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Effect of Summer Monthly Temperatures on Light Tree Ring Formation in Three Larch Species (*Larix*) in the Northern Forest–Tundra of Siberia

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Abstract—Studies in the northern forest–tundra of Siberia have been performed to estimate temperature conditions in individual months of the growing season that have an effect on the formation of light tree rings in three larch species: *Larix sibirica, L. gmelinii,* and *L. cajanderi.* The threshold air temperatures for light ring formation have been determined and found to be similar in all the species. Differences in temperature response are conditioned mainly by the longitudinal climate gradient rather than by species-specific features.

Keywords: Siberian forest–tundra, larch, light tree rings, temperature

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Air temperature is the main limiting factor for tree growth at high latitudes of Siberia, which controls the processes of carbon cycle in plants: its photosynthetic assimilation, deposition in plant tissues, and release by respiration. There are threshold temperatures that initiate different phenophases in conifers, including tree ring formation [1–4], and optimal environmental conditions for different phases of radial tree-ring growth, which may be specific for each conifer species.

Conifer trees growing at the northern tree line occasionally produce tree rings with poorly developed, relatively light-colored latewood, which are referred to as light rings (LRs) [5]. The latewood zone in such rings contains a reduced number of mature tracheids [6, 7] or consists of tracheids with large lumens and thin cell walls [7–9], with both types of LRs occurring in the same conifer species [7]. Their formation is explained by the fact that, at high latitudes, a relatively cold summer (or part of it) and/or a relatively short growing season often lead to incomplete development and maturation of tracheids [8–11].

Mork's index [12] commonly used to distinguish between earlywood and latewood tracheids based on the wall-to-lumen ratio is inapplicable to LRs, and the terms "latewood zone" and "latewood tracheids" can be used only conditionally in this case. In general, LRs are characterized by a low wood density and poor lignification of tracheid walls because of a reduced rate of carbon assimilation and deposition.

The frequency of LRs in conifers growing at the northern tree line is fairly high, and their formation is explained by the effect of climatic factors, primarily temperature [13, 14]. In larch growing in the southern forest–tundra and northern taiga of Western Siberia, LRs are formed in years with May and June temperatures below the long-term average by 2.2°C and August temperature, by 2°C [11]. However, no such information is available for the northern forest–tundra of Western, Central, and Eastern Siberia.

The purpose of this study was to evaluate temperature conditions at which LRs are formed in different larch species growing at the northern tree line in the Siberian Subarctic.

STUDY REGION, MATERIAL, AND METHODS

Climatic conditions. The study region is located in the subarctic forest–tundra of Siberia (66°–72° N, 66°–167° E), where the main climate-forming factors are irregularity of solar radiation input during the year, heterogeneity of substrate in the cold and warm seasons, and the pattern of atmospheric circulation. The duration of insolation at the onset of the growing season reaches 24 hours a day. The albedo of the substrate surface varies from a maximum of ~90% in winter to a minimum of ~10% at the onset of the growing season, when the surface becomes heterogeneous. Climate continentality increases in the west–east direction.

The climate in the north of Western Siberia is conditioned by both warm air masses from the Atlantic and cold arctic air masses penetrating deep into the continent. The influence of the Atlantic sector of the Arctic, manifested in relatively high precipitation, extends eastward up to the Kotui River (101° E). The

Table 1. Characteristics of weather stations

No.	Station	Latitude N	Longitude E	Elevation a.s.l., m	Observation period, years
1	Salekhard	66.53°	66.53°	15	1882–2017
2	Dudinka	69.40°	86.17°	16	1906–2017
3	Volochanka	70.97°	94.50°	37	1936–2017
4	Kyusyur	70.68°	127.4°	36	1912–2017
5	Yubileynaya	70.75°	136.22°	25	1935–2017
6	Srendekolymsk	67.45°	153.69°	20	1887–2017

thermal regime east of this river and in the north of Eastern Siberia depends not so much on atmospheric circulation as on solar radiation input, and climate is characterized by high snow evaporation in the period until daily average temperature transition through 0°C and low annual precipitation.

The growing season is no longer than 2.5 months, precipitation falls mainly during the warm season (up to 50% of the annual amount in July to August). Sporadic frosts may occur throughout the growing season. Soils are gley and gley-podzol, permafrost is widespread; the depth of its seasonal thawing decreases from 3 m in the west to 1.5 m in the east of Siberian Subarctic. The depth of soil thawing in July, under the canopy of close and sparse larch forests, varies from 15 to 75 cm, and the monthly average soil temperature at a depth of 20 cm in July does not exceed 4.0–8.0°C [15–17].

Weather stations. Meteorological data for the study were obtained from six weather stations (Salekhard, Dudinka, Volochanka, Kyusyur, Yubileynaya, and Srendekolymsk) located at low elevations a.s.l. (not in the mountains) along the northern tree line of conifers, which formed a 4000-km meridional transect covering the western and eastern distribution limits of different larch species (Table 1, Fig. 1). Records of monthly average and daily average temperatures over the period of May to September from each station were analyzed to determine the onset and end dates of the growing season by two criteria: stable transition of daily average temperature through 5°C and through 8°C [18]. Since stations 1 and 6 were located 100 km south of sampling areas, the corresponding temperature values were recalculated based on Climate Explorer, CRUTEM 4.1 grid data [19].

Sample collection and processing. The main tree species growing at the northern tree-line in high latitudes of Siberia are Siberian larch (*L. sibirica* Ledeb.), Dahurian larch (*L. gmelinii* (Rupr.) Rupr.), and Cajander larch (*L. cajanderi* Mayr). From each of these species, 12–25 cores were taken at breast height (1.3 m) in six study sites located at 300 to 1100 km from each other, forming a meridional transect in the northern forest–tundra (Table 2). Sampling was carried out in two habitats, one in the east and the other in the west of the species range [20]. To exclude the influence of interspecific hybridization at the range boundaries, the eastern *L. sibirica* sites and the western *L. gmelinii* sites were located at distances of 100 and 200 km from the boundary between their ranges, with *L. gmelinii* range being separated from *L. cajanderi* range by the Verkhoyansk Ridge. Soil moisture regime in all study sites is normal; permafrost is present, but the soil thaws in summer to a depth of no less than 60–80 cm.

The surface of cores was thoroughly smoothed out in the laboratory, and they were cross-dated using TSAP [21] and COFECHA software [22] to determine

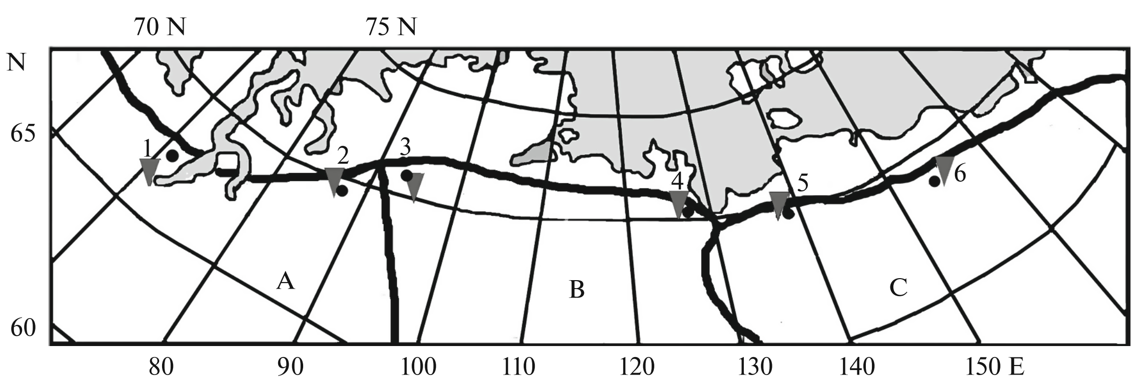

Fig. 1. Schematic map of sampling area: (▾) weather stations, (●) sampling sites. Bold line shows boundaries of the ranges of three larch species (A, B, C).

Table 2. Characteristics of study sites (L.s., *Larix sibirica*; L.g., *L. gmelinii*; L.c., *L. cajanderi*)

No.	Latitude N	Longitude E	Elevation a.s.l., m	Species	Starting year	Chronology length, years	Number of cores
1	67°33′	67°32′	35	L.s.	1890	120	25
2	69°23′	86°13′	20	L.s	1925	85	21
3	71°20′	93°50′	70	L.g.	1540	451	24
4	71°06′	127°17′	70	L.g.	1425	567	15
5	70°15′	138°10′	80	L.c.	1301	691	12
6	69°17′	154°46′	50	L.c.	1412	580	14

the exact years of LR formation. The length of the common chronologies varied from 85 to 690 years, averaging 450 years, but only the period covered by meteorological observations and available larch wood samples (1936–1990) was considered in further analysis.

The proportion of LRs relative to the total number of rings per sample in each year was calculated for each study site, and chronologies of LR frequency were constructed on this basis. Our analysis was then limited to the years when LRs were formed in more than one sample.

The data on monthly average temperatures from six weather stations were processed by one-way ANOVA to evaluate differences in these temperatures between the groups of years with and without LRs in different larch species and reveal correlation between LR chronologies and monthly average temperature.

RESULTS

Climatic conditions of the growing season according to data from weather stations. Two out of six stations forming the meridional transect—Salekhard and Srendekolymsk—are located no farther than 150 km from the Arctic Circle, while the others are 300–400 km north of it. The average June temperature is 8.2°C in Salekhard and 11.3°C in Srendekolymsk. It gradually rises along the transect, since climate continentality increases from the west to the east, but shows an abrupt increase in the region of Srendekolymsk. The average July temperature decreases in the west–east direction, slightly rising in Srendekolymsk due to southern location of this station. The average August temperature barely changes along the transect but shows the same trend (Fig. 2).

The average summer temperature (June–August) is 11.1°C in Salekhard, 11.2°C in Srendekolymsk, and about 9.7°C in the regions of all other stations. Temperatures averaged over the transect are 7.5°C in June, 12.9°C in July, 9.4°C in August, and 10.2°C for the three summer months.

Differences in the onset dates of the growing season were revealed. Daily average temperature transitions through 0, 5°, and 8°C occur earliest at more southern Salekhard and Srendekolymsk stations. The latest transitions are observed at the Dudinka station, even though it is located farther south than the remaining three stations. The onset of the growing season at stations 3 and 5 located in the western part of larch range at 70° N is shifted to later dates, compared to eastern stations 4 and 6 (Fig. 3).

The timing of decrease in daily average temperature to 5° and 8°C varies along the transect. The warm season is the longest at stations located in Western Siberia, especially as concerns temperature transition through the 5°C threshold. Transitions through 5° and 8°C at other stations occur on approximately the same dates, regardless of a more southern or eastern location of a given station.

The total length of the period with temperatures above 5°C is 103 days in Salekhard, 108 days in Srendekolymsk, and 89–90 days in other locations. The main differences in the length of the growing season are conditioned by transition through the threshold temperatures in June.

Monthly average air temperatures over the period of 1936 to 1990 at the Salekhard and Srendekolymsk stations proved to be significantly higher than those in the corresponding study sites located farther north: the June, July, and August temperatures recorded at the Salekhard station are 2.3°, 2.1°, and 1.9°C degrees higher, and those recorded at the Srendekolymsk station are 1.1°, 1.0 °, and 0.7°C higher, respectively.

Light ring chronologies. The number of years when larch trees formed LRs varied from 9 to 27 over the period of 1936 to 1990. The frequency of LR formation along the transect differed depending on climatic periods (Fig. 4).

All the three larch species produced LRs morphologically defined to different extents. In some LRs, the latewood zone (according to its shape and position) consisted of thin-walled tracheids. This zone in such rings accounted for 20–35% of the total ring width, which is characteristic of the normal latewood zone in any of the three species [23]. Rings of a different type had a very narrow zone consisting of completely formed latewood tracheids, which accounted for less than 15% of the total ring width [7] (Fig. 5).

In *L. sibirica*, LRs with a wide latewood zone consisting of thin-walled tracheids occurred most fre-

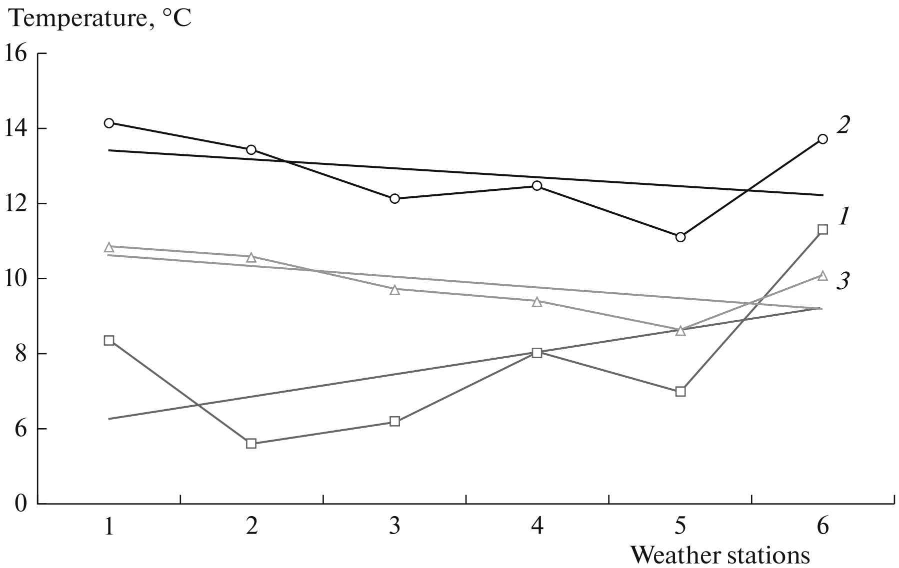

Fig. 2. Dynamics of temperature in (*1*) June, (*2*) July, and (*3*) August at weather stations (numbered as in Table 1).

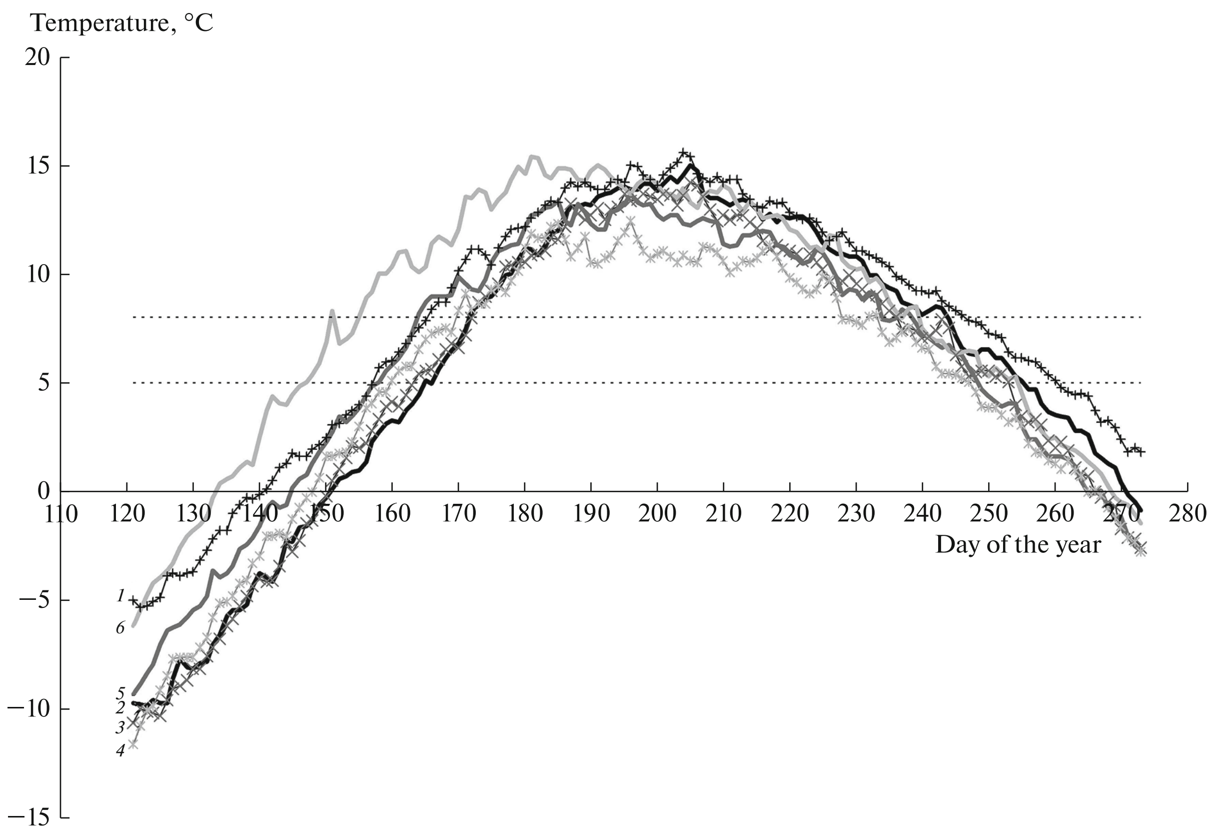

Fig. 3. Dynamics of temperature in May to September (days 121–273 of the year) at weather stations 1–6 (see Table 1). Temperature transitions through 5 and 8°C are indicated by dotted lines.

quently over the above period, with the proportion of years marked by their formation reaching 100% in study site 1 and 93% in study site 2. These proportions in the other two species were lower: in *L. gmelinii*, 60 and 33% in study sites 3 and 4; in *L. cajanderi*, 33 and 18% in study sites 5 and 6. LRs produced in other years has a thin latewood zone with mature tracheids. Moreover, the latewood zone in some LRs was so

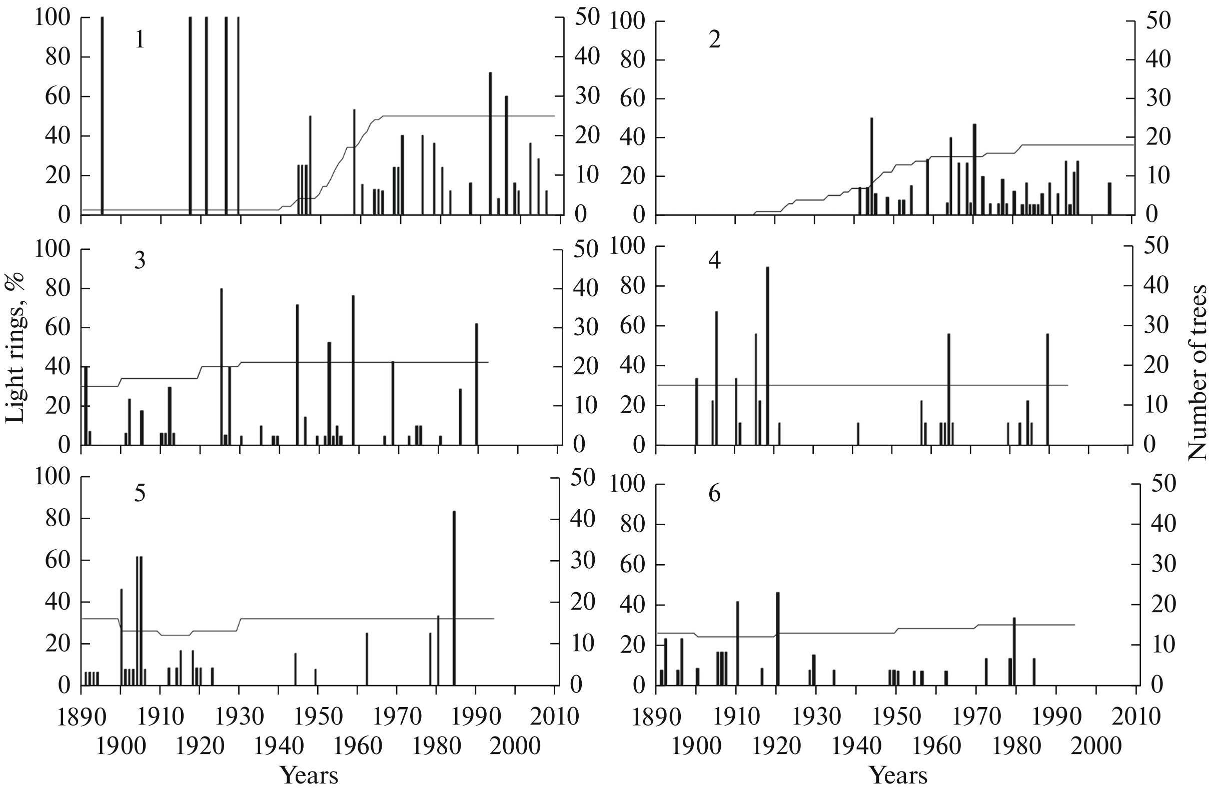

Fig. 4. Light tree ring chronologies. Bars show the proportion of light rings relative to the total number of tree rings in a given year; a line, the number of samples. Sampling sites (1–6) are numbered as in Fig. 1.

indistinct that cross-dating of individual series was necessary for their identification, but they occurred sporadically: in *L. cajanderii* (study site 5) in 1984 and in *L. gmelinii* (study site 3) in 1989 (Central Siberia).

Climatic signal from LRs in different larch species. Correlation analysis revealed relationships between the number of LRs and the average air temperatures of summer months, which proved to have certain species-specific features. In *L. sibirica*, the number of LRs is significantly correlated with the average temperatures of May, August, and, in the western part of the range, of July. *Larix gmelinii* shows such correlations with June and August temperatures at the western boundary of its range and with June and July temperatures at the eastern boundary. Chronologies for *L. cajanderi* show correlation with the June temperature and, at the eastern range boundary, also with the July temperature. Thus, a distinct signal of August temperature was revealed in chronologies from areas lying west of the Putorana Plateau, and that of June temperature, in *L. gmelinii* and *L. cajanderi* growing beyond the plateau (Table 3).

Significant differences were revealed when comparing the mean values of monthly average temperatures and their variances. The formation of LRs in *L. sibirica* occurs at average August temperatures below 9.5°C, with temperatures above 9.7°C providing for the complete formation of latewood. August temperatures in years with and without LRs differ by up to 1.5°C. June is a cold month within *L. sibirica* range, with the monthly average temperature being no higher than 6°C even in years with LRs, while July is relatively warm. June and July temperatures do not differ between years with and without LRs, except for the July temperatures recorded at the Dudinka station (Table 4).

Larix gmelinii produces LRs when June temperatures are below 4°C at the western boundary and below 6°C at the eastern boundary of its range, with the average July temperature being no higher than 11°C. The influence of August temperatures is ambiguous: temperatures below 7.7°C in the western part of the range promote LR formation, while temperatures below 8.6°C in the eastern part have no such effect.

Larix cajanderi produces LRs at June temperatures below 7.3°C at the eastern boundary of its range. Temperatures recorded at its western boundary in years with LRs are still lower (about 5°C), but the processes of LR formation probably begin when temperature decreases below 7.3°C. July and August temperatures do not differ between years with and without LRs.

Irrespective of larch species, the difference between June temperatures in years with and without LRs decreases from the west to the east; the difference

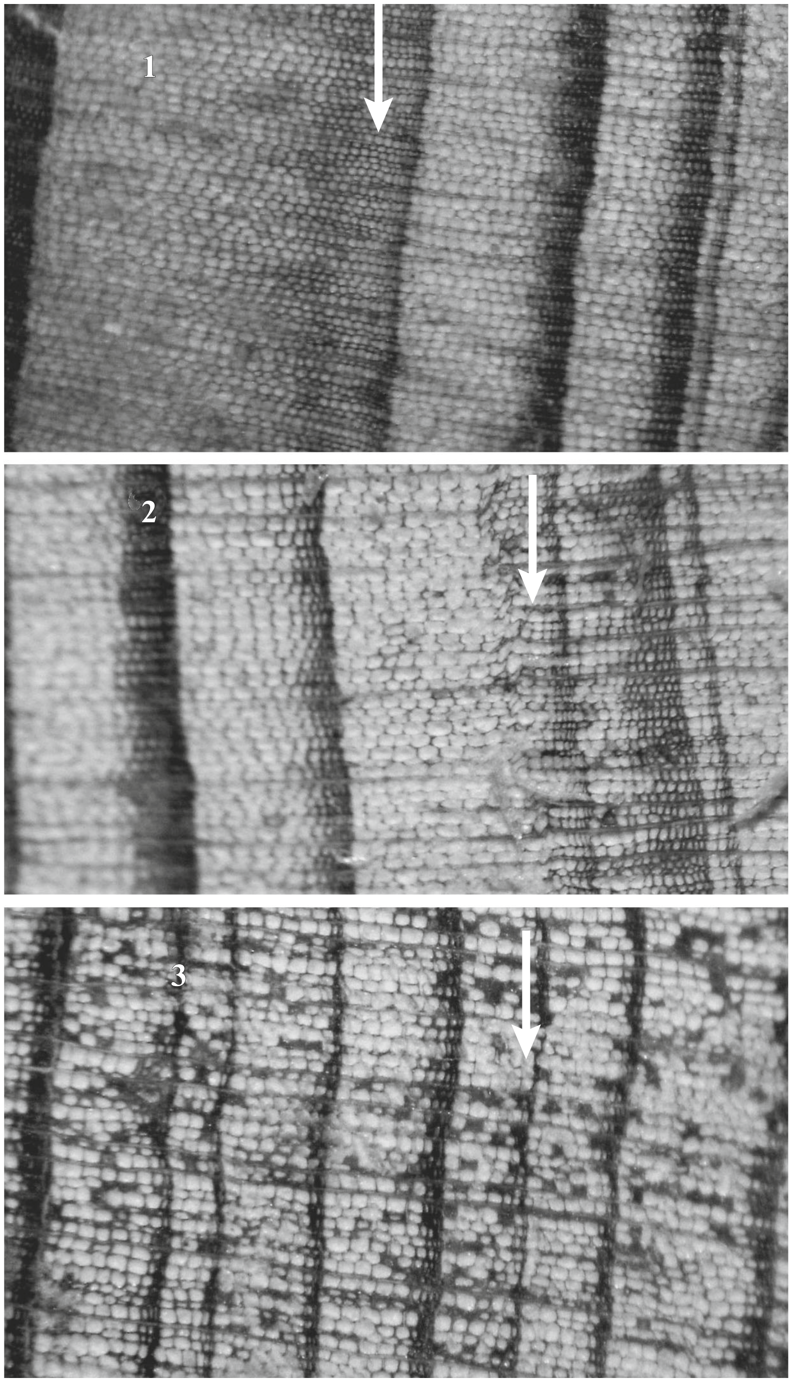

Fig. 5. Light tree rings in (1) *Larix sibirica,* (2) *L. gmelinii,* and (3) *L. cajanderi.* The light ring latewood is indicated by an arrow. Magnification 32×.

between July temperatures remans at the same level; and that between August temperatures decreases.

DISCUSSION

Internal factors having an effect on the formation of tracheids play an important role when plants grow under optimal or suboptimal conditions, whereas their formation under extreme climatic conditions of the Siberian Subarctic strongly depends on environmental factors, primarily ambient temperature.

Latewood is most sensitive to climatic changes, and this is reflected in anatomical parameters of tree rings [1–3, 24]. Light rings represent extreme variants of latewood formation where mature tracheids are formed in a smaller amount than is normal for a given

Table 3. Correlation between the proportion of light rings and monthly average air temperature

Study site no.	Oct_p	Nov_p	Dec_p	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept
1	–0.05	–0.09	–0.15	0.12	0.00	–0.25	–0.12	**–0.32**	–0.17	**–0.26**	**–0.34**	–0.15
2	0.21	0.17	0.02	0.09	0.14	0.02	–0.17	**–0.26**	–0.23	–0.10	**–0.29**	0.21
3	0.03	–0.22	–0.08	0.11	0.03	0.04	–0.05	0.05	**–0.31**	–0.23	**–0.43**	–0.21
4	–0.19	0.05	0.13	0.03	0.21	0.12	–0.08	0.06	**–0.30**	**–0.30**	–0.18	–0.16
5	–0.12	0.01	–0.03	0.21	–0.12	–0.10	0.01	0.10	**–0.29**	–0.20	–0.12	**–0.29**
6	–0.08	–0.13	–0.14	0.14	–0.04	0.02	0.02	–0.08	**–0.28**	**–0.33**	–0.25	–0.10

Correlation coefficients significant at $p < 0.05$ are boldfaced; significant coefficients for June, July, and August are on gray background. Lowercase index (p) indicates months of previous year.

Table 4. Differences in summer monthly average temperatures between years with and without LR. A tilde (~) indicates values calculated from grid data.

Study site no.	June				July				August			
	Temperature, °C			*p-level*	Temperature, °C			*p-level*	Temperature, °C			*p-level*
	without LR	with LR	difference		without LR	with LR	difference		without LR	with LR	difference	
1	~6.2 ± 2.1	~5.4 ± 2.6	0.8	–	~12.2 ± 1.9	~12.3 ± 1.3	0.1	–	~9.7 ± 2.6	~8.5 ± 2.5	1.2	*
2	6.0 ± 7.5	4.6 ± 8.2	1.4	–	14.1 ± 4.2	12.7 ± 1.7	1.4	*	10.7 ± 2.4	9.5 ± 3.2	1.2	*
3	5.8 ± 2.8	3.8 ± 2.3	2.0	*	12.9 ± 2.1	11.2 ± 2.3	1.6	*	9.4 ± 1.8	7.7 ± 1.7	1.6	*
4	8.1 ± 3.1	6.0 ± 3.1	2.1	***	12.4 ± 1.6	11.5 ± 2.3	0.9	–	9.3 ± 3.1	8.6 ± 1.5	0.7	–
5	6.9 ± 1.5	5.2 ± 1.9	1.7	**	10.8 ± 1.6	9.9 ± 2.2	0.8	–	8.0 ± 1.5	7.9 ± 2.0	0.1	–
6	~10.1 ± 4.1	~7.3 ± 2.2	2.6	***	~13.0 ± 4.2	~11.4 ± 3.7	1.6	*	~9.0 ± 3.5	~8.2 ± 0.9	0.6	–

Significance level (*p-level*): $*p < 0.05$, $**p < 0.01$, $***p < 0.001$; (–) not significant.

species or the latewood zone consists of thin-walled tracheids. Both structural variants of LRs can be found in the three larch species even in the same year, but differences in the frequency of their formation are observed. Since LRs of both types ubiquitously occur in larch species, these differences depend mainly on climatic conditions in the study region rather than on species-specific features.

The growth and differentiation of tracheids in larch species follow the same pattern. When temperatures at the onset of the growing season reach the threshold level, the cambial cells start dividing and produce xylem mother cells, which immediately enter the extension growth phase to form immature tracheids. This phase is confined to the first half of the growing season. Cambial activity slows down in July because of rise in temperature [1, 3]; the processes of cell extension also slow down or cease under the influence of external factors (low or very high temperature, insufficient or excessive moisture leading to physiological drought); as a result, cells are formed whose shape resembles that of latewood cells, which subsequently mature into latewood tracheids [25]. They reach maturity as a result of deposition of secondary cell wall components, and these processes can be limited by both climatic factors and availability of substrate (H_2O, CO_2).

Most LRs in *L. sibirica* have a wide latewood zone with thin-walled tracheids. This is evidence that tracheids have undergone all phases of growth and cell differentiation before the processes of carbon storage, secondary cell wall formation, and maturation have ceased under the effect of low temperature at the end of the growing season. This is explained by a relatively long warm period at the end of the growing season in Western Siberia, compared to that in Central and Eastern Siberia. The average air temperature in June in Western Siberia remains below the threshold leading to the initiation of cambial activity (8°C). Therefore, no correlation of LR formation with this temperature has been revealed, and its decrease by 0.8–1.5°C does not influence the processes of late tracheid maturation. It is known that July temperature influences tree ring width [26], but it has no significant effect on LR formation, since no substantial differences in this temperature between years with and without LRs have been revealed. A decrease in August temperature by 1°C (provided that the 9.5°C threshold has been reached) leads to retardation of cell wall maturation and production of LRs in *L. sibirica*.

Light rings in *L. gmelinii* contain signals from all summer months, which is explained by the diversity of environmental conditions in Central Siberia. The western part of *L. gmelinii* range (western and northwestern slopes of the Putorana Plateau) is exposed to Atlantic air masses, and the pattern of atmospheric circulation is similar to that in Western Siberia, with a relatively cold June and a relatively warm August [16]. As a result, LRs with thin-walled latewood are mainly formed, but there also may be LRs where the latewood zone is very thin or even absent. In the eastern part of the range, which lies beyond the Anabar Plateau and is characterized by a sharply continental climate, temperatures in June (rather than in July) have an effect on annual tree increment [26] and anatomical structure of tree rings. Temperatures in August become so low that their effect on the deposition of secondary cell walls becomes statistically insignificant, although it has been noted that the monthly average air temperature in years with LR formation is generally lower than its long-term average values for years when structurally complete tree rings have been formed.

There is multiple evidence that LR formation mainly depends on temperatures at the end of the growing season (August) [8, 9, 14, 27], but it has been found that this process in *L. cajanderi* is significantly influenced by conditions in the first half of the growing season. This is because the main phases of tree ring formation are shifted to June. The farther to the east, the closer the correlation of tree ring width with June temperature and the weaker its correlation with July temperature [26]. The average June temperatures exceed 8°C, and cambial activity is therefore sufficiently high in this month. However, if June is cold, the processes of cell division and extension growth will be retarded, resulting in the formation of a small number of late tracheids, and the latewood zone will be very narrow. Low temperatures in August have no significant effect on secondary cell wall formation, because the main processes of tracheid maturation take place in July. However, the effect of August temperatures on LR formation is not excluded in the southern forest–tundra zone of Eastern Siberia, where the growing season is longer.

In all cases of LR formation considered above, regardless of larch species, July temperatures above 10°C (which account for tree ring width) did not differ statistically between years with and without LRs.

Thermal regulation of processes occurring at the onset of the growing season, namely, needle and shoot growth, may have an indirect influence on the formation of late tracheids (the thickness of their walls) exerted via the carbon storage cycle. It is known that photosynthesis is possible at low and even subzero temperatures, and therefore CO_2 supply is not limited during the growing season, whereas the transport of assimilates, local carbon metabolism, and, consequently, linear shoot growth and young needle growth are largely dependent on temperature [27, 29]. Moreover, LR formation depends not only on monthly average temperature but also on its monthly dynamics, decrease to critical values, and the occurrence of frosts in late spring, summer, and early autumn.

Thus, the growing season includes several periods with threshold temperatures resulting in LR formation. Normal progression of latewood formation and late tracheid maturation in larch, regardless of species, is possible if monthly average temperatures are above 6°C in June and 9.5°C in August. Temperatures below these thresholds lead to reduction in the number of latewood tracheids and the thickness of their cell walls. Biosynthesis of cell wall components in conifers ceases when air temperature decreases to the threshold values, and these values are therefore more important for tracheid maturation than cooling by no less than 1.5–2.5°C

CONCLUSIONS

Light rings in three larch species growing at the northern tree line in the Siberian Subarctic contain temperature signals of the three summer months. The temperature response differs between the species, with the climatic signal in LRs gradually shifting from August to June along the west–east transect.

Larch trees growing in the northern forest–tundra of the Siberian Subarctic produce LRs at temperatures below certain threshold values. Air temperatures influencing the processes of polysaccharide synthesis and deposition and of cell wall formation in late tracheids appear to be similar in different larch species, averaging about 6°C in June and 8–9.5°C in August.

Climatic conditions during the growing season are specific for each larch species, which leads to the formation of different LR types. Their formation in *L. sibirica* occurs under the influence of low August temperature; the same applies to *L. gmelinii* in the western part of its range, while the main role in the eastern part is played by June and July temperatures; and latewood formation in *L. cajanderi* is influenced by June temperatures. These species-specific features of temperature sensitivity in different summer months have been acquired under the effect of differences in environmental conditions determined by geographic and climatic factors in the northern forest–tundra of the Siberian Subarctic.

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COMPLIANCE WITH ETHICAL STANDARDS

The authors declare that they have no conflict of interest. This article does not contain any studies involving animals or human participants performed by any of the authors.

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