1940 and 1960 has increased since about 1975, following the increase in temperature to some extent. The stage thus should have been set for a new recruitment wave into tundra areas in northwest Russia. However, no new recruitment of trees in our sample sites and other areas in northwest Russia (see also Esper and Schweingruber 2004) has been taking place since 1982.

Influence of Site Conditions

To gain a better understanding into the possible factors hampering new tree recruitment, we should briefly look at the environmental setting at our study sites. At the landscape scale, forest islands at our research sites were located on well-drained soils and are bordered by peatlands or upland tundra. Peatlands are usually water-logged, and have shallow active layers (Zoltai 1995). Upland tundra is characterized by a shallow active layer, high soil moisture contents and cryoturbatic features. The treeline species of the region, *Picea obovata*, has difficulty growing on permafrost-influenced soils, and modeling results show that the distribution of cold and wet soils is most likely controlling landscape distribution of established trees (Virtanen and others 2004).

Our ground-based studies corroborated these modeling results at smaller scales. Nearly all recruitment during the mid twentieth century took place in areas where active layer depth presumably was relatively deep, because single *P. obovata* trees had previously established there (Figure 6; Table 1). The establishment in the middle of the twentieth century thus most likely represented infilling rather than a true treeline advance. Only at one site (site 2, the northernmost site) did new trees establish about 50 m beyond the forest borders, but the active layer depth in the newly formed woodland was, at least in 2007, notably deeper than in adjacent tundra. Either active layer depth there was already deeper in 1950, or the successful establishment of trees has led to a deeper active layer since then. Both trajectories are possible, because permafrost conditions and tree growth are coupled and influence each other. Although underlying permafrost prohibits drainage, permafrost degradation will result in a deeper active layer with generally improved drainage and the formation of well-drained microtopographic features (Lloyd and others 2003). Tall woody vegetation that might otherwise have been unable to colonize permafrost-influenced cold, poorly drained soils

might now be able to successfully expand into these areas (Allard and others 1996; Lloyd and others 2003).

Tree advance into tundra can also alter the current state of permafrost distribution by first initiating a positive feedback on permafrost degradation as a result of increased snow trapping and decreased albedo. As snow insulates the soil, the cold cannot penetrate as deeply into the soil and refreezing of the ground in winter is diminished (Liston and others 2002; Lloyd and others 2003; Sullivan 2010). In addition, forested sites with low albedo absorb more solar energy than tundra sites with high albedo resulting in higher soil heat flux and an increase in active layer depth (Thompson and others 2004). On the other hand, once a forest is established, increased tree cover can increase permafrost thickness and decrease active layer depth due to shading and interception of snowfall (Chapin and others 2000; French 2007; Thompson and others 2004). Both factors could lead to dampening feedbacks on permafrost degradation (Lloyd and others 2003).

At our sites, however, it is most likely that the first step in a conversion from tundra to woodland was permafrost degradation, because neither the literature, nor our results indicate a recruitment of *P. obovata* in areas with a shallow active layer. Observations at the micro-scale corroborate these conclusions, as most spruce trees and seedlings at our sites had established on slightly elevated features (mainly hummocks) with higher soil temperatures, better nutrient supply and lower soil moisture. These microsites are generally more conducive to tree growth and establishment (Chapin and others 2005) and at the treeline in northwest Alaska, the local *P. glauca* preferentially established on such suitable microsites (Sullivan and Sveinbjörnsson 2010). It is thus most likely that the occurrence of permafrost and cold and wet soils controls *P. obovata* distribution on the landscape, plot and micro-scale at our sites and that no further treeline advance into tundra has taken place simply because no suitable tundra sites with deep active layers were available.

Influence of Seed Production and Early Cold Spells?

However, one would expect establishment and survival of seedlings within the current woodland and forest plots, where active layer depth is sufficient for tree growth. Our results did not show any new establishment within these plots since 1982 (see also Esper and Schweingruber 2004).
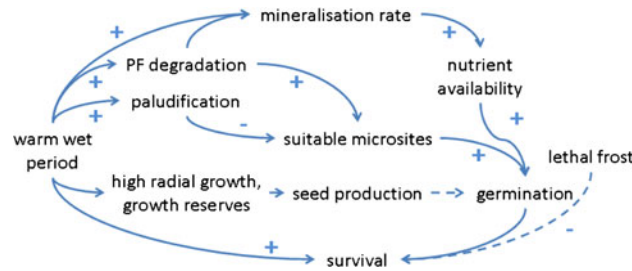
Figure 8. The conceptual model of successful recruitment of *P. obovata* at treeline in our study sites shows the complex interactions between climate, microsite conditions and *Picea* ecology. Because all relationships (indicated by *arrows* and (+) for amplifying and (−) for dampening effect) are scalar (that is, the stronger the process, the stronger the feedback), recruitment is influenced by all factors and their interaction. Especially seed production/germination and lethal frosts can influence survival of new individuals.

Successful recruitment is a function of germination and mortality and it is difficult to determine whether populations establish because of high germination or low mortality rates (MacDonald and others 2008). The conceptual model (Figure 8) offers two possible pathways to drastically reduce successful recruitment: (1) no viable seed production and (2) lethal events after germination.

Cones were present in the majority of trees at all field sites at least in the forest plots. However, our germination trials showed only a very limited amount of viable seeds. Effects of the germination experiment set-up, if present, were most likely minimal, because a commercial seed source from the more southern boreal zone handled similarly did show a germination rate of 80%, even though germination requirements of the more southerly seed source might have differed to some extent. Along an elevational gradient in the southern Urals, *P. obovata* trees at treeline produce fewer and smaller cones, fewer seeds and show lower seedling survival rates than stands further downslope (Koshkina and others 2008), concurrent with our observations from the latitudinal gradient. The lack of viable seed might thus be one reason for the lack of establishment, but because of the small sampling depth, this result has to be interpreted with some caution.

After germination, survival of seedlings is strongly influenced by the climatic conditions the following years. Three main climatic differences between the late twentieth century period (of no observed recruitment) and the earlier/mid twentieth century period (of strong recruitment) exist: The late twentieth century is characterized by (1) generally very low early winter temperatures (Figure 7), 2) the absence of a pronounced winter warming (data not shown) and 3) the occurrence of several years with very early and strong
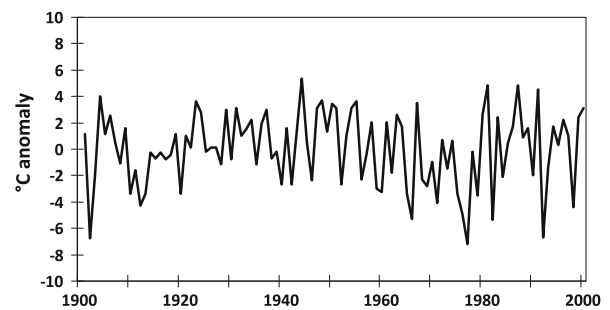

Figure 9. Anomaly of October mean monthly temperatures (in °C versus mean 1901–2002). Very cold (>4°C colder than average) Octobers occurred 1902, 1912, 1966, 1971, 1977, 1982, 1992, and 1998.

autumnal frosts, as indicated by the anomalies of October temperatures from the long-term mean (Figure 9). In a meta-analysis of treeline dynamics, treeline advance was more likely in areas of strong winter warming (Harsch and others 2009), in line with our results of no advance during a period of nearly no winter warming.

Frost severity has far more impact on seedling survival, damage, and subsequent growth than frost exposure time in *P. glauca* (Bigras and others 2004), suggesting that single events can have a significant impact on seedling survival. This seems to be especially true if the cold spell comes suddenly at the end of summer (Thomas 2000), before the establishment of a contiguous snow cover. Damage can be effects of cold on shoots and roots or indirectly by abrasive, blown snow in tundra. Seedlings on top of hummocks would be especially vulnerable in very cold years, because snowfall is generally lower in cold years and the available, blown snow accumulates first in inter-hummock spaces. This would (1) leave the hummock tops exposed longer to drifting snow and (2) result in

lower soil temperatures inside the hummocks due to poorer insulation. Species such as *P. glauca* and possibly *P. obovata*, which do not tolerate cold soil conditions might be strongly affected (Dumais and others 2002), especially in their first year of growth (Koshkina and others 2008). To test these hypotheses, controlled experiments, or data on seedling mortality in the field with concomitant measurements of soil temperatures in hummock or inter-hummock spaces under varying snow regimes (for example, mid and late twentieth century) are necessary. Although the absence of any early winter warming does lend credibility to our line of thoughts, the beginning of the early cold spells (∼1966) is earlier than the end of the successful recruitment, indicating only a weak relationship. At this point, we thus cannot fully explain the missing recruitment since 1982, but propose a combination of lack of viable seed and seedling mortality due to cold spells as a hypothesis, but one which must await further testing.

CONCLUSIONS

Treeline dynamics depend on many factors interacting at various scales and can alter albedo and carbon storage at high latitudes, resulting in an important feedback mechanism to the global climate system. Establishment of trees north of the treeline requires both favorable climatic conditions and suitable microsites. In NW Russia, general radial growth patterns and establishment periods of the treeline forming species *Picea obovata* were similar across our four study sites and mainly related to generally warmer and wetter conditions. Main establishment waves at our sites occurred between 1850 and 1880, and during a major and continental scale establishment in the 1950s and 1960s. Then, summer and winter temperatures (the regional climate driver) seem to have been favorable for radial growth and seed production, and no evidence exists for early cold spells possibly reducing survival of young seedlings. Micro-site conditions might play a role hindering the expansion of *P. obovata* into permafrost-affected areas, because active layer depth was similar in all plots with trees and seedlings but decreased sharply in treeless tundra. The lack of establishment after 1982 at permafrost-free sites might be due to a combination of low seed quality and high mortality of seedlings due to the absence of general winter warming in the last decades of the twentieth century and early strong fall frosts. Our results therefore suggest that for a successful establishment of *P. obovata* in tundra areas of NW Russia, further

permafrost degradation and generally warmer winters might be a prerequisite.

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