

Alexander Kirdyanov · Malcolm Hughes
Eugene Vaganov · Fritz Schweingruber · Pavel Silkin

The importance of early summer temperature and date of snow melt for tree growth in the Siberian Subarctic

Received: 5 May 2000 / Accepted: 11 July 2002 / Published online: 24 August 2002
© Springer-Verlag 2002

Abstract Wood material for at least 12 larch trees at six sites [*Larix sibirica* Ldb, *Larix gmelinii* (Rupr.) Rupr, *Larix cajanderi* Mayr] near the northern timberline in Siberia was analyzed to investigate influence of climatic factor changes on tree-ring growth at high latitudes. Tree-ring cell size, maximum latewood density and ring width measured by means of image analysis and X-ray radiodensitometry and calculated latewood cell-wall thickness were used. Correlation analysis of tree-ring structure parameter chronologies with temperatures averaged over periods of 5 days (pentad) shows that early summer temperature (mean for 5–6 pentads, depending on the region, starting from the middle of June) and date of snow melt are the most important factors that define seasonal growth and tree-ring structure. Analysis of instrumental climatic data indicates that a positive trend of early summer temperature was combined with winter precipitation (October–April) increase and this combination leads to later snow melt. Based on the results of tree-ring growth modelling, it was shown that later snow melt (hence, delayed initiation of cambial activity and, as a result, decrease of wood production) explains the changes in the relationship between tree ring width and summer temperature dynamics observed after the 1960s for a large area of the Siberian Subarctic. The understanding of the role of winter precipitation in controlling ring growth, through its effect on the timing of cambial activation, suggests the possibility of using ring structure parameters to create reconstructions of past winter precipitation variations.

Keywords Dendrochronology · Tree-ring growth · Tree-ring structure · Early summer temperature · Snow cover

Introduction

Temperature is the most important limiting factor for all growth processes of trees at high latitudes (Shiyatov 1986; Jacoby and D'Arrigo 1989; D'Arrigo et al. 1992; Briffa et al. 1995, 1998a, 1998b; Vaganov et al. 1996). Seasonal course of temperature has a very strong effect on seasonal kinetics of tree-ring formation and tracheid production (Kandelaki and Dem'yanov 1982; Vaganov et al. 1994, 1996). Creber and Chaloner (1984) indicated that growth initiation timing in boreal and temperate climates is defined to a great extent by temperature. Data on physiology of cambium activity indicate that, in conditions where temperature strongly limits tree radial growth, temperature must be higher than some threshold and the thawing of the soil upper layer after snow melt must have begun so that radial growth can commence (Kandelaki 1979; Tranquillini 1979; Schweingruber 1996). It strongly influences duration of wood production season at high latitudes because the new cell production usually ceases there by the middle of August (Mikola 1962). Thus, according to Leikola (1969), 0.5°C deviation in mean April–May temperature caused significant shifts in the starting dates of cambial activity.

Most of researches pointed out the positive influence of temperature on tree-ring growth for the region where temperature is the leading limiting environmental factor: at high latitudes tree-ring width variations correlate well with average summer temperature (June–August) and maximum latewood density show the significant connection to mean temperature of a longer interval (May–September) (D'Arrigo et al. 1992; Briffa 1992; Briffa et al. 1998a, 1998b). Vaganov (1996) found the significant increase of tracheid diameter in earlywood of larch tree rings near the northern timberline associated with the long-term summer temperature increase. On the other

A. Kirdyanov (✉) · E. Vaganov · P. Silkin
V.N.Sukachev Institute of Forest SB RAS, Akademgorodok,
Krasnoyarsk, 660036, Russia
e-mail: institute@forest.akadem.ru
Tel.: +7-3912-433686, Fax: +7-3912-433686

M. Hughes
Laboratory of Tree-Ring Research, University of Arizona, Tucson,
AZ 85721, USA

F. Schweingruber
Swiss Federal Institute for Forest, Snow and Landscape Research,
Zuricherstrasse 111, 8903 Birmensdorf, Switzerland

Table 1 The main statistical characteristics of tree-ring width (TRW), cell size, cell-wall thickness and maximum latewood density chronologies

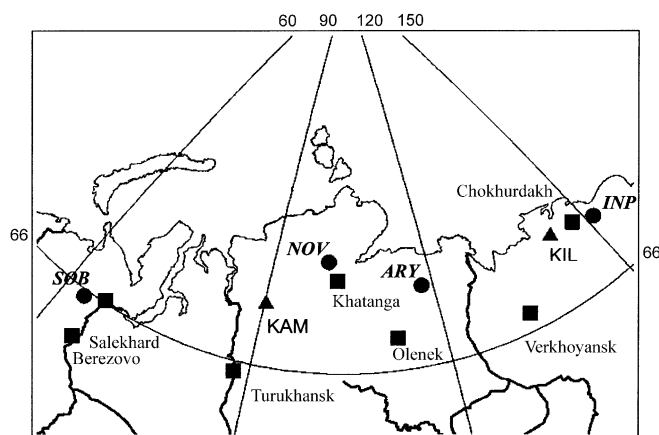
Site	Tree-ring parameter	No. of trees measured	Period	Mean \pm SD	Coefficient of		
					variation	sensitivity	autocorrelation of the first order
SOB	TRW indices	19	1563–1992	1.00 \pm 0.37	37.0%	0.470	0.08
NOV	TRW indices	14	1500–1990	1.00 \pm 0.41	41.0%	0.510	–0.01
	Size of the first cell	5	1890–1990	38.7 \pm 3.29 μ m	8.5%	0.089	0.20
	Size of the fourth cell	5	1890–1990	42.5 \pm 4.31 μ m	10.1%	0.088	0.43
	Size of the 12th cell	5	1890–1990	17.8 \pm 2.70 μ m	15.2%	0.132	0.42
KAM	Cell-wall thickness		1890–1990	3.8 \pm 0.81 μ m	21.3%	0.224	0.25
	Maximum density (*100)	12	1574–1990	75.4 \pm 9.85 g/cm ³	13.1%	0.146	0.04
	TRW indices	12	1545–1990	1.00 \pm 0.39	39.0%	0.490	–0.02
ARY	TRW indices	25	1600–1990	1.00 \pm 0.35	35.0%	0.420	0.11
INP	TRW indices	25	1325–1994	1.00 \pm 0.34	34.0%	0.410	0.04
	Size of the first cell	5	1890–1994	43.9 \pm 2.64 μ m	6.0%	0.060	0.19
	Size of the fourth cell	5	1890–1994	45.6 \pm 3.06 μ m	6.7%	0.063	0.29
	Size of the 12th cell	5	1890–1994	16.4 \pm 2.58 μ m	15.7%	0.147	0.28
KIL	Cell-wall thickness		1890–1990	3.5 \pm 0.67 μ m	19.1%	0.189	0.27
	Maximum density (*100)	19	1434–1990	74.5 \pm 9.50 g/cm ³	12.8%	0.130	0.15
	TRW indices	55529	1493–1994	1.00 \pm 0.32	32.0%	0.390	0.07

hand, some authors reported the opposite results. Denne (1971), in experiments with Scots pine seedlings, showed that temperature increase from 17.5°C to 27.5°C produced only a 10% increase in tracheid diameter. A negative influence of temperature on tracheid wall thickness in *Pinus sylvestris* L. (Antonova and Stasova 1993) and *Larix sibirica* Ldb. (Antonova and Stasova 1997) is also in contrast to the results of dendroclimatic analysis of latewood maximum density, because maximum density is mainly determined by latewood cell-wall thickness.

To explore the influence of climatic factors on larch tree-ring growth and to find the most important intervals of a year when variability of tree-ring structure is defined by these factors, tree-ring measurements of larch from the northern timberline in the Siberian Subarctic were used in our work. In addition to tree-ring width measurements (Cook and Kairiuktis 1990) data on cell and density structure of tree-rings (Schweingruber 1988; Vaganov 1990) were used to characterize particularities of tree seasonal growth.

Materials and methods

Wood material from six larch sites from the forest-tundra zone of Siberia was analyzed (Fig. 1). Cores were collected from *Larix sibirica* Ldb. (site SOB), *Larix gmelinii* (Rupr.) Rupr. (sites KAM, NOV, ARY) and *Larix cajanderi* Mayr (sites KIL and INP). The choice of these sites was defined by the presence of long records of daily temperature data. For samples from four sites (SOB, NOV, ARY, INP) tree-ring width was measured and dendroclimatic analysis of standardized chronologies was carried out. Individual chronologies were detrended by fitting a cubic smoothing spline with TREND program (Rimer 1991) to eliminate growth trends. In some cases the theoretical curve was edited to reduce the influence of non-climatic factors (mainly forest fires) on tree-ring growth (Vaganov et al. 1996). To remove the effect of autocorrelation, each standardized series was transferred to residual chronology

**Fig. 1** The map of site and meteorological station locations (squares – meteorological stations, circles – tree-ring width sites, triangles – tree-ring width and tree-ring structure sites)

gy through autoregressive (AR) modelling. For two other sites the following chronologies of tree-ring structure parameters were used, in addition to tree-ring width: cell size, maximum latewood density and cell-wall thickness. Maximum latewood density was obtained from density profiles measured by means of densitometry using DENDRO-2003 (Schweingruber 1988). Chronologies of cell-wall thickness variability were calculated according to Vaganov (1996) using maximum density and cell size in latewood chronologies. Cell chronologies were obtained from averaged individual cell files standardized to the same cell number (15) (Vaganov et al. 1985). Standardization of individual cell files was done to compare tree rings with different cell numbers. Cell size chronologies of the first cell in each tree ring (representing the beginning of the growth season), the fourth cell (earlywood formation), and the 12th cell (formation of latewood) were obtained. Local chronologies were calculated by averaging measurements made for individual trees (12–19 trees for tree-ring width, 15–20 trees for maximum latewood density, 5 trees for cell sizes). Chronology statistics are presented in Table 1.

Correlation coefficients of tree-ring width chronologies with temperature of pentads (mean temperature of 5 consecutive days) fixed to calendar dates were calculated. Long instrumental records of daily temperature from the nearest meteorological stations [Berezovo (1936–1990), Khatanga (1936–1989), Olenek (1936–1990), Chokurdakh (1948–1989)] were used.

The seasonal dynamics of temperature vary to a great extent from year to year. For example, the date after which temperature stays consistently above 0°C can differ by up to 25–30 days. Therefore, it is not strictly appropriate to correlate tree-ring parameters with temperatures for pentads whose dates are fixed relative to the calendar. Doing this will result, in some years, in tree-ring data being correlated with the temperature of a period when there is no growth and, for other years, when growth is in an active, or even a very active, phase. It makes more sense to correlate tree-ring structure parameters with pentad temperatures where the dates of the pentad are fixed relative to the date of cambium initiation defined by tree physiology and climatic data. As soil temperature is a very important parameter for tree growth on permafrost soil (Pozdnyakov 1986), an attempt was made to connect the date of the beginning of growth and date of snowmelt.

The date of snowmelt was calculated from temperature and winter precipitation data according to a simple method (Kuzmin 1961):

$$m = b \Sigma T_+ \quad (1)$$

where m is the intensity of snow melt, b is the integral temperature coefficient of snow melt (millimeters of melted water per °C of positive mean daily air temperatures) dependent on latitude, inclination, humidity, wind speed, etc (Kuzmin 1961) and ΣT_+ is the sum of positive mean daily air temperatures. The coefficient b was defined empirically based on instrumental data on snowmelt timing. The dates calculated correlate very well with available observed snow melt data ($n=16$, $R=0.82$, $F=28.8$, $P<0.0001$) and their standard deviation, maximum and minimum values are similar.

In addition to daily data monthly temperature and precipitation from Khatanga, Chokurdakh and monthly data available for a longer period (since the 1880s) from meteorological stations Salekhard, Turukhansk, Verkhoyansk were used. On the basis of these data winter precipitation was calculated as a cumulative precipitation during the period with negative monthly temperature – from October of the previous year until April of the current year.

A simulation model of seasonal tree-ring growth and cell production (Vaganov et al 1990; Fritts et al. 1991; Fritts and Shashkin 1995) was used to calculate tree-ring width variations from daily temperature, precipitation and light data, taking snow melt and soil thawing into account. The model has a specific block devoted to the soil thawing dynamic, so that, for example, it takes into account such possibilities as frequent refreezing and thawing. Tree-ring width changes simulated on the base of climatic data were compared with the chronologies measured.

Results

Correlation of pentad temperature data with tree-ring width chronologies shows (Fig. 2) that the most important interval of growth season when temperature influences cell production is quite short: 4 pentads (17 June–6 July) with significant correlation for the western site (SOB), 5 pentads (17 June–11 July) – for the sites NOV and ARY, 7 pentads (7 June–11 July) – for the site INP. This interval is essentially the period of early season temperature increase. Mean temperature (averaged over several years) of the first pentad which shows significant positive correlation with tree-ring width decrease from the west to the east: 10°C for the western site, 6–7°C for

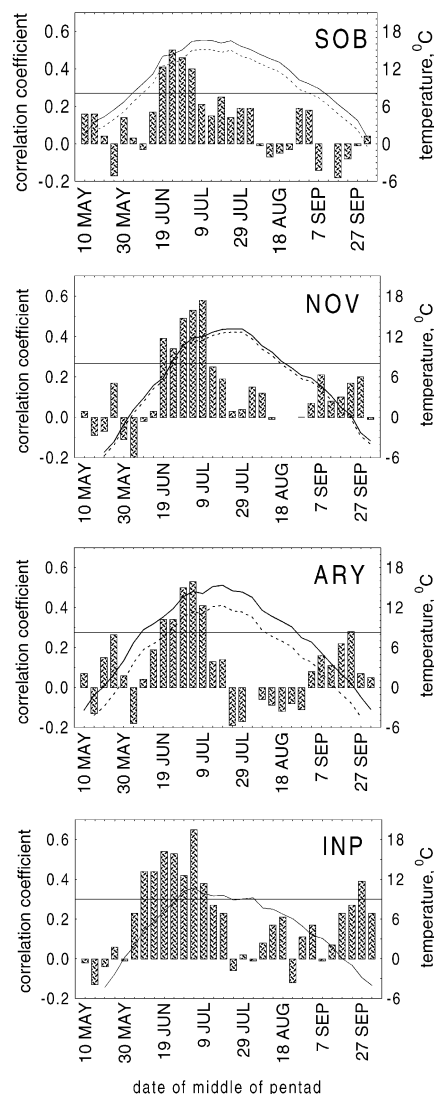
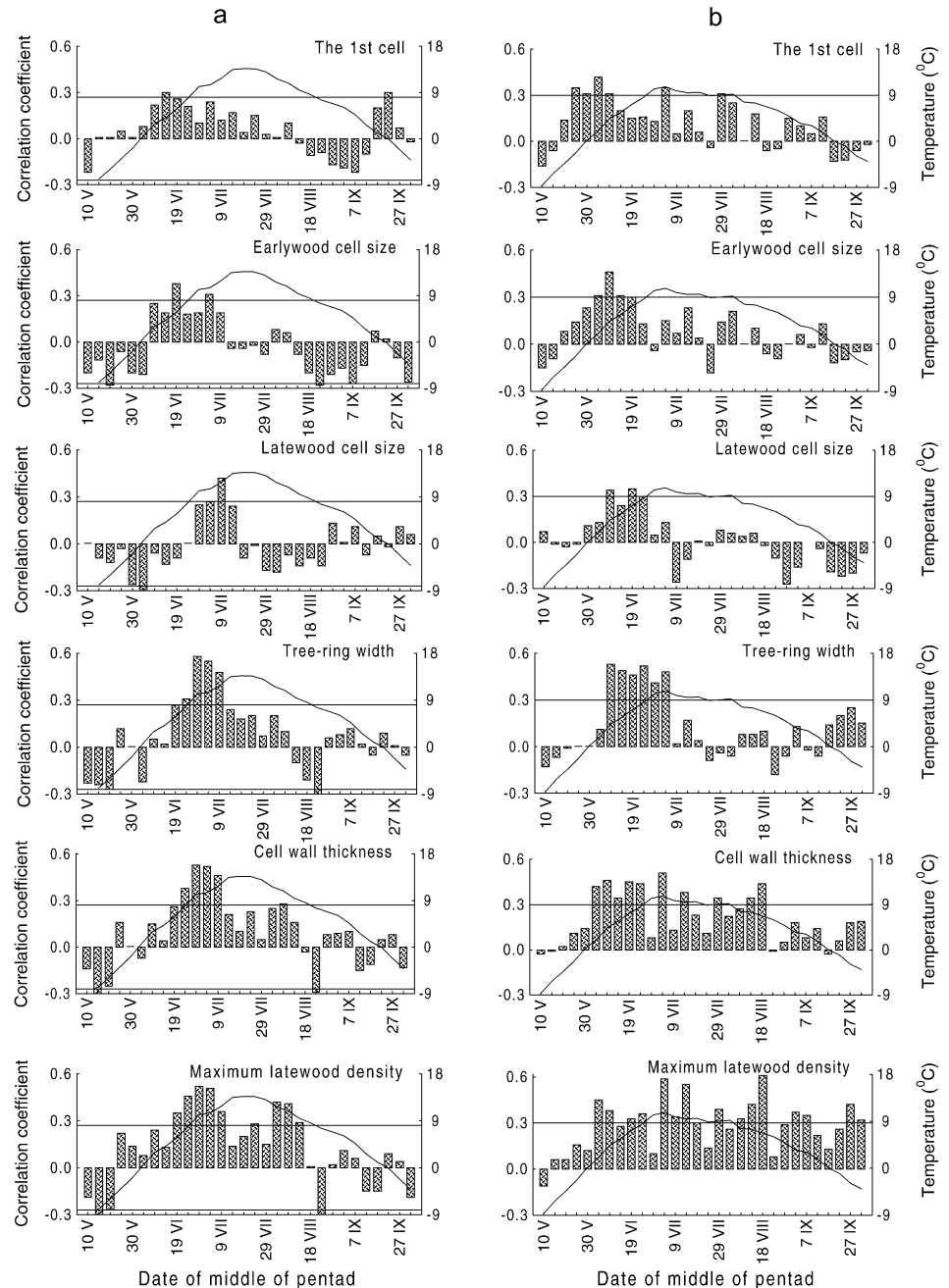


Fig. 2 Correlation between temperature of pentads and tree-ring width indices for four sites near the northern timberline. Values above the horizontal solid line are statistically significant ($P<0.05$). Solid line – Mean of temperature data from meteorological station close to ring width site: SOB (Berezovo), NOV (Khatanga), ARY (Olenek), INP (Chokurdakh), dotted line – temperature corrected to the site

the sites in the middle of the latitudinal transect, 4°C for the eastern site. The periods of the season with significant correlation between tree-ring width and temperature are much shorter than the period with temperature higher than 5°C, increasing from 21% at the western site through 35% at the middle sites to 50% at the eastern site.

The size of the first cell in the tree ring correlates significantly with temperature in one pentad (12–16 June) for the Taymir site (KAM) and with four pentads (22 May–11 June) for the Indigirka river site (KIL) (Fig. 3). The most important intervals for earlywood cells shift to the later dates (17–21 June and 2–21 June for the two sites respectively). The highest correlations with late-

Fig. 3 Correlation between temperature of pentads and parameters of tree rings for the Taymir (a) and the Indigirka river (b) sites (KAM and KIL, respectively). Values above the horizontal solid line are statistically significant ($P < 0.05$). Line – Mean temperature [1936–1989 for Khatanga (a), and 1948–1989 for Chokurdakh (b)]

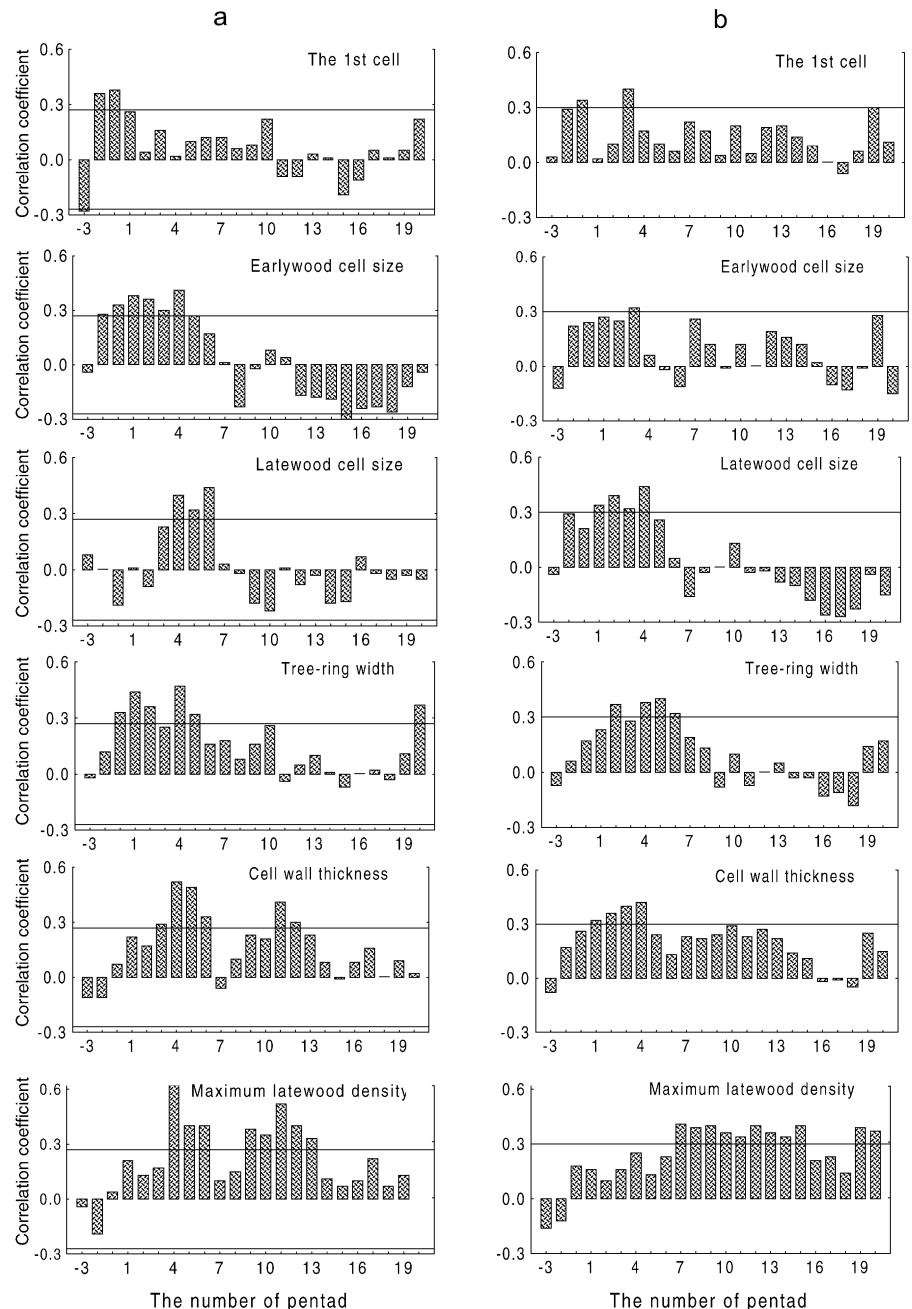


wood cell sizes are later still (7–11 July, 7–26 June respectively). Pentads when latewood cell-wall thickness shows significant correlation with temperature are the same as for tree-ring width (cell production) at the Taymir site. For the Indigirka river site, latewood cell-wall thickness correlates with almost all the period with temperature $> 0^{\circ}\text{C}$. The period when temperature influences maximum latewood density is longer, for example, 4 June–2 October for the Indigirka river site.

Results of correlation between tree-ring structure parameters and temperature of pentads where the dates of the pentads being fixed relative to the date of snow melt rather than to the calendar are presented on Fig. 4. The

size of the first cell is significantly correlated with the temperature of two pentads before the date of snowmelt. The size of earlywood cells correlates with the temperatures of several pentads just after snowmelt and the size of latewood cells with temperature of pentads after snow melt, obviously during the period when these cells are being produced. The correlation of temperature with cell-wall thickness and maximum latewood density changed when pentad dates were fixed relative to snow melt rather than the calendar. These two tree-ring structure parameters are dependent primarily on temperature in the second half of the season. The variability of tree-ring width is explained by the temperature of pentads

Fig. 4 Correlation between temperature of pentads calculated according to the date of snow melt and tree-ring structure parameters (the Taymir site (a), the Indigirka river site (b)). Values above the *horizontal solid line* are statistically significant ($P < 0.05$)



immediately after snow melting (the first part of the growth season).

Comparison of correlation between tree-ring parameters and pentad temperature with fixed dates and dates adjusted to the date of snow melt shows that early summer temperature and the date of snow melt are the main climatic factors that define seasonal growth and tree-ring structure of conifers near the northern timberline. Multiple regression models of tree-ring width indices calculated with early summer temperature (mean temperature of the period with significant correlation between tree-ring width and pentad temperature (Fig. 3): 17 June–11 July for Taymir and 7 June–6 July for Indigirka regions) and

snow-melt date as independent variables show strong agreement with instrumental data (Table 2). Comparison of the mean ring widths formed at the years with very early and very late snowmelt confirms the influence of snowmelt date on tree-ring width (Fig. 4, Table 3). These data indicate that tree-ring width indices are higher in years with earlier snow melting.

We examined the dynamics of early summer temperature, calculated dates of snow melting and winter precipitation, which influences snow melt date, for meteorological stations in the regions investigated and in others located at a short distance to south which had longer records (Fig. 5). Early summer temperature has a clear

Table 2 Parameters of multiple regression model of TRW indices with early summer temperature and the date of snow melting as independent variables. *T* Taymir region (Khatanga), *I* Indigirka region (Chokurdakh)

Region	Coefficients of regression model		<i>R</i>	<i>R</i> ²	<i>F</i>	<i>P</i> <
	Temperature	Date of snow melting				
T	0.089	0.009	0.71	0.504	20.3	0.00001
I	0.121	0.014	0.73	0.539	22.8	0.00001

Table 3 Tree-ring width indices for years with early and late snow melting. *T* Taymir region (Khatanga), *I* Indigirka region (Chokurdakh)

Region	Early snow melting			Late snow melting		
	Number	Mean	SD of years	Number	Mean	SD of years
T	12	1.25	±0.19	10	0.88	±0.25
I	9	1.06	±0.28	9	0.92	±0.22

Table 4 Parameters of trends of early summer temperature, winter precipitation (October–April) and dates of snow melting. *S* Region of Salekhard, *T* region of Taymir, *I* region of the Indigirka river

Region	Temperature trend (°C per 10 years)		Precipitation trend (mm per 10 years)		Date of snow melting trend (days per 10 years)	
	Trend during the (Period)	Trend during 1981–1990	Trend during the (Period)	Trend during 1981–1990	Trend during the (Period)	Trend during 1981–1990
S	+0.15° (1883–1992)	+0.13°	+11.4 mm (1892–1986)	–36.3 mm	+3.7 days (1936–1989)	+14.1 days
T	+0.25° (1933–1995)	–0.70°	+22.6 mm (1933–1990)	+22.2 mm	+2.6 days (1936–1989)	–0.3 days
I	+0.03° (1945–1991)	+0.14°	+3.9 mm (1961–1991)	+18.0 mm	+1.4 days (1948–1989)	–3.3 days

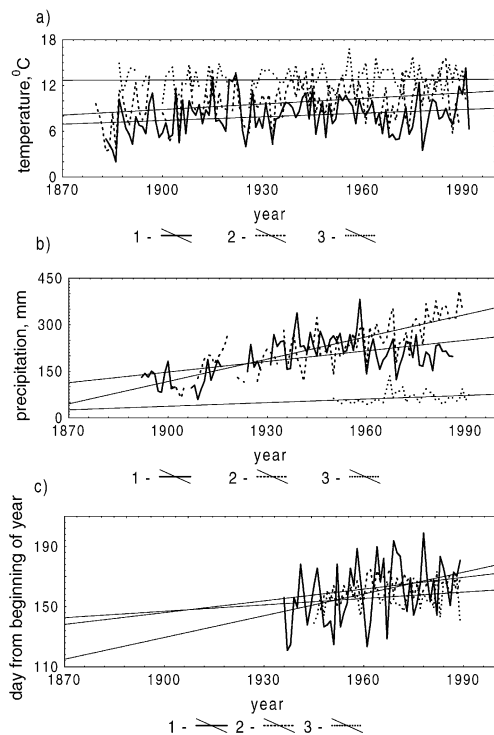


Fig. 5 Variability of early summer temperature (a), winter precipitation (b) and calculated dates of snow melting (c) for meteorological stations at Salekhard (1), Turukhansk (2) and Verkhoyansk (3). In each case, a straight line shows the trend over the period of record

positive trend during the last century. Winter precipitation also shows a positive trend. In calculated dates of snow melt, these two processes with different directions (temperature accelerates growth, winter precipitation shifts the start of cambium activity to later dates) lead to later activation of tree growth season. Further, the higher values of winter precipitation the higher their influence: in the wet western and middle regions of the Siberian Subarctic, the shift of snow-melt dates will be larger than in the drier eastern regions (Table 4). Trends defined for the short run of instrumental data at the meteorological stations closest to the tree sites and for all the data differ significantly. For example, for sites from middle and eastern Siberia there is a tendency for earlier snow melt during the 1981–1990 period. But for the longer period of observation there is a positive trend of snow melt dates (later seasonal growth).

To show the importance of date of snow melt and early summer temperature for tree-ring growth the spatial dynamic of long-term average winter precipitation and rate of late spring–early summer temperature increase (difference of the average temperature of June and May) was considered for the northern Siberia region (Fig. 6). Monthly temperature and precipitation data for 18 meteorological stations located along the nine longitudinal transects (near the northern timberline and 200 km southwards) from longitude 70°E to longitude 165°E in the Subarctic region (Vaganov et al. 1996) were used to show the dynamic. It is obvious the increase of the rate

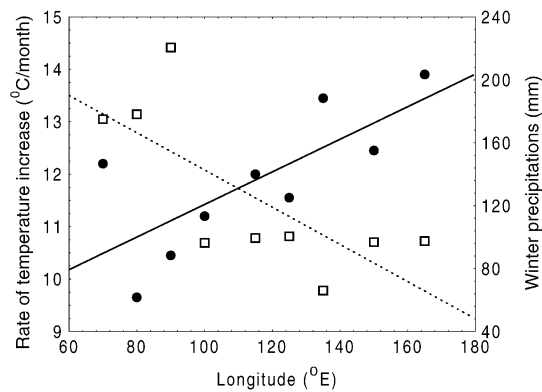


Fig. 6 Spatial dynamic of long-term average winter precipitation (rectangle) and rate of late spring – early summer temperature increase (difference of the average temperature of June and May) (circles) in the northern Siberia region. Straight lines shows the trends of considered temperature (solid line) and precipitation (dotted line) observed in the direction from the west to the east

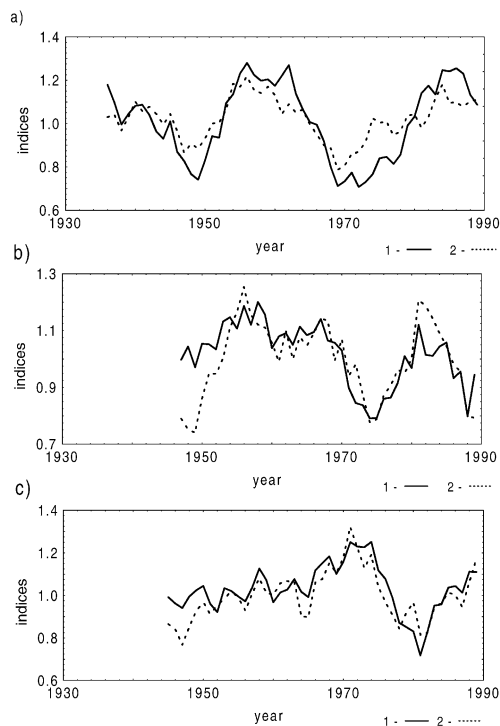


Fig. 7 Tree-ring width index dynamics at sites SOB (a), NOV (b), INP (c). Solid line – Measured data, dotted line – simulation by tree-ring growth model. Data are smoothed by 5-year averaging

of late spring–early summer temperature change and decrease of the mean winter precipitation from the west to the east. Such tendencies lead to a faster snowmelt and, consequently, to cambium initiation at lower temperatures to the east.

As a further demonstration of the combined roles of the timing of cambial initiation [linked to date of snow melt and hence winter precipitation (Groisman et al. 1994a)] and early summer temperature in controlling tree-ring width in the Subarctic, we use a simulation

model of seasonal tree-ring growth and cell production. Chronologies generated for three sites using this model are very similar to those collected and measured (SOB, NOV and INP) (Fig. 7). Correlations between smoothed modelled and observed chronologies are 0.86 (1936–1989), 0.84 (1947–1989), and 0.71 (1945–1989), respectively from the west to the east. It is important that these relationships do not deteriorate after the 1960s.

Discussion

The results show that summer temperature is one of the most important external factors that define tree-ring growth at the northern tree line. It is obvious the positive influence of temperature on tracheid production, their dimensions, latewood cell-wall thickness and maximum latewood density. Whilst cell sizes and tree-ring width depend on temperature of the first part of the season, cell-wall thickness and maximum density are mainly defined by temperature of that interval of the season when the processes of cell-wall formation and maturation take place. This is consistent with knowledge of the physiology of tree-ring and cell-wall growth. Thus, significant correlation of size of the first cell with temperature of 10 days before the date of snowmelt corresponds with data about the stage of cambium initiation (swelling) before production of new xylem cells (Zimmerman and Brown 1971). This stage is connected with the beginning of new needle development and one can often see trees near the northern timberline with new needle development when the soil is still under snow (Shiyatov 1969; Gorchakovskii and Shiyatov 1985). High temperature during the first part of a season also leads to formation of a wider cambial zone and consequently to higher cell production through the season (wider tree rings) (Bannan 1955; Wilson 1964; Gregory and Wilson 1968; Vaganov et al. 1985).

Significant correlation of maximum latewood density, defined by latewood cell sizes and latewood cell-wall thickness, as well with early summer temperature as temperature of some periods in August–September can be explained by the fact that enlargement and wall thickening stages of cell development require several weeks to complete tracheid differentiation (1.5–2.5 months) and seasonal course of temperature is very important for photosynthesis (quantity of substances assimilated during the summer) and, consequently cell-wall thickness. For example, temperature defines cell production and cell size at the stage of division in cambial zone, and for maximum latewood density the temperature of the period when photosynthesis and secondary wall thickening take place is also important.

It is a major aim of dendroclimatic investigations of tree growth in northern (subarctic) latitudes, and near upper timberline in alpine regions, to determine the nature of the connection between tree-ring width variability and temperature, this being the main factor that limits tree

growth. However, our results show that, even here, tree growth response has a markedly “biological” character. Temperature variation is not the only factor which defines tree growth. The date of cambial initiation is another very important climate-linked factor for tree-ring growth. This date is connected with the date of snow-melt, and consequently with winter precipitation. Tree-ring structure parameters (cell size, cell-wall thickness, density) show that both temperature and the date of cambial initiation are very important for tree-ring growth and cell production. In other words, our analysis of tree growth shows results that are consistent with numerous findings on seasonal tree-ring formation (Lobjanidze 1961; Wilson and Howard 1968; Gregory 1971; Skene 1972; Savidge 1993; Larson 1994) if one uses temperature dynamics where the actual date of cambial activation is taken into consideration.

Results indicate that to study the limiting influence of external factors on tree-ring growth it is necessary to estimate exactly the ranges of strong limitation by each of them and to work in these ranges. Thus, Vaganov (1996) showed that if summer temperature varies from 5°C to 14°C then tracheid diameters of larch grown near the northern timberline are significantly affected by temperature. In the regions where temperature is 12–19°C (slightly higher the limiting values) its effect on tracheid diameters diminishes (Vaganov 1996). In Denne’s experiments (1971) the temperature range from 17.5 to 27.5°C was chosen. These temperatures are close to optimum for growth and, as a result, there was no pronounced effect of temperature on tracheid dimensions. It is also important to take into consideration all the environmental factors that can influence tree-ring growth (temperature, water supply, light intensity, etc.). Thus, in the case of Antonova and Stasova’s data (1993, 1997) there was no control of water content in soil during latewood tracheid production and formation. Consequently, a negative effect of temperature on cell-wall thickness could be connected to water loss from soil due to increased evapotranspiration.

In our work use of data on combined influence of two environmental factors (data of snow melting and early summer temperature) helps to explain the observation of Briffa et al. (1998a, 1998b) of divergence in the trends of summer temperature and tree-ring width (and, to a greater extent, maximum latewood density) in high northern latitudes after 1960, so that both the slope of the relationship, and the correlation between the two variables decline. This effect is particularly marked at decadal and longer time scales, and for the northern regions of Siberia, although it is weaker to the east. Several possible causes of the effect have been suggested, including: a possible increase of water stress related to the summer temperature increase (Barber et al 2000; Lloyd and Fastie 2002) or/and an increase of UV radiation having a strong influence on the biomass accumulation of evergreen trees (Tevini 1994; Laasko and Huffunen 1998).

Our results suggest a different cause for this change in the relationships between tree-ring width, maximum

latewood density and summer temperature, namely increasing winter precipitation. It leads to delayed snow-melt; hence delayed initiation of cambial activity, and, as a result, decreasing wood production. Instrumental data confirm the existence of a steady upward trend of annual (and consequently winter) precipitation in the northern regions of Canada and Russia (Findlay et al. 1994; Groisman and Easterling 1994; Groisman et al. 1994b) and increase of snow storage in north Eurasia (Krenke et al. 2001).

Tendency to earlier snow melt (cambium initiation at lower temperature) in eastern Siberia because of lower winter precipitation and faster increase in late spring–early summer temperatures (Fig. 6) can explain the difference in temperature of the first pentad which shows significant positive correlation with tree-ring width obtained for the study sites located in the west, middle and east of Siberia (10°C, 6–7°C and 4°C respectively) (Fig. 2).

The results have a number of implications for the study of both natural and anthropogenic variability in the Subarctic. The understanding of the role of winter precipitation in controlling ring growth, through its effect on the timing of cambial activation, suggests the possibility of using ring width and the size of the first cell formed each year to create reconstructions of past winter precipitation variations. It also permits an improvement of the biological basis of summer temperature reconstructions. Similarly, our results lead to a testable working hypothesis to explain the earlier and increased spring greening of the boreal forest seen in remotely sensed primary productivity for the period 1981–1990 (Myneni et al. 1997). This in turn has important implications for the study of the global carbon cycle, and the changes it may undergo in a changing climate. In particular, possible future changes in winter precipitation should be taken into account, as well as changing growth season temperatures, in the development of models and scenarios concerning the role of the forest of the Siberian Subarctic in the carbon cycle.

Acknowledgements This paper was carried out with the financial support of RFFI (grant 00-15-97980), Krasnoyarsk Scientific Foundation – SEC “Yenisey” (grant 1M0007) and RFFI-DFG (grant 98-04-04074).

References

- Antonova GF, Stasova VV (1993) Effects of environmental factors on wood formation in Scots pine stems. *Trees* 7:214–219
- Antonova GF, Stasova VV (1997) Effects of environmental factors on wood formation in larch (*Larix sibirica* Ldb.) stems. *Trees* 11:462–468
- Bannan MW (1955) The vascular cambium and radial growth in *Thuja occidentalis* L. *Can J Bot* 33:113–138
- Barber VA, Juday GP, Finney BP (2000) Reduced growth of Alaskan white spruce in the twentieth century from temperature-induced drought stress. *Nature* 405:668–673
- Briffa KR (1992) Increasing productivity of ‘natural growth’ conifers in Europe over the last century. In: Bartholin TS, Berglund BE, Eckstein D, Schweingruber FH (eds) *Proceeding of the*

- International Dendrochronological Symposium on Tree Ring and Environment, LUNDQUA Rep 34:64–71
- Briffa KR, Jones PD, Schweingruber FH, Shiyatov SG, Cook ER (1995) Unusual twentieth-century summer warmth in a 1,000-year temperature record from Siberia. *Nature* 376:156–159
- Briffa KR, Schweingruber FH, Jones PD, Osborn TJ, Harris IC, Shiyatov SG, Vaganov EA, Grudd H (1998a) Trees tell of past climates: but are they speaking less clearly today? *PhilosTrans R Soc London B* 353:65–73
- Briffa KR, Schweingruber FH, Jones PD, Osborn TJ, Shiyatov SG, Vaganov EA (1998b) Reduced sensitivity of recent tree-growth to temperature at high northern latitudes. *Nature* 391:678–682
- Cook ER, Kairiukstis LA (eds) (1990) *Methods of Dendrochronology. Application in Environmental Sciences*. Kluwer, Dordrecht
- Creber GT, Chaloner WG (1984) Influence of environmental factors on wood structure of living and fossil trees. *Bot Rev* 50:357–448
- D'Arrigo RD, Jacoby GC, Free RM (1992) Tree-ring width and maximum latewood density at the North American tree line: parameters of climatic change. *Can J For Res* 22:1290–1296
- Denne MP (1971) Temperature and tracheid development in *Pinus sylvestris* seedlings. *J Exp Bot* 22:362–370
- Findlay BF, Gullett DW, Malone L, Reyecraft J, Skinner WR, Vincent L, Whitewood R (1994) Canadian national and regional standardized annual precipitation departures. In: Boden TA, Kaiser DP, Sepanski RJ, Stoss FW (eds) *Trends '93: a compendium of data on global change*. ORNL/CDIAC-65. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, Oak Ridge, Tenn. USA, pp 800–828
- Fritts HC, Shashkin AV (1995) Modeling tree-ring structure as related to temperature, precipitation, and day length. In: Lewis TE (ed) *Tree rings as indicators of ecosystem health*. CRC, New York, pp 17–58
- Fritts HC, Vaganov EA, Sviderskaya IV, Shashkin AV (1991) Climatic variation and tree-ring structure in conifers: a statistical simulative model of tree-ring width, number of cells, cell wall-thickness and wood density. *Clim Res* 1:37–54
- Gorchakovskii PL, Shiyatov SG (1985) *Phyto-indication of environmental conditions and nature processes in high altitudes* (in Russian). Nauka, Moscow
- Gregory RA (1971) Cambial activity in Alaskan white spruce. *Am J Bot* 58:160–171
- Gregory RA, Wilson BF (1968) A comparison of cambial activity of white spruce in Alaska and New England. *Can J Bot* 46:733–734
- Groisman PY, Easterling DR (1994) Area-averaged precipitation over the contiguous United States, Alaska, and Canada. In: Boden TA, Kaiser DP, Sepanski RJ, Stoss FW (eds) *Trends '93: a compendium of data on global change*. ORNL/CDIAC-65. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, Oak Ridge, Tenn. USA, pp 786–798
- Groisman PY, Karl TR, Kight RW (1994a) Observed impact of snow cover on the heat balance and the rise of continental spring temperatures. *Science* 263:19
- Groisman PY, Kopteva VV, Belokrylova TA, Karl TR (1994b) Area-averaged precipitation over the main part of the former USSR. In: Boden TA, Kaiser DP, Sepanski RJ, Stoss FW (eds) *Trends '93: a compendium of data on global change*. ORNL/CDIAC-65. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, Oak Ridge, Tenn. USA, pp 906–910
- Jacoby GC, D'Arrigo RD (1989) Reconstructed Northern Hemisphere annual temperature since 1671 based on high-latitude tree-ring data from North America. *Clim Change* 14:39–49
- Kandelaki AA (1979) Larch wood formation on Taymir. (in Russian) *Lesovedenie* 6:64–69
- Kandelaki AA, Demyanov VA (1982) Dynamics of tree ring formation of trees in Putoran mountains. (in Russian) *Lesovedenie* 5:46–49
- Krenke AN, Kitaev LM, Turkov DV (2001) Climate role of changes in snow cover during the warming period (in Russian). *Izvestiya RAN* 4:44–51
- Kuzmin PP (1961) Snow melting process (in Russian). *Gidrometeoizdat*, Leningrad
- Laasko K, Hufnunen S (1998) Effects of ultraviolet-B radiation (UV-B) on conifers. *Environ Pollut* 99:313–328
- Larson PR (1994) *The vascular cambium. Development and structure*. Springer, Berlin Heidelberg New York
- Leikola M (1969) The influence of environmental factors on the diameter growth of young trees. *Acta For Fenn* 92:1–44
- Lloyd AH, Fastie CL (2002) Spatial and temporal variability in the growth and climate response of treeline trees in Alaska. *Clim Change* 52:481–509
- Lobjanidze EO (1961) Cambium and tree ring formation. (in Russian) AS USSR, Tbilisi
- Mikola P (1962) Temperature and tree growth near the northern timberline. In: Kozłowski TT (ed) *Tree growth*. Ronald, New York, pp 265–287
- Myneni RB, Keeling CD, Tucker CJ, Asrar G, Nemani RR (1997) Increased plant growth in the northern high latitudes from 1981–1991. *Nature* 337:388–392
- Pozdnyakov LK (1986) *Forestry on permafrost soil* (in Russian). Nauka, Novosibirsk
- Rimer T (1991) *TREND. User's guide for personal computers*. Gottingen University Press, Gottingen
- Savidge RA (1993) Formation of annual rings in trees. In: Rensing L (ed) *Oscillations and morphogenesis*. Dekker, New York, pp 343–363
- Schweingruber FH (1988) *Tree ring: basics and applications of dendrochronology*. Reidel, Dordrecht
- Schweingruber FH (1996) *Tree rings and environment*. Dendroecology. Haupt, Berne
- Shiyatov SG (1969) Snow cover on the upper timberline and its influence on woody plants. In: *Papers of Institute of Plant and Animal Ecology* (in Russian). UB AS USSR, Sverdlovsk, pp 141–157
- Shiyatov SG (1986) *Dendrochronology of the Polar timberline in Ural* (in Russian). Nauka, Moscow
- Skene DS (1972) The kinetics of tracheid development in *Tsuga canadensis* Carr and its relation to tree vigour. *Ann Bot* 36:179–187
- Tevini M (1994) Physiological changes in plants related to UV-B radiation: an overview. In: Biggs RH, Joyner MEB (eds) *Stratospheric ozone depletion. UV-B radiation in the biosphere*. Springer, Berlin Heidelberg New York, pp 37–56
- Tranquillini W (1979) *Physiological ecology of the alpine timberline*. Springer, Berlin Heidelberg New York
- Vaganov EA (1990) The tracheidogram method in tree-ring analysis and its application. In: Cook E, Kairiukstis L (eds) *Methods of dendrochronology*. Kluwer, Dordrecht, pp 63–75
- Vaganov EA (1996) Mechanisms and simulation model of tree ring structure developing in conifers (in Russian). *Lesovedenie* 1:3–15
- Vaganov EA, Shashkin AV, Sviderskaya IV, Vysotskaya LG (1985) *Histometric analysis of woody plant growth* (in Russian). Nauka, Novosibirsk
- Vaganov EA, Sviderskaya IV, Kondratyeva EN (1990) Climatic conditions and tree ring structure: simulation model of tracheidogram (in Russian). *Lesovedenie* 2:37–45
- Vaganov EA, Vysotskaya LG, Shashkin AV (1994) Season growth and structure of larch tree rings at the northern timberline (in Russian). *Lesovedenie* 5:3–15
- Vaganov EA, Shiyatov SG, Mazepa VS (1996) *Dendroclimatic investigation in Ural-Siberian Subarctic* (in Russian). Nauka, Novosibirsk
- Wilson BF (1964) A model for cell production by the cambium of conifers. In: Zimmermann MH (ed) *The formation of wood in forest trees*. Academic Press, New York, pp 19–34
- Wilson BF, Howard RA (1968) A computer model for cambial activity. *For Sci* 14:77–90
- Zimmerman MH, Brown CL (1971) *Trees: structure and function*. Springer, Berlin Heidelberg New York