Original article
УДК 581.412:581.824.1:630.181
DOI: 10.37482/0536-1036-2025-6-33-47

A Strategy for Adapting the Hydraulic System of Woody Plants to Various Tiers of the Floodplain Forest of the Enmyvaam River (Chukotka)

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Received on May 19, 2024 / Approved after reviewing on October 26, 2024 / Accepted on October 28, 2024

Abstract. The article examines the features of the anatomical structure of the hydraulic system of 17 species from 13 genera of 6 families of woody flowering plants, which belong to different tiers of the floodplain forest growing along the Enmyvaam River (hypoarctic tundra). It has been found that 1st-tier trees have the most advanced hydraulic system. It consists only of libriform fibers and vascular segments of a short-cylindrical, cylindrical fibrous shape with simple perforations, punctate alternate, closed, and close-set intervascular porosity, single-row, mostly homogeneous rays, apotracheal and paratracheal parenchyma. This is most likely due to the particularly intense water exchange regime in tall trees, whose crowns are more susceptible to harsh environmental influences. Shrubs and low-growing trees of the 2nd tier demonstrate the presence of both archaic and evolutionarily advanced features in approximately equal quantities in the stem wood. For example, in the genera *Alnus* and *Sorbus*, there is a combination of libriforms with fibrous and vascular tracheids; vessel segments with scalariform, reticulate, and simple perforations, apotracheal and paratracheal parenchyma, and heterogeneous and homogeneous palisade rays. As for the species of the genus *Salix*, they have a highly developed hydraulic system, similar to that of the 1st-tier plants. Small shrubs and dwarf shrubs of the 3rd tier, living in areas with excessive absolute and relative humidity and sometimes extremely low lighting, have the widest range of specific adaptive features acquired as a result of adaptation to the extreme conditions of high latitudes.

Keywords: xylem, wood, water-conducting tissue, hydraulic system, woody plants, adaptation, floodplain forest, tundra
Acknowledgements: The work was carried out within the framework of the topic "Evolutionary and Ecological Patterns of the Structural and Systematic Diversity of Modern and Fossil Plants Based on the Collection Funds of the Botanical Museum of the Komarov Botanical Institute of the Russian Academy of Sciences (Saint Petersburg)".

For citation: Chavchavadze E.S., Shchekalev R.V., Grabovskiy A.A., Romanova V.O. A Strategy for Adapting the Hydraulic System of Woody Plants to Various Tiers of the Floodplain Forest of the Enmyvaam River (Chukotka). *Lesnoy Zhurnal* = Russian Forestry Journal, 2025, no. 6, pp. 33–47. https://doi.org/10.37482/0536-1036-2025-6-33-47

Научная статья

Стратегия адаптации гидросистемы древесных растений к различным ярусам пойменного леса реки Энмываам (Чукотка)

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Поступила в редакцию 19.05.24 / Одобрена после рецензирования 26.10.24 / Принята к печати 28.10.24

Аннотация. Рассмотрены особенности анатомического строения гидросистемы 17 видов из 13 родов 6 семейств древесных цветковых растений, которые относятся к различным ярусам пойменного леса, произрастающего вдоль реки Энмываам (гипоарктическая тундра). Выяснено, что деревья 1-го яруса обладают наиболее совершенной водопроводящей системой. В ее состав входят только волокна либриформа и членики сосудов коротко-цилиндрической, цилиндрической волокновидной формы с простыми перфорациями, точечной очередной, сомкнутой и сближенной межсосудистой поровостью, 1-рядные в основном гомогенные лучи, апотрахеальная и паратрахеальная паренхима. Это связано, скорее всего, с особо напряженным режимом водного обмена у высокоствольных деревьев, кроны которых сильнее подвержены влиянию окружающей среды. Кустарники и низкорослые деревья 2-го яруса демонстрируют наличие в древесине ствола в примерно равных количествах как архаичных, так и эволюционно продвинутых черт. Например, у родов *Alnus* и *Sorbus* наблюдается сочетание либриформа с волокнистыми и сосудистыми трахеидами; члеников сосудов с лестничными, сетчатыми и простыми перфорациями, апотрахеальной и паратрахеальной паренхимы, гетерогенных и гомогенно-палисадных лучей. Что касается видов рода *Salix*, то они обладают близкой к совершенной гидросистемой, как и представители растений 1-го яруса. Небольшие кустарники и кустарнички 3-го яруса, обитающие в местах с избыточной абсолютной и относительной влажностью и порой чрезвычайно слабым освещением, характеризуются самым большим диапазоном специфических приспособительных особенностей, приобретенных в результате адаптации к экстремальным условиям высоких широт.

Ключевые слова: ксилема, древесина, водопроводящая ткань, гидросистема, древесные растения, адаптация, пойменный лес, тундра

Благодарности: Работа выполнена в рамках темы «Эволюционные и экологические закономерности структурного и систематического разнообразия современных и ископаемых растений на основе коллекционных фондов Ботанического музея Ботанического института им. В.Л. Комарова РАН (г. Санкт-Петербург)».

Для цитирования: Chavchavadze E.S., Shchekalev R.V., Grabovskiy A.A., Romanova V.O. A Strategy for Adapting the Hydraulic System of Woody Plants to Various Tiers of the Floodplain Forest of the Enmyvaam River (Chukotka) // Изв. вузов. Лесн. журн. 2025. № 6. С. 33–47. https://doi.org/10.37482/0536-1036-2025-6-33-47

Introduction

A floodplain forest is a special type of forest biocenosis that grows in a temporarily flooded area of a river valley (floodplain). In Russia, these forests are found in all natural zones, from arid steppes to tundra. The highest density of forest stands is observed in taiga floodplain forests, where canopy closure reaches 80 %, while in the southern and northern directions it decreases to 15 % [9]. The species composition of woody plants in floodplain forests depends on climatic conditions, flooding schedule, chemical composition of water and soil sediments, as well as the thickness and the granulometric composition of the latter.

In the wettest areas with prolonged flooding, particularly resistant plants grow, such as birch, wild rosemary, currant and, above all, willow [13, 16, 18].

Floodplain forests have a beneficial effect on the climate, strengthen the soil, improve water use conditions, and provide habitats for commercial fish, birds, and animals. Moreover, in the dry steppes and tundra, these forests are the only source of wood, which is widely used by the local population in their economy.

We have surveyed the forested plain in the lower reaches of the Enmyvaam River, which originates from Lake Elgygytgyn and flows into the Belaya River (the Anadyr River basin) (Fig. 1).

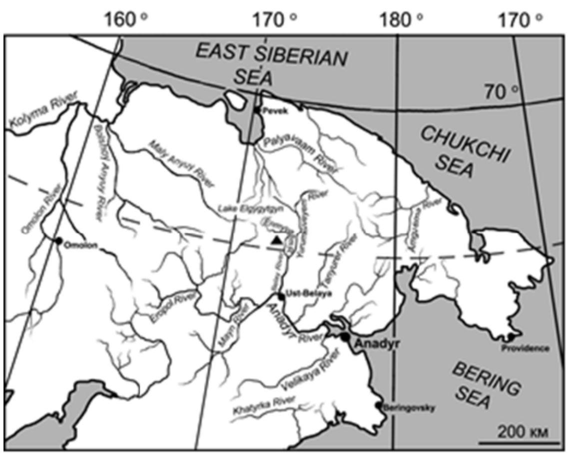


Fig. 1. The area of interest

In the upper and middle reaches, the Enmyvaam River flows through a mountain range, and in its lower reaches, through a plain surrounded by swamps and small lakes. The river is 285 km long, with the floodplain on both sides of the main channel extending in width from 500 to 1,000 m or more. The characteristic appearance of the river phytocenosis (Fig. 2) is provided by the chosenia forests of different ages, which, combined with fragrant poplar, tall willows and grass-shrub populations, occupies almost its entire space [18].

Fig. 2. The photos of forest floodplain phytocenoses along the Enmyvaam River: *a* – the left bank of the middle reaches of the Enmyvaam River, the beginning of the chosenia forest; *b* – the right bank of the Enmyvaam River near the confluence of the Telerennatveem River: 1st tier – *Chozenia arbutifolia* (Pall.) A. Skvorts; 2nd tier – *Salix schwerinii* E.L. Wolf, *Salix boganidensis* Trautv.; 3rd tier – *Betula divaricata* Ledeb., *Ribes triste* Pall., *Rosa acicularis* Lindl.; *c* – the lower reaches of the Enmyvaam River, the Ust-Belsky reindeer herding farm «Sernaya». Poplar-chosenia forest: 2nd tier – *Alnus fruticosa* Rupr.; all plants of the 3rd tier, except *Spirea salicifolia* L. and *Dasiphora fruticosa* L.; *d* – the lower reaches of the Enmyvaam River near the confluence of the Vap'anayvaam (Mukhomornaya) River. The poplar-chosenia forest with fallen poplars in the 1st tier; *e* – the chosenia-poplar forest: 1st tier – *Chosenia arbutifolia* (Pall.) A. Skvorts. and *Populus suaveolens* Fisch. ex Poit. et A.Vilm.; 2nd tier – *Betula cajanderi* Sukaczev.; 3rd tier – thickets of *Ribes triste* Pall; *f* – the chosenia-poplar forest with a predominance of *Populus suaveolens* Fisch. ex Poit. et A. Vilm.; 2nd tier – *Salix boganidensis* Trautv., *Alnus fruticosa* Rupr. and *Sorbus sibirica* (Hedl.) Krylov; 3rd tier – *Betula divaricata* Ledeb., *Ribes triste* Pall., *Rosa acicularis* Lindl., *Pinus pumila* (Pall.) Regel.

The near-edge floodplain forests feature unique young chosenia trees towering up to 5 m and occasional willow, alder, rowan and other shrubs. The entire floodplain area is covered underwater during the spring and summer floods which last for 15 to 25 days. The central part of the floodplain with a thick layer of sand deposits is home to mature chosenia-poplar forests, called “groves” in the Anadyr River basin. The species composition of woody plants in such groves is not very rich (about 50 species); they are typically dominated by 3 to 5 species characterized by a particularly active vegetative regeneration. Researchers of the Chukotka flora, botanists, geographers, taxonomists, and ecologists note that this feature is inherent in all chosenia groves of the Anadyr River basin [6, 13, 14, 16–20, 39]. Therefore, the research we have undertaken is not only of a specific, but also of a general nature.

Our study has been aimed at investigating the structural features of the water-conducting tissue of woody flowering plants by tiers of the floodplain forest in the lower reaches of the Enmyvaam River and determining the ways of adaptation of the secondary xylem and its elements of the studied plants to an unstable (fluctuating) water schedule in the conditions of the hypoarctic tundra.

Research Objects and Methods

As a research material, in 2017, the samples of angiosperm wood have been collected in various areas of the lower reaches of the Enmyvaam River. Additionally, the samples from the dendrological collection of the Botanical Museum, Herbarium and the Laboratory of Far North Vegetation of the Botanical Institute of the Russian Academy of Sciences have been used.

The samples of each species have been taken in triplicate: at breast height (1.3 m from the ground) for tall 1st-tier trees and at a height of 1/3 of the stem length from the ground for scrub trees. The samples of large shrubs have been selected from medium-sized branches at a distance of 2 cm from the root collar. Cross-sections of the wood of small shrubs and 3rd-tier dwarf shrubs have been taken just above the root collar; in the case of creeping forms, samples have been taken below the living crown, raised above the ground. The stem samples of small plants have not exceeded 1 cm in diameter. The sections of micro-preparations have been carried out on a freezing microtome from Reichert (Austria) in 3 projections: transverse (TrP), radial (RP), and tangential (TaP). Xylotomic descriptions and micrometry have been carried out using conventional methods [9, 23, 38] and the method of digital encoding of features, including 20 groups and 160 of their variations [32]. In our descriptions, we have adhered to the terminology proposed by the International Association of Wood Anatomists – IAWA [36] and the glossary in the Atlas of Wood and Paper Fibers [1]. The structural analysis of the hydraulic system has been carried out using an Axio Scope A1 Zeiss photon microscope and a Jeol JSM-6390 LA scanning electron microscope.

In the presented work, we have studied 17 species (Table 1) from 13 genera of 6 families of woody angiosperms.

The 1st tier comprises tall trees, up to 20 m high, including *Chosenia arbutifolia* (Pall.) A. Skvorts. and fragrant poplar – *Populus suaveolens* Fisch. ex Poit. & A. Vilm.

The 2nd tier is formed by small trees and shrubs (from 2 to 12 m), including sharpleaf willow (*Salix schwerinii* E.L.Wolf), Boganida willow (*Salix boganidensis* Trautv.), European green alder (*Alnus fruticosa* Rupr.) and Siberian rowan (*Sorbus* *sibirica* Hedl.). A special focus is on the Cajander birch (*Betula cajanderi* Sukaczev.) (up to 14 meters high), which forms small groves in large clearings of the floodplain forest.

Table 1

The studied species of floodplain forests in the lower reaches of the Enmyvaam River

Genus (family)	Life form	High, m	Site
1st tier			
Populus suaveolens Fisch. (Salicaceae)	Tree	<20	Floodplain of the Vanakvaam (Sernaya) River
Chosenia arbutifolia (Pall.) A. Skvorts. (Salicaceae)			Floodplains of the Telerennetveem, Vanakvaam (Sernaya) and Vapanayvaam Rivers
2nd tier			
Betula cajanderi Sukacz. (Betulaceae)	Tree	<15	Floodplain of the Vapanayvaam (Sernaya) River, Mukhomornoye weather station
Salix schwerinii E. Wolf (Salicaceae)	Tree, shrub	<12	Floodplain of the Vapanayvaam (Sernaya) River, Ust-Belsky reindeer herding farm
S. boganidensis Trautv. (Salicaceae)	Shrub	<12	
Alnus fruticosa Rupr. (= *Duschekia fruticosa* (Rupr.) Pouzar) (Betulaceae)		<10	
Sorbus sibirica Hedl. (Rosaceae)	Tree, shrub	<10	Floodplain of the Varenon River
3rd tier			
Betula divaricata Ledeb. (= *B.middendorffii* Trautv. et C.A. Mey.) (Betulaceae)	Shrub	<1.5	Floodplain of the Vapanayvaam (Sernaya) River, Mukhomornoye weather station
Potentilla fruticosa L. (= *Pentaphylloides fruticosa* (L.) O. Schwarz) (Rosaceae)		<1.5	
Spiraea salicifolia L. (Rosaceae)		<1.5	
Ledum decumbens (Ait.) Lodd. ex Steud. (= *L. palustre* L. subsp. *decumbens* (Ait.) Hult.) (Ericaceae)		<0.4	
Ribes triste Pall. (Grossulariaceae)		<1	Floodplain of the Vapanayvaam (Sernaya) River, Ust-Belsky reindeer herding farm
Rosa acicularis Lindl. (Rosaceae)		<0.8	
Betula exilis Sukacz. (Betulaceae)		<0.4	Floodplain of the Varenon River
Empetrum subholarcticum V. Vassil. (Empetraceae)	Dwarf shrub (creeping)	<0.2	
Vaccinium uliginosum L. (Ericaceae)	Shrub	<0.4	
V. vitis-idaea L. (Ericaceae)		<0.2	

The 3rd tier is occupied by scrub and dwarf shrubs (from 0.2 to 2 m high), including Middendorf's spreading birch (*Betula divaricata* Ledeb.), dwarf birch (*B. exilis* Sukaczev), shrubby cinquefoil (*Potentilla fruticosa* L.), willow-leaved meadowsweet (*Spiraea salicifolia* L.), swamp redcurrant (*Ribes triste* Pall.), prickly wild rose (*Rosa acicularis* Lindl.), wild rosemary (*Ledum decumbens* Small), bog bilberry (*Vaccinium uliginosum* L.), lingonberry (*Vaccinium vitis-idaea* L.) and crowberry (*Empetrum subholarcticum* V.N. Vassil.).

This paper adopts the classification and size of families by A.L. Takhtadzhyan [30]. The names of taxa and authors have been verified according to IPNI [12], POWO [24], etc. [8, 25, 26].

Results and Discussion

The composition of wood of all the considered species is relatively uniform. In addition to the permanent elements, such as vascular segments, axial and radial parenchyma cells, it can comprise, for instance, only fibrous tracheids (pp. *Empetrum*, *Vaccinium*, *Ledum*) or only libriform fibers, often septate (pp. *Chosenia*, *Populus*, *Salix*). In the hydraulic system of small plants of the 2nd and especially, 3rd-tiers, tracheid-like vessels with 1 to 2 perforations on the lateral wall are sporadically encountered.

The wood of the species examined (Fig. 3–5) is typically scatter-vascular, occasionally combined with semi-ring-vascular (pp. *Empetrum*, *Ribes*, *Sorbus*, *Rosa*). Very narrow growth layers often have only one layer of vessels at the annual ring boundary in early wood. The vessel segments are extremely small, very small or fairly small in diameter – up to 25 μm, from 25 to 50 μm and from 50 to 100 μm, respectively [38]. In chosenia and poplar species, the vessel segments are of short-cylindrical, cylindrical and fibrous shape, with the length exceeding the diameter by 2 to 7, 4 to 7 and 7 to 11 times, respectively, or, more often fibrous (p. *Betula cajanderi*). In small shrubs, dwarf shrubs and prostrate shrubs of the *Betula*, *Ledum* and *Empetrum* genera, the vessel segments are mainly fibrous and elongate-fibrous, rarely cylindrical, with the length exceeding the diameter by 7 to 11, over 11 and 4 to 7 times, respectively. The vessel segment membranes are thin to moderately thickened and thickened (2.2, 3.2 and 4.0 μm) with rostels from barely noticeable to medium (pp. *Chosenia*, *Populus*, *Betula*, *Salix*).

The most important water-conducting elements in the secondary xylem are various types of perforation plates and intervascular porosity. Thus, the perforations of the species considered are quite diverse: scalariform and, less frequently, scalariform-reticulate (pp. *Betula*, *Alnus*, *Ribes*, *Ledum*); solely simple (pp. *Chosenia*, *Populus*, *Salix*, *Potentilla*, *Spiraea*, *Rosa*); simple, occasionally combined with scalariform (pp. *Sorbus).* All types of plates from scalariform to simple are observed in *Vaccinium uliginosum* plants (Fig. 5). The intervascular porosity is equally diverse being represented by several types, both primitive (scalariform, transitional combined with opposite, as in representatives of the genera *Betula* and *Alnus*) and more specialized (mixed and alternate in various combinations, as in representatives of the genera *Spiraea* and *Ledum*). Representatives of the genera *Ribes*, *Vaccinium* and *Empetrum* demonstrate all the listed types of porosity. The species of the genus *Salix* are distinguished by alternate closed and close-set free porosity (Fig. 3).

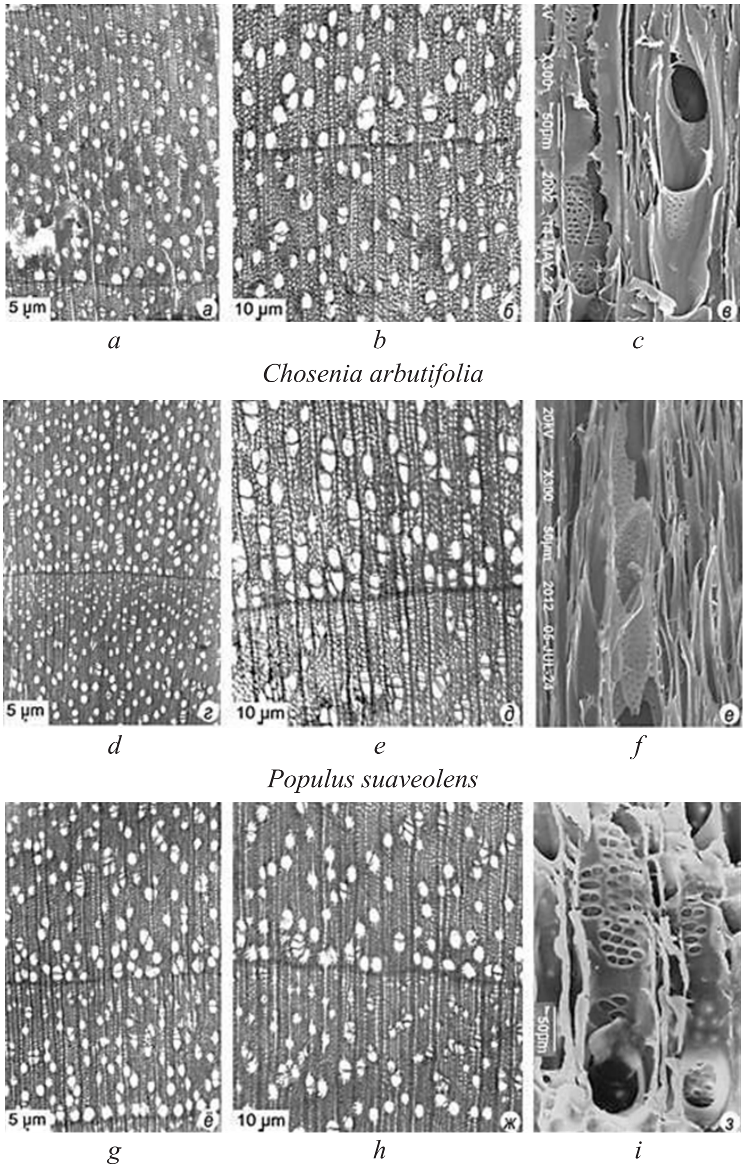
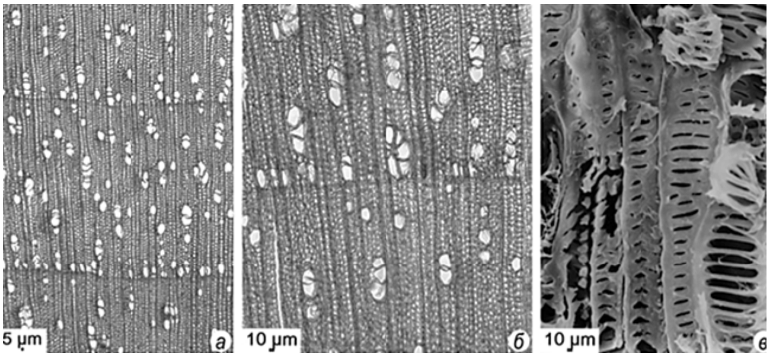
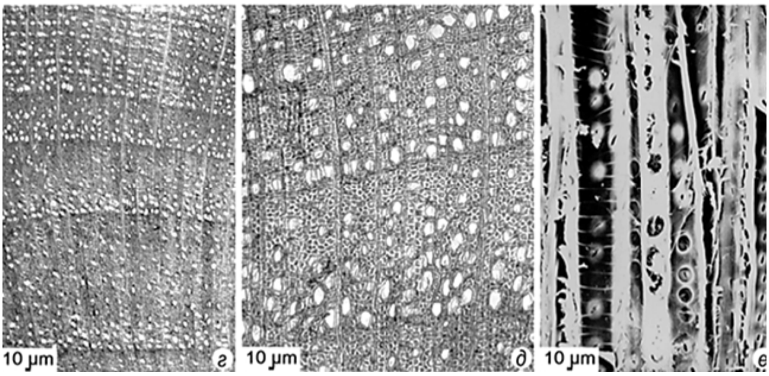


Fig. 3. The structural elements of the secondary xylem of woody plants (*Chosenia arbutifolia*, *Populus suaveolens*, *Salix schwerinii*): *a* – scattered-vascular type of wood, the even boundary of the annual ring is emphasized in the late wood by 1–3 cells flattened in the radial direction (TrP); *b* – scattered-vascular type of wood, the pores in the early part of the annual ring are slightly larger than in the late part (TrP); *c* – fragment of a vessel segment with simple perforations and alternate intervascular porosity (RP); *d* – scattered-vascular type of wood, with numerous pores, and a smooth boundary of the annual ring (TrP); *e* – scattered-vascular type of wood, with large pores often concentrated in the early wood near the boundary of the annual ring (TrP); *f* – vascular segments with simple perforations and alternate intervascular porosity (RP); *g* – scattered-vascular type of wood, the boundary of the annual ring is emphasized in the early wood by larger pores, and in the late wood by 2–3 libriform cells flattened in the radial direction (TrP); *h* – the boundary of the annual ring is slightly wavy, and the number of pores in the late wood is less than in the early wood (TrP); *i* – vessels with simple perforations and alternate close-set intervascular porosity (RP)



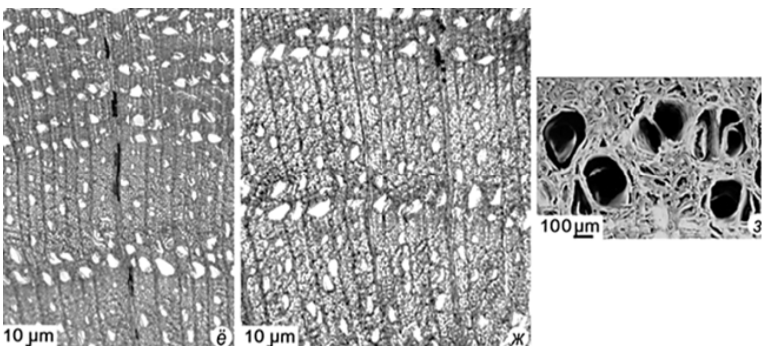
a *b* *c*

Alnus fruticosa



d *e* *f*

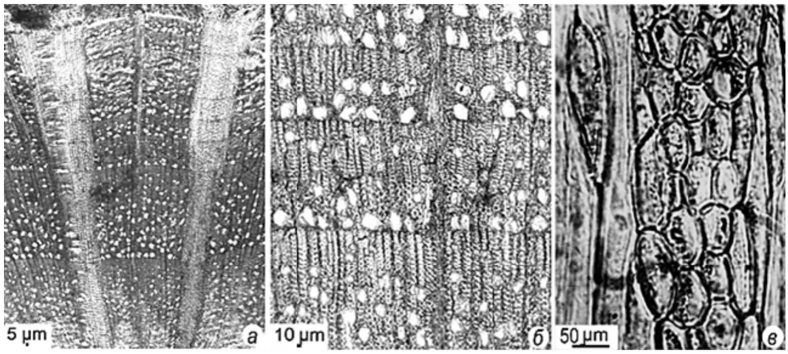
Sorbus sibirica



g *h* *i*

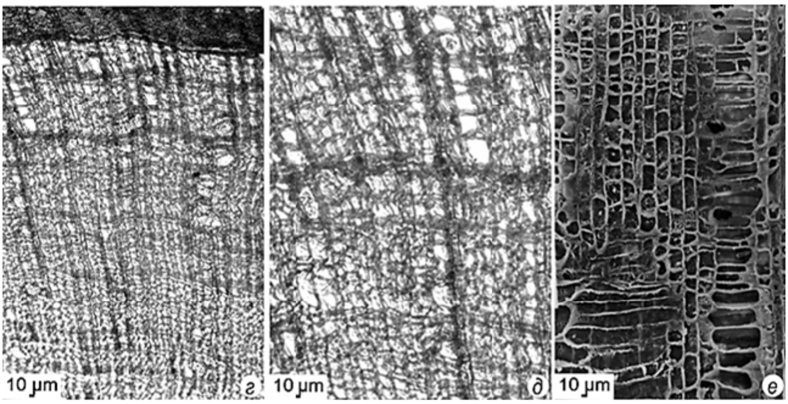
Rosa acicularis

Fig. 4. The structural elements of the secondary xylem of woody plants (*Alnus fruticosa*, *Sorbus sibirica*, *Rosa acicularis*): *a* – scattered-vascular type of wood, with slightly wavy boundaries of annual rings (TrP); *b* – scattered-vascular type of wood, the pores are single or more often in groups (TrP); *c* – vessel segments with scalariform perforations (RP); *d* – scattered-vascular type of wood with a tendency to semi-ring-vascularity, with narrow growth layers, slightly wavy boundaries, and narrow pores (TrP); *e* – scattered-vascular type of wood with a tendency to semi-ring-vascularity, with larger pores located along the boundary of the annual ring (TrP); *f* – fragment of fibrous and vascular tracheid with rounded and oval bordered pores (TaP); *g* – wood with a tendency towards the ring-vascular type, the boundaries of the annual rings are emphasized by 1–3 tracheal elements flattened in the radial direction (TrP); *h* – boundaries of the annual ring are emphasized in the early wood by 1 or 2 layers of larger pores (TrP); *i* – pores are single and paired (TrP)



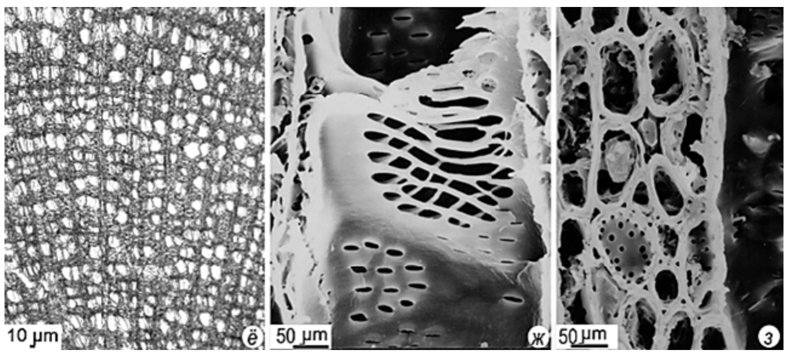
a *b* *c*

Spiraea salicifolia



d *e* *f*

Betula exilis



g *h* *i*

Vaccinium uliginosum

Fig. 5. The structural elements of the secondary xylem of woody plants (*Spiraea salicifolia*, *Betula exilis*, *Vaccinium uliginosum*): *a* – scattered-vascular type of wood with wide multi-row rays and small pores (TrP); *b* – scattered-vascular wood with a tendency to ring-vascularity, the boundary of annual rings is emphasized in the early wood by 1–12 elements flattened in the radial direction (TrP); *c* – fragment of a 4-row ray (TaP); *d* – wood with 9 annual rings and wavy boundaries, emphasized by 1–3 fibrous elements flattened in the radial direction (TrP); *e* – scattered-vascular type of wood, with single and grouped pores, or the ones in radial chains of 3 to 6 (TrP); *f* – fragment of a heterogeneous ray (TaP); *g* – scattered-vascular type of wood with unclear annual ring boundaries and false annual rings (TrP); *h* – fragment of a vessel segment with reticulate perforation and alternate intervascular porosity (RP); *i* – fragment of a 4–5-row ray (TaP)

Fibrous tracheids, from moderately thickened to fairly thick (3.5 to 4.5 μm), occupy the largest volume in wood. On their radial walls there are bordered pores of oval and oval-elongated shapes with the apertures repeating their outlines. Libriform, or simple-pore fibers, have thicknesses ranging from 2.8 to 4.5 μm. Thinner membranes are observed in those life forms that include shrubs, dwarf shrubs and prostrate shrubs while thickened membranes are in the plant life-forms that include trees, small trees and tall shrubs, more specifically, *Chosenia*, *Populus*, *Betula cajanderi*, *Alnus*, etc. In addition, some species have vascular tracheids in the water-conducting tissue – non-perforated cells with signs of a mechanical fiber and a vessel segment, similar to it in shape and porosity type – *Betula*, *Spiraea.* The axial parenchyma is most often sparse, apotracheal, either diffuse or chain-like, with several cells in short chains scattered randomly among fibrous elements (pp. *Salix*, *Ledum*, *Spiraea*, *Potentilla*, *Rosa*) or relatively abundant (pp. *Alnus*, *Betula*, *Vaccinium*, *Empetrum*). Representatives of the genera *Spiraea*, *Ribes*, *Potentilla*, *Rosa*, *Salix* and *Betula* have, in addition to the apotracheal, sparse paratracheal vasicetric parenchyma.

The overwhelming majority of the species considered are characterized by heterogeneous rays. However, some of the examined plants of the genera *Chosenia*, *Populus*, *Salix* and *Sorbus* have heterogeneous rays with a tendency to homogeneous ones and even homogeneous rays. Representatives of the genera *Rosa*, *Vaccinium*, *Empetrum*, *Alnus*, *Betula*, *Ledum*, *Potentilla*, *Spiraea* and *Ribes* sometimes exhibit heterogeneous rays in combination with homogeneous palisade rays. The ray width (number of rows) in the studied species is quite diverse: from single-row in *Chosenia*, *Populus*, *Salix* and *Empetrum,* single-row and partially double-row in *Ledum* and *Potentilla* to single-row, double-row and multi-row in *Ribes*, *Vaccinium*, *Betula*, *Spiraea* and *Rosa*.

The ray height (number of layers) shows considerable instability. A low layering index is observed in *Betula* and *Empetrum*, up to 10–12 cells, while in *Ribes*, *Vaccinium* and *Salix* it is higher – 30–35 cells. Frequently, narrow, low rays, merging at their ends, significantly increase the height. 2 and 3-row rays often demonstrate short, single-row endings in *Ribes*, *Vaccinium* etc. However, this feature is fairly unstable and is rarely used in definitions.

Analyzing the quantitative indicators of the hydraulic system of woody plants from layer to layer, it should be noted, that as the habitat conditions deteriorate and the growth energy (habitus) decreases, the average values of xylotomic characteristics change: the width of the annual rings and the diameter of pores decrease, while the density of the vessels, in contrast, increases. This quantitative redistribution of traits is a non-specific response of the water-conducting tissue to any deterioration in conditions and serves as an important factor in the struggle of plants for existence [4, 5, 27, 31, 33]. In larger 1st and 2nd-tier plants of the genera *Chosenia*, *Populus*, *Salix*, *Betula* and *Sorbus*, the xylotomic indices of the secondary xylem are slightly higher (Table 2) than in representatives of small habits of the genera *Spiraea*, *Ledum*, *Rosa* etc. [7, 15].

Comparative xylotomic studies of the hypoarctic tundra floodplain forest species should preferably be carried out taking into account the plant life form, age and habitat conditions. It is important to bear in mind that the environmental effect on the plant is but a whole combination of soil and climatic factors that impact the plant's external and internal structure in its entirety rather than only individual structural features [35].

Table 2

The quantitative xylotomic indices of the species considered

Species	Annual ring width, mm	Quantity of vessels, pcs/mm²	Tangential pore size, μm	Length, μm		Number of rays, pcs/mm
				vessel segment	fibrous element	
1st tier						
Chosenia arbutifolia	1.3 / 32.7	93 / 14.3	46.6 / 31.7	420 / 29.3	755 / 20.1	12 / 23.9
Populus suaveolens	1.5 / 34.1	130 / 22.2	70.0 / 33.0	412 / 26.1	942 / 21.8	19 / 27.3
2nd tier						
Betula cajanderi	1.0 / 21.9	40 / 11.2	45.0 / 29.4	910 / 31.4	1,000 / 26.1	14 / 19.8
Salix schwerinii	0.8 / 23.7	280 / 29.6	27.5 / 25.2	500 / 25.5	680 / 22.1	8 / 14.2
S. boganidensis	0.7 / 29.3	550 / 34.2	25.0 / 26.1	575 / 21.8	650 / 21.8	9 / 13.8
Alnus fruticosa	1.4 / 32.5	183 / 23.1	50.0 / 30.0	559 / 23.7	683 / 19.7	19 / 22.3
Sorbus sibirica	1.2 / 31.7	150 / 24.1	38.7 / 19.7	450 / 21.4	1,200 / 25.4	18 / 20.9
3rd tier						
Betula divaricata	0.2 / 17.5	161 / 15.3	24.6 / 20.7	370 / 12.1	486 / 16.3	17 / 13.9
Potentilla fruticosa	0.1 / 15.4	147 / 18.3	32.2 / 21.0	232 / 18.5	413 / 16.6	21 / 12.8
Spirea salicifolia	0.23 / 22.0	687 / 16.9	24.5 / 30.0	158 / 21.1	259 / 10.6	22 / 13.0
Ribes triste	0.3 / 21.1	640 / 21.4	21.1 / 34.2	134 / 35.1	196 / 13.8	28 / 27.8
Rosa acicularis	0.3 / 22.2	381 / 12.0	34.0 / 20.0	230 / 14.4	342 / 15.2	23 / 10.1
Betula exilis	0.2 / 30.2	147 / 16.6	27.9 / 26.9	179 / 23.5	361 / 14.4	17 / 11.4
Ledum decumbens	0.07 / 26.6	857 / 11.3	21.0 / 19.9	218 / 13.1	320 / 11.7	26 / 11.2
Empetrum subholarcticum	0.2 / 17.6	548 / 12.9	22.8 / 26.7	184 / 17.9	239 / 11.5	23 / 16.6
Vaccinium uliginosum	0.1 / 35.4	869 / 12.5	22.7 / 18.9	130 / 12.5	196 / 13.7	26 / 11.5
V. vitis-idaea	0.1 / 35.4	850 / 14.2	22.0 / 24.7	125 / 19.4	191 / 11.7	26 / 17.2

Note: The denominator indicates the magnitude of the index variability, %.

The examined anatomical features of the secondary xylem of woody species from different tiers of the floodplain forest in the vicinity of the Enmyvaam River have shown that the water-conducting system of the 1st-tier trees is the most sophisticated of all. It consists only of libriform fibers and vessel segments of a short-cylindrical, cylindrical and fibrous shape with simple perforations, punctate alternate, closed and close-set porosity, with single-row mainly homogeneous rays, apotracheal and paratracheal parenchyma. The perfection of the hydraulic system of 1st-tier plants is most likely associated with a more intense water exchange regime in tall trees, whose crowns are more exposed to the harsh environmental influences of the Far North, that is, insolation, wind, temperature and humidity [10, 34].

The 2nd-tier shrub and scrub tree wood demonstrate the occurrence of both archaic and evolutionarily advanced features in almost equal proportions. In *Alnus* and *Sorbus* species, for example, it's a combination of libriforms with fibrous and vascular tracheids; vessel segments with scalariform, reticulate and simple perforations, apotracheal and paratracheal parenchyma, heterogeneous and homogeneous palisade rays. As for the species of the genus *Salix*, they have a very sophisticated hydraulic system, just like the 1st-tier plants. Both belong to the same *Salicaceae* family.

The 3rd-tier small and dwarf shrubs, occupying the sites with excessive absolute and relative humidity and sometimes extremely weak lighting, demonstrate the widest range of specific adaptive features acquired through the adaptation to the extreme conditions of high latitudes [2, 6]. It has been noted that in the plants of 2 lower tiers, with the exception of representatives of the genus *Salix,* there is no clear division into water-conducting, mechanical and storage elements since the fibrous tracheids present in it partially take over these functions [3, 11, 22, 28, 29, 37].

As a phylogenetic group of woody plants, the genus *Salix* has been formed in the dynamic conditions of river floodplains where plants have developed a special set of adaptive traits called «ecological dualism», enabling them to successfully grow in an environment with an unstable water regime, from flooding in a low floodplain to summer drought in a high floodplain [21].

It has been discovered that the overwhelming majority of plants of the hypoarctic tundra floodplain forests, irrespective of the tier, demonstrate a primitive, scattered-vascular type of wood that does not require a long growing season or significant energy expenditure for its formation [22]. However, this indicates the physiological necessity of such a feature rather than the specialization level of the taxa in question.

Importantly, the study has revealed the simultaneous presence of traits of varying specialization degrees (heterobathmy) in the wood of all the studied species of the Enmyvaam River floodplain forest which increase their genetic flexibility and adaptive abilities to occupy various ecological niches in the Far North pessimal conditions.

Conclusion

Thus, the study of the structural features of the secondary xylem in woody flowering plants through the adaptation to the floodplain forest conditions of the Enmyvaam River (hypoarctic tundra) allows to reveal, using the example of model genera and species, certain patterns in the formation of the water-conducting system and adaptive strategies of multi-tiered forest phytocenoses of a number of tributaries of the Anadyr River basin (Chukotka).

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Конфликт интересов: Авторы заявляют об отсутствии конфликта интересов
Conflict of interest: The authors declare that there is no conflict of interest

Вклад авторов: Все авторы в равной доле участвовали в написании статьи
Authors' Contribution: All authors contributed equally to the writing of the article