

BASE-TO-TIP RADIAL GROWTH AND ANATOMICAL STRUCTURE OF STAG-HEADED LARCH TREES ON PERMAFROST: CAUSES AND EMPIRICAL PRIORITIES

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Abstract

*In the northern larch forests of Siberia growing on permafrost soils the top drying phenomenon is widely spread. Its causes remain unclear. We suggest that an acute water deficiency in continuous climate warming could trigger the process of top drying in larch trees. In order to validate this hypothesis, dendroclimatic and wood anatomy approaches were used. A comparative analysis of the base-to-tip radial growth dynamics and wood anatomical structure in healthy and stag-headed Gmelin larch trees (*Larix gmelinii* (Rupr.) Rupr.), growing in the even-aged forest on the permafrost soil of the north-facing slope (64°19'23" N, 100°13'28" E) was made. The tree ring width, as well as lumen radial size and wall thickness of tracheids were measured at 1/4, 1/2 and 3/4 of the stem height and 20-25 cm below the top, in 15 healthy and 12 stag-headed trees. Decreasing trends of the aforementioned parameters from tree base to top were found in all the trees, which was especially evident in the stag-headed trees. Wood anatomical structure in the upper part of the stag-headed stems underwent modifications over the last 20 years: there occurred tree ring boundaries became indistinct, disturbance of the tracheid rows, thinning of early- and latewood tracheid walls. Using sliding climate correlations with the indexed radial increments it was found that the trees on the north-facing slope could suffer from water deficiency from the end of May until the late June. The presence of both stag-headed and neighboring healthy trees on the north-facing slope can be explained by high variability of soil hydrothermal growth conditions due to very high spatial mosaic moss-lichen cover, common to the north-facing slopes. The trees, growing in these unfavorable local hydrothermal conditions under continuous climate warming could experience an extremely acute water deficiency, leading to top drying out.*

Keywords: north-facing slope, larch forest, stag-headed trees, radial increment, tracheid, lumen radial size, wall thickness, weather factors, water deficiency

1. INTRODUCTION

In connection with the current climate warming, complete or partial shrinkage and death of trees in coniferous forests have become widely spread [1]. Researchers believe this phenomenon to be related to frequent droughts which can result in the dehydration of organs and tissues of trees [2].

In the Siberian north-taiga stands composed of Gmelin larch (*Larix gmelinii* (Rupr.) Rupr.), developing on permafrost, stag-headed trees occur universally. The questions concerning the reasons of top drying, or whether this drying will be followed by the death of the whole tree, as well as some other questions remain without answer. The existence of stag-headed trees can also be due to water deficiency which has become more acute due to the current climate warming.

Stag-headed trees are more frequently found on north-facing slopes under extreme hydrothermal soil conditions. Trees growing on such slopes are suppressed, a lot of them have dry tops, low biometric indicators and rates of growth in height and diameter [3]; they also characterized by low intensity of photosynthesis [4].

Our research was aimed at confirming the hypothesis (using the dendroclimatic technique and xylotomic analysis) that top drying in the northern larch stands growing on permafrost soils on the north-facing slopes occurs due to available water deficiency. Indeed, water moves upward in the stem due to base-to-tip decreasing of water potential along the stem [2], that produces changes in

functioning of cambium and differentiation of its derivatives. Mean water moving rate is imposed by difference between leaf water potential depending on transpiration, and soil water potential. The cambium activity is indirectly influenced by weather conditions through varying of available soil water (through soil water potential). Thus, both of these impacts on cambium are included in the characteristics of tree radial growth at various heights in the stem. They are certain to be reflected in radial growth dynamics and wood anatomical structure of tree rings.

2. MATERIALS AND METHODS

2.1. Materials

Our research was carried out near the field station of the Institute of Forest, SB RAS (Evenkia, the settlement Tura, 64°19' NL, 100°13' EL) in 2009 and 2013. The climate of the region is extremely continental. According to the data of the meteorological station "Tura" (the period of from 1934 to 2009), the average temperature in January was -36.0 °C, in July it was +16.5 °C, and the annual average temperature amounted to -9.0 °C, with the average annual precipitation being 366 mm. The growth season continues 70–80 days. The period without frosts on the soil amounts only as few as 53–56 days, or about 70 % of the whole growth season length. There is snow cover of up to 40–50 cm, which, on average, lasts for 207 days [5].

The study plot was located in a larch forest composed of Gmelin larch (*Larix gmelinii* (Rupr.) Rupr.), (*Ledum* sp., *Vaccinium* sp., lichen and green mossy forest type). The stand formed after the strong ground fire in 1899 (dated by A.A. Knorre [6]) on permafrost soils of the north-facing slope, with the slope being 7–8° (Fig.1). To our evaluation, about 60% of the trees were stag-headed. No evidence of the presence of wood-damaging insects was found during exploration.

The stand density was 4075 trees per hectare, wood stock was 41.7 m³/ha, and yield class was Vb. At the end of July 2009, the stag-headed trees were noticeably smaller than the neighboring healthy trees of the same age: the mean DBH value was by 27% lower (47.4 and 65.2 mm, respectively), while the mean value of their stem height were by 26% lower (7.36 and 8.29 m), and the crown length was by 14.6% smaller (3.79 and 4.44 m) then those of the healthy trees [7].



Fig. 1. The study plot on the slope of the northern exposure. The Gmelin larch forest consisting of healthy and stag-headed trees (A). The map of the study site location (B) near Tura in the Central Evenkia

The soil was homogeneous cryohydromorphic cryozems [8] of middle loamy granulometric composition (the fraction of physical clay being 41%). Rather high humidity of active soil level. Water run-off above the permafrost surface was fixed. The thickness of the moss-lichen cover was 7–15 cm, the depth of the organic level being 11–25 cm [7]; the depth of the root layer does not exceed 25 cm

[9]. The larch root system was commonly located on the soil surface beneath moss-lichen cover [5, 9]. During the whole growth period, melting soil layer had rather low temperature. At the end of July the soil at a depth of 10 cm heated up only to 6.5 °C, with the volume humidity being 40% [10]. The plot under study was characterized by high spatial tessellation of the moss-lichen cover, along with the high spatial mosaicity of hydrothermal properties of active soil layer [11]. The latter is obvious from the data in the Fig. 2 presented high variation of seasonally thawed soil layer depth along the transect across the study plot. Long-time observations over the period of years resulted, on average, to 42 ± 10 cm of seasonally thawed soil layer depth on the frost heave hillocks and 6 ± 6 cm on the pools. The comparatively small depth of the seasonal soil thawing results from thermo-isolating quite thick moss-lichen cover (7–15 cm), preventing the heat penetration in the spring-summer period.

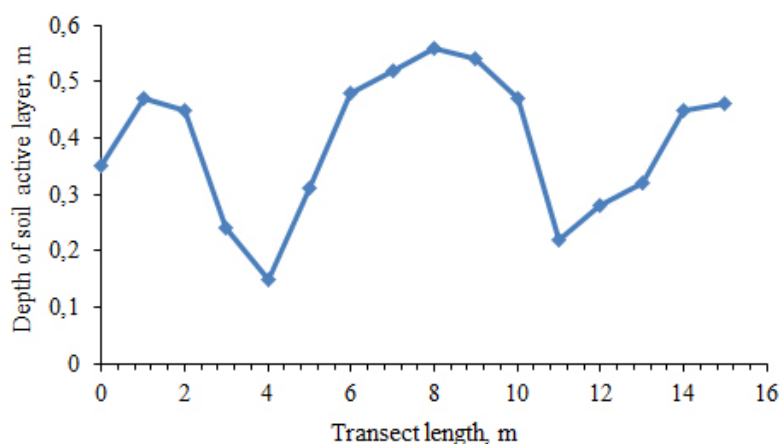


Fig. 2. High variation of seasonally thawed soil layer depth along transect across the study plot.

2.2. Methods

Within the study plot, we chose thirteen trees free from defect tops and twelve neighboring stag-headed trees for our examination. The disks were made at 1/4, 1/2, 3/4 of the stem heights and 20–30 cm below apex. In the stag-headed trees the uppermost disks were made 1–3 cm below the boundary between the living part which had no visible deteriorations and the upper dead part of the stem.

Cross-sections 15–20 μm thick were made from the disks using a sliding microtome, which were then used to prepare temporary samples for microscopy. Safranin was used to stain the samples. 65 disks taken from healthy trees as well as 60 ones from the stag-headed trees were examined.

Tree ring widths were measured on the disks along two radii. Most measurements were made using the LINTAB v3.0 (accuracy of 0.01 mm). The widths of very narrow and hardly distinguished tree rings, which formed near tops were measured using prepared cross-sections by the complex device Axio Imager MAT, Version 04.14.2005 (Karl Zeis Light AGMicroscopy).

Tree-ring chronologies were constructed by the standard techniques [12, 13, 14] using the software “Arstan” and “Cofecha” widely used in dendrochronology. The age trends were approximated by the negative exponential functions. The indexed chronologies were analyzed for 1934–2009.

In order to distinguish time periods within a growth season when climatic factors impacted (air temperature, precipitation) significantly on radial increment, sliding climate correlations were estimated. The calculations were made with the optimal for high latitudes [15] values of the “window for averaging” amounting to 20 days and values of the “step” amounting to 5 days from April, 10 to August, 28. In the latter period climatic factors could be expected to influence in tree ring growth in northern forests. The daily values of the air temperature and precipitation at the meteorological station

“Tura” were taken from the site «National Weather Service. Internet Weather Source» <ftp://ftp.ncdc.noaa.gov/pub/data/ghcn/daily>

For wood anatomical characteristics measurement, we chose the disks taken from five stag-headed and five healthy trees at the same abovementioned stem heights. Cross-sections of 15 μm thick for microscopy were made. And. Lumen radial size was measured along 2–5 tracheid rows in ten outmost tree rings formed in the period of 2000–2009, using the installation for computer image analysis Axio Imager MAT, Version 04.14.2005 (Karl Zeis Light AG Microscopy). For healthy and stag-headed trees, 170 – 380 cells were measured at 1/4 of the stem height, 160 – 280 cells at 1/2 of the height, 135 – 325 cells at 3/4 of the height and 55 – 425 cells were measured near the top.

3. RESULTS

We achieved the aim of this paper by solving several questions in tandem.

Did the current climate warming result in radial growth dynamics of the healthy larch trees in the forest stand under study?

The sliding correlations of 20 day- mean radial increment with mean air temperatures were compared for two time periods differed in climate conditions: 1943–1970 (Fig. 3A) and 1970–2009 (Fig. 3B). The second period is characterized by a clear trend of spring-early summer air temperature towards increasing. Fig 3 shows that the response of the trees to the air temperature in the warmer period (B) turned out to be considerably higher in spring-early summer period.

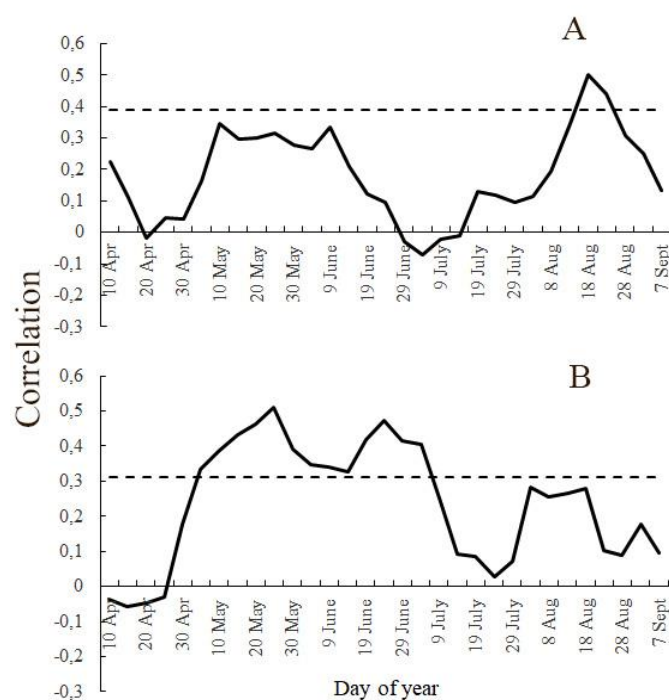


Fig. 3. Sliding 20-day-correlation functions of indexed DBH radial increments of healthy larch trees with the air temperature data for the periods 1943–1970 (A) and 1970–2009 (B). (The dotted line is the level of significance).

Did healthy and stag-headed larch trees differ in sensitivity to climatic factors in the period of current climate warming?

For stag-headed and healthy trees, sliding climate correlations of the radial increment at various stem heights were calculated and analyzed, reconstructing in detail the intra-seasonal influence of weather

conditions to stem growth (Fig. 4). The calculation of the functions was carried out for the period 1985–2009, when climate warming according to the meteorological data was more pronounced. No noticeable difference was found between response periods for the stag-headed and healthy trees, as evidenced by the correlation curves at the corresponding height levels. Slight difference between these groups of trees in correlation coefficients were noticed only in the upper levels of the stem height: 3/4 and under the top.

In Fig. 4 there are presented two time intervals when the radial increment of stag-headed and healthy trees reliably correlates with the climatic factors. The first period is typical only for the upper part of the stems (for 3/4 of the stem height and at the top), it lasts about two weeks (third decade of April - early May) and is negatively correlates with air temperature. The indicated period precedes the beginning of the radial growth of Gmelin larch in this area [16]. Abnormally high air temperatures at the end of April can "trigger" the onset of the process of pre-seasonal cambium reactivation. However, in high latitudes, the abnormally warm period in spring is inevitably followed by frosty periods; thus, the process of cambium reactivation can be suspended, to negatively affect the width and anatomical structure of the annual ring. Frequent frost rings in larch trees at the polar tree line [17] can be considered as evidence for cambium damages in early spring.

The second period is characterized by a positive correlation of the radial increment at all levels of stem height of the stag-headed and healthy trees with both climatic factors (air temperature and precipitation) from the end of May to the 20th of June. In the stag-headed trees, the temperature effect on the increment at the top is observed from the end of May to mid-June, while in the healthy trees it is observed a little longer: from the end of May to the end of June. No significant differences are observed in the response of the radial growth to precipitation between these two groups of the trees in Fig. 4. So, it is obvious, that dendrochronological method of sliding response functions could not reveal difference in reaction to climate factor influence between stag-headed and healthy trees.

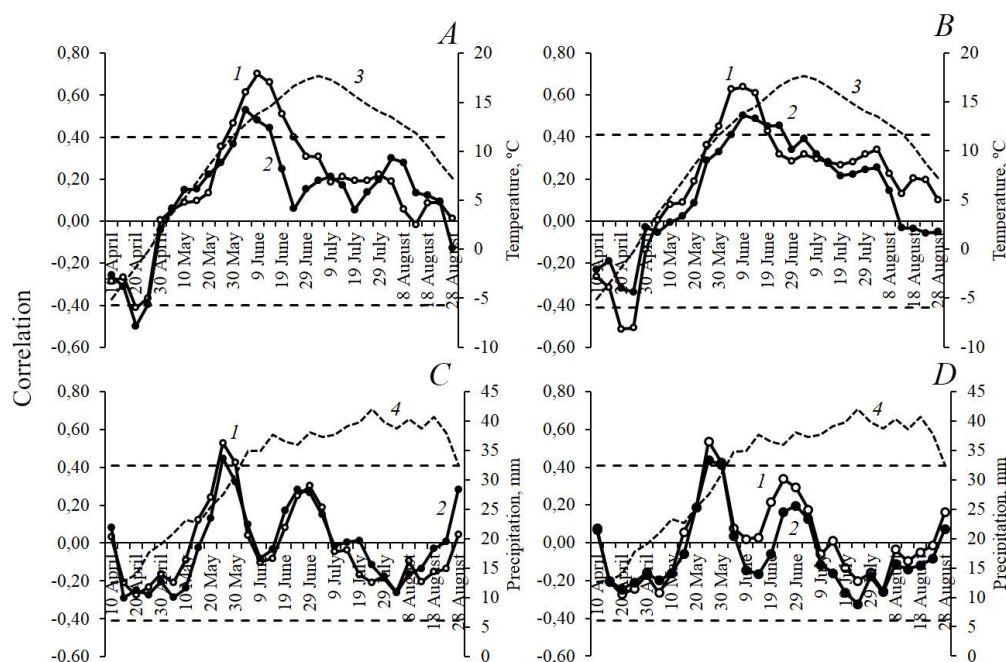


Fig. 4. Sliding 20-day-correlation functions of the indexed radial increments with air temperature and precipitation data for the period 1985–2009. A, C – stag-headed trees, B, D – healthy trees. 1 – 3/4 of the stem height; 2 – beneath the top. 3 and 4 – sliding 20-day-average values of daily temperature and precipitation for 1985–2009. The correlation coefficients $R \geq 0.41$ are significant at $P \geq 0.95$.

On the other side, when available water deficiency is the reason of top drying process, xylem anatomy must reflect it.

Do healthy and stag-headed trees differ in wood anatomical structure?

The microscopic examination revealed modifications in the anatomical structure of the annual rings formed at 3/4 of the stem height and beneath the top of in the stag-headed trees (Fig.5A). They were absent lower in the stem, i.e. at 1/2 and 1/4 of the stem height, and were the most pronounced at the dry tops. Modifications were totally absent in the stems of the healthy trees (Fig. 5B).

Modifications in stag-headed trees appeared at different years in the middle of 1980-th, but since 2000 they already had a clearly pronounced character. The rows of tracheids in the growth rings were destroyed, the latewood tracheids were formed with relatively thinner walls; thus, in the several outmost rings near the bark it occurred difficult or sometimes impossible to distinguish the growth rings themselves (the example in Fig.5A).

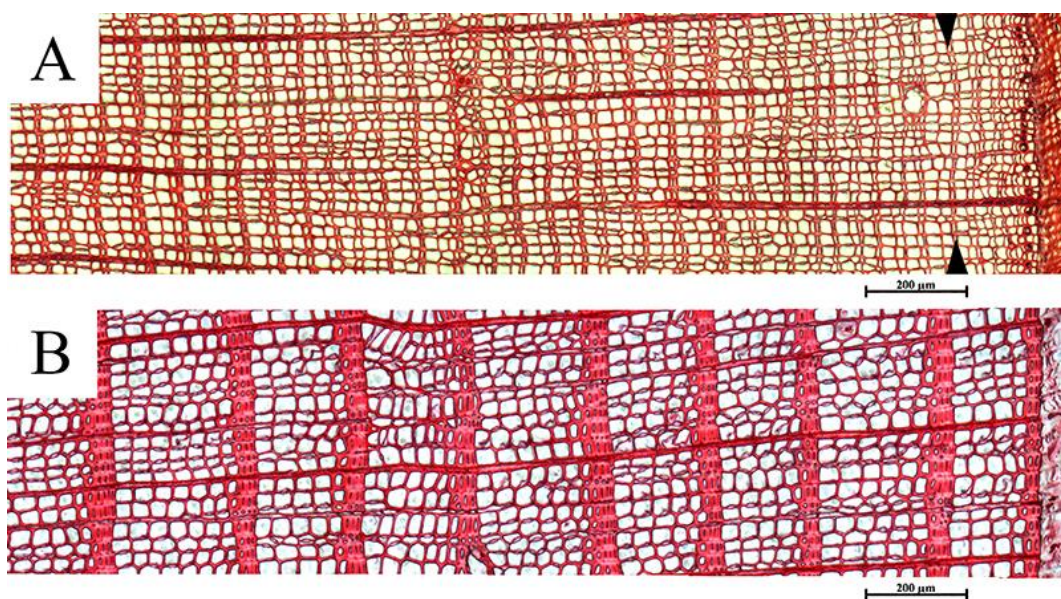


Fig. 5. Wood anatomical structure beneath the tops of the stag-headed (A) and healthy (B) larch trees. The year of appearing xylem modifications (2000) is denoted by arrows. The outmost tree rings in (A) and (B) are 2013.

Tracheids in xylem experiences water transport in the stem from roots to the crown. Efficiency of water conduction depends on tracheid lumen size, and safety of conduction system depends on tracheid wall thickness.

Do stag-headed and healthy trees differ in tracheid characteristics?

The anatomical characteristics (radial lumen size and tracheid wall thickness) measured on the cross sections over five radial rows were averaged for the entire time interval considered: 2000–2009. The average values and standard deviations are shown in Fig. 6.

The stag-headed and healthy trees were compared:

- by the trends from the bottom to top;
- by the average values at the corresponding levels of height in the stems of stag-headed and healthy trees.

The comparative analysis using the *t*-test revealed the following.

- In the stag-headed and healthy trees, the average size of the tracheid lumen and wall thickness at 1/4 of the stem height is significantly larger than that beneath top. Thus, one can make a conclusion about

a decreasing trends of these indicators upwards along the stem. In our case, they are more pronounced in the stag-headed trees as compared to the healthy ones (Fig. 6). It is worth noting that the decreasing trend in average tracheid size upwards the stem is typical of all the trees [18]. Contrary to them, we obtained trends for lumen and wall thickness data separately. The average wall thickness of tracheids has a more pronounced tendency to decrease with the stem height rather than the lumen size (Fig. 6).

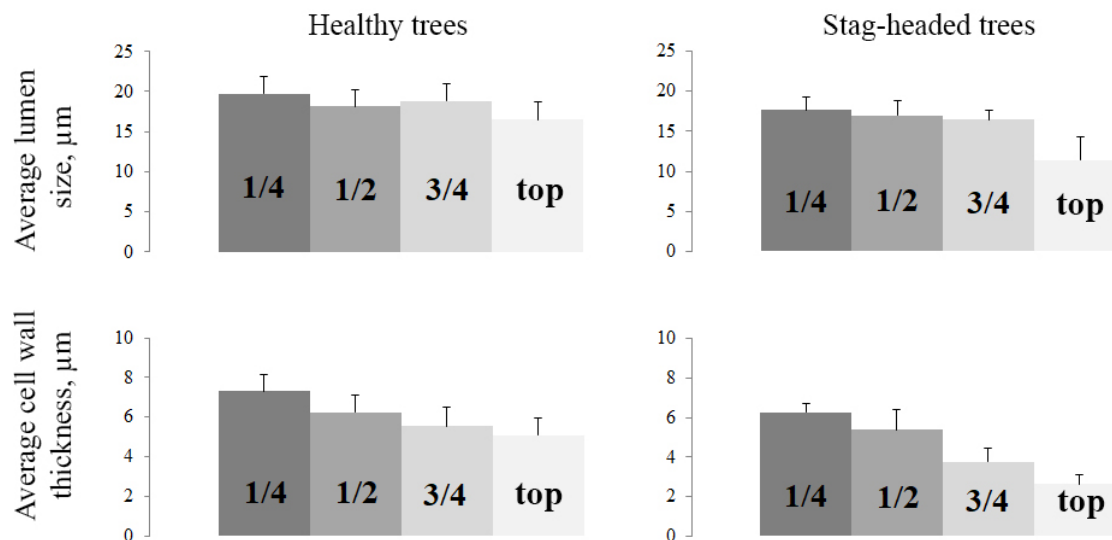


Fig. 6. Average lumen size and cell wall thickness in the healthy and stag-headed trees at 1/4, 1/2, 3/4 of the stem height and beneath the top (2000 – 2009).

- The difference between the stag-headed and healthy trees in terms of anatomical parameters was clearly manifested near the tops: in the stag-headed trees, the average radial size of the lumen is definitely (at $P \geq 0.95$) smaller (by 1.3 times), and the tracheid walls are about 2 times thinner than in the healthy trees. Both groups of trees differ slightly in the average radial size of the lumen and average thickness of the tracheid walls at lower heights in the stems.

4. DISCUSSION

The results of dendroclimatic analysis (Fig. 4) showed that abundant precipitation and increased air temperature from the end of May to the late June have a noticeable positive effect on the radial growth rate of all the trees in the stand, both stag-headed and healthy ones. This is the time of the start and intensive radial growth of Gmelin larch in the study area [16]. But on the north-facing slope, the active soil layer still has rather low temperature, close to zero [3]. Precipitation turns out to be the main source of water for plants during this period. Its temperature is higher than that in soil surface so that affects soil warming. Thus, in the years with quite low air temperature and precipitation from the end of May to the late June, the trees may well experience available water deficiency.

Changes in the hydrothermal properties of permafrost soils during the current warming (Fig. 3) may well lead to the emergence and aggravation of the existing water deficiency. The results of dendroclimatic studies of the dynamics of the stable carbon isotope in the annual rings of Gmelin larch from the permafrost zone showed that in recent decades trees have indeed experienced an ever increasing deficiency of available water [19]. The negative impact of the latter affected the trees in the stand in different ways. Different responses of the trees were manifested in the wood anatomical structure beneath tops rather than in the radial increment response to the climatic factors. Modifications appearing in the anatomical structure (Fig. 5A) indicates a violation of the very process of meristematic cell differentiation in the certain trees which then have become stag-headed. In this case, quite narrow annual rings are formed, consisting of a small number of thin-walled tracheids

having small lumens. The water conduction efficiency of such tracheids is relatively low (according to Poiseuille's law), and this aggravates water supply to the tree tops dramatically. The latter leads to a decrease in photosynthesis, and, accordingly, in carbohydrates amount consumed for the synthesis of tracheid walls. At the same time, some trees in the stand (here, referred to as "healthy") are not so sensitive in water deficiency. These trees with living tops have a clear boundary of growth rings and rather large earlywood tracheids (Fig. 5B and Fig. 6), more efficient for transporting water.

The difference in the local hydrothermal soil conditions on the study plot (Fig. 2) is here considered the main factor determining the differentiation of individual trees in response to water deficiency. Indeed, the study plot is characterized by a high spatial mosaicity of the thawing depth of the active soil layer (see Fig. 1) and, accordingly, a high spatial heterogeneity of its hydrothermal properties. Among the trees studied, those growing in more unfavorable soil conditions (higher moisture and lower temperature) turned out to be the most "sensitive" available water deficiency (as it is called "physiological draught"). The latter led to the formation of small tracheids (low turgor [20, 21]) with relatively thin cell walls (substrate starvation [22]), which are ineffective for top water supply.

5. CONCLUSIONS

The dendroecological and wood anatomy results confirm the hypothesis that all trees on the north-facing slope experience water available deficiency from the end of May to the late June. The negative impact of the latter affected the trees in the stand in different ways. Different responses of the trees were manifested in the anatomical structure in various heights of the stem rather than in the response of radial increments on climatic factors. A decreasing trend in the lumen sizes and thicknesses of the tracheid walls upwards to top was observed. The trend is more pronounced in the stag-headed trees as compared to the healthy ones. The presence of modifications in the xylotomic structure of annual increments beneath the drying tops indicates a violation of the water transport process. The tops, being in more severe water supply conditions, resulted in dry tops of more "sensitive" tree. The growth conditions which are not the same for all the trees in the stand can be associated with the high spatial heterogeneity of hydrothermal soil conditions due to the high spatial tessellation of the thermos-isolated moss-lichen cover. The variability of its thermal insulation properties is determined by the spatial distribution and ratio of microassociations of dominant species *Pleurozium schreberi*, *Aulacomnium turgidum*, *Hylocomium splendens* [11].

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