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Russian Arctic warming and 'greening' are closely tracked by tundra shrub willows

BRUCE C. FORBES*1, MARC MACIAS FAURIA†‡1 and PENTTI ZETTERBERG§

*Arctic Centre, University of Lapland, FI-96101 Rovaniemi, Finland, †Biogeoscience Institute, University of Calgary, Calgary, Alberta, Canada T2N 1N4, ‡Department of Ecology, University of Barcelona, Barcelona, Catalonia 08028, Spain, §Ecological Research Institute, University of Joensuu, FI-80101 Joensuu, Finland

Abstract

Growth in arctic vegetation is generally expected to increase under a warming climate, particularly among deciduous shrubs. We analyzed annual ring growth for an abundant and nearly circumpolar erect willow (Salix lanata L.) from the coastal zone of the northwest Russian Arctic (Nenets Autonomous Okrug). The resulting chronology is strongly related to summer temperature for the period 1942-2005. Remarkably high correlations occur at long distances (>1600 km) across the tundra and taiga zones of West Siberia and Eastern Europe. We also found a clear relationship with photosynthetic activity for upland vegetation at a regional scale for the period 1981-2005, confirming a parallel 'greening' trend reported for similarly warming North American portions of the tundra biome. The standardized growth curve suggests a significant increase in shrub willow growth over the last six decades. These findings are in line with field and remote sensing studies that have assigned a strong shrub component to the reported greening signal since the early 1980s. Furthermore, the growth trend agrees with qualitative observations by nomadic Nenets reindeer herders of recent increases in willow size in the region. The quality of the chronology as a climate proxy is exceptional. Given its wide geographic distribution and the ready preservation of wood in permafrost, S. lanata L. has great potential for extended temperature reconstructions in remote areas across the Arctic.

Keywords: climate change, dendrochronology, NDVI, remote sensing, Salix lanata, trend analysis

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Introduction

The general consensus is that growth in arctic vegetation is expected to increase under a warming climate (ACIA, 2005; IPCC, 2007). Remote sensing data reveal that tundra vegetation in North America may be responding to the recent warming via enhanced photosynthetic activity (Goetz et al., 2005; Verbyla, 2008). At a circumpolar scale, the highest photosynthetic activity and strongest growth trends are reported in locations characterized by erect shrub tundra (Raynolds et al., 2006). Live leaf phytomass from deciduous shrubs, shown to have increased in northern Alaska during the second half of the last century (Sturm et al., 2001; Tape et al., 2006), is believed to be a key driver of the observed trends (Jia et al., 2003; Goetz et al., 2005; Verbyla, 2008). In the Eurasian Arctic, ground-level quantification of deciduous shrub growth is missing.

Correspondence: Bruce C. Forbes, tel. $+358\,40\,847\,9202$; fax $+358\,16\,341\,2777$, e-mail: bforbes@ulapland.fi

¹Contributed equally to this work.

Retrospective analyses that could quantify the relationship between summer warmth and deciduous shrub growth would help to fill a critical gap in our understanding of the 'greening' already underway.

The resolution of proxy climate records varies considerably, but few natural archives offer annually resolved records of past arctic climates (Zalatan & Gajewski, 2006). Ice cores and lake varve sequences can provide annual or even seasonal records of past climatic conditions, but can be subject to error from missing years, and replication, which would help reduce the error associated with dating, is typically not possible. Relatively few studies to date have exploited arctic woody species for dendroclimatology. These have either (1) used evergreen shrubs, (2) found precipitation or snow regime growth responses, and/or (3) not produced complete chronologies (Walker, 1987; Woodcock & Bradley, 1994; Johnstone & Henry, 1997; Rayback & Henry, 2006; Schmidt et al., 2006; Zalatan & Gajewski, 2006; Bär et al., 2007; Nikolaev & Samsonova, 2007; Forchhammer et al., 2008), or (4) produced floating chronologies for archaeological dating (Shiyatov & Hantemirov, 2000), i.e. the time periods represented were not continuous up until the present. Yet until now, no studies have managed to produce a response function relating deciduous tundra shrub growth to temperature, despite mounting evidence in the last few years for a link between summer warmth and increasing live leaf phytomass in portions of the tundra biome ('greening' of the Arctic; Jia et al., 2003; Goetz et al., 2005; Raynolds et al., 2008; Verbyla, 2008).

Salix lanata L. (sensu latu) is an abundant deciduous dioecious willow with nearly circumpolar geographic distribution from the northern boreal forest (foresttundra transition zone) to the northern limits of the Low Arctic (dwarf and prostrate shrub zone), except in Greenland where it is absent (Hultén & Fries, 1986). Other than at its northern range limits, the plant is typically erect, attaining a height of 1-3 m under favorable conditions with adequate snow cover (Jonsell, 2000; Tolmachev, 2000), but it also grows horizontally in response to chronic snow loading and readily roots adventitiously when stems come into contact with the ground. Several authors have commented on the difficulties involved with reliably cross-dating arctic willows (Beschel & Webb, 1963; Woodcock & Bradley, 1994), but this species does produce well-defined growth rings. Moreover, preserved dead Salix material from at least two tundra species (S arctica Pall. and S. dasyclados Wimm.) has been previously cross-dated, suggesting the potential for extending chronologies from living material (Woodcock & Bradley, 1994; Shiyatov & Hantemirov, 2000).

The aims of the present study are to: (i) develop a ring width chronology using S. lanata from the East European Arctic; (ii) investigate the growth-climate relationship and thus the potential for proxy climate reconstruction of this abundant and geographically widespread species; and (iii) explore possible evidence for a tundra shrub growth trend to match an ostensible arctic 'greening' detected by the Normalized Difference Vegetation Index (NDVI, Jia et al., 2003; Goetz et al., 2005; Raynolds et al., 2006; Verbyla, 2008).

Study area

The study area lies in the Nenets Autonomous Okrug (Fig. 1), about 20 km southeast of the coastal port of Varandei, between the lakes Big Toravei and Small Toravei (68°40″N, 58°30″E). This is a region of low arctic tundra (Walker et al., 2005) with uplands characterized by dwarf shrub heath, Sphagnum-sedge mires in the lowlands, and dense copses of Salix spp. 50-250 cm tall in moist to saturated riparian habitats and along lake margins with rolling, moderate slopes. A supervised classification based on very high-resolution Quickbird-2 satellite imagery determined the local ground cover of erect *Salix* copse to be $\approx 20\%$ (Fig. 2). The study area is

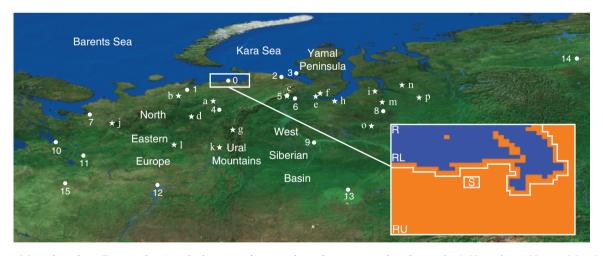


Fig. 1 Map of northern Eurasia showing the location of meteorological stations used in this study: 0, Varandei; 1, Naryan Mar; 2, Ust Kara; 3, Marre Sale; 4, Pechora; 5, Ra Iz; 6, Salekhard; 7, Arkhangelsk; 8, Tarko Sale; 9, Khanty Mansisk; 10, Vytegra; 11, Vologda; 12, Kazan; 13, Omsk; 14, Khatanga; 15, Moscow. The study area is highlighted by an empty white rectangle and expanded in the lower-right corner of the image, which depicts the different NDVI areas used in the study. R, regional NDVI (whole area); RU, Regional-Upland; RL, Regional-Lowland; S, site. Lowercase letters and white stars indicate the location of the boreal tree-ring width chronologies, developed by F. Schweingruber and available at the International Tree-Ring Data Bank at the National Oceanic and Atmospheric Administration Paleoclimatology Program and World Data Center for Paleoclimatology (http://www.ncdc.noaa.gov/paleo/treering.html), which were compared with the Salix lanata chronology presented in this study: a, Shchely Bozh; b, Chariyakha river; c, Polar Urals; d, Kedvaran; e, Shchuchye River; f, Khadyta River; g, Ukyu; h, Nadym River; i, Khadutte River; j, Voroney; k, Krasnovishersk; l, Nyuchpas; m, Malchoyakha River; n, Indikyakha River; o, Lower Vangapur River; p, Sidorovsk.

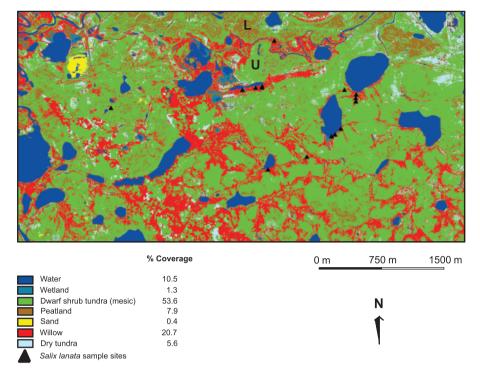


Fig. 2 Supervised land classification of the sampling area on a very high resolution Quickbird-2 image, taken on 5 August 2005. The percentages of land cover for each class are shown. Note the sharp change between the upland (U) and lowland (L) at the northern edge of the image, the lowlands having a much greater proportion of peatland.

situated within subzone D of the Circumpolar Arctic Vegetation Map (CAVM; Walker et al., 2005). The boundary between subzones C and D separates drier northern tundra on mineral soils from southern relatively moist tundra with moss carpets. This is approximately equivalent to the boundary between the high and low arctic (Bliss, 1997). Subzone D is characterized by erect shrubs (>40 cm tall) in protected locations, such as riparian habitats and at the foot of steep slopes, particularly along lakeshores. Substrates are classified as peaty tundra gley soils with high organic content (Ponomarev et al., 2004). During 1995-2005, mean summer (June-August) temperature at Varandei, the nearest weather station, was 7.5 °C and snow cover depths between December and April averaged 68 cm. This region has experienced an estimated warming trend of 1-2 °C for the month of July during the main study period 1942-2005 (NASA-GISS, 2009). Winter temperatures (December-February) for the same period do not reveal a warming trend, although from 1981 to 2005 temperature has increased from 0.2 to 0.5 °C (NASA-GISS, 2009). This study will focus on the growing season (June-August) in order to address the aforementioned literature gap concerning the relationship between summer warmth and deciduous phytomass at the regional scale.

Materials and methods

Field methods

168 slices 2-3-cm-thick were collected from 40 discrete individuals spread across 15 sample sites over an area of approximately 3×2.5 km in the summer of 2006. These represent 'upland' tundra that is relatively lowlying ($\approx 25 \,\mathrm{m\,a.s.l.}$) but still topographically distinct from the adjoining mire-dominated coastal lowland that is generally $\leq 100 \,\mathrm{cm} \,\mathrm{a.s.l.}$ (Fig. 2). A minimum of four slices between the root collar and the upper canopy was taken from each individual in order to properly account for reaction wood, which forms in response to mechanical stress, e.g. wind exposure, snow loading, soil movement, and can result in asymmetric stem growth. In the few cases of obtaining two or more samples from among dense, polycormic clonal copses, care was taken to differentiate between distinct genets. Whenever possible, neighboring female (7) and male (24) plants were used in order to test for potential variations in stem growth resulting from differential allocation to reproductive effort or stem production.

Olofsson *et al.* (2009) have recently argued that herbivory must be considered in order to understand how a changing climate may or may not affect shrub

abundance. The leaves and twigs of S. lanata constitute important forage for several herbivores, including reindeer (Rangifer tarandus L.; Podkorytov, 1995). In smaller erect individuals and related prostrate taxa, such as S. arctica Pall., herbivory could be a source of dendrochronological error within years (Schmidt et al., 2006), and early- and mid-season browsing and trampling are demonstrated to significantly reduce Salix biomass in shrubs ≤ 80 cm in height (Kitti et al., 2009). In the study area, which comprises designated pasture territory used by nomadic Nenets herders, Salix spp. are potentially grazed in late summer up to a level of $\sim 1.8 \,\mathrm{m}$. We found no evidence of browsing in the field, and only erect individuals with heights ranging 2-2.5 m were sampled.

Climate and remote sensing data

Continuous climate records in the arctic tundra tend to be relatively short-term and spatially restricted to coastal areas where most meteorological stations are located, particularly in North America (Zalatan & Gajewski, 2006). In the East European North (Fig. 1), data sources north of treeline are patchy, spatially and temporally, and the distances between stations can be great. At nearby Varandei, continuous climate records extend back only to the 1990s. Mean monthly temperature data from 12 stations in Northern Russia, 225 to 1725 km from the study site and covering the period 1942-2004, were obtained from the National Climatic Data Center (NCDC, http://www.ncdc.noaa.gov/oa/ncdc.html). Monthly precipitation and temperature data from five nearby (i.e. distances < 400 km) Russian Arctic stations for 1961-2000 were available at the National Snow and Ice Data Center (NSIDC) at Boulder, Colorado. Further, we used mean monthly surface temperature data from a 2.5° latitude per 2.5° longitude regional grid covering the period 1948-2005 from the NCEP Reanalysis database, provided by the NOAA-CIRES Climate Diagnostics Centre, Boulder, Colorado (http://www.cdc.noaa. gov/).

NDVI data are derived from the National Oceanic and Atmospheric Administration (NOAA) Advanced Very High Resolution Radiometer (AVHRR) meteorological satellites, and serve as a strong proxy for gross photosynthesis. They are therefore useful for estimating levels of total live aboveground phytomass and leaf area index (LAI) in tundra vegetation (Goetz et al., 2005; Riedel et al., 2005; Raynolds et al., 2006). We obtained biweekly NDVI records from the Global Inventory Modeling and Mapping Studies (GIMMS) dataset, available through the Global Land Cover Facility (http://glcf.umiacs.umd.edu/data/gimms/). The dataset (Tucker et al., 2005) has been corrected for calibra-

tion, view geometry, volcanic aerosols, and other effects not related to vegetation change, and covers the period 1981-2005 at 8 km resolution. We computed regional averages of NDVI for four areas which varied in extension and in physiographic characteristics (Fig. 1): (i) Site comprised of a small area in the immediate vicinity of the sampling site (4 pixels, 256 km²); (ii) Regional, a broad area around the site (648 pixels, 41472 km²); (iii) Regional-Upland, as (ii) but excluding coastal pixels and thus with a smaller fraction of mires, peatlands, and water bodies and a higher fraction of well-drained land (576 pixels, 36864 km²); and (iv) Regional-Lowland, as (ii) but including only coastal pixels, which showed consistent lower NDVI values due a combination of cooler temperatures (immediate proximity to the Barents Sea) and higher fraction of water bodies (72 pixels, 4608 km²).

Data analysis

Wood samples were sanded and measured with a precision of 0.01 mm. Cross-dating of the ring width measurement series was performed following standard dendrochronological procedures (Fritts, 1976). Individual ring width measurements showed a characteristic age-related trend, with early suppressed growth followed by a relatively sharp growth increase (Supporting information, Fig. S1). Such a growth pattern was interpreted as the time the individual shrub takes to reach the 'canopy' of the respective thicket from which it was sampled. Ring width measurements were initially detrended using a 32-year smoothing spline (Cook & Peters, 1981). The Expressed Population Signal (EPS), which is a function of series replication and mean interseries correlation, was used to define the reliable part of the chronology (EPS \pm 85%, Wigley et al., 1984). Other descriptive statistics were calculated for each chronology to permit comparisons with other dendrochronological data sets (Fritts, 1976).

Dendrochronology in northern Russia has been restricted to the boreal forest and forest-tundra zones, with research focused on the conifers *Larix sibirica* Ldb., L. gmelini Pilger, L. cajanderi Mayr, Picea obovata Ldb. and Pinus sylvestris L. (e.g. Shiyatov et al., 1996). That is, the resulting S. lanata chronology cannot be compared with any other Russian tundra shrub chronology. In order to test its agreement with other ring width chronologies in the region, a network of existing 16 tree-ring width chronologies from various species in the northern boreal forest located south of our study site, and developed by F. Schweingruber (Fig. 1; Table 1) was correlated against the S. lanata chronology. Measurement data for each chronology was obtained from the International Tree-Ring Data Bank at the National Oceanic and Atmospheric Administration Paleoclimatology Program and

Table 1 Network of northern boreal forest tree-ring chronologies developed by F. Schweingruber and available at the International Tree-Ring Data Bank at the National Oceanic and Atmospheric Administration Paleoclimatology Program and World Data Center for Paleoclimatology (http://www.ncdc.noaa.gov/paleo/treering.html)

Code	Site	Lat	Lon	Species	Full period	Distance to site (km)	Pearson's correlation
a	Shchely Bozh	66.22	56.33	Picea obovata	1784–1990	180	0.320*
b	Chariyakha River	66.88	51.95	Pinus sylvestris	1653-1990	295	0.419**
С	Polar Urals	66.87	65.63	Larix sibirica	914-1990	360	0.491**
d	Kedvaran	64.25	53.57	Larix sibirica	1674-1991	450	0.277***
e	Shchuchye River	66.82	69.28	Larix sibirica	1710-1990	490	0.320*
f	Khadyta River	67.20	69.83	Larix sibirica	1782-1990	500	0.546**
g	Ukyu	62.60	58.80	Picea obovata	1616-1991	590	0.178
h	Nadym River	66.22	71.67	Larix sibirica	1740-1990	610	0.418**
i	Khadutte River	67.47	76.77	Larix sibirica	1585-1990	790	0.381**
i	Voroney	63.43	43.55	Larix sibirica	1729-1990	830	0.231***
k	Krasnovishersk	60.38	57.12	Larix sibirica	1730-1991	830	0.172
1	Nyuchpas	60.70	51.38	Pinus sylvestris	1651-1991	850	0.176
m	Malchoyakha River	66.08	77.68	Larix sibirica	1780-1990	870	0.282*
n	Indikyakha River	68.25	80.18	Larix sibirica	1592-1990	920	0.288*
O	Lower Vangapur River	63.07	76.32	Larix sibirica	1804-1994	990	0.206
p	Sidorovsk	66.67	82.33	Larix sibirica	1750–1990	1050	0.250***

Code shows the lowercase letters corresponding to each site in Fig. 1.

Lat, latitude; Lon; longitude, in decimal degrees; full period, total time span covered by each chronology; distance to site (km) is the distance (straight line) from the *S. lanata* site to each boreal forest site; Pearson's correlations were computed over the maximum common time span (1942–1990) and between the residual chronologies.

World Data Center for Paleoclimatology (http://www.ncdc.noaa.gov/paleo/treering.html). Individual measurement series were standardized by negative exponential functions or nonascending straight lines to remove the age-related growth trend, a common procedure in northern boreal forest stands (e.g. Macias *et al.*, 2004).

Response functions between the ring width residual chronology and monthly climate data (temperature and precipitation) for the five closest climate stations (distance to the site $\leq 400 \, \text{km}$) were performed using the program DendroClim2002 (Biondi & Waikul, 2004) for the period 1961–2000, for which we had full climatic data. Response function coefficients are multivariate estimates from a principal component regression model calculated to avoid colinearity between predictors commonly found in multivariable sets of meteorological data. Significance and stability of coefficients were assessed by 1000 bootstrap estimates obtained by random extraction with replacement from the initial data set. Climate-growth relationships were analyzed from the previous September to August of the growth year. Correlations between climate and the boreal forest treering width chronologies were computed in order to put the climate signal of our *S. lanata* chronology in context. Finally, relationships between shrub growth and NDVI

data measurements were assessed by linear Pearson's correlation coefficients.

Owing to the very flexible 32-year smoothing spline applied to the individual ring-width series in the standardization process, any mid to low-frequency component will be missing in the resulting ring width chronology. However, assessing decadal shrub-growth trends is of great interest in order to investigate if current temperature and NDVI trends can be related to increased deciduous shrub growth. We attempted a recovery of the longer-term component of the chronology by applying the Regional Curve Standardization approach (RCS; Briffa et al., 1992) to the individual growth series, a method specifically designed to preserve low frequency variability in ring width chronologies (Fig. S2). Sampling from the root collar at the base of each stem provided the best available material from the live portion of the individual.

Results

A reliable ring width chronology (STD32) was produced for the period 1942–2005 (Fig. 3a), with very high interseries correlation and chronology statistics (Table 2). Owing to the flexible spline used in the standardization process, the chronology was largely free of low

^{*}P < 0.1; **P < 0.05; and ***P < 0.01.

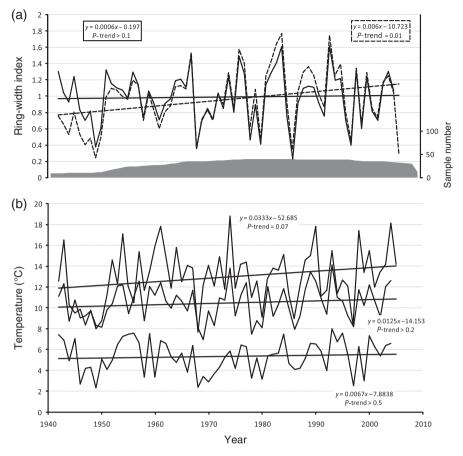


Fig. 3 (a) Salix lanata ring width STD32 – continuous line, standardized with a 32 years smoothing spline – and RCS – dashed line, standardized with the regional curve standardization procedure - chronologies, period 1942-2005 (see Materials and methods for further explanation). Sample depth (number of individuals) is shown as a filled grey area. Note the clear low frequency component in the chronology obtained by RCS, specifically designed to preserve it, suggesting a significant increase in Salix lanata growth for the period 1942–2005; (b) summer season (defined as June-August average) temperature series for a coastal lowland (Marre Sale – 69.72°N, 66.82°E, lower), an interior lowland (Naryan Mar - 67.63°N, 53.03°E, middle) and an upland interior (Salekhard - 66.53°N, 66.67°E, upper) meteorological stations close to the studied stand for the same period 1942-2005, obtained from the National Climatic Data Center (NCDC, http://www.ncdc.noaa.gov/oa/ncdc.html, see Materials and methods). Linear fits, their equations, and the trend-associated P-values are displayed. Note the lower coastal temperatures and the fact that the positive trend for summer temperature in Salekhard (upland interior) is remarkably similar to that of the RCS chronology.

frequency variability. No difference was found in the ring width between male and female individuals. Positive correlations were found when comparing the S. lanata chronology with the network of northern boreal forest chronologies (common period 1942-1990; Table 1): correlations were significant (P < 0.05) with nine out the 16 chronologies, and at distances >900 km. Our S. lanata chronology strongly correlated with the Polar Urals chronology (r = 0.49, P < 0.001), successfully used in Northern Hemisphere temperature reconstructions (e.g. Esper et al., 2002).

Response function coefficients revealed a very strong summer (especially July and August) temperature signal, and no precipitation signal. Figure 4 depicts the average response function coefficients for the five records of monthly temperature and precipitation, summarizing the overall ring width vs. climate relationships. June temperature was found to be significant when using the Naryan Mar record – the closest meteorological station, located 225 km from the study site. The only significant positive response to December temperature was found for Salekhard (400 km from the site). Correlation coefficients with summer temperature (defined as the June to August average) for a set of climate stations covering the 62-year period 1942-2004 were extremely high (r>0.7) at distances up to 300 km; Table 3A). Omsk summer temperatures, in the southern Ural Region, were very highly related to the chronology despite this station being some 1650 km distant from the sample sites. Correlations between STD32 and gridded summer

Table 2 Salix lanata ring width chronology statistics

	-		0,		
Time span	EPS> 85% since	n (n)	rg (SD)	+ (SD)	r
Time span	65% SINCE	$n_c (n_s)$	18 (3D)	ι (SD)	r
Raw data					
1921–2005	1942	119 (40)	0.682	51 (12)	0.734
1921-2003	1942	119 (40)		31 (12)	0.734
			(0.363)		
MS	SD	r1			
IVIS	3D	<i>r</i> 1			
Standard chi	onologu				
0.416	0.359	0.0	75		
0.410	0.559	0.0	17.5		
MS	SD				
-					
Residual chr	onology				
0.409	0.363				
EPS	VarPC1%	Ç	SNR		
	Vall C170		J1 11 (
Period 1942-	-2005 (Detrend	led Series)			
0.958	0.552	2	22.97		
		·-			

EPS, Expressed Population Signal; n_c , number of cores; n_s , number of shrub individuals; rg, mean radial growth (mm); SD, standard deviation; t, mean series length (years); r, mean correlation between individual and mean chronology; MS, mean sensitivity; r1, first-order autocorrelation; SNR, signal-to-noise ratio, which is a measure of the common variance in a chronology scaled by the total variance of the chronology; VarPC1%, variance explained by the first principal component.

temperature data for 1948–2005 are depicted in Fig. 5, with very high coefficients occurring at long distances, especially towards the south-east into the West Siberian Basin well into the boreal zone.

Moreover, our *S. lanata* chronology consistently showed a stronger summer temperature signal than the network of northern boreal forest tree-ring chronologies when tested against the set of climate stations across Northern Russia for the common period 1942–1990 (Table S1). Table 3B shows this in the case of the Polar Urals *L. sibirica* chronology, well known to paleoclimatologists and located 360 km south-east of our sampling site.

Fifteen-day NDVI values (1981–2005) peaked in the second half of July (interpreted as peak total biomass) and sharply dropped in the second half of September, being highest and lowest in the Regional-Upland and Regional-Lowland zones, respectively (Fig. 6a). NDVI values for the Site area (256 km²) were closer to the Regional-Upland NDVI values. Relationships between NDVI and temperature for a set of stations located within a radius <400 km from the site peaked in the second half of June (interpreted as peak productivity), but were high since the second half of May, when

Table 3 (A) Pearson's correlation coefficients between *S. lanata* residual ring width chronology and summer temperature (defined as the June to August average) for 12 climate stations covering the 62-year period 1942–2004 (see Fig. 1). (B) Pearson's correlation of Polar Urals *L. Sibirica* ring with residual chronology (*Polar Urals*, see text) and *S. lanata* residual ring width chronology *vs.* summer temperature for the stations in (A), covering the period 1942–1990

	A	В		
Station	$r(r^2)$	x (km)	Polar Urals	S. lanata
Naryan Mar	0.721 (0.520)**	225	0.34	0.67
Marre Sale	0.701 (0.491)**	300	0.53	0.65
Salekhard	0.591 (0.350)**	400	0.32	0.56
Arkhangelsk	0.280 (0.078)*	880	-0.01	0.3
Tarko Sale	0.551 (0.304)**	930	0.39	0.52
Khanty	0.537 (0.288)**	950	0.45	0.48
Mansisk				
Vytegra	0.01 (0.000)	1290	-0.09	0.12
Vologda	0.047 (0.002)	1320	-0.08	0.17
Kazan	0.165 (0.027)	1475	-0.01	0.25
Omsk	0.535 (0.286)**	1650	0.47	0.5
Khatanga	-0.016 (0.000)	1700	0.03	0.07
Moscow	-0.162 (0.026)	1725	-0.17	-0.01

^{**}Significant at P < 0.01.

significant snow cover remains on the ground but *Salix* spp. are already experiencing bud-break and the first leaves begin to emerge from the snow-free portions of the canopy. Figure 6b shows the correlation patterns between NDVI and the Naryan Mar record, which were exactly the same when using the other meteorological stations (not shown). Finally, NDVI values for the first half of July had higher correlations with June T, suggesting a \sim 1–2 week lag between T and NDVI (not shown).

Shrub annual growth strongly correlated to summer (especially the first half of July but also the second) NDVI values (Fig. 6c; 1981–2005). Correlation coefficients were highest for the Regional-Upland area, and lowest for the Regional-Lowland NDVI, although the patterns were the same for all areas. The stronger link between shrub radial growth and Regional-Upland NDVI with respect to Site NDVI might be due to the relatively low aerial coverage of erect willow shrub habitat within the Site area (Fig. 2).

The application of the RCS method successfully preserved mid- to low-frequency components of shrub growth. RCS curve shows a clear lower frequency component that indicates a significant increase in

^{*}Significant at P < 0.05.

x, distance to the study site; r, Pearson's correlation coefficient; r^2 , variance explained.

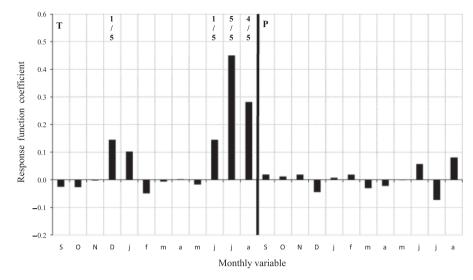


Fig. 4 Averaged response function coefficients for Salix lanata residual ring width chronology vs. monthly temperature (right, T) and precipitation (left, P) over five meteorological stations within the area (distances up to 400 km), obtained from the National Snow and Ice Data Center (NSIDC, see Materials and methods): Naryan Mar, Pechora, Ra Iz, Salekhard, and Ust Kara. Response function coefficients calculated separately for each meteorological station (not shown) resulted in the same overall pattern. Analyses were performed from September before the growing season to current August for the period 1961-2000 for which there is available T and P monthly meteorological data. Months abbreviated with capital letters correspond to the year previous to the growing season. Positive (negative) coefficients indicate positive (negative) ring-width vs. climate relationships. Fractions in the upper part of the plot indicate the number of times the response coefficients were found significant (P < 0.05); for example, 4/5 in August T means that the relationship between ringwidth and August T was found significant when analyzed against four out of the five climate records used. No fraction is displayed when no significant coefficients were found.

S. lanata L. radial growth along the study period (Fig. 3a), in a similar manner to summer season temperatures in meteorological stations located in the Regional-Upland area (Fig. 3b).

Discussion

Results show that S. lanata ring width growth in northern Russia is strongly related with summer temperature, as well as with NDVI. Although the present study was conducted on a single site, the large areas over which the chronology is related to both instrument and proxy climate records suggest that it is regionally representative. Assuming these solid relationships to be causal, the results would indicate that summer warming has enhanced deciduous shrub growth, which in turn has been responsible for the observed increases in NDVI.

Growth in arctic vegetation is generally expected to increase under a warming climate (ACIA, 2005; Chapin et al., 2005; Walker et al., 2006; IPCC, 2007). This greening within the tundra biome contrasts with a relative browning in the boreal forest zone (Goetz et al., 2005; Verbyla, 2008). Remote sensing evidence for the widespread greening comes largely from North America (Sturm et al., 2001; Goetz et al., 2005; Tape et al., 2006; Verbyla,

2008). Dendrochronological data relevant to the 'divergence problem' – i.e. divergent trends of temperature and tree growth in much of the circumboreal coniferous forest - derive from both North American and Eurasian taiga regions (Shiyatov et al., 1996; Briffa et al., 1998; Lopatin et al., 2006; D'Arrigo et al., 2008). To date, net increases in tundra phytomass detected by various remote sensing procedures are widely attributed to the contribution from erect deciduous shrubs, a key plant functional group of which Salix spp. comprise one the largest components north of the latitudinal treeline. The main driver for this woody encroachment into tundra areas is presumed to be recent decadal climatic warming (Sturm et al., 2001; Bunn et al., 2005; Goetz et al., 2005; Raynolds et al., 2008). Deciduous shrubs have been demonstrated to respond to experimental and observed increases in summer temperature at Toolik Lake, Alaska (Chapin et al., 1995; Hobbie & Chapin, 1998; Wahren et al., 2005). It remains nonetheless difficult to confirm the extent of large-scale vegetation changes across the circumpolar Arctic (Callaghan et al., 2005), although there is strong indication from the International Tundra Experiment for warming-related shrub increases well beyond Alaska (Walker et al., 2006). Based on these findings, Verbyla (2008) speculates that the observed increase in annual maximum

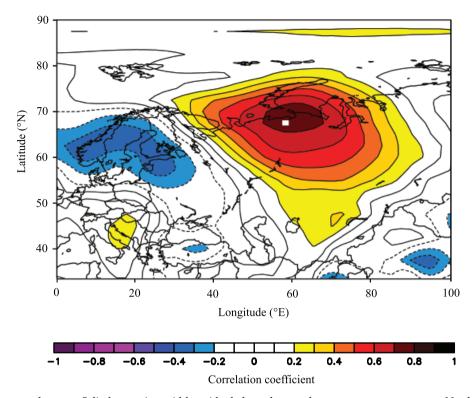


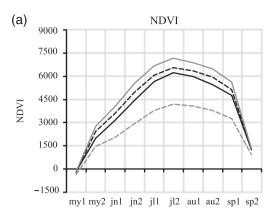
Fig. 5 Correlation map between Salix lanata ring width residual chronology and summer temperature over North-Western Eurasia. Data consists on June to August mean surface temperature from a 2.5° latitude per 2.5° longitude grid, obtained from the NCEP Reanalysis database (http://www.cdc.noaa.gov/, see Materials and methods). Time period is 1948–2005. Location of the Salix lanata chronology is shown as a white filled square. Note the high correlations occurring at long distances, especially towards the southeast into the West Siberian Basin well into the boreal zone.

NDVI in arctic Alaska and adjoining Canada may be due to an increase in height and cover of shrubs and graminoids. Similarly, Raynolds *et al.* (2008) conclude that increases in NDVI are also likely to occur where vegetation physiognomy changes to include larger plant life forms, such as the boundaries between graminoids and erect shrubs. This study presents the first complete chronology from an erect deciduous tundra shrub detailing a response function that relates shrub growth, summer temperature and NDVI.

Our results demonstrate that shrub ring width in an abundant tundra willow with a nearly circumpolar distribution is strongly related to summer temperature for the period 1942–2005. Remarkably high correlations occur at large distances across the tundra and taiga zones of Eastern Europe and the West Siberian Basin, mirroring the large spatial correlation of summer temperatures in this area. Correlations with Summer T are consistently higher than those used for boreal forest temperature reconstructions in Eurasia (e.g. Grudd et al., 2002; Hantemirov & Shiyatov, 2002; Helama et al., 2002), comparable only with a study with the evergreen arctic shrub Empetrum hermaphroditum Lange ex Hagerup in the mountains of central Norway (Bär

et al., 2007). We also found a clear relationship with NDVI for upland vegetation at a regional scale for the period 1981-2005, confirming a parallel greening trend reported for similarly warming portions of arctic North America (Jia et al., 2003; Goetz et al., 2005; Verbyla, 2008). Despite the inherent difficulties in preserving the low-frequency component of a ring width chronology while efficiently removing its age-related trend, the RCS growth curve suggests a significant increase in willow growth over the last six decades, parallel to the summer temperature increase for the region (NASA-GISS, 2009, most visible in the stations located in the upland tundra, and least visible in the coastal areas). These findings are in line with studies that have surmised an increase in the height and cover of erect shrubs as a key component of the reported tundra greening signal detected via NDVI since the early 1980s (Jia et al., 2003; Tape et al., 2006; Walker et al., 2006; Raynolds et al., 2008; Verbyla, 2008). Furthermore, the growth trend agrees with observations by the indigenous Nenets here and on neighboring Yamal Peninsula concerning recent increases in willow height and abundance (Forbes & Stammler, 2009). Their local observations provide an independent source of qualitative knowledge that help





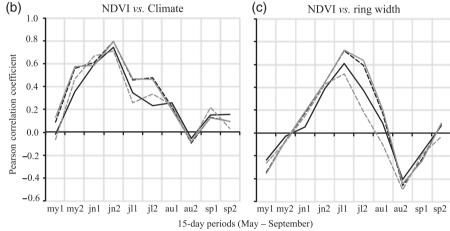


Fig. 6 (a) Average 15-day NDVI values indicating peak total biomass in the second half of July. Note that the highest and lowest overall NDVI values correspond to the Upland and Lowland regions, respectively; (b) relationships between Regional 15-day NDVI and monthly temperature for Naryan Mar meteorological station (as in Fig. 1, obtained from the National Climatic Data Center - NCDC, http://www.ncdc.noaa.gov/oa/ncdc.html, see Materials and methods), indicating peak productivity in the second half of June; (c) correlation between Salix lanata residual ring width chronology and 15-day NDVI values, indicating a peak in the first half of July. Correlations computed from May to September (i.e. growing season) for the common period 1981–2005. NDVI regions: black continuous line, Site; black dashed line, Regional; grey continuous line, Regional-Upland; grey dashed line, Regional-Lowland (see Fig. 1 and materials and data for definition and display of the areas).

to confirm not only the quantitative data, but also their social-ecological relevance since changes in shrub height and phytomass have direct and indirect impacts on their livelihood. For example, herders note that when the tallest shrubs exceed the antler height of standing reindeer, animals can disappear from sight when browsing within thickets and subsequently be lost during migration (Forbes & Stammler, 2009).

Before the present investigation, the most direct evidence for a regional response derived largely from a time series air photo analysis of increasing shrub abundance over a 50-year period on the Alaskan North Slope (Sturm et al., 2001; Tape et al., 2006). That particular study is cited in support of a number of recent remote sensing analyses examining the broader scale relationship between summer warmth, tundra greening and NDVI in North America (Walker et al., 2002; Jia et al., 2003, 2006; Goetz et al., 2005; Raynolds et al., 2006, 2008; Tape et al., 2006). Together these analyses rest on the reasonable assumption that temporal changes to NDVI resulting from climate change might replicate the differences that occur along spatial climate gradients because increased warming is expected to enhance shrub growth (Walker et al., 2002). Satellite-based analyses have found that the amount of shrubs is strongly spatially correlated with NDVI and summer warmth, particularly in acidic tundra, arguably making it a meaningful indicator of aboveground plant biomass at both local and regional scales (Walker et al., 2002; Raynolds et al., 2006, 2008). In support of this, fieldbased work employing hand-held sensors recently determined that shrub phytomass, especially its live foliar

deciduous component, was the major factor controlling NDVI across a variety of northern Alaskan vegetation types (Riedel *et al.*, 2005). Jia *et al.* (2003) likewise reported that 88% of the variance of deciduous shrub foliar biomass was explained with ground-measured NDVI. Our data provide support for extending these interpretations (1) retrospectively and (2) to the western Eurasian Arctic, which until now has lacked ground-level quantification of a steady increase in willow shrub growth to match the region's demonstrated warming trend in recent decades.

We have determined S. lanata L. to be a remarkably high quality proxy for six decades of summer temperature over vast swaths of the tundra and taiga zones of West Siberia and the East European Arctic. The observed higher performance of S. lanata as a summer temperature proxy at a regional scale when compared with other high quality ring-width-based temperature proxies further confirms this. Given the divergence problem, it is important to develop suitable archives for reconstructing climate regimes in remote locations lacking long-term meteorological records, especially in the tundra zone. The lack of precipitation signal in the presented S. lanata chronology suggests that the drought stress-caused temperature decoupling in boreal trees – proposed as one of the main mechanisms for the divergence problem (e.g. D'Arrigo et al., 2008) - does not affect this deciduous tundra shrub, at least in the studied area. The ready preservation of shrub wood in permafrost substrates (Shiyatov & Hantemirov, 2000) and lakes, coupled with the abundant and broad distribution of S. lanata L., makes this species an excellent candidate for extending reliable climate reconstructions much further into the past. Although the sharp growth releases experienced by S. lanata individuals when reaching the canopy within their respective thickets implies potential difficulties in climate signal recovery, these are not insurmountable given a large number of samples and the use of appropriate standardization methods. The strength of the regional relationship we found between shrub growth and NDVI agrees well with a recent circumpolar analysis (Raynolds et al., 2006). Our analysis provides the best proxy assessment to date that deciduous shrub phytomass has increased significantly in response to an ongoing summer warming trend. Furthermore, the results fill an important gap since ground-level data on decadal phytomass trends are otherwise lacking for the Russian Arctic. These findings have relevance for tundra biodiversity, surface hydrology, and feedbacks resulting in atmospheric heating. This is because an increase in shrub abundance lies at the crux of a range of critical regime shifts in the tundra biome including net ecosystem productivity, species loss, snow cover, and energy balance as driven

by albedo (ACIA, 2005; Chapin *et al.*, 2005; Walker *et al.*, 2006; IPCC, 2007). Given the vast expanses of shrub tundra across northern Russia (Walker *et al.*, 2005), and the large geographic range of *S. lanata* L. (Hultén & Fries, 1986), additional chronologies from this species in different landscapes would help to confirm if the trends reported here are circumpolar.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure. S1. Individual ring width measurements (mm) of *Salix lanata* at the study site in Eastern European Arctic. The arithmetic mean of all the individual series is shown as a thick black line to illustrate the overall growth pattern more clearly. Note the characteristic age-related trend, with suppressed growth in the early years followed by a relatively sharp growth increase. The vertical red line marks the year 1942, from which the chronology has enough sample depth to be considered reliable (see *Materials and Methods* and *Results*).

Figure. S2. Thin black line is the average ageing curve resulting from all the *Salix lanata* ring-width cores aligned by age. A 32-year cubic spline function with 50 percent cut-off was fitted to the averaged series (thick black line), representing the *Regional Growth Curve*.

Table S1. Pearson correlation coefficients between the network of northern boreal forest tree-ring width chronologies developed by F. Schweingruber (see Fig. 1, Table 1) and the average temperature for June to August from a network of meteorological stations in northern Russia (see Fig. 1, Table 3). Correlations computed over the common period 1942–1990. Significant coefficients (p < 0.05) are shown in bold. The last line shows ring-width vs. summer T correlations for the S. lanata chronology created in the present study. Note the overall higher coefficients shown by the S. lanata chronology.

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