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Formation of Two Xylem Frost Injuries in One Annual Ring in Siberian Spruce under Conditions of Western Siberian Forest-Tundra

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Abstract—The phenomenon of the formation of two damaged xylem layers in one frost ring is described in Siberian spruce grown in western Siberian forest-tundra. Temperature conditions providing for the formation of pathological cell and tissue structures are determined. The relationship between the formation of double frost injuries and cold periods is demonstrated.

Key words: tree rings, frost injury of xylem, *Picea obovata*, frosts, western Siberian forest-tundra.

Extreme climatic events during the growing period—late spring and early autumn frosts, when air temperature falls below zero at night and rises above zero in the daytime—have a strong effect on the functioning and stability of ecosystems and the yielding capacity of agricultural crops (Gol'tsberg, 1948). In coniferous species, such temperature drops often lead to injuries in the cambial zone, which is composed of young xylem cells and cambial cells. A typical frost injury within a tree ring includes the following zones (from the center to the periphery of the trunk): (1) thin-walled and crumpled tracheids, (2) a dark layer consisting of strongly compressed dead cells, (3) contorted and swollen (bulb-shaped) radial rays, and (4) larger parenchymal cells and deformed tracheids. The annual rings containing a layer of xylem cells injured and destroyed by frosts are referred to as frost rings (Bailey, 1925; Glock, 1951; Glerum and Farrar, 1966; Lenz, 1967; Nilov and Chertovskoi, 1975; Stöckli and Schweingruber, 1996; Knufinke, 1998; Hantemirov *et al.*, 2000).

Studies on revealing, analyzing, and dating the frost rings are important for determining the threshold values and the range of plant resistance to low temperatures and reconstructing the chronology of extreme temperatures in the past over periods significantly greater than the period of meteorological observations. Published data mostly concern the formation of one frost injury in a tree ring. Stöckli and Schweingruber (1996), Knufinke (1998), and Gurskaya (1999) are the only authors who described the formation of two frost injuries during one growing season in Swiss mountain pine (*Pinus mugo* ssp. *uncinata*) and European larch (*Larix decidua* Mill.) growing in the subalpine belt of the Alps.

We found that the annual rings of Siberian spruce (*Picea obovata* Ledeb.) growing in western Siberian forest-tundra often contain not only single, but also double frost injuries of xylem. In this work, we describe the cases of double frost injuries in Siberian spruce and analyze temperature conditions providing for the formation of such pathological structures.

STUDY REGION, OBJECTS, AND METHODS

Wood samples (crosscuts and cores) were taken from 100 young and medium-aged Siberian spruce trees at heights of 0.2 and 1.0 m; in 18 trees, samples were also taken along the entire length of the trunk at 1-m intervals. The trees grew at three sites located on the left bank of the Ob River, 3–5 km northwest of the city of Labytnangi, at an elevation of 60–80 m a.s.l. In this region, Siberian spruce grows together with Siberian larch (*Larix sibirica* Ledeb.) and birch (*Betula tortuosa* Ledeb.) in shrub-moss-lichen open forests.

Wood samples contained 10–120 annual rings. The date of formation was determined for each ring by the method of cross-dating (Stokes and Smiley, 1968). Frost rings were revealed visually on the carefully smoothed surface of the sample. Microphotographs of tree rings with two layers of injured xylem, formed in 1913 (a) and 1918 (b), are shown in Fig. 1. The relative location of injured xylem layers were determined within the following five zones of a tree ring: *ew0*, the beginning of earlywood; *ew1*, the first half of earlywood; *ew2*, the second half of earlywood; *lw1*, the first half of latewood; and *lw2*, the second half of latewood. In each ring with two frost injuries, the average numbers of tracheid cells before the first injury, between injuries, and after the second injury were calculated in order to determine their relative location within the ring. To determine temperature conditions under which

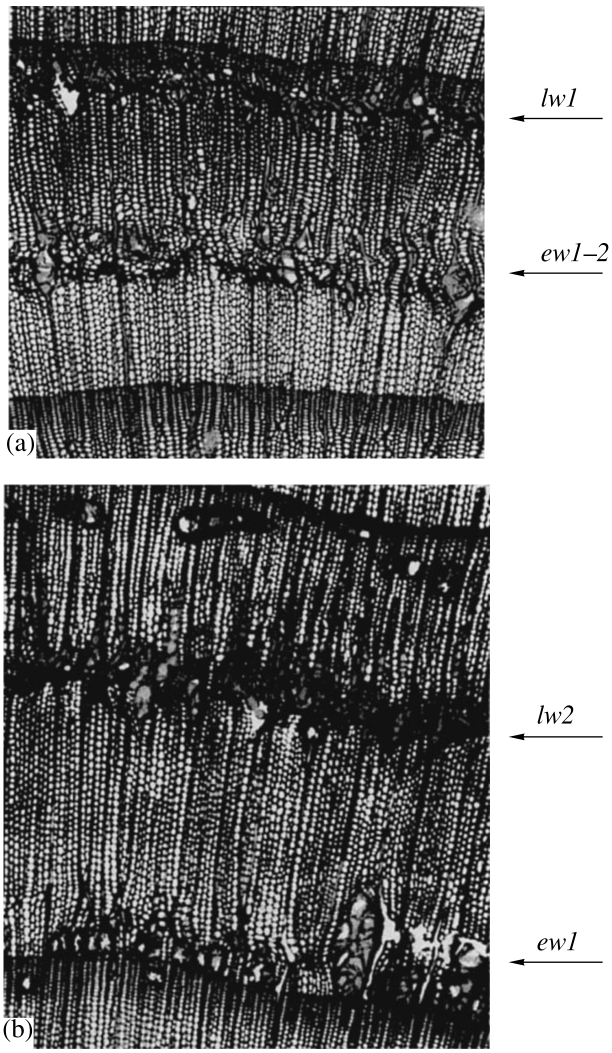

Fig. 1. Photographs of double xylem injuries in frost rings formed in (a) 1913 and (b) 1919: *ew1*, the first half of earlywood; *ew1–2*, the transitional zone between the first and second halves of earlywood; *lw1*, the first half of latewood; *lw2*, the second half of latewood. Magnification 25×.

frost injuries were formed, we used data on the minimum and daily average air temperatures at a height of 2 m between 1883 and 1999, which were obtained at the Salekhard meteorological station situated 15–20 km away from the study area. The dates on which the daily average air temperature rose above and fell below 5°C were taken as the beginning and the end of the growing period, respectively (Orlova, 1962).

RESULTS

Chronology of Double Frost Injuries

Both single and double frost injuries of xylem were found in the annual rings of Siberian spruce wood. Single injuries were more frequent. Over the past 120 years, frost rings appeared in 84 growing seasons, including 73 seasons with single and 11 seasons with both single and double injuries. Double injuries were found in the tree rings formed in 1881, 1882, 1884, 1891, 1893, 1895, 1896, 1913, 1917, 1918, and 1945. It is noteworthy that the frequency of the rings with double injuries between 1881 and 1919 (ten cases) was much higher than that of 1920–1999 (one case). According to meteorological data from the Salekhard station, these periods differed in the temperature conditions of summer months (Fig. 2). The average temperature in June to August was 10.7°C in 1883–1919 and 11.4°C (i.e., 0.7°C higher) in 1920–1999. The difference in air temperature was much greater in June (1.3°C) than in July (0.5°C) and August (0.2°C). As can be seen from Fig. 2, the majority of the rings with double xylem injury were formed in the summer periods with cold and moderate temperatures, except for 1945, when the average temperature in June to August was 1.7°C above the norm. According to dendroclimatic reconstructions (Shiyatov, 1995), the summer periods of 1881 and 1882 were also cold.

Characteristics of Frost Rings and Temperature Conditions

Both single and double frost injuries of xylem were formed only in the undergrowth and young Siberian spruce trees with a trunk diameter and height no greater than 3 cm and 4 m. The cambial zone of such trees quickly cools to the ambient air temperature, because the heat-insulating layer of bark and bast is thin (no more than 2 mm) and the heat capacity of trunks is small. These trees usually have no more than 20–25 annual rings. This is why frost injuries of xylem in older and thicker trees occurred only in the rings located in the central part of the trunk. Moreover, double frost injuries were only found in the lower parts of trunks, at a height of up to 2 m. The undergrowth and young trees usually had no frost rings formed in the same year at the heights of 0.2 and 1 m (i.e., the same frost injuries did not occur at both heights simultaneously). Double injuries at a height of 0.2 m were found in 17 trees; at a height of 1 m, in two trees; and at a height of 2 m, in only one tree.

Below, we characterize frost rings with double injuries of xylem that were formed in the years for which the data of meteorological observations are available and the rings formed in 1881 and 1882, for which such data are absent.

Frost ring 1884 was formed before the beginning of observations at the minimum temperature at the Salekhard station; hence, the dates and severity of frosts were reconstructed on the basis of data on changes in the daily average temperature. Five wood samples contained the ring of this year, and the rings with double injuries were found in two of them. The first layer of damaged xylem was in *ew1*, and the second layer, in *lw2*. The first layer occupied approximately 50–60% of the ring circumference and lacked the zone of dead cells. The second layer contained all the four zones of frost injury and extended over 90–100% of the ring circumference. This is evidence that the first frost was weak, whereas the second was severe. The summer of this year was very cold: the average air temperature in June–August was 7.9°C (Fig. 3), and the daily average temperature rose above 5°C on June 14. After several warm days, when the daily average temperature reached 13°C, there was a relatively long cold spell (June 18–25) with daily temperatures falling to 4°C. Seven radial rows of normal cells were formed before the first injury. The second frost injury in *lw2* was caused by a sharp temperature drop on July 1–4, when the daily average temperature decreased from 16 to 6°C. Fifteen radial rows of normal cells were formed between these injuries, which is evidence for their active division in late June, when air temperature was high. Temperature conditions after the second frost injury were favorable, and this resulted in the formation of three normal cell layers.

Frost ring 1891. Among the six studied rings of this year, double injuries were found in two rings. The first injury was formed in *ew2*, and the second, in *lw2*. Both injuries contained all four zones and occupied 50–60% of the ring in its widest part. The summer of this year was the coldest summer over the period of instrumental observations: the average temperature in June–August was 7.8°C. The beginning of the growing season was characterized by sharp changes in air temperature. The rise of daily average temperature above 5°C occurred three times: on June 11, 15, and 18 (Fig. 3). The minimum daily temperature at a height of 2 m had the lowest value on June 17 (close to 0°C), but this could hardly cause frost injury in *ew2*, because seven radial rows of normal cells were formed before this injury. The first injury was formed in response to a sharp temperature drop on July 5–7, when the minimum temperature at a height of 2 m was 1.6°C. The second injury coincided with the cold spell on July 21–23, when the minimum temperature was 2.8°C. Five radial rows of normal cells were formed between these injuries, and five rows were formed after the second injury.

Frost ring 1893. A double frost injury was found in one out of six samples. The first injury was in *ew2*, and the second, in *lw1*. Both injuries contained all four zones and occupied 50–60% of the ring circumference. The temperature of summer months was close to the norm for the period between 1883 and 1919. The first rise of daily average temperature above 5°C was recorded on June 4. After two relatively warm days, a long cold spell occurred, and the minimum temperature on some days decreased below zero. After the next rise on June 18, air temperature remained high for eight days, and this led to the formation of 20 radial rows of normal cells. The temperature dropped sharply on June 27, when its minimum value was 1.6°C. This cold spell was responsible for the xylem injury in *ew2*. The next cold spell on July 3–5, with a minimum temperature of 3.2°C, resulted in the formation of the second layer of damaged cells in *lw1*. Eleven radial rows of normal cells were formed between the injuries, and seven rows were formed after the second injury.

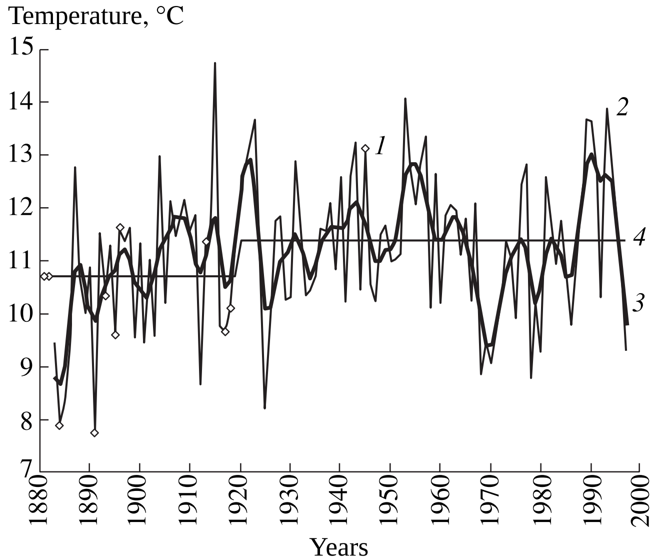

Fig. 2. Variation of average air temperature in June–August at the Salekhard meteorological station between 1883 and 1999: (*1*) the years of formation of double xylem injuries, (*2*) annual average temperature, (*3*) annual average temperature smoothed by means of cubic spline, (*4*) temperature averaged over the periods from 1883 to 1919 and from 1920 to 1999.

Frost ring 1895. The presence of a double frost injury was revealed in five out of eight samples. The first injury was in *ew2*, and the second, in *lw1*. Both injuries contained all four zones of damaged cells and occupied the entire ring circumference. In that year, the average temperature in June–August was 1.1°C lower than the norm. The daily average temperature rose above 5°C on June 8 (see Fig. 3). However, air temperature remained low until June 22: its average values did not exceed 11°C, and the minimum values ranged from 2 to 7°C. However, 14 rows of normal cells were formed in this period. A significant decrease of temperature was observed between June 23 and 28, especially on the last two days, when the minimum temperature at a height of 2 m was only 0.6°C. As a result, a frost injury appeared in *ew2* throughout the ring circumference. Between June 29 and July 8, both average and minimum temperatures were very high (25 and 20.5°C, respectively), and this provided for the formation of 20 normal cell rows after the first injury. This was followed by a cold spell between July 9 and 16, with the daily average and minimum temperatures of 10 and 5.1°C. After three days, the next cold spell occurred during which these temperatures were even lower. These two cold spells resulted in the formation of the layer of injured cells in *lw1*. Thereafter, six radial rows of normal cells were formed.

Frost ring 1896. A double frost injury in the ring of that year was found in one out of eight samples. The

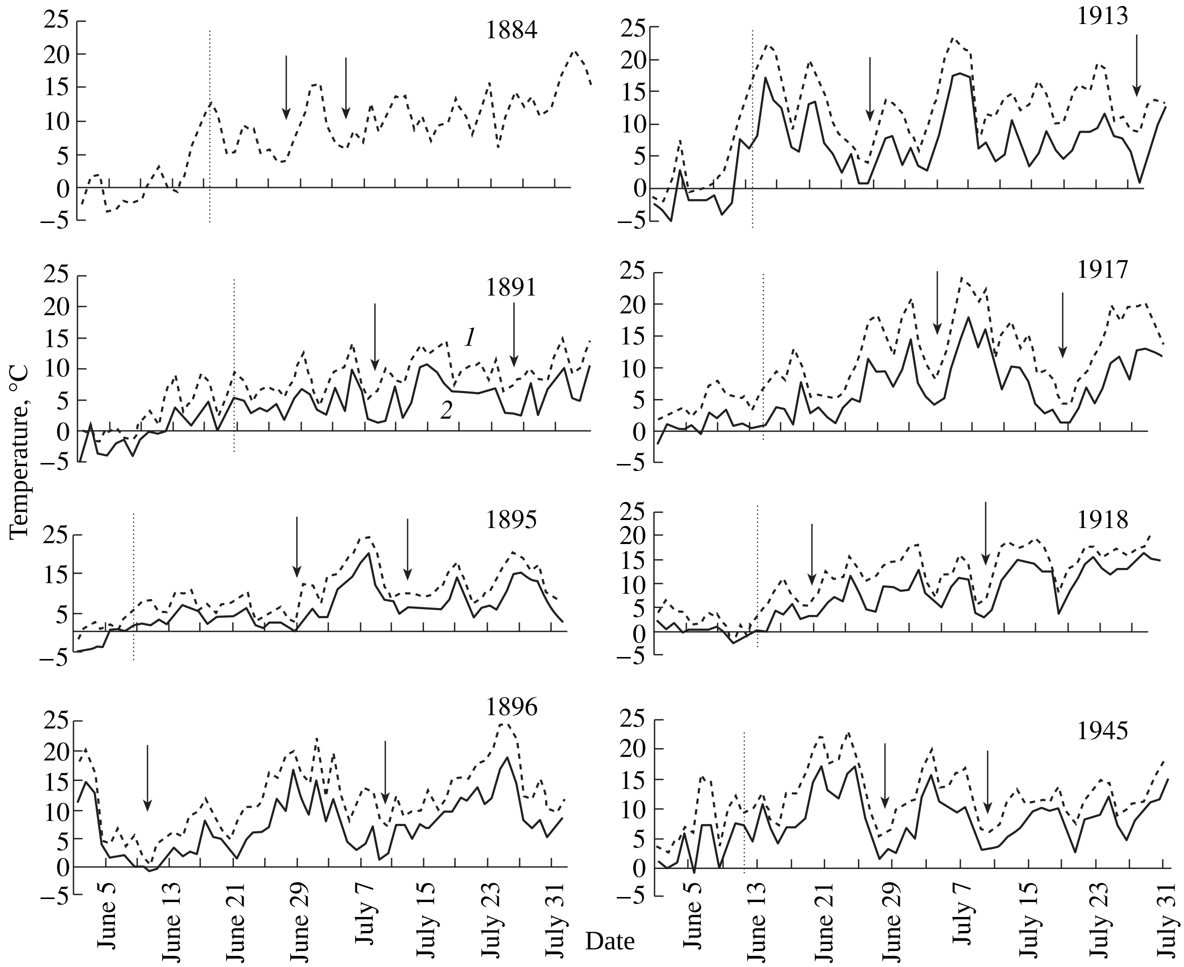

Fig. 3. Variations of daily average (*1*) and minimum (*2*) air temperatures in the years of formation of frost rings with double xylem injuries. Vertical lines show the rise of daily average temperature above 5°C, arrows show frosts responsible for xylem injuries.

first injury was in *ew2*, and the second injury, in *lw2*. The first injury contained four zones of injured cells and occupied the entire ring circumference. The second injury was less severe: dead cells were virtually absent, and only contorted medullar rays and deformed cells occupied 50–60% of the ring in its widest part. The summer period of that year was characterized by an unusually early rise of daily average temperature above 5°C (on May 17) and the alternation of relatively long warm and cold periods (Fig. 3). The temperature in June–August exceeded the norm by 0.9°C. Favorable thermal conditions at the beginning of the growing period provided for active cell division and the resulting formation of 31 normal cell rows. During the first long cold spell (June 4–22), the minimum temperature at the height of 2 m decreased below zero (on June 10). This frost caused the first injury in *ew2* throughout the ring circumference. The following warm period (from June 22 to July 4), in which the daily average and minimum temperatures increased to 21 and 17°C, respectively, was favorable for radial growth and provided for the formation of 20 normal cell rows. The second long cold spell was recorded between July 5 and 14, when the minimum temperature at a height of 2 m decreased to 1.6°C. This caused the formation of the second layer of damaged cells with contorted medullar rays in *lw2*. Temperature conditions in the second half of July were favorable, and nine radial rows of normal cells were formed after the second injury.

Frost ring 1913. Double frost injuries were found in five out of twenty samples. The first injury was at the boundary between *ew1* and *ew2*, and the second injury was in *lw1* (Fig. 1a). Both layers contained all four zones typical of frost injuries and extended throughout the ring circumference. The temperature in June–August was close to the norm (11.3°C) that year. The daily average temperature rose above 5°C on June 10 (Fig. 3). Mid-June was very warm, and 11 radial rows of normal cells were formed before the first injury. The first frost was recorded on June 25–26, when the minimum temperature at a height of 2 m decreased to 0.8°C. As a consequence, a distinct layer of damaged cells appeared, after which 23 rows of normal cells were formed. The second cold spell occurred on July 28–29, when the minimum temperature was 1.4°C. It resulted in the formation of a layer of injured cells in *lw1*. Temperature conditions in the first half of August were favorable, and nine rows of normal cells were formed after the second injury.

Frost ring 1917. A double frost injury was found in one out of fifteen wood samples. Both injuries were in latewood: one in *lw1* and the other in *lw2*. The temperature in June–August was 1°C below the norm. The daily average temperature rose above 5°C on June 10 but remained low (not higher than 13°C) over the next 20 days (Fig. 3). It became much warmer in the beginning of July, but soon (on July 3–4) a cold spell occurred, and the minimum temperature decreased to 4.5°C. As a result, a layer of slightly deformed cells and contorted medullar rays was formed over 50% of the ring circumference. The second damaged layer in *lw2*, with a small number of dead cells distributed throughout the ring circumference, was formed by a severe frost on July 19–20, when the minimum temperature at a height of 2 m decreased to 1.7°C. In the rings of this year, almost all earlywood cells (16 radial rows) appeared before the first injury. Both frosts occurred in July, when the formation of latewood cells began. After the second frost, virtually no normal cells were formed, and the anatomical structure of xylem regenerated in the beginning of the next (1918) growing season.

Frost ring 1918. The presence of a double frost injury was found in two out of fourteen wood samples. The first injury was in *ew1*, and the second, in *lw2*. The temperature in June–August was 10.2°C, i.e., 0.5°C below the norm. The daily average temperature reliably rose above 5°C on June 15. The first cold spell occurred on June 18–20 (the minimum temperature was 2.9°C) and caused a slight injury in *ew1* (deformed cells and strongly contorted medullar rays) over 50% of the ring circumference. Five radial rows of normal cells were formed before the first injury, and 24 rows were formed between the first and second injuries. The next cold spell continued from July 9 to 12: the daily average temperature decreased from 16 to 6°C, and the minimum temperature decreased from 12 to 3.4°C. In addition, another short-term cold spell occurred on July 20–21, when the minimum temperature was 4°C. These two cold spells caused cell damage and death in *lw2* throughout the ring circumference, as the interval between them was only 8 days, too short for the recovery of cambial cells (Fig. 3). The ring of 1918 lacked the typical thick-walled latewood cells and normal cells formed after the second injury. This is evidence that the effect of the double cold spell between July 9 and 21 was so severe that cambial cells were damaged and failed to recover prior to the reliable fall of daily average temperature below 0°C. As a consequence, the cambium continued to produce deformed cells and medullar rays in the beginning of the next growing period (Fig. 1b), although there were no frosts at that time.

Frost ring 1945. The presence of a double frost injury was found in four out of eight wood samples. The first injury was in *ew2*, and the second, in *lw1*. Both layers contained all four zones typical of frost injuries and covered the entire ring circumference. This fact suggests that cold spells were strong and occurred in the middle of the growing period. In that year, the temperature in June–August was 1.7°C above the norm, and the rise of daily average temperature above 5°C occurred in the first ten-day period of June. During the first strong and long cold spell (June 27–30), the minimum temperature at a height of 2 m decreased to 1.9°C (Fig. 3), which resulted in damage to xylem cells in *ew2*. The decrease of the minimum temperature to 3.4°C during the second cold spell (July 9–11) caused a frost injury in *lw1*. The layer of 11 cell rows was formed before the first injury, five rows were formed between injuries, and nine rows of normal cells were formed after the second injury.

Frost ring 1881. The presence of a double frost injury was found in two out of five wood samples. The first injury was in *ew1*, and the second, in *ew2*. Both layers contained all four zones typical of frost injuries and occupied the entire ring circumference. Six radial rows of normal cells were formed before the first injury; seven rows, between injuries; and nine rows, after the second injury. The severity of frosts and the thermal conditions of summer months in that year may be estimated by analyzing frost injuries of xylem and on the basis of dendroclimatic reconstructions. The temperature in June and July was 0.8°C below the norm (Shiyatov, 1995). Both cold spells were severe and occurred in the beginning and the middle of the growing period. The first cold spell continued 3–5 days; the average temperature was probably 4–5°C, and the minimum temperature could have decreased to 1–2°C (as in 1895, when a similar double injury occurred). The frost injury in *ew2* was similar to those in the latewood of rings formed in 1895, 1913, and 1945; i.e., the corresponding severe cold spell in 1881 probably lasted for one or two days between July 5 and 15.

Frost ring 1882. A double frost injury was found in one out of five wood samples. The first layer of damaged cells was formed in the very beginning of the growing season of Siberian spruce (*ew0*). This layer lacked the zone of dead cells, but the zone with strongly contorted medullar rays and deformed cells was distinct. Similar pathologies were found in the annual rings of 1910 and 1953, which had only one frost injury. The second xylem injury in *lw2* was similar to those in the rings of 1917 and 1918 and contained all four zones typical of severe frost injuries. Both injuries were in the widest part of the ring and occupied 80% of its circumference. Only single normal cells appeared before the first injury; most of them were formed between the injuries (23 radial rows), and no such cells were found after the second injury. The summer of 1882 was extremely cold: air temperature in June and July was 2.2°C below the norm (Shiyatov, 1995). The first moderately severe frost was in the beginning of the period of radial tree growth. The minimum temperature decreased below zero for several days, and the frost continued for no less than ten days, as in 1910 and 1953. The second strong frost was in the end of the growing period, between July 10 and 25. It continued for at least two days; the minimum temperature at a height of 2 m was 3–4°C, and the daily average temperature was about 7°C.

DISCUSSION

Under conditions of high latitudes and continental climate, as in western Siberian forest-tundra, cold spells accompanied by frosts occur throughout the growing period (Orlova, 1962). In the study region, frosts are observed not only in late spring and early autumn, but also in summer, so that the period without frosts is reduced in some years to 10–15 days. The key role in the occurrence of frosts belongs to the advection of cold air masses from the Arctic, because of which the daily average air temperature may decrease below zero for several days. In most cases, however, these air masses initially have a low above-zero temperature, and their further cooling in the night and morning hours occurs due to heat loss by radiation. Hence, frosts of the transitional, advective-radiational type prevail in this region.

Special experiments on the effects of subzero temperatures on the seedlings of woody plants (Glerum and Farrar, 1966) showed that typical frost injuries appear in xylem at temperatures from 0 to –8°C. In the study region, most frost injuries in Siberian spruce appeared on the days when the minimum air temperature in the meteorological box (2 m above the ground) was low but above zero (0.6–6°C). Only one injury in the ring of 1986 was formed at subzero temperatures. According to Stöckli and Schweingruber (1996), frost injuries in Swiss mountain pine in the Alps occurred at both subzero and low above-zero temperatures (measured at the nearest meteorological station). Orlova (1962) noted that the continental climate of western Siberia in summer is characterized by distinct temperature gradients in the ground air layer (25–30 cm), which result from heat loss by radiation at night and the flow of cold air to depressions. The difference between temperatures at the ground surface and in the meteorological box reaches 7–10°C, and strong frosts on the ground and grass stand may occur when the temperature in the meteorological box reaches 5°C. Gol'tsberg (1948) reported similar values of temperature inversion during frosts at a height of 2 m and on the ground surface. Moreover, the prevalence of above-zero temperatures in records made at the Salekhard station during frosts is explained by the fact that, until the early 1960s, the meteorological box was located on a cape near the vast expanse of water at the confluence of the Polui and Ob rivers, whereas the sites at which the frost rings were studied were 3–7 km away from the Ob floodplain. All these facts suggest that the xylem injuries described above were indeed caused by exposure to cold.

The question concerning the mechanism of frost ring formation is still open. The most widespread opinion is that frost injuries result from cell sap dehydration combined with cell compression upon water freezing (Glerum and Farrar, 1966). Stöckli and Schweingruber (1996) proposed the hypothesis that the main cause of frost injuries is water stress developing under the effect of simultaneous transpiration and cell sap freezing. Our data show that most frost injuries in Siberian spruce occurred when air temperature sharply decreased from 15–20°C to subzero values. An additional damaging factor in such cases is that the fragile cells of the cambial zone may be mechanically compressed by bark and bast because of a great temperature drop between the surface and inner parts of the trunk (Soraurer, 1922, cited from Glerum and Farrar, 1966). Special experiments showed that similar xylem injuries may occur upon slight mechanical compression of the trunk with micrometric calipers (Glerum and Farrar, 1966).

Double injuries in the same annual ring of Siberian spruce proved to appear in the years when frosts occurred in the early and middle growing season. In most cases, the first and second frosts were in June and July, when the cambial and mother cells were at the stage of active proliferation and daughter cells were at the stage of extension. Frosts in early August were rare, and frosts in the second half of this month had no damaging effect on cambium and fully developed xylem cells. The earliest frost that resulted in the formation of a frost ring occurred on June 10, 1896; the latest frost, on July 28–29, 1913. In 1891 and 1917, both frosts responsible for a double injury occurred in July.

Frosts cause damage to cambial cells, dividing mother cells, and young xylem cells (Glerum and Farrar, 1966). After a hard frost, no less than 10–15 days are necessary for complete regeneration of cambium. Severely damaged cambium may fail to regenerate by the onset of winter and continue producing abnormal cells and tissues in the beginning of the next growing period. This phenomenon manifested itself especially clearly in the rings of 1918 and 1919. In July 1918, two frosts occurred within 8 days (Fig. 3), and the cambial cells failed to regenerate completely by the end of the growing period, since no normally developed cells appeared in the ring after the second frost. The ring of the next year contained deformed tracheids, dilated parenchymal cells, and slightly contorted medullar rays, which continued to form in the early period of tree growth, although no frosts occurred at that time. This is why the boundary between the rings of 1918 and 1919 was indistinct (Fig. 1b).

Thus, double xylem injuries in frost rings of Siberian spruce growing in western Siberian forest-tundra occur with a fairly high frequency (11 cases over the last 120 years). They are the indicators of extreme temperatures in the period of plant growth. The presence of two frost injuries is evidence that the growing seasons in the corresponding years were extremely severe, with the period without frosts lasting for only two to three weeks. The use of xylem injuries as indicators of frosts offers new possibilities in determining the dates and frequencies of frosts over long periods of time. This is important for various micro- and mesoclimatic studies, especially in the mountain regions with sparse meteorological stations located mostly in river valleys.

REFERENCES

Bailey, I.W., The "Spruce Budworm" Biocoenose-1: Frost Rings as Indicators of the Chronology of Specific Biological Events, *Bot. Gaz.*, 1925, vol. 80, pp. 93–101.

Glerum, C. and Farrar, J.L., Frost Ring Formation in the Stem of Some Coniferous Species, *Can. J. Bot.*, 1966, vol. 44, no. 7, pp. 879–886.

Glock, W.S., Cambial Frost Injuries and Multiple Growth Layers at Lubbock, Texas, *Ecology*, 1951, vol. 32, no. 1, pp. 28–36.

Gol'tsberg, I.A., Geographic Distribution of Hazardous Frosts, *Trudy Glavnoi geofizicheskoi observatorii* (Proceedings of the Main Geophysical Observatory), Leningrad: Gidrometeoizdat, 1948, issue 12 (74), pp. 5–52.

Gurskaya, M.A., Frost Rings in Siberian Larch in the Northern Ob Region, *Aktual'nye problemy biologii* (Current Problems in Biology), Syktyvkar, 1999, p. 51.

Hantemirov, S.M., Gorlanova, L.A., and Shiyatov, S.G., Pathological Tree-Ring Structures in Siberian Juniper (*Juniperus sibirica* Burgsd.) and Their Use for Reconstructing of Extreme Climatic Events, *Ekologiya*, 2000, no. 3, pp. 185–192.

Knufinke, A., *Frostringe in Lärchen* (*Larix decidua* Mill.) *und deren Beziehung zu Wetter und Standort*. Dargestellt an Material aus der Waldgrenz-Aufforstung Stillberg: Diplomarbeit an der Universität Bielefeld, Fakultät für Biologie, Davos, Schweiz, 1998.

Lenz, O., Action de la neige et du gel sur les arbres de montagne en particulier sur leur forme et l'anatomie de la tige, *Mitt. Schweiz Anst. forstl. Versuchswesen*, 1967, vol. 43, no. 3, pp. 289–316.

Nilov, V.N. and Chertovskoi, V.G., On the Effects of Frosts on Spruce Undergrowth, *Ekologiya*, 1975, vol. 6, no. 4, pp. 47–52.

Orlova, V.V., *Klimat SSSR: Zapadnaya Sibir'* (Climate of the Soviet Union: West Siberia), Leningrad: Gidrometeoizdat, 1962, part 4.

Shiyatov, S.G., Reconstruction of Climate and the Upper Timberline Dynamics since AD 745 by Tree-Ring Data in the Polar Ural Mountains, *Publication of the Academy of Finland, 6/95*, Painatuskeskus, 1995, pp. 144–147.

Stöckli, V.B. and Schweingruber, F.H., *Tree Rings as Indicators of Ecological Processes: the Influence of Competition, Frost and Water Stress on Tree Growth, Size, and Survival*, Basel, 1996.

Stokes, M.A. and Smiley, T.L., *An Introduction to Tree-Ring Dating*, Chicago: Univ. of Chicago Press, 1968.