БОТАНИЧЕСКИЙ ЖУРНАЛ, 2023, том 108, № 7, с. 690–708

СООБЩЕНИЯ

SIGNIFICANCE OF COORDINATION BETWEEN STEM XYLEM TRAITS AND LEAF GAS EXCHANGE PARAMETERS DURING ADAPTATION FORMATION IN SOME BOREAL SPECIES OF KARELIA

© 2023 г. V. B. Pridacha[1],*, T. V. Tarelkina[1], Ya. A. Neronova[1], and N. V. Tumanik[1]

[1]Forest Research Institute, Karelian Research Centre of RAS
Pushkinskaya Str., 11, Petrozavodsk, 185910, Russia
**e-mail: pridacha@krc.karelia.ru*

Received March 02, 2023; revised May 30, 2023; accepted June 06, 2023

Assessment of the resistance of forest communities and individual species to external impacts requires research on the possible response of species, communities and ecosystems in different regions to the changes expected in the natural environment and climate. This study aimed to assess the variability of stem xylem anatomical and hydraulic traits and their coordination with leaf CO_2/H_2O exchange parameters in evergreen gymnosperm and deciduous angiosperm tree species during natural reforestation after clear-cutting of boreal pine forest in the European North. We analysed the effects of plant growth conditions and climatic factors on the structural and functional traits of regrowing trees in Scots pine (*Pinus sylvestris* L.), silver birch (*Betula pendula* Roth) and aspen (*Populus tremula* L.) during four growing seasons in a clear-cut site and under bilberry-type pine forest canopy in the middle taiga of Karelia. Stem xylem anatomical and hydraulic traits and leaf CO_2/H_2O exchange parameters in the different tree species mainly demonstrated a similar response to changes in plant growth conditions and climate. In the clear-cut, both Scots pine and the angiosperm tree species had the highest tracheid and vessel hydraulic diameters and xylem potential hydraulic conductivity while at the same time having the lowest specific density of tracheids and vessels. Analyzing the interannual variation of climatic factors we found that the variability of annual increments was the highest in all the species as compared to the other xylem traits, which were more conservative. Coordination between stem xylem hydraulic traits and stomatal conductance, rates of photosynthesis and transpiration, and their variability in evergreen gymnosperm and deciduous angiosperm tree species under environmental factors indicate different hydraulic behavior (isohydric/anisohydric) strategies in silver birch, aspen, and Scots pine. The predicted increase in the frequency of heat waves and droughts at Northern latitudes will promote the competitive ability of Scots pine and aspen, which build a more efficient and safer hydraulic structure compared to silver birch by raising CO_2 gas exchange and productivity in dry conditions.

Keywords: woody plants, hydraulic conductivity, photosynthesis, transpiration, environmental factors

DOI: 10.31857/S000681362306008X, **EDN:** ZLUYYI

The assessment of the resistance of communities and individual species to external impacts has currently received great attention (IPCC, 2013; FAO, 2020). However, the question of possible responses of species (Niinemets, 2010; Bussotti et al., 2015; Reich et al., 2018), communities, and ecosystems in different regions to various external impacts (Price et al., 2013; Groisman et al., 2017; Oliveira et al., 2021) still remains open due to uncertainty in the assessment of the ability of natural ecosystems to recover functionally from catastrophic disturbances. This problem is especially acute in the European North considering changes in the frequency, pattern, and severity of extreme environmental conditions over the past few decades.

Perennial plants, and particularly trees, contribute the most significantly to the biomass of terrestrial ecosystems (Bonan, 2008). Through their ontogeny, woody plants are continuously exposed to variations of biotic and abiotic environmental factors. An understanding of wood formation under variable natural environment and climate conditions is one of the central interests of plant anatomists and ecophysiologists (Fritts, 1976; Vaganov et al., 2006; Hacke, 2015), since the xylem, being the main water conducting tissue in terrestrial plants, supplies water and nutrients to the plant's photosynthetic and growing tissues. The efficiency and safety of xylem functioning largely determine the growth, productivity and survival of plants (Hacke, Sperry, 2001; Fonti et al., 2010; Gleason et al., 2016). The ratio of the transport, storage, and structural support functions of tree xylem can change over the gradient of ecological conditions as a result of adaptive transformations (Lachenbruch, McCulloh, 2014; Kawai et al., 2022). The responses may, however, differ significantly among species due to specific growth strategies and xylem anatomy features (Hacke, 2015).

The traits of xylem hydraulic structure, such as the arrangement, length, diameter, wall thickness and pit features of conducting elements, determine the water transport safety and efficiency (Sperry et al., 2006; Venturas et al., 2017; Sviderskaya et al., 2021). With longer conducting elements, water passes through the pits fewer times, which reduces total xylem hydraulic resistance (Choat et al., 2008). At the same time, the wider conducting elements increase the risk of embolism in both evergreen gymnosperm and deciduous angiosperm tree species (Bouche et al., 2014; Hacke et al., 2017). This leads to the reduced competitive ability of trees with large vessels during frosts and severe drought (Olson et al., 2018). Diffuse-porous species, like members of the genus *Populus* L., lower the risk of cavitation and hydraulic failure under water stress by producing numerous and interconnected vessels with narrow lumens (Rodriguez-Zaccaro et al., 2021). The xylem of ring-porous species with large vessels, namely *Quercus* spp., has been observed to be highly vulnerable to embolism as water transport happens only in the outermost tree ring (Fonti et al., 2010; Benson et al., 2022). Evergreen gymnosperm tree species have a more universal structure of the xylem compared to deciduous angiosperm tree species, with large thin-walled tracheids in earlywood and smaller thick-walled tracheids in latewood, which perform different functions – efficient water transport in earlywood and, to a greater extent, mechanical support in latewood (Hacke, 2015). Presumably, differences in the tracheid characteristics of earlywood and latewood help conifers adapt to variation in environmental conditions, especially to frosts and droughts (Zheng et al., 2022).

Woody plants utilize multiple strategies to avoid xylem dysfunction caused by embolism (Nardini et al., 2018; Anderegg et al., 2019). For example, at a certain value of leaf water potential, stomatal restriction of transpiration water loss occurs (Buckley, 2019) reducing the rate of xylem dehydration. The degree and intensity of such hydraulic regulation vary among species and depend on the age, height, xylem structure, and functional type of plant (Manzoni et al., 2013; Gleason et al., 2016; Martinez-Vilalta, Garcia-Forner, 2017). According to our data (Sazonova et al., 2019), stomatal restriction of water loss through transpiration in boreal Scots pine trees begins when the water potential of foliated shoot reaches −1.0...−1.1 MPa. Dehydration of stem xylem in boreal silver birch trees occurs at higher values of the foliated shoot water potential (Pridacha et al., 2018) since the Ψ range corresponding to the maximum rate of water flux in silver birch is shifted towards higher values (−0.4...−0.6 MPa) compared to Scots pine (−0.6...−0.85 MPa). This “threshold” value of Ψ has significant physiological implications as it points to the relationship between the regulatory mechanisms of xylem water fluxes and water losses through transpiration in conifer and angiosperm tree species (Brodribb, Cochard, 2009; Urli et al., 2013). Another important regulator of water transport is radial water fluxes between xylem, phloem, and the living parenchyma cells which connect them hydraulically and thus can buffer against water status fluctuations caused by water loss from leaves and water supply to roots (Sevanto et al., 2011; Stroock et al., 2014). In turn, the plant hydraulic structure, which determines both qualitatively and quantitatively the plant’s ability to conduct water from the roots to the leaves, controls the maximum stomatal conductance and thus affects photosynthesis (Brodribb et al., 2017; Hacke et al., 2017; Xiong, Nadal, 2020). This close functional coordination ensures the stability and competitiveness of plants in changing environmental conditions.

Members of genera *Pinus* L., *Betula* L., and *Populus* L. are common in the temperate and arctic zones of Northern Eurasia and are the main forest-formative tree species for boreal forests. Due to their wide ecological amplitude, *Pinus sylvestris* L., *Betula pendula* Roth, and *Populus tremula* L. are convenient objects for studying the mechanisms by which plants adapt to environmental impacts. In a previous study of the functional traits of evergreen gymnosperm and deciduous angiosperm tree species along the “clear-cut site – bilberry-type pine forest” gradient of environmental factors, we revealed some non-specific changes in stomatal conductance and rates of photosynthesis and transpiration in Scots pine, silver birch, and aspen and, vice versa, species-specific changes in the photosynthetic efficiency of water use and nitrogen use (Pridacha et al., 2021). Here, to clarify the causes of such species-specific response, we assessed the variability of stem xylem anatomical and hydraulic traits and their coordination with leaf CO_2/H_2O exchange parameters in a evergreen gymnosperm (*Pinus sylvestris*) and in deciduous angiosperm (*Betula pendula* and *Populus tremula*) tree species during natural reforestation after clear-cutting of boreal pine forest. The key working hypothesis was that different tree species co-occurring in the European North, regardless of the species’ ecological and biological traits, would respond similarly to changes in environmental factors limiting plant growth and productivity. To test this hypothesis, we analysed the effects of plant growth conditions (habitat) and climatic factors (temperature and total precipitation in the growing season) on the structural and functional traits of Scots pine, silver birch, and aspen in a clear-cut site and under the canopy of an undisturbed bilberry-type pine forest in southern Karelia during four growing seasons.

MATERIAL AND METHODS

Study area and vegetation. This study was carried out in the European part of the middle taiga (southern Karelia, Russia) on two adjacent sample plots (SP) sit-

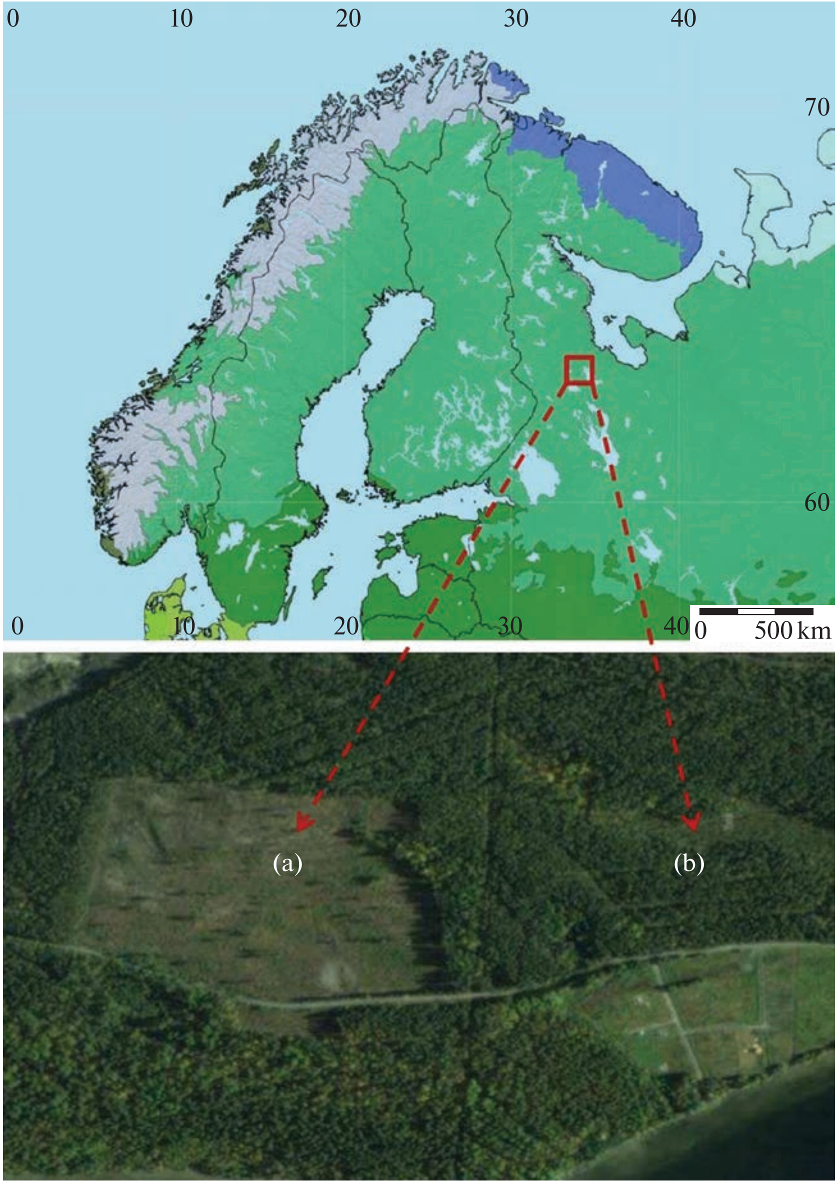

Fig. 1. Map of the study area. Locations of the clear-cut SP (a) and the forest SP (b), respectively.

uated in a 10-year-old clear-cut Scots pine stand (62°10′28.1″N, 33°59′58.8″E) and a mature 95-year-old bilberry-type pine stand (62°10′10.8″N, 34°00′05.4″E) in July-August in the period from 2016 to 2019 (Fig. 1). The climate in the study area is of the Subarctic type (Peel et al., 2007), characterized by a relatively evenly distribution of precipitation over a year (550–750 mm annual mean). The monthly mean air temperatures in January and July are –11°C and +16°C, respectively (Gromtsev, 2003). The growing season with daily mean air temperatures above +5°C lasts about 155 days from May to September. Total incoming solar radiation over the growing season does not exceed 1130 MJ m^{-2}. Previously, we noted (Pridacha et al., 2021) that moisture conditions during the growing seasons (May through September) of 2016–2019 were characterized by alteration of wetter (490 mm) and drier (250 mm) periods. The beginning of 2018 and 2019 growing seasons showed relatively dry weather conditions. The total precipitation of the 2016 growing season was higher than the long-term climate means (Nazarova, 2015) throughout the growing season. The growing season's temperature pattern in 2016–2019 varied ($-0.9 \le \Delta T \le +2.1$) from warmer (2016 and 2018) to colder seasons (2017 and 2019). For this study, we used seasonal mean temperature and seasonal total precipitation from May to September in 2016–2019 according to the Kondopoga weather station (https://rp5.ru) located 20 km away from SPs.

The main condition for selecting SPs was the presence of at least 150 regrowth trees on the plots (Pridacha et al., 2021). The diameter at breast height (DBH) and tree height (H) were measured for each tree in each plot, and the average DBH and H for the plots were calculated independently. The measurement of the biometric parameters of all Scots pine, silver birch and aspen regrowth trees in the clear-cut and forest SPs allowed us to select the model trees for each species having the average DBH and H in both plant communities. The species sampled were Scots pine (*Pinus sylvestris*), silver birch (*Betula pendula*), and aspen (*Populus tremula*) regrowth trees of the same age group (10–15 years old) growing in the clear-cut site and under the canopy of bilberry-type pine forest. The age of a tree was determined by the rings on cross-section of wood sampled at the root collar in 5 trees of each species in both SPs. Our previous study showed (Pridacha et al., 2021) that the young growing stand formed in the clear-cut site mainly consisted of Scots pine (about 70%) with a mix of silver birch and aspen trees. The heights of Scots pine, silver birch, and aspen trees in the clear-cut site were 2.3 ± 0.1, 3.4 ± 0.2, and 1.8 ± 0.5 m, and their diameters were 1.6 ± 0.1, 1.8 ± 0.2, and 1.2 ± 0.4 cm, respectively. The mature tree stand of bilberry-type pine forest mainly consisted of Scots pine (90%) with a mix of silver birch (10%). The heights of regrowing Scots pine, silver birch, and aspen plants in the mature pine stand were 1.4 ± 0.0, 2.2 ± 0.1, and 3.2 ± 0.3 m, and their diameters were 0.4 ± 0.0, 0.9 ± 0.1, and 1.4 ± 0.2 cm, respectively. Characteristics of SPs (regrowth density, co-occurring species) and soil properties were described in detail in previous paper (Pridacha et al., 2021). The soil in both SPs was sandy Podzol and the bulk of roots was concentrated within the upper 2–25 cm depth soil layer. The water table in the clear-cut and the forest SPs was at about the same depth (1.2 m).

Stem xylem traits. To determine xylem traits the fragments of stem 2.0 cm long were sawn at 0.2 m height from 5 model trees of each species in both SPs on August 30, 2019. It should be noted that in the study area, the period of cambial growth lasts from May to the first decade of August (Kishchenko, Vantenkova, 2013, 2014). Since the differentiation of vessels passes quickly (Jin et al., 2018), all vessels in silver birch and aspen were fully formed by the date of selection. In Scots pine, the thickening of latewood tracheid cell walls can continue for 30–60 days after the cessation of cambial divisions (Vaganov et al., 2006). Therefore, only fully differentiated latewood tracheids were selected for measurements in Scots pine. Two samples were taken from each saw cut, from the northern and from the southern sides, which were fixed in 70° alcohol. Thin cross-sections (15–20 μm) were cut from each sample using Frigomobil 1205 freezing microtome (Reichert–Jung, Heidelberg, Germany) and stained with 1% safranin aqueous solution. The sections were mounted in glycerol on glass slides and observed under an AxioImager A1 light microscope (Carl Zeiss, Germany) at ×10 magnification. Images (Fig. 2) were recorded using an ADFPRO03 camera (ADF Optics, China) and ADF Image Capture software (ADF Optics, China).

Anatomical measurements were performed according to the recommendations (IAWA list..., 1989, Scholz et al., 2013). For xylem traits analysis, a series of annual rings over the period 2016–2019 was selected. We took 6 digital images per tree. Digital images were processed with ImageJ v. 1.50 (NIH, USA) to measure xylem increments, cell wall thickness, and radial diameters of the lumen of xylem conducting elements, and to count the number of tracheids and vessels per unit xylem area (Table 1). Xylem anatomical traits in pine, birch and aspen were measured separately for the northern and the southern sides of the stem, and then the results were pooled together for each tree. For tracheid diameter and tracheid wall thickness, 50 tracheids were randomly measured in earlywood and latewood subsection for each conifer tree. The parameters of vessels were measured in 100 replications for each deciduous tree.

The hydraulic diameter D_h was calculated as follows (Tyree, Zimmermann, 2002):

$$D_\mathrm{h} = \left[\frac{\Sigma d^4}{n}\right]^{\frac{1}{4}} \qquad (1)$$

where n is the number of vessels (tracheids) measured and d is the diameter of the vessel (tracheid).

Potential hydraulic conductivity $K\mathrm{p}$ was calculated according to the Hagen–Poiseuille law (Sterck et al., 2008):

$$K\mathrm{p} = \left(\frac{\pi\rho_\mathrm{w}}{128\eta}\right) \times N \times D_\mathrm{h}^4 \qquad (2)$$

where ρ_w is the density of water at 20°C (998.2 kg m^{-3}), η is the viscosity of water at 20°C (1.002×10^{-3} Pa s) and N is vessel (tracheid) density. Vessel (tracheid) density was the ratio of the total number of vessels (tracheids) to the cross-sectional area (Chen et al., 2020).

Leaf gas exchange parameters. All gas exchange measurements were performed using the portable photosynthesis system LI-6400XT (LI-COR Inc., USA) fitted with the standard 2 × 3 cm leaf chamber and a light source LI-6400-02B LED (LI-COR Inc., USA) in July 2016–2019. Field measurements of stomatal conductance (g_s, mol $\mathrm{m}^{-2}\ \mathrm{s}^{-1}$), photosynthesis ($A$, μmol $\mathrm{m}^{-2}\ \mathrm{s}^{-1}$) and transpiration ($E$, mmol $\mathrm{m}^{-2}\ \mathrm{s}^{-1}$) in the leaves (needles) of trees in both SPs were conducted between 10 a.m. and 4 p.m. on fully expanded leaves without visible damage located in the middle third of the crown. The measurements were conducted on three leaves per tree in five model trees per species in both SPs. The water potential (Ψ, MPa) was measured in a detached foliated shoot using the Plant Moisture Vessel device, SKPM 1400 (Skye Instru-

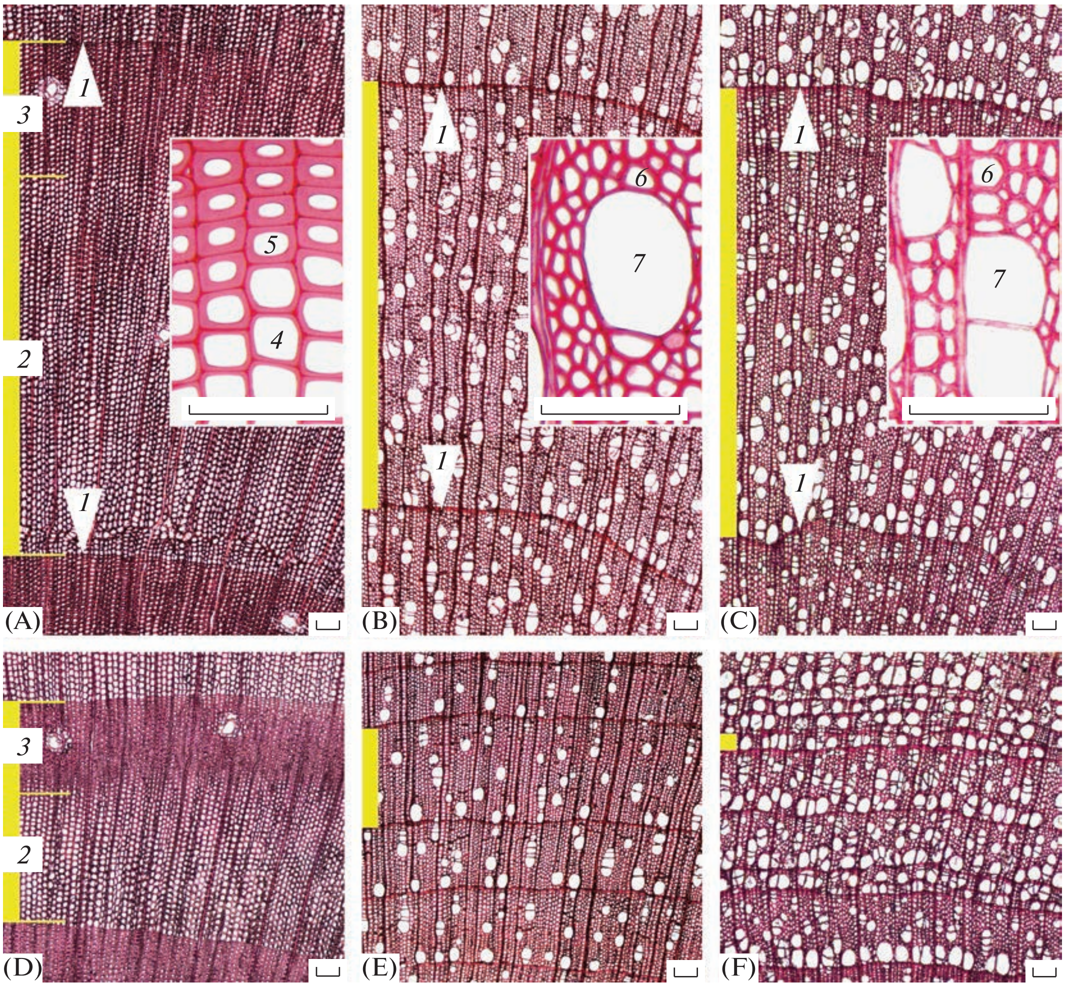

Fig. 2. Examples of light microscopy images of transverse sections of wood anatomy of evergreen gymnosperm and deciduous angiosperm tree species growing in the clear-cut SP (A, B, C) and the forest SP (D, E, F). The 2017 annual increment is indicated by yellow. The numbers indicate the following: 1 – growth ring boundaries, 2 – earlywood, 3 – latewood, 4 – earlywood tracheid, 5 – latewood tracheid, 6 – fiber, 7 – vessel. It should be noted that the wood structure of *Betula pendula* (B, E) and *Populus tremula* (C, F) is diffuse-porous with large vessels. Conducting elements of xylem in *Pinus sylvestris* (A, D) are earlywood and latewood tracheids. Scale bar = 100 µm.

ments Ltd., United Kingdom) simultaneously with measuring of photosynthesis and transpiration rates. The methodological details of the leaf CO_2/H_2O exchange measurements and data on leaf functional traits were presented in previous paper (Pridacha et al., 2021). The present study focused on stem xylem changes and their relationship with leaf gas exchange parameters across the gradient of environmental factors.

Statistical analysis. The data were analyzed with Statistica 13.3 (TIBCO Software Inc., USA). The normality of the data was checked using the Shapiro-Wilk test. The effect of plant growth conditions ($df = 1$) and the year of the experiment ($df = 3$) on stem xylem traits of the coniferous and deciduous tree species was assessed by two-factor analysis of variance. To identify interannual variability of key characteristics, the values of stem xylem traits were normalized relative to their means per 2016–2019 for each tree species. Pearson correlation coefficients (r) and P value were used to evaluated bivariate relationships between xylem traits and the growing-season climatic factors in 2016–2019 (seasonal mean air temperature and seasonal total precipitation from May to September). The diagrams and tables show the means and their standard errors. Significant differences between the means were estimated using Tukey's test. This study was carried out using equipment of the Core Facility of the Karelian Research Centre RAS.

RESULTS

The analysis of the effects of plant growth conditions (habitat) and the year of the experiment (year) on the stem xylem traits formed during four growing seasons in pine, birch, and aspen trees (Table 2) showed

Table 1. List of the stem xylem traits measured in this study with designations and units

Symbol	Traits	Units
	Anatomic traits	
TRW	Tree-ring width	mm
N_{EW}	Number of earlywood tracheids per unit xylem area	N mm^{-2}
N_{LW}	Number of latewood tracheids per unit xylem area	N mm^{-2}
WT_{EW}	Earlywood tracheid cell wall thickness	µm
WT_{LW}	Latewood tracheid cell wall thickness	µm
LD_{EW}	Lumen diameter of earlywood tracheids	µm
LD_{LW}	Lumen diameter of latewood tracheids	µm
TD_{EW}	Diameter of earlywood tracheids	µm
TD_{LW}	Diameter of latewood tracheids	µm
LW	Latewood	%
N	Number of vessels per unit xylem area	N mm^{-2}
FWT	Fiber cell wall thickness	µm
VWT	Vessel cell wall thickness	µm
FLD	Fiber lumen diameter	µm
VLD	Vessel lumen diameter	µm
FD	Fiber diameter	µm
VD	Vessel diameter	µm
	Hydraulic traits	
Dh_{EW}	Hydraulic diameter of earlywood tracheids	µm
Dh_{LW}	Hydraulic diameter of latewood tracheids	µm
Dh	Vessel hydraulic diameter	µm
Kp_{EW}	Potential hydraulic conductivity of earlywood tracheids	kg m^{-1} MPa^{-1} s^{-1}
Kp_{LW}	Potential hydraulic conductivity of latewood tracheids	kg m^{-1} MPa^{-1} s^{-1}
Kp	Potential hydraulic conductivity	kg m^{-1} MPa^{-1} s^{-1}

that in most cases the key characteristics were more significantly influenced by the "habitat" factor than by the year. Importantly, for all the species the change of plant growth conditions had the greatest effect on xylem increment width and the smallest effect on cell wall thickness in xylem conducting elements.

Effects of plant growth conditions on stem xylem traits. A comparison of the 2016—2019 averaged values of stem xylem traits in pine, birch, and aspen in the clear-cut and forest SPs revealed a similar response of various species to the habitat change (Table 3). Thus, TRW values in pine, birch, and aspen in the clear-cut SP were 5, 7, and 9-fold, respectively, higher than corresponding levels in the trees in the forest SP. Decrease in TRW values in all tree species growing in the forest SP resulted, in particular in pine, to an increase in the content of latewood (44%) compared with the clear-cut SP (31%). At the same time, the number of vessels (tracheids) per unit xylem area (N) in pine, birch, and aspen in the forest SP was higher than in the clear-cut SP by 45—50, 9, and 45%, respectively. On the other hand, VLD and FLD, VD and FD values in the angiosperm tree species in the clear-cut SP were, respectively, 1.2—1.5 (in birch) and 1.2—1.3-fold (in aspen) higher than in the forest SP. The xylem of conifer trees in the clear-cut SP also featured tracheids with large lumen diameters. Pine LD_{EW} and LD_{LW}, as well as of TD_{EW}, TD_{LW} increased 1.3—1.7-fold in the clear-cut SP versus the forest SP. The influence of plant growth conditions on the cell wall formation, however, was less significant. The differences in the wall thickness of xylem conducting elements between pine, birch, and aspen in the clear-cut and the forest SPs were only 2—4, 3—11, and 5—13%, respectively.

The greatest increase in Dh values in the clear-cut SP was found in birch (41%) and the smallest in aspen (30%) and pine both in early and late wood (30%). The Kp value increase in the clear-cut SP was the highest in birch (3.3-fold) and the lowest in pine (1.9—2.3-fold) and aspen (1.9-fold). Comparison of xylem

Table 2. Results of two-way ANOVA for the effect of habitat and year of the experiment on stem xylem traits in Scots pine, silver birch, and aspen trees

Dependent variables	n	Factors					
		Habitat		Year		Habitat × Year	
		p	η^2	*p*	η^2	*p*	η^2
				Pinus sylvestris			
TRW	10	***	72.3	***	7.7	***	5.3
N_{EW}	10	***	38.3	***	1.3	***	11.4
N_{LW}	10	***	35.8	***	1.4	***	9.5
WT_{EW}	10	**	1.1	**	1.9	***	3.2
WT_{LW}	10	ns	0.4	***	4.8	***	13.0
LD_{EW}	10	***	38.2	ns	0.4	***	9.7
LD_{LW}	10	***	43.6	***	7.1	***	1.4
TD_{EW}	10	***	35.5	ns	0.3	***	10.7
TD_{LW}	10	***	35.1	***	6.4	***	4.0
LW	10	***	24.1	***	8.3	***	28.7
Dh_{EW}	10	***	46.2	ns	0.4	***	14.0
Dh_{LW}	10	***	44.2	***	7.4	***	5.2
Kp_{EW}	10	***	22.4	*	0.7	***	9.2
Kp_{LW}	10	***	22.1	***	5.8	***	3.6
Kp	10	***	31.6	*	0.8	***	7.1
				Betula pendula			
TRW	10	***	89.5	***	1.9	***	1.1
N	10	***	2.8	***	17.3	***	29.7
FWT	10	***	0.6	***	2.4	***	1.1
VWT	10	***	5.0	***	2.5	***	1.2
FLD	10	***	29.6	***	0.8	***	2.1
VLD	10	***	44.4	***	1.9	***	1.2
FD	10	***	25.8	ns	0.1	***	2.6
VD	10	***	44.5	***	1.9	***	1.4
Dh	10	***	70.6	***	4.1	***	2.1
Kp	10	***	80.8	***	2.3	***	1.2
				Populus tremula			
TRW	10	***	80.3	***	1.4	***	0.6
N	10	***	33.2	***	15.9	***	3.8
FWT	10	***	1.2	***	2.7	***	0.9
VWT	10	***	6.3	***	2.6	***	0.9
FLD	10	***	27.1	***	1.8	***	1.6
VLD	10	***	25.1	***	3.5	***	1.3
FD	10	***	24.3	***	1.3	***	2.2
VD	10	***	26.7	***	3.1	***	1.3
Dh	10	***	52.5	***	6.0	***	2.8
Kp	10	***	41.4	***	4.0	***	2.7

Note. n – number of trees; η^2 – effect size, %. Here and below: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, ns – not significant ($p > 0.05$). For the designations of xylem traits see Table 1.

Table 3. Stem xylem traits of Scots pine, silver birch, and aspen trees in the clear-cut site (SP1) and under pine forest canopy (SP2) averaged over the 2016–2019 period

Parameter	SP1	SP2
Pinus sylvestris		
TRW	2.4 ± 0.0 *a* (34)	0.5 ± 0.0 *b* (40)
N_{EW}	393 ± 5 *a* (26)	586 ± 5 *b* (24)
N_{LW}	611 ± 7 *a* (23)	888 ± 11 *b* (25)
WT_{EW}	4.6 ± 0.0 *a* (18)	4.8 ± 0.0 *b* (18)
WT_{LW}	8.2 ± 0.1 *a* (19)	8.1 ± 0.1 *a* (15)
LD_{EW}	49.5 ± 0.5 *a* (19)	35.1 ± 0.4 *b* (25)
LD_{LW}	20.3 ± 0.3 *a* (27)	12.1 ± 0.2 *b* (29)
TD_{EW}	58.7 ± 0.5 *a* (17)	44.6 ± 0.4 *b* (20)
TD_{LW}	36.7 ± 0.3 *a* (18)	28.2 ± 0.2 *b* (17)
LW	33.1 ± 0.5 *a* (29)	43.1 ± 0.4 *b* (19)
Dh_{EW}	59.6 ± 0.4 *a* (14)	45.7 ± 0.3 *b* (15)
Dh_{LW}	37.2 ± 0.3 *a* (15)	28.6 ± 0.2 *b* (14)
Kp_{EW}	127.5 ± 3.3 *a* (52)	68.1 ± 2.1 *b* (62)
Kp_{LW}	33.9 ± 1.2 *a* (72)	14.9 ± 0.3 *b*(42)
Kp	161.4 ± 3.4 *a* (43)	83.0 ± 2.2 *b* (53)
Betula pendula		
TRW	1.9 ± 0.0 *a* (20)	0.3 ± 0.0 *b* (42)
N	121 ± 1 *a* (17)	131 ± 1 *b* (12)
FWT	2.3 ± 0.0 *a* (20)	2.2 ± 0.0 *b* (24)
VWT	2.6 ± 0.0 *a* (20)	2.4 ± 0.0 *b* (24)
FLD	10.4 ± 0.1 *a* (21)	7.6 ± 0.1 *b* (27)
VLD	51.5 ± 0.3 *a* (18)	34.6 ± 0.3 *b* (27)
FD	14.9 ± 0.1 *a* (16)	12.0 ± 0.1 *b* (21)
VD	56.7 ± 0.3 *a* (17)	39.3 ± 0.3 *b* (25)
Dh	58.6 ± 0.1 *a* (7)	41.6 ± 0.2 *b* (16)
Kp	36.0 ± 0.2 *a* (19)	10.8 ± 0.2 *b* (50)
Populus tremula		
TRW	1.6 ± 0.0 *a* (30)	0.2 ± 0.0 *b* (58)
N	162 ± 1 *a* (31)	234 ± 1 *b* (23)
FWT	2.7 ± 0.0 *a* (22)	2.6 ± 0.0 *b* (25)
VWT	3.2 ± 0.0 *a* (21)	2.9 ± 0.0 *b* (25)
FLD	12.2 ± 0.1 *a* (21)	9.1 ± 0.1 *b* (27)
VLD	49.7 ± 0.3 *a* (25)	34.0 ± 0.2 *b* (25)
FD	17.7 ± 0.1 *a* (17)	14.4 ± 0.1 *b* (20)
VD	56.2 ± 0.3 *a* (23)	42.7 ± 0.2 *b* (22)
Dh	58.6 ± 0.2 *a* (14)	45.1 ± 0.1 *b* (9)
Kp	45.5 ± 0.4 *a* (34)	24.5 ± 0.2 *b* (35)

Note. Values in parentheses are the values of coefficient of variation (*C.V.*, %). Different small letters (*a*, *b*) indicate significant differences of the mean values between plant growth conditions ($p < 0.05$). For the designations of xylem traits see Table 1.

Table 4. Correlations between xylem structural and functional traits and the growing season climatic factors in silver birch trees in the clear-cut SP (below diagonal) and the forest SP (above diagonal) in the 2016–2019 period

Traits	TRW	N	FWT	VWT	FLD	VLD	FD	VD	Dh	Kp	T_{air}	P
TRW		**–0.57**	0.44	0.44	**0.50**	0.41	**0.58**	0.44	**0.70**	**0.63**	*n.s.*	**0.57**
N	0.24		–0.10	–0.09	–0.12	–0.26	–0.14	–0.26	–0.41	–0.32	*n.s.*	–0.36
FWT	–0.17	–0.17		**0.89**	0.28	0.32	**0.64**	0.43	**0.58**	**0.57**	*n.s.*	*n.s.*
VWT	–0.17	–0.17	**0.78**		0.28	0.32	0.46	**0.58**	**0.58**	**0.57**	*n.s.*	*n.s.*
FLD	0.16	–0.14	*n.s.*	*n.s.*		0.17	**0.92**	0.20	0.28	0.28	*n.s.*	0.25
VLD	0.11	–0.31	*n.s.*	*n.s.*	0.09		0.27	**0.99**	**0.56**	**0.55**	–0.12	*n.s.*
FD	0.08	–0.19	0.36	0.11	**0.92**	0.09		0.34	0.47	0.46	*n.s.*	0.19
VD	0.09	–0.33	0.12	0.32	0.09	**0.99**	0.13		**0.61**	**0.59**	–0.11	*n.s.*
Dh	0.22	**–0.75**	0.07	0.08	0.25	0.43	0.26	0.43		**0.98**	–0.21	*n.s.*
Kp	**0.55**	–0.39	*n.s.*	*n.s.*	0.27	0.38	0.25	0.38	**0.88**		–0.32	–0.11
T_{air}	0.39	**0.70**	*n.s.*	*n.s.*	–0.11	–0.24	–0.12	–0.23	**–0.52**	–0.18		0.21
P	0.36	**0.57**	–0.26	–0.27	–0.09	–0.25	–0.18	–0.26	**–0.62**	–0.48	0.21	

Note. For the designations of xylem traits see Table 1. T_{air} – mean air temperature for the period from May to September, °C; P – total precipitation for the period from May to September, mm. Significant correlations ($p \leq 0.01$) are shown. Moderate and strong correlations ($|r| \geq 0.5$) are indicated in bold.

traits between the deciduous species showed that aspen had higher values of N (by 34–78%), VWT (20–22%), and Kp (27%) than birch in both SPs. The Kp value in pine was 4–8- and 3–4-fold that of birch and aspen in the clear-cut SP and the forest SP, respectively. Importantly, pine WT_{LW} and N_{LW} were 2- and 1.5-fold that the WT_{EW} and N_{EW} values in both SPs.

Effects of interannual climate variability on stem xylem traits. A comparative analysis of interannual dynamics of normalized values of xylem traits in different habitats showed that in most cases the variability of the parameters in birch, aspen (Fig. 3), and pine (Fig. 4) during the 2016–2019 period was within 10 and 15%, respectively, of their means for this period. We found that the most variable parameter was TRW for aspen (43–55%) and birch (22–38%) in the forest SP, and for pine (20–38%) in both SPs. The number of vessels (tracheids) per unit xylem area (N) was also showed high variability in birch in the clear-cut SP (15–19%), and in aspen (15–23%) and pine (16–18%) in both SPs. Pine exhibited a considerable change in the LW value in the clear-cut SP (20–38%) and the LD_{LW} value in the forest SP (20%) over the four-year period. An important pattern common for all the species is a high interannual variability of the Kp value, which was found in aspen in the clear-cut SP (13–21%), and in birch (14–22%) and pine (22–35%) in both SPs.

Relationships between stem xylem traits and climatic factors. Assessing the relationships between structural and functional traits and climatic factors in the period from May through September 2016–2019 we revealed some differences between the species. For birch in the clear-cut SP (Table 4) positive correlations were found for Kp with Dh ($r = 0.88$) and TRW ($r = 0.55$), VLD with VD ($r = 0.99$), FLD with FD ($r = 0.92$), FWT with VWT ($r = 0.78$), while a negative correlation was detected between N and Dh ($r = -0.75$). Growing-season averaged temperature and total precipitation were positively correlated with N ($r = 0.70$ and $r = 0.57$, respectively) and negatively related to Dh ($r = -0.52$ and $r = -0.62$, respectively) of birch trees in the clear-cut SP.

There were more of significant correlations in birch in the forest SP (20) than in the clear-cut SP (10). The Kp value in birch trees growing in the forest SP was positively correlated with Dh ($r = 0.98$) and TRW ($r = 0.63$), VD ($r = 0.59$), VWT ($r = 0.57$), FWT ($r = 0.57$), and VLD ($r = 0.55$). Correlations of the Dh parameter followed the strength and direction patterns of Kp correlations with xylem traits. We also detected positive correlations of VD with VLD ($r = 0.99$) and VWT ($r = 0.58$), FD with FLD ($r = 0.92$) and FWT ($r = 0.64$), FWT and VWT ($r = 0.89$). TRW was positively correlated with FD ($r = 0.58$) and FLD ($r = 0.50$), and negatively related to N ($r = -0.57$). Silver birch trees in the forest SP exhibited also positive correlations between TRW and total precipitation over the growing season ($r = 0.57$).

In contrast with birch, the number of significant correlations in aspen (Table 5) was higher in the clear-cut SP (16) than the forest SP (8). The N parameter in aspen trees growing in the clear-cut SP was negatively correlated with Dh ($r = -0.85$), TRW ($r = -0.64$), Kp ($r = -0.58$), VLD ($r = -0.56$), and VD ($r = -0.55$). Similarly to birch, aspen in the clear-cut SP showed positive correlations of VD with VLD ($r = 0.99$) and VWT ($r = 0.51$), FD with FLD ($r = 0.92$) and FWT ($r = 0.53$), FWT with VWT ($r = 0.69$). Aspen Kp in the clear-cut SP was positively correlated with Dh ($r = 0.90$), VD ($r = 0.55$), and VLD ($r = 0.54$). Positive

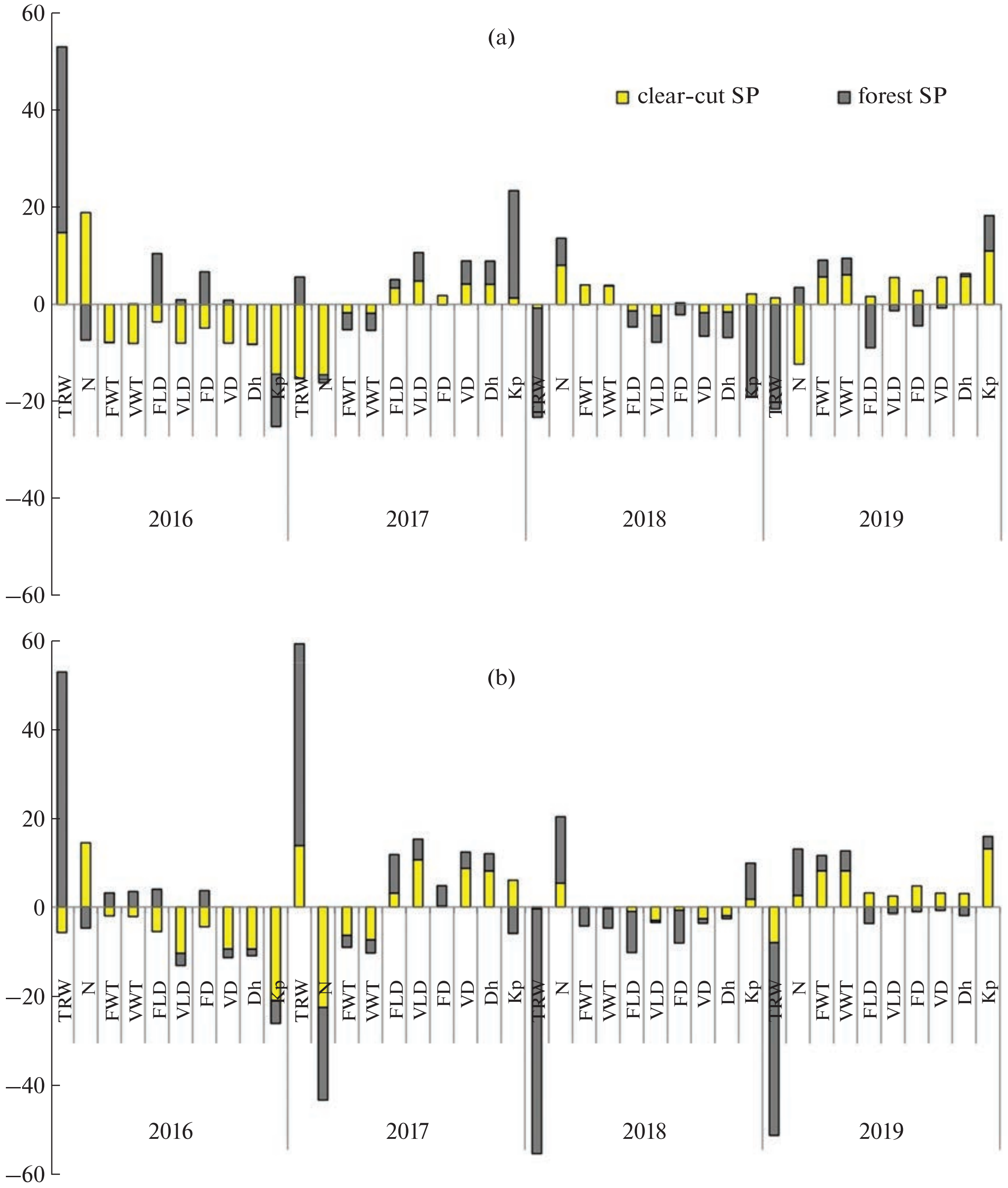

Fig. 3. Variability (%) of stem xylem traits in *Betula pendula* (a) and *Populus tremula* (b) in the clear-cut and forest SPs in the period from 2016 to 2019. For the designations of xylem traits see Table 1.

correlations in aspen in the clear-cut SP were also detected for Dh with VD ($r = 0.62$), VLD ($r = 0.62$), and TRW ($r = 0.54$).

As well as in the clear-cut SP, aspen trees in the forest SP showed a negative correlation between N and TRW ($r = -0.51$). Positive correlations in this habitat were found for VD with VLD ($r = 0.99$) and VWT ($r = 0.50$), FD with FLD ($r = 0.89$) and FWT ($r = 0.53$), FWT and VWT ($r = 0.60$), Kp and Dh ($r = 0.81$). Like in birch, aspen TRW in the forest SP was positively correlated with precipitation over the growing season ($r = 0.60$).

In pine, like in birch, the number of significant correlations (Table 6) was higher in the forest SP (28) than in the clear-cut SP (18). Positive correlations in pine trees in the clear-cut SP were found for TD_{EW} with LD_{EW} ($r = 0.99$), TD_{LW} with LD_{LW} ($r = 0.89$) and WT_{LW} ($r = 0.56$), Dh_{EW} with TD_{EW} ($r = 0.78$) and LD_{EW} ($r = 0.76$), Dh_{LW} with TD_{LW} ($r = 0.84$) and

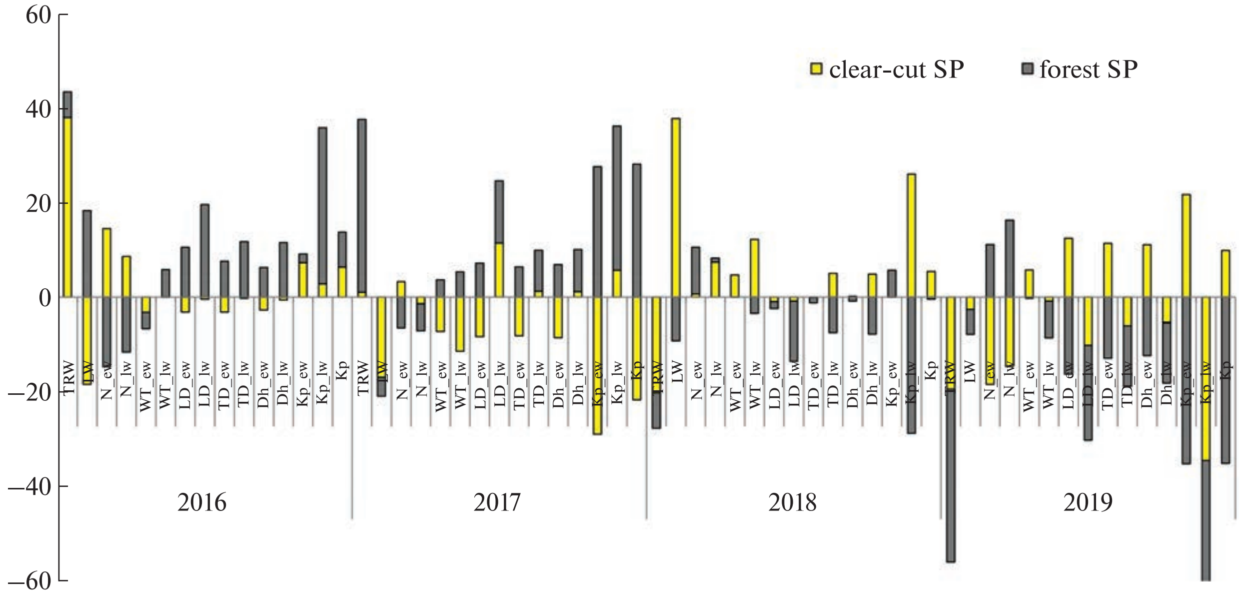

Fig. 4. Variability (%) of stem xylem traits in *Pinus sylvestris* in the clear-cut and forest SPs in the period from 2016 to 2019. For the designations of xylem traits see Table 1.

LD_{LW} ($r = 0.78$). In early and late wood, correlations of similar strength and direction were also detected for Kp_{EW} with Dh_{EW} ($r = 0.82$), TD_{EW} ($r = 0.65$), and LD_{EW} ($r = 0.63$), and Kp_{LW} with Dh_{LW} ($r = 0.92$), TD_{LW} ($r = 0.77$), and LD_{LW} ($r = 0.74$). Pine Kp in the clear-cut SP was positively correlated with Kp_{EW} ($r = 0.93$), Dh_{EW} ($r = 0.72$), TD_{EW} ($r = 0.58$), and LD_{EW} ($r = 0.54$). Pine TRW was positively correlated with precipitation over the growing season ($r = 0.67$), and LW with growing-season mean temperatures ($r = 0.51$).

In the forest SP, correlations between pine xylem traits are comparable in strength and direction to those in pine trees in the clear-cut SP. Meanwhile, positive correlations in trees growing in the forest SP were detected for LW with Dh_{LW} ($r = 0.56$) and Kp_{LW} ($r = 0.51$), Dh_{LW} with WT_{LW} ($r = 0.55$), N_{LW} with N_{EW} ($r = 0.51$). Pine in this habitat also showed negative correlations of Dh_{LW} with N_{LW} ($r = -0.64$) and N_{EW}

Table 5. Correlations between xylem structural and functional traits and the growing season climatic factors in aspen trees in the clear-cut SP (below diagonal) and the forest SP (above diagonal) in the 2016–2019 period

Traits	TRW	N	FWT	VWT	FLD	VLD	FD	VD	Dh	Kp	Tair	P
TRW		**−0.51**	0.14	0.14	0.22	0.16	0.25	0.17	0.12	−0.18	−0.27	**0.60**
N	**−0.64**		−0.11	−0.11	−0.32	−0.09	−0.32	−0.11	−0.27	0.25	0.43	−0.31
FWT	0.05	*n.s.*		**0.60**	0.10	0.06	**0.53**	0.21	*n.s.*	*n.s.*	*n.s.*	*n.s.*
VWT	0.05	*n.s.*	**0.69**		0.10	0.06	0.21	**0.50**	*n.s.*	*n.s.*	*n.s.*	*n.s.*
FLD	0.24	−0.26	0.15	0.15		*n.s.*	**0.89**	*n.s.*	*n.s.*	−0.21	−0.17	0.14
VLD	0.42	**−0.56**	0.06	0.06	0.24		*n.s.*	**0.99**	0.40	0.33	−0.09	*n.s.*
FD	0.22	−0.23	**0.53**	0.17	**0.92**	0.23		0.11	*n.s.*	−0.18	−0.15	0.14
VD	0.42	**−0.55**	0.16	**0.51**	0.25	**0.99**	0.28		0.40	0.32	−0.08	*n.s.*
Dh	**0.54**	**−0.85**	0.07	0.07	0.32	**0.62**	0.30	**0.62**		**0.81**	−0.18	*n.s.*
Kp	0.35	**−0.58**	0.10	0.10	0.28	**0.54**	0.28	**0.55**	**0.90**		0.09	−0.11
Tair	−0.16	0.36	*n.s.*	*n.s.*	−0.13	−0.25	−0.10	−0.25	−0.37	−0.19		0.21
P	*n.s.*	0.13	−0.14	−0.14	−0.15	−0.17	−0.17	−0.18	−0.31	−0.36	0.21	

Note. For the designations of xylem traits see Table 1. T_{air} – mean air temperature for the period from May to September, °C; P – total precipitation for the period from May to September, mm. Significant correlations ($p \leq 0.01$) are shown. Moderate and strong correlations ($|r| \geq 0.5$) are indicated in bold.

Table 6. Correlations between xylem structural and functional traits and the growing season climatic factors in Scots pine trees in the clear-cut SP (below diagonal) and the forest SP (above diagonal) in the 2016–2019 period

Traits	TRW	LW	N_{EW}	N_{LW}	WT_{EW}	WT_{LW}	LD_{EW}	LD_{LW}	TD_{EW}	TD_{LW}	Dh_{EW}	Dh_{LW}	Kp_{EW}	Kp_{LW}	Kp	Tair	P
TRW		0.15	–0.34	–0.18	*n.s.*	*n.s.*	0.28	0.36	0.29	0.26	0.40	0.32	0.23	0.37	0.27	–0.23	0.34
LW	–0.43		–0.19	–0.29	*n.s.*	0.22	*n.s.*	0.48	*n.s.*	0.47	*n.s.*	**0.56**	–0.16	**0.51**	*n.s.*	0.11	**0.51**
N_{EW}	0.18	*n.s.*		**0.51**	*n.s.*	–0.35	–0.28	–0.40	–0.30	–0.47	–0.38	**–0.59**	*n.s.*	–0.45	*n.s.*	*n.s.*	–0.42
N_{LW}	0.16	*n.s.*	0.43		*n.s.*	–0.40	–0.19	–0.45	–0.17	**–0.54**	–0.18	**–0.64**	0.18	–0.23	0.14	*n.s.*	–0.37
WT_{EW}	0.19	0.22	*n.s.*	0.11		*n.s.*	–0.11	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*
WT_{LW}	–0.18	0.39	*n.s.*	0.11	*n.s.*		*n.s.*	0.27	*n.s.*	**0.70**	*n.s.*	**0.55**	*n.s.*	0.43	*n.s.*	*n.s.*	0.33
LD_{EW}	0.14	*n.s.*	–0.30	*n.s.*	0.28	*n.s.*		0.25	**0.98**	0.20	**0.76**	0.25	**0.64**	0.29	**0.66**	*n.s.*	0.36
LD_{LW}	0.21	*n.s.*	0.20	0.20	0.12	0.11	–0.29		0.25	**0.87**	0.32	**0.74**	*n.s.*	**0.69**	0.19	*n.s.*	**0.52**
TD_{EW}	0.17	*n.s.*	–0.30	*n.s.*	0.43	*n.s.*	**0.99**	–0.26		0.21	**0.76**	0.26	**0.64**	0.31	**0.66**	*n.s.*	0.34
TD_{LW}	*n.s.*	0.15	0.17	0.22	0.12	**0.56**	–0.23	**0.89**	–0.19		0.27	**0.83**	*n.s.*	**0.72**	0.12	*n.s.*	**0.55**
Dh_{EW}	0.22	*n.s.*	–0.41	*n.s.*	0.42	*n.s.*	**0.76**	–0.32	**0.78**	–0.27		0.32	**0.85**	0.40	**0.87**	*n.s.*	0.41
Dh_{LW}	*n.s.*	0.17	0.20	0.24	0.14	0.42	–0.28	**0.78**	–0.24	**0.84**	–0.31		*n.s.*	**0.88**	0.14	–0.14	**0.65**
Kp_{EW}	0.35	*n.s.*	0.12	0.29	0.35	*n.s.*	**0.63**	–0.24	**0.65**	–0.20	**0.82**	–0.24		0.22	**0.99**	*n.s.*	0.16
Kp_{LW}	0.22	0.13	0.27	0.47	0.26	0.34	–0.19	**0.74**	–0.13	**0.77**	–0.18	**0.92**	*n.s.*		0.36	–0.23	**0.64**
Kp	0.41	*n.s.*	0.21	0.45	0.43	0.11	**0.54**	*n.s.*	**0.58**	*n.s.*	**0.72**	*n.s.*	**0.93**	0.29		*n.s.*	0.24
Tair	*n.s.*	**0.51**	0.16	0.26	0.15	0.41	*n.s.*	–0.11	*n.s.*	*n.s.*	*n.s.*	0.11	0.17	0.15	0.21		0.21
P	**0.67**	–0.40	0.42	0.28	–0.20	*n.s.*	–0.24	*n.s.*	–0.26	*n.s.*	–0.31	*n.s.*	*n.s.*	0.10	*n.s.*	0.21	

Note. For the designations of xylem traits see Table 1. T_{air} – mean air temperature for the period from May to September, °C; P – total precipitation for the period from May to September, mm. Significant correlations ($p \leq 0.01$) are shown. Moderate and strong correlations ($|r| \geq 0.5$) are indicated in bold.

($r = -0.59$), and TD_{LW} with N_{LW} ($r = -0.54$). It is noteworthy that the effect of precipitation to pine latewood parameters was higher in the forest SP as compared to the clear-cut SP: Kp_{LW} ($r = 0.64$), Dh_{LW} ($r = 0.65$), TD_{LW} ($r = 0.55$), LD_{LW} ($r = 0.52$), and LW ($r = 0.51$).

Coordination between stem xylem traits and leaf gas exchange parameters. The analysis of the effect of environmental conditions on leaf CO_2/H_2O gas exchange parameters in pine, birch, and aspen that we have previously performed in the same SPs and individuals in July in the 2016–2019 period (Pridacha et al., 2021) allowed us to assess coordination among xylem functional traits and stomatal conductance, and rates of photosynthesis and transpiration. Comparisons of the variability of the xylem and leaf characteristics in birch, aspen, and pine in most cases showed a different response of various species to the habitat change (Fig. 5). Thus, birch proved to be more conservative in the response to changes in ecological conditions in terms of xylem anatomical traits ($\Delta N = 9\%$) but showed the highest variability of functional characteristics of the xylem ($\Delta Kp = 234\%$ and $\Delta Dh = 41\%$) and leaf ($\Delta g_s = 49\%$, $\Delta E = 39\%$, and $\Delta A = 36\%$) than other species. Aspen, as opposed to birch, showed a greater variation of xylem structure ($\Delta N = 45\%$) simultaneously with higher conservatism in the functional traits of the xylem ($\Delta Kp = 86\%$ and $\Delta Dh = 30\%$) and leaf ($\Delta g_s = 32\%$, $\Delta A = 27\%$ and $\Delta E = 19\%$). In pine, the variability of most of structural and functional characteristics was similar to those of aspen ($\Delta Kp = 95\%$, $\Delta N = 50\%$, $\Delta Dh = 30\%$, $\Delta A = 25\%$), and some showed similarity to the variability in birch ($\Delta g_s = 45\%$, $\Delta E = 39\%$). Importantly, the highest variability of the water potential of foliated shoots between the clear-cut and the forest SPs was found for aspen ($\Delta\Psi = 13\%$) and lower for pine ($\Delta\Psi = 8\%$). This parameter in birch had similar values in both SPs ($\Delta\Psi$, $p > 0.05$).

DISCUSSION

The seasonal and interannual variability of xylem anatomical characteristics in woody plants is known to reflect the processes of cells division in the cambial zone, radial cell enlargement and cell wall formation, which are under hormonal and genetic control and influenced directly and indirectly by external environmental conditions (Fritts, 1976; Vaganov et al., 2006; Hacke, 2015).

Effects of plant growth conditions on stem xylem traits. Our previous study (Pridacha et al., 2021) of soil and plant cover characteristics as well as meteorological parameters in the clear-cut SP and the forest SP revealed significant differences between the habitat conditions of SPs. The differences were manifested in the lower nutrient availability in the organic horizon of the disturbed soil of the clear-cut SP versus the forest SP. The ground vegetation in the clear-cut SP featured a higher diversity of light-demanding species of vascular plants and, vice versa, a pronounced degradation of the moss and lichen layer compared to the forest SP. Microclimate in the clear-cut SP in July 2016–2019 featured higher mean daytime values of photosynthetically active radiation (1218 μmol m^{-2} s^{-1}), water vapour pressure deficit (2.2 kPa), air (27.1°C) and soil (16.1°C) temperatures compared to the forest SP (240 μmol m^{-2} s^{-1}, 1.3 kPa, 22.4°C and 13.8°C, respectively). At the same time, the mean values of field soil moisture of the root layer (0–50 cm) in the clear-cut SP and the forest SP were similar (10.5 and 10.3%, respectively).

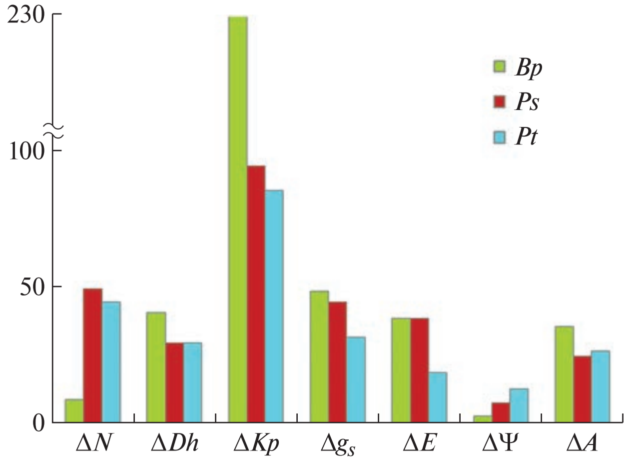

Fig. 5. Variability (%) of stem xylem traits and leaf gas exchange parameters of *Betula pendula* (*Bp*), *Pinus sylvestris* (*Ps*), and *Populus tremula* (*Pt*) across plant growth conditions in the 2016–2019 period. For the designations of xylem traits see Table 1; g_s – stomatal conductance, A – photosynthesis rate, E – transpiration rate, Ψ – water potential.

The contrasting habitat conditions in the clear-cut SP and the forest SP have significantly influenced the cambial activity and formation of xylem structure in all tree species (Table 2). Both pine and the angiosperm tree species in the clear-cut site demonstrated the highest values of TRW, vessel (tracheid) cell wall thickness, lumen radial diameter in the vessels (tracheids), Dh, and Kp (Table 3). The unidirectional increase in the lumen diameter of xylem vessels (tracheids) in pine and the angiosperm trees growing in the high-light conditions of the clear-cut SP was apparently due to a general intensification of growth processes in all tree species, in particular extension growth of cells (Olson et al., 2014). In turn, the increase of the Kp value in the trees from the clear-cut SP is supposed to promote water supply to leaves and the processes of photosynthesis and transpiration (Bussotti et al., 2015; Brodribb et al., 2017), in agreement with our data on the highest values of stomatal conductance and rates of photosynthesis and transpiration in conifer and angiosperm tree species in the clear-cut SP (Pridacha et al., 2021).

In the process of xylogenesis, substantial amounts of organic matter get bound as cell wall polysaccharides (Deslauriers et al., 2009; Simard et al., 2013). The increase in cell wall thickness in the xylem of angiosperm trees growing in the clear-cut SP and getting sufficient amounts of light can be explained by a higher supply of photoassimilates from the leaves to the stem xylem cells, in also agreement with higher photosynthesis rates in birch and aspen in the clear-cut SP (Pridacha et al., 2021). On the contrary, the reduction in the cell wall thickness of earlywood tracheids in pine trees from the clear-cut SP with a simultaneous increase in their lumen diameter might be a consequence of cells expansion. The reduction in this parameter in pine may have the aim of enhancing the water supply to compensate for the transpiration losses under high light conditions in the clear-cut SP as compared to the forest SP. At the same time, the patterns we observed in the thickness of cell walls of early- and latewood tracheids in pine have been attributed both to the various functions of early- and latewood cells (Sperry et al., 2006; Hacke, 2015) and to cambial activity decline during the growing season (Antonova, Stasova, 1997; Olano et al., 2014). Indirect evidence of the higher metabolic cost of water conducting elements in pine xylem due to a higher contribution to the weight of cell walls compared to angiosperm tree species is the higher specific carbon content per unit needle area that we observed in pine in both SPs (Pridacha et al., 2021).

Effects of climatic factors on stem xylem traits. The fact that TRW showed the highest interannual variability (Fig. 3, 4) among all other xylem traits in all tree species was quite predictable given that this parameter is highly sensitive to variations in the natural environment and climate (Babushkina et al., 2019; Nola et al., 2020). The high variability of TRW is in good agreement with the moisture conditions during the study period (2016–2019), characterized by alternation of wetter and drier periods. A majority of xylem anatomical characteristics in pine, birch, and aspen demonstrated higher conservatism in interannual variability than TRW. Moderate variability of the normalized values of anatomical parameters in the 2016–2019 period suggests that different species respond similarly to interannual variation of air temperature and precipitation close to the region's climate normal. This pattern may also indicate the ability of the tree species to adapt to a wide range of environmental conditions (Tikhova et al., 2017; Pridacha et al., 2018; Sazonova et al., 2019). Non-specific changes in xylem anatomical and hydraulic traits in pine and the angiosperm species might be due to the similarity of their evolutionarily developed adaptations to changing environmental conditions since these species grow in the regions with the same climatic variability.

At the same time, species-specific sensitivity of xylem anatomical features to climate factors has been reported for woody plants (Anderegg, 2015; Sperry, Love, 2015). Thus, pine radial growth in the northern European Russia showed a positive correlation with warm and moist conditions in the current growing season, whereas TRW in spruce strongly correlated with cool and moist conditions in the previous growing season (Hughes et al., 2019). We have also detected species-specific features in correlations between stem xylem traits and climatic factors in the period from May to September 2016–2019, which differed between the two habitats (Tables 4, 5, 6). The angiosperm trees under forest canopy showed a significant ($|r| > 0.5$) positive correlation between TRW and precipitation in the current growing season, whereas for pine in this habitat precipitation had a positive effect on latewood characteristics. In the clear-cut site, the warm and moist conditions in the current growing season promoted LW and TRW in pine, while in birch they had a positive effect on N and a negative effect on Dh. In aspen in the clear-cut SP, no strong correlations were found ($|r| < 0.5$) between xylem traits and air temperature (precipitation) in the current growing season. A strong positive effect of precipitations on latewood width in pine has also been reported for the South Siberian forest-steppe zone (Arzac et al., 2018).

Associations among stem xylem traits. Correlation analysis showed that in most cases the angiosperm tree species (Tables 4 and 5) exhibited correlations of similar strength and direction for the parameters characterizing cell wall formation (VWT and FWT), extension growth (VLD and VD), cell generation (TRW and N), and water supply (Dh and Kp). Similar patterns were found in pine as well (Table 6). The interspecies comparison of xylem traits revealed similar Dh values in pine and the angiosperm trees while Kp increased along the birch < aspen < pine sequence in both SPs. This fact might be due to the increase in N, which also occurred along the birch < aspen < pine sequence in both SPs. It is noteworthy that the actual hydraulic conductivity may differ from the Kp value as calculations of the latter do not take into account the axial dimension of the vessel (tracheid), the number and structural and functional characteristics of the pits linking the vessels (tracheids). We know on the other hand that tracheids in gymnosperms should experience greater specific hydraulic resistance than vessels in angiosperms given that tracheids are approximately 10 times shorter than vessels of the same diameter (Pittermann et al., 2005). Conifers, however, solve this problem by maximizing the number of tracheids per unit of wood area and maintaining the functional activity of sapwood for several years compared to the single outermost ring in ring-porous angiosperms (Venturas et al., 2017). Also, angiosperms are known to have functional limitations on the maximum vessel diameter meant to make the xylem more resistant to embolism after frosts (Hacke et al., 2017). Conifers, on the other hand, feature a nearly 60 times higher efficiency in conducting water by the torus-margo pit structure in tracheids compared to inter-vessel pit of angiosperms (Pittermann et al., 2005). Owing to this functional feature, conifers can reduce the hydraulic resistance of the xylem and, furthermore, compete with angiosperms in hydraulic efficiency and safety (Choat et al., 2012). At the same time, many recent studies demonstrate fairly close agreement between the estimates of xylem hydraulic conductivity and cavitation resistance obtained by physical, optical, and microscopic methods (Gauthey et al., 2020; Chen et al. 2021). Therefore, we feel it quite safe to use the obtained xylem traits for comparisons among tree species.

The comparison of xylem anatomical and hydraulic parameters demonstrated a clear relationship of N – Dh – Kp in all the species. Variations of the number and diameter of xylem conduits play an important role in the adaptation of woody plants to the habitat conditions (Hacke, 2015). Wider vessels conduct water more effectively while smaller and more numerous vessels are less prone to embolism (Fonti et al., 2010; Chen et al., 2020). In the trees growing in the forest SP an increase in N led to a reduction in Dh and Kp in all the species, whereas in the clear-cut SP, on the contrary, a reduction in N promoted Dh and Kp in all the species. The increase in N in pine, birch, and aspen can be explained by their compensatory response to reduced xylem hydraulic conductivity versus that in the clear-cut SP. The Kp reduction observed in all the species in the forest SP is likely a result of the limited availability of soil moisture due to higher competition for water resources in a mature tree stand, caused in particular by moisture interception by roots of adult trees. Besides, the significant increase in N in aspen at the forest SP apparently enables the water exchange rate, in particular stomatal conductance and transpiration rate, to be reduced less than in other species in this habitat (Pridacha et al., 2021). Another supposition is that the higher VWT values in aspen versus birch in both SPs would drive increased resistance to xylem dysfunction due to possible vessel destruction by high internal negative pressure. This is also indirectly evidenced by previously detected highest values of the calcium biological absorption coefficient and calcium content in leaves in aspen versus other species (Pridacha et al., 2021), considering that calcium enhances cell wall rigidity as it forms Ca-pectate complexes with pectin components (Lambers, Oliveira, 2019). This fact, however, does not reduce the Kp value in aspen. Higher Kp values in aspen versus birch in both SPs are due to higher N, which enhances the hydraulic efficiency of the xylem on the one hand and provides the resistance to xylem embolism caused by water potential drop on the other, as mentioned also by other researchers (Rodriguez-Zaccaro et al., 2021).

Coordination between stem xylem traits and leaf gas exchange parameters. Analysis of coordination between stem xylem traits and leaf gas exchange parameters in different species shows the water-use strategies to be different in birch, aspen, and pine. An increase in N along with similar values of Dh in all the species promotes Kp. In view of this, the hydraulic structure seems to be more efficient and safer in aspen and pine due to higher N and Kp values and thicker cell walls of vessels (tracheids) in the xylem. High xylem resistance to cavitation usually helps plants to survive under drier environments (Fonti et al., 2010; Hacke, 2015). Hence, aspen and pine can be expected to be more resistant to the water stress than birch. In the habitat gradient, aspen and pine exhibit higher variability of xylem structural characteristics (ΔN) simultaneously with greater conservatism in its functional parameters (ΔDh and ΔKp) as well as more variable water potential of shoots (Fig. 5), indicating an anisohydric water-use strategy. Birch, on the contrary, tends to the isohydric water-use strategy, as corroborated by the results of other authors (Klein, 2014; Meinzer et al., 2016; Hochberg et al., 2018; Sellin et al., 2019). The greater conservatism of the xylem structure in birch (ΔN) simultaneously with the greater variability of its functional traits (ΔDh and ΔKp) with the most pronounced changes in stomatal conductance (Δg_s) and transpiration rate (ΔE) helps maintaining the homeostasis of the water potential of shoots (ΔΨ) across the habitats. This isohydric behavior leads to the most significant change in the rate of photosynthesis (ΔA) along the gradient of ecological conditions in birch as compared to aspen and pine. On the other hand, the less strict stomatal control (Δg_s) for reducing transpiration water loses (ΔE) and preventing water stress in aspen facilitates a higher photosynthetic activity (ΔA) than in birch. The strategy of adaptation to the habitat change in pine is a compromise, with structural and functional parameter responses similar to both aspen (ΔN, ΔDh and ΔKp, ΔΨ, ΔA), and to birch (Δg_s and ΔE), which probably provides the conifer with adaptation advantage over the deciduous species in a wide range of ecological conditions.

Importantly, the patterns described above were revealed for local climate, forest and soil conditions. We admit that under more contrasting climatic, topographic and edaphic conditions the functional relationships may prove to be different (Kannenberg et al., 2022). Further experimental and modeling studies are necessary to assess more accurately and comprehensively the effects of spatial and temporal variability of abiotic factors on the structural and functional traits of evergreen gymnosperm and deciduous angiosperm tree species.

CONCLUSIONS

The results of this experimental study supported our working hypothesis that evergreen gymnosperm and deciduous angiosperm tree species respond similarly to changes in plant growth conditions and climate in the European North. In most cases, different tree species demonstrated a unidirectional response of stem xylem traits and leaf gas exchange parameters to changes in the habitat and interannual variability of climatic factors. At the same time, some interspecific differences were found in the coordination of structural and functional traits and their variability. The patterns revealed suggest that the predicted increase in the frequency of extreme weather events at high northern latitudes, namely periods of heavy heat and drought, will promote the competitive ability of Scots pine and aspen, which build a more efficient and safer hydraulic structure compared to silver birch, whose xylem is more vulnerable to drought-induced cavitation, by raising CO_2 gas exchange and productivity in drier environments. This assessment is important for better understanding the direction and magnitude of the flora composition and ranges of boreal plant species in changing the natural environment and the climate.

ACKNOWLEDGEMENTS

The authors are grateful to colleagues A.N. Pekkoev, D.E. Semin and L.I. Semenova for assistance in sampling and carrying out anatomical analyses within the study; to T.A. Sazonova for the support on the study. The study was supported by the Russian Foundation of Basic Research (grant 17-04-01087-a) and the Karelian Research Centre of the Russian Academy of Sciences (Forest Research Institute KarRC RAS).

REFERENCES

Anderegg W.R.L. 2015. Spatial and temporal variation in plant hydraulic traits and their relevance for climate change impacts on vegetation. – New Phytol. 205: 1008–1014. https://doi.org/10.1111/nph.12907

Anderegg W.R.L., Anderegg L.D.L., Kerr K.L., Trugman A.T. 2019. Widespread drought-induced tree mortality at dry range edges indicates that climate stress exceeds species' compensating mechanisms. – Glob. Change Biol. 25: 3793–3802. https://doi.org/10.1111/gcb.14771

Antonova G.F., Stasova V.V. 1997. Effects of environmental factors on wood formation in larch (*Larix sibirica* Ldb.) stems. – Trees. 11 (8): 462–468.

Arzac A., Babushkina E.A., Fonti P., Slobodchikova V., Sviderskaya I.V., Vaganov E.A. 2018. Evidences of wider latewood in *Pinus sylvestris* from a forest-steppe of Southern Siberia. – Dendrochronologia. 49: 1–8. https://doi.org/10.1016/j.dendro.2018.02.007

Babushkina E.A., Belokopytova L.V., Zhirnova D.F., Vaganov E.A. 2019. Siberian spruce tree ring anatomy: imprint of development processes and their high-temporal environmental regulation. – Dendrochronologia. 53: 114–124. https://doi.org/10.1016/j.dendro.2018.12.003

Benson M.C., Miniat C.F., Oishi A., Denham S.O., Domec J.C., Johnson D.M., Missik J.E., Phillips R.P., Wood J.D., Novick K.A. 2022. The xylem of Anisohydric *Quercus alba* L. is more vulnerable to embolism than isohydric codominants. – Plant Cell Environ. 45: 329– 346. https://doi.org/10.1111/pce.14244

Bonan G.B. 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. – Science 320: 1444–1449. https://doi.org/10.1126/science.1155121

Bouche P.S., Larter M., Domec J.C., Burlett R., Gasson P., Jansen S., Delzon S. 2014. A broad survey of hydraulic and mechanical safety in the xylem of conifers. – J. Exp. Bot. 65: 4419–4431. https://doi.org/10.1093/jxb/eru218

Brodribb T.J., Cochard H. 2009. Hydraulic failure defines the recovery and point of death in water-stressed conifers. – Plant Physiol. 149: 575–584. https://doi.org/10.1104/pp.108.129783

Brodribb T.J., McAdam S.A.M., Carins Murphy M.R. 2017. Xylem and stomata, coordinated through time and space. – Plant Cell Environ. 40: 872–880. https://doi.org/10.1111/pce.12817

Buckley T.N. 2019. How do stomata respond to water status? – New Phytol. 224: 21–36. https://doi.org/10.1111/nph.15899

Bussotti F., Pollastrini M., Holland V., Brüggemann W. 2015. Functional traits and adaptive capacity of European forests to climate change. – Environ. Exp. Bot. 111: 91–113. https://doi.org/10.1016/j.envexpbot.2014.11.006

Chen Y.J., Maenpuen P., Zhang Y.J., Barai K., Katabuchi M., Gao H., Kaewkamol S., Tao L.B., Zhang J.L. 2021. Quantifying vulnerability to embolism in tropical trees and lianas using five methods: can discrepancies be explained by xylem structural traits? – New Phytol. 229: 805–819. https://doi.org/10.1111/nph.16927

Chen Z., Zhu S., Zhang Y., Luan J., Li S., Sun P., Wan X., Liu S. 2020. Tradeoff between storage capacity and embolism resistance in the xylem of temperate broadleaf tree species. – Tree Physiol. 40: 1029–1042. https://doi.org/10.1093/treephys/tpaa046

Choat B., Cobb A.R., Jansen S. 2008. Structure and function of bordered pits: new discoveries and impacts on whole-plant hydraulic function. – New Phytol. 177: 608–626. https://doi.org/10.1111/j.1469-8137.2007.02317.x

Choat B., Jansen S., Brodribb T.J., Cochard H., Bhaskar R., Bucci S.J., Delzon S., Feild T.S., Gleason S., Jacobson A.L., Lens F., Maherali H., Martinez-Vilalta J., Mayr S., Mencuccini M., Mitchell P.J., Nardini A., Pittermann J., Pratt R.B., Sperry J.S., Westoby M., Wright I.J., Zanne A. 2012. Global convergence in the vulnerability of forests to drought. – Nature. 491: 752–755. https://doi.org/10.1038/nature11688

Deslauriers A., Giovannelli A., Rossi S., Castro G., Fragnelli G., Traversi L. 2009. Intra-annual cambial activity and carbon availability in stem of poplar. – Tree Physiol. 29: 1223–1235. https://doi.org/10.1093/treephys/tpp061

FAO. 2020. Global Forest Resources Assessment 2020 – Key findings. Rome. 16 p. https://doi.org/10.4060/ca8753en

Fonti P., von Arx G., García-González I., Eilmann B., Sass-Klaassen U., Gärtner H., Eckstein D. 2010. Studying global change through investigation of the plastic responses of xylem anatomy in tree rings. – New Phytol. 185 (1): 42–53. https://doi.org/10.1111/j.1469-8137.2009.03030.x

Fritts H.C. 1976. Tree rings and climate. London. 567 p.

Gauthey A., Peters J.M.R., Carins-Murphy M.R., Rodriguez-Dominguez C.M., Li X., Delzon S., King A., López R., Medlyn B.E., Tissue D.T., Brodribb T.J., Choat B. 2020. Visual and hydraulic techniques produce similar estimates of cavitation resistance in woody species. – New Phytol. 228: 884–897. https://doi.org/10.1111/nph.16746

Gleason S.M., Westoby M., Jansen S., Choat B., Hacke U.G., Pratt R.B., Bhaskar R., Brodribb T.J., Bucci S.J., Cao K.F., Cochard H., Delzon S., Domec J.C., Fan Z.X., Feild T.S., Jacobsen A.L., Johnson D.M., Lens F., Maherali H., Martínez-Vilalta J., Mayr S., McCulloh K.A., Mencuccini M., Mitchell P.J., Morris H., Nardini A., Pittermann J., Plavcová L., Schreiber S.G., Sperry J.S., Wright I.J., Zanne A.E. 2016. Weak tradeoff between xylem safety and xylem-specific hydraulic efficiency across the world's woody plant species. – New Phytol. 209: 123–136. https://doi.org/10.1111/nph.13646

Groisman P., Shugart H., Kicklighter D., Henebry G., Tchebakova N., Maksyutov S., Monier E., Gutman G., Gulev S., Qi J., Prishchepov A., Kukavskaya E., Porfiriev B., Shiklomanov A., Loboda T., Shiklomanov N., Nghiem S., Bergen K., Albrechtova J., Chen J., Shahgedanova M., Shvidenko A., Speranskaya N., Soja A., de Beurs K., Bulygina O., McCarty J., Zhuang Q., Zolina O. 2017. Northern Eurasia Future Initiative (NEFI): facing the challenges and pathways of global change in the twenty-first century. – Prog. Earth Planet. Sci. 4: 41. https://doi.org/10.1186/s40645-017-0154-5

Gromtsev A.N. (ed.). 2003. Biotic diversity of Karelia: conditions of formation, communities and species. Petrozavodsk. 244 p. (In Russ. and Eng.)

Hacke U.G. (ed.). 2015. Functional and Ecological Xylem Anatomy. Springer, Cham. 281 p. https://doi.org/10.1007/978-3-319-15783-2

Hacke U.G., Sperry J.S. 2001. Functional and ecological xylem anatomy. – Perspect. Plant Ecol. Evol. Syst. 4 (2): 97–115.

Hacke U.G., Spicer R., Schreiber S.G., Plavcová L. 2017. An ecophysiological and developmental perspective on variation in vessel diameter. – Plant Cell Environ. 40: 831–45. https://doi.org/10.1111/pce.12777

Hochberg U., Rockwell F.E., Holbrook N.M., Cochard H. 2018. Iso/Anisohydry: a plant-environment interaction rather than a simple hydraulic trait. – Trends Plant Sci. 23: 112–120. https://doi.org/10.1016/j.tplants.2017.11.002

Hughes M.K., Olchev A., Bunn A.G., Berner L.T., Loslebe M., Novenko E. 2019. Different climate responses of spruce and pine growth in Northern European Russia. – Dendrochronologia. 56: 125601. https://doi.org/10.1016/j.dendro.2019.05.005

IAWA list of microscopic features for hardwood identification. 1989. – IAWA Bulletin. 10: 219–332.

IPCC Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. 2013. Cambridge. 1535 p.

Jin K., Liu X., Wang K., Jiang Z., Tian G., Yang S., Shang L., Ma J. 2018. Imaging the dynamic deposition of cell wall polymer in xylem and phloem in Populus×euramericana. – Planta. 248: 849–858. https://doi.org/10.1007/s00425-018-2931-9

Kannenberg S.A., Guo J.S., Novick K.A., Anderegg W.R.L., Feng X., Kennedy D., Konings A.G., Martínez-Vilalta J., Matheny A.M. 2022. Opportunities, challenges and pitfalls in characterizing plant water-use strategies. – Funct. Ecol. 36: 24–37. https://doi.org/10.1111/1365-2435.13945

Kawai K., Minagi K., Nakamura T., Saiki S.T., Yazaki K., Ishida A. 2022. Parenchyma underlies the interspecific variation of xylem hydraulics and carbon storage across 15 woody species on a subtropical island in Japan. – Tree Physiol. 42 (2): 337–350. https://doi.org/10.1093/treephys/tpab100

Kishchenko I.T., Vantenkova I.V. 2013. Sezonnyj rost listvennyh lesoobrazuyushchih vidov v taezhnoj zone Rossii (na primere Karelii) [Seasonal growth of deciduous forest-forming species in the taiga zone of Russia (on the example of Karelia)]. Petrozavodsk. 94 p. (In Russ.).

Kishchenko I.T., Vantenkova I.V. 2014. Sezonnyj rost hvojnyh lesoobrazuyushchih vidov v taezhnoj zone Rossii (na primere Karelii) [Seasonal growth of coniferous forest-forming species in the taiga zone of Russia (by the example of Karelia)]. Petrozavodsk. 163 p. (In Russ.).

Klein T. 2014. The variability of stomatal sensitivity to leaf water potential across tree species indicates a continuum between isohydric and anisohydric behaviours. – Funct. Ecol. 28: 1313–1320. https://doi.org/10.1111/1365-2435.12289

Lachenbruch B., McCulloh K.A. 2014. Traits, properties, and performance: how woody plants combine hydraulic and mechanical functions in a cell, tissue, or whole plant. – New Phytol. 204: 747–764. https://doi.org/10.1111/nph.13035

Lambers H., Oliveira R.S. 2019. Plant physiological ecology. Springer Nature Switzerland AG. 736 p.

Manzoni S., Vico G., Katul G., Palmroth S., Jackson R.B., Porporato A. 2013. Hydraulic limits on maximum plant transpiration and the emergence of the safety–efficiency trade-off. – New Phytol. 198: 169–178. https://doi.org/10.1111/nph.12126

Martinez-Vilalta J., Garcia-Forner N. 2017. Water potential regulation, stomatal behavior and hydraulic transport under drought: deconstructing the iso/anisohydric concept. – Plant Cell Environ. 40: 962–976. https://doi.org/10.1111/pce.12846

Meinzer F.C., Woodruff D.R., Marias D.E., Smith D.D., McCulloh K.A., Howard A.R., Magedman A.L. 2016. Mapping 'hydroscapes' along the iso- to anisohydric continuum of stomatal regulation of plant water status. – Ecol. Lett. 19: 1343–1352. https://doi.org/10.1111/ele.12670

Nardini A., Savi T., Trifilò P., Gullo M.A. 2018. Drought stress and the recovery from xylem embolism in woody plants. – Progress in Botany. 79: 197–232. https://doi.org/10.1007/124_2017_11

Nazarova L.E. 2015. Precipitation over the territory of Karelia. – Transactions of KarRC RAS. 9: 114–120 (In Russ.).
https://doi.org/10.17076/lim56

Niinemets U. 2010. Responses of forest trees to single and multiple environmental stresses from seedlings to mature plants: Past stress history, stress interactions, tolerance and acclimation. – Forest Ecol. Manag. 260: 1623–1639.
https://doi.org/10.1016/j.foreco.2010.07.054

Nola P., Bracco F., Assini S., von Arx G., Castagneri D. 2020. Xylem anatomy of *Robinia pseudoacacia* L. and *Quercus robur* L. is differently affected by climate in a temperate alluvial forest. – Ann. For. Sci. 77 (8).
https://doi.org/10.1007/s13595-019-0906-z

Olano J.M., Linares J.C., García-Cervigón A.I., Arzac A., Delgado A., Rozas V. 2014. Drought-induced increase in water-use efficiency reduces secondary tree growth and tracheid wall thickness in a Mediterranean conifer. – Oecologia. 176 (1): 273–283.
https://doi.org/10.1007/s00442-014-2989-4

Oliveira R.S., Eller C.B., Barros F.d.V., Hirota M., Brum M., Bittencourt P. 2021. Linking plant hydraulics and the fast–slow continuum to understand resilience to drought in tropical ecosystems. – New Phytol. 230: 904–923.
https://doi.org/10.1111/nph.17266

Olson M.E., Soriano D., Rosell J.A., Anfodillo T., Donoghue M.J., Edwards E.J., León-Gómez C., Dawson T., Martínez J.J.C., Castorena M., Echeverría A., Espinosa C.I., Fajardo A., Gazol A., Isnard S., Lima R.S., Marcati C.R., Méndez-Alonzo R. 2018. Plant height and hydraulic vulnerability to drought and cold. – Proc. Natl. Acad. Sci. USA. 115 (29): 7551–7556.
https://doi.org/10.1073/pnas.1721728115

Olson M.E., Anfodillo T., Rosell J.A., Petit G., Crivellaro A., Isnard S., León-Gómez C., Alvarado-Cárdenas L.O., Castorena M. 2014. Universal hydraulics of the flowering plants: vessel diameter scales with stem length across angiosperm lineages, habits and climates. – Ecol. Lett. 17: 988–997.
https://doi.org/10.1111/ele.12302

Peel M.C., Finlayson B.L., McMahon T.A. 2007. Updated world map of the Koppen-Geiger climate classification. – Hydrol. Earth Syst. Sci. 11: 1633–1644.
https://doi.org/10.5194/hess-11-1633-2007

Pittermann J., Sperry J.S., Hacke U.G., Wheeler J.K., Sikkema E.H. 2005. Torus-margo pits help conifers compete with angiosperms. – Science 310: 1924.
https://doi.org/10.1126/science.1120479

Price D.T., Alfaro R.I., Brown K.J., Flannigan M.D., Fleming R.A., Hogg E.H., Girardin M.P., Lakusta T., Johnston M., McKenney D.W., Pedlar J.H., Stratton T., Sturrock R.N., Thompson I.D., Trofymow J.A., Venier L.A. 2013. Anticipating the consequences of climate change for Canada's boreal forest ecosystems. – Environ. Rev. 21: 322–365.
https://doi.org/10.1139/er-2013-0042

Pridacha V.B., Sazonova T.A., Novichonok E.V., Semin D.E., Tkachenko Yu.N., Pekkoev A.N., Timofeeva V.V., Bakhmet O.N., Olchev A.V. 2021. Clear-cutting impacts nutrient, carbon and water exchange parameters in woody plants in an east Fennoscandian pine forest. – Plant Soil. 466: 317–336.
https://doi.org/10.1007/s11104-021-05058-w

Pridacha V.B., Tikhova G.P., Sazonova T.A. 2018. The effect of abiotic factors on water exchange in coniferous and deciduous plants. – Transactions of KarRC RAS. 12: 76–86 (In Russ.).
https://doi.org/10.17076/eb878

Reich P.B., Sendall K.M., Stefanski A., Rich R.L., Hobbie S.E., Montgomery R.A. 2018. Effects of climate warming on photosynthesis in boreal tree species depend on soil moisture. – Nature. 562: 263–267.
https://doi.org/10.1038/s41586-018-0582-4

Rodriguez-Zaccaro F.D., Henry I.M., Groover A. 2021. Genetic regulation of vessel morphology in *Populus*. – Front. Plant Sci. 12.
https://doi.org/10.3389/fpls.2021.705596

Sazonova T.A., Bolondinskii V.K., Pridacha V.B. 2019. Resistance to moisture transport in the conductive system of Scots pine. – Russ. J. For. Sci. 6: 556–566 (In Russ.).
https://doi.org/10.1134/S0024114819060081

Scholz A., Klepsch M., Karimi Z., Jansen S. 2013. How to quantify conduits in wood? – Front. Plant Sci. 4: 56.
https://doi.org/10.3389/fpls.2013.00056

Sellin A., Taneda H., Alber M. 2019. Leaf structural and hydraulic adjustment with respect to air humidity and canopy position in silver birch (*Betula pendula*). – J. Plant Res. 132: 369–381.
https://doi.org/10.1007/s10265-019-01106-w

Sevanto S., Hölttä T., Holbrook N.M. 2011. Effects of the hydraulic coupling between xylem and phloem on diurnal phloem diameter variation. – Plant Cell Environ. 34: 690–703.
https://doi.org/10.1111/j.1365-3040.2011.02275.x

Simard S., Giovannelli A., Treydte K., Traversi M.L., King G.M., Frank D., Fonti P. 2013. Intra-annual dynamics of non-structural carbohydrates in the cambium of mature conifer trees reflects radial growth demands. – Tree Physiol. 33: 913–923.
https://doi.org/10.1093/treephys/tpt075

Sperry J.S., Hacke U.G., Pitterman J. 2006. Size and function in conifer tracheids and angiosperm vessels. – Am. J. Bot. 93: 1490–1500.
https://doi.org/10.3732/ajb.93.10.1490

Sperry J.S., Love D.M. 2015. What plant hydraulics can tell us about responses to climate-change droughts. – New Phytol. 207: 14–27.
https://doi.org/10.1111/nph.13354

Sterck F.J., Zweifel R., Sass-Klaassen U., Chowdhury Q. 2008. Persisting soil drought reduces leaf specific conductivity in Scots pine (*Pinus sylvestris*) and pubescent oak (*Quercus pubescens*). – Tree Physiol. 28 (4): 529–36.
https://doi.org/10.1093/treephys/28.4.529

Stroock A.D., Pagay V.V., Zwieniecki M.A., Holbrook N.M. 2014. The physicochemical hydrodynamics of vascular plants. – Annu. Rev. Fluid Mech. 46: 615–642.
https://doi.org/10.1146/annurev-fluid-010313-141411

Sviderskaya I.V., Vaganov E.A., Fonti M.V., Fonti P. 2021. Isometric scaling to model water transport in conifer tree rings across time and environments. – J. Exp. Bot. 72: 2672–2685.
https://doi.org/10.1093/jxb/eraa595

Tikhova G.P., Pridacha V.B., Sazonova T.A. 2017. The influence of air temperature and relative humidity on dynamics of water potential in *Betula pendula* (Betulaceae) trees. – Sib. J. For. Sci. 1: 56–64 (In Russ.). https://doi.org/10.15372/SJFS20170106

Tyree M.T., Zimmermann M.H. 2002. Xylem Structure and the Ascent of Sap. 2nd Edn. Berlin, Heidelberg, New York. 365 p.

Urli M., Porté A.J., Cochard H., Guengant Y., Burlett R., Delzon S. 2013. Xylem embolism threshold for catastrophic hydraulic failure in angiosperm trees. – Tree Physiol. 33: 672–83. https://doi.org/10.1093/treephys/tpt030

Vaganov E.A., Hughes M.K., Shashkin A.V. 2006. Growth dynamics of conifer tree rings images of past and future environments. Berlin. 367 p.

Venturas M.D., Sperry J.S., Hacke U.G. 2017. Plant xylem hydraulics: what we understand, current research, and future challenges. – J. Integr. Plant Biol. 59 (6): 356–389. https://doi.org/10.1111/jipb.12534

Xiong D., Nadal M. 2020. Linking water relations and hydraulics with photosynthesis. – Plant J. 101 (4): 800–815. https://doi.org/10.1111/tpj.14595

Zheng J., Li Y., Morris H., Vandelook F., Jansen S. 2022. Variation in tracheid dimensions of conifer xylem reveals evidence of adaptation to environmental conditions. – Front. Plant Sci. 13. https://doi.org/10.3389/fpls.2022.774241

ЗНАЧЕНИЕ СОГЛАСОВАННОСТИ ПРИЗНАКОВ КСИЛЕМЫ СТВОЛА И ПАРАМЕТРОВ ГАЗООБМЕНА ЛИСТА ПРИ ФОРМИРОВАНИИ АДАПТАЦИИ У НЕКОТОРЫХ БОРЕАЛЬНЫХ ВИДОВ В КАРЕЛИИ

В. Б. Придача[a,#], **Т. В. Тарелкина**[a], **Я. А. Неронова**[a], **Н. В. Туманик**[a]

[a] *Институт леса Карельского научного центра РАН*
ул. Пушкинская, 11, Петрозаводск, 185910, Россия
[#] *e-mail: pridacha@krc.karelia.ru*

Оценка устойчивости лесных сообществ и отдельных видов к внешним воздействиям требует проведения исследований возможных ответных реакций видов, сообществ и экосистем в разных регионах на прогнозируемые изменения природной среды и климата. Целью исследования было оценить изменчивость анатомических и гидравлических характеристик ксилемы и их согласованность с показателями CO_2/H_2O-газообмена у голосеменного и покрытосеменных древесных растений в ходе естественного лесовосстановления на вырубке сосняка черничного в условиях Европейского Севера. Для этого провели анализ влияния фитоценотических условий и климатических факторов на структурно-функциональные характеристики подроста сосны обыкновенной (*Pinus sylvestris* L.), березы повислой (*Betula pendula* Roth) и осины (*Populus tremula* L.) на сплошной вырубке и под пологом сосняка черничного в течение четырех вегетационных периодов в условиях среднетаежной подзоны Карелии. Выявлена преимущественно схожая направленность реакций анатомических и гидравлических характеристик ксилемы и показателей CO_2/H_2O-газообмена листа разных видов на изменение фитоценотических условий и климатических факторов. На вырубке как у сосны, так и у листопадных видов отмечены максимальные значения гидравлического диаметра трахеид и сосудов, потенциальной гидравлической проводимости ксилемы и, напротив, минимальные значения удельной плотности трахеид и сосудов. В межгодовой динамике климатических факторов у всех видов выявлена максимальная изменчивость годичных приростов по сравнению с большей консервативностью других характеристик ксилемы. Вместе с тем показаны межвидовые особенности согласованности гидравлических характеристик ксилемы, устьичной проводимости, интенсивности фотосинтеза и транспирации и их изменчивость у систематически разных видов, которые указывают на разные стратегии гидравлического поведения (isohydric/anisohydric) у березы, осины и сосны. Прогнозируемое увеличение повторяемости периодов сильной жары и засухи в высоких широтах усилит конкурентоспособность сосны и осины, формирующих более эффективную и безопасную гидравлическую структуру относительно березы, посредством роста CO_2-газообмена и продуктивности в засушливых условиях.

Ключевые слова: древесные растения, гидравлическая проводимость ксилемы, фотосинтез, транспирация, факторы среды

БЛАГОДАРНОСТИ

Авторы выражают благодарность коллегам А.Н. Пеккоеву, Д.Е. Семину и Л.И. Семеновой за помощь в отборе проб и проведении анатомических исследований; Т.А. Сазоновой за поддержку в проведении исследования. Финансовое обеспечение исследований осуществлялось из средств федерального бюджета на выполнение государственного задания КарНЦ РАН (Институт леса КарНЦ РАН) и при финансовой поддержке РФФИ (грант 17-04-01087-а).