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Variability of Anatomical Characteristics of the Wood of Mountain Ash (*Sorbus aucuparia* L.) in the Conditions of the North Caucasus

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Abstract. The article presents the results of a study of the structure of the wood of mountain ash (*Sorbus aucuparia* L.) in the mountains of the North Caucasus. The direction of adaptive changes occurring in the elements of the secondary xylem of the plant at various heights, including extreme ones, is shown. The conclusions of a number of studies have been confirmed that the basic reaction of mountain ash with an increase in altitude and a decrease in growing capacity, as well as an increase in the intensity of transpiration, is a decrease in plant size and a narrowing of the annual growth of the stem in diameter. At the same time, a number of quantitative changes occur in the wood itself, mainly aimed at optimizing the water-transporting function. With increasing altitude, as water supply conditions become more stringent, maintaining normal water balance is achieved by narrowing the diameters of vessels and increasing their number per unit area. The increase in the total area of the pores occurs due to an increase in the number of narrow, single vessels. The quantitative anatomical changes established during the study are adaptive in nature. In the storage parenchyma of wood, there is an increase in the density and linear dimensions of the rays. The volume of the radial parenchyma at a relatively constant average ply value occurs due to an increase in the height of the cells composing the ray. It is noted that sufficient water balance and enrichment of *Sorbus aucuparia* wood with living cells of the axial and radial parenchyma increases the viability and plasticity of the entire organism, covers the energy costs for reparation processes, and also stimulates the possibility of vegetative reproduction in conditions unfavorable for seed renewal. A significant range of fluctuations in the quantitative characteristics of mountain ash wood elements increases its adaptive capabilities, helping it to occupy a variety of ecological niches in nature, as evidenced by the wide range of this species.
Keywords: mountain ash, wood, xylem, water-transporting tissue, annual ring, xylotomic signs, adaptation, the North Caucasus

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Научная статья

Изменчивость анатомических характеристик древесины рябины обыкновенной (*Sorbus aucuparia* L.) в условиях Северного Кавказа

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Аннотация. Представлены результаты исследования структуры древесины рябины обыкновенной (*Sorbus aucuparia* L.) в условиях гор Северного Кавказа. Показано направление адаптационных изменений в элементах вторичной ксилемы растения на различных, в т. ч. предельных, высотах. Подтверждены выводы ряда исследований о том, что базовой реакцией рябины с подъемом в горы и снижением энергии роста, а также увеличением интенсивности транспирации является уменьшение размеров растения и снижение годового прироста ствола по диаметру. Одновременно с этим в древесине происходит ряд количественных изменений, связанных главным образом с оптимизацией водопроводящей функции. С высотой, по мере ужесточения условий водоснабжения, сохранение нормального водного баланса достигается сужением сосудов и увеличением их числа на единицу площади древесины ствола. Возрастание суммарной площади просветов происходит за счет повышения числа узких одиночных сосудов. Установленные в ходе исследования количественные анатомические изменения носят адаптивный характер. В запасающей паренхиме древесины увеличиваются густота и линейные размеры лучей. Объем лучевой паренхимы при относительно постоянной средней слойности нарастает за счет увеличения высоты слагающих луч клеток. Отмечено, что достаточный водный баланс и обогащение древесины *Sorbus aucuparia* живыми клетками аксиальной и лучевой паренхимы повышают жизнеспособность и пластичность всего организма, покрывают энергетические затраты на репарационные

процессы, а также стимулируют возможность вегетативного размножения в неблагоприятных для семенного возобновления условиях. Значительный диапазон флуктуации количественных признаков элементов древесины рябины повышает ее адаптивные возможности, помогая занимать в природе разнообразные экологические ниши, о чем свидетельствует широкий ареал этого вида.
Ключевые слова: рябина обыкновенная, древесина, ксилема, водопроводящая ткань, годичное кольцо, ксилотомические признаки, адаптация, Северный Кавказ

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Introduction

Adaptation of plants to a variety of environmental situations, including extreme ones, represents one of the problems that ecological botany investigates. Mountain forests occupy a significant place in the vegetation cover of Russia with woody plants constituting the basis. The increasing frequency of natural disasters, such as forest fires, floods and mudflows, has led to a reduction in forest areas, including in the mountainous regions of our country. The Restoration of the affected areas and the creation of new artificial stands require a well-founded approach, knowledge of the biological and environmental characteristics of all the components included in the various layers of a mountain forest. One of these components is mountain ash (*Sorbus aucuparia* L.).

Ecological and anatomical studies of woody plants in connection with their altitude-based distribution provide significant clarity in solving these problems, which makes it possible to understand the directions of their structural adaptation to mountain conditions [33]. Such research is becoming increasingly relevant in our time. The ecology of forest-forming species is one of the foundations of mountain forestry, the development of which serves as a guarantee of effective and balanced forestry activities [11, 12, 30].

Our study aims to investigate the quantitative xylotomic characteristics of mountain ash in connection with the altitude above sea level in the mountains of the North Caucasus.

Research Objects and Methods

In mountainous areas, with an increase in altitude above sea level, changes in physical-geographical, phytocenotic, and edaphic conditions, and altitudinal zonality of the climate manifests itself. It is believed that for every 100 m of elevation the temperature decreases by slightly less than 0.5 °C. At the same time, the relative humidity and the amount of precipitation increases, atmospheric pressure decreases, and the ratio of direct and diffuse radiation, as well as the movement of air masses and other factors change [4, 5, 9]. The listed characteristics change with altitude in an interconnected manner, exerting a certain effect on the habitat conditions of plants. On this basis, we consider altitude above sea level as a complex environmental factor.

The species selected for our study has become mountain ash, a tree of 4 to 15 (20) m high with a stem diameter of up to 18–20 cm in diameter. In Russia, it is a widespread species in the forests of the European part and the North Caucasus, growing as undergrowth in coniferous and coniferous-deciduous forests. Mountain ash is quite winter-hardy, drought-resistant and undemanding to soil resources [10]. In the mountains of the North Caucasus it is found everywhere from an altitude of 850 to 2,500 meters above sea level (hereinafter – masl), predominantly on northern slopes [2, 8, 28, 29].

Mountain ash has a diffuse-porous type of wood with distinct annual rings. Their border is represented by a narrow strip of radially flattened fibrous tracheids and terminal parenchyma cells. The transition from spring to summerwood can be both gradual and relatively abrupt. Vessels are all of the same type and numerous, with their number and size slightly decreasing towards summerwood. In cross-section, the pores of the vessels are of angular, round and oval shape, positioned singly or, less often, in pairs and small groups of 3 to 4, their diameter varies within 15–50 μm. The perforation plates are mostly simple, located on transverse, strongly beveled or lateral walls. In pessimal habitat conditions, scalariform perforation plates with a small number (1 to 3) of crossbars are found; reticulate perforation plates are even less common.

Fibrous tracheids with fairly thickened walls make up the bulk of the wood. The bordered pores on the walls of the tracheids are rounded; the apertures are elongated, often slit-like, reaching the border limits, often intersecting.

The axial parenchyma is diffuse, more often metatracheal from scanty to abundant. The rays are 2-to-3-rowed, homogeneous and slightly heterogeneous, in cross section they are usually narrower than the vessels; meeting the latter, the rays bend, bypassing them. On the tangential section, the rays are represented by two types of cells: those elongated along the axis of the tree make up single-rowed rays or are located at the edge of a three-rowed ray with smaller, rounded cells in the middle of it. In a radial section, the cells that make up the central part of the rays are horizontally elongated; the marginal cells are often slightly higher than the middle ones.

The material for our study has been collected in the western part of the North Caucasus on the territory of the Tersky Ridge along the Kerigo, Tyualoy, Chanty-Argun, and Sharo-Argun Rivers (Table 1). The samples of wood for analysis of the anatomical structure have been collected from individual *Sorbus aucuparia* specimens of up to 40 years of age. The collectors have observed the principle of the equivalence of the ecological conditions of growth of individual plants (for example, the comparability of slope exposure).

Individually growing specimens have been selected on the slopes of the northern rhumb mountains with approximately the same stem diameters, except for the material collected at the upper limits of the forest belt. In tall plants, transverse cuts have been taken at a height of 30 cm from the soil surface, and in low-growing specimens at a height of 10 cm. This made it possible to obtain a sufficient amount of material for further research (30 trees for each height). After measuring the width of the annual rings, 2 to 4 segments (depending on the diameter of the disk) have been cut out to study the linear dimensions of the structural elements of wood in the definitive xylem zone.

Table 1

The description of the research objects

Altitude, masl	Slope exposure	Habitat
1,400	North	The left flank of the Kerigo River gorge (lower reach) – the right tributary of the Chanty-Argun River. Floodplain forest
1,900	Northwest	The right flank of the Tyualoy River gorge – the left tributary of the Kerigo River. Mixed forest
2,450		The vicinity of the Tebulo Pass (side ridge). The upper reach of the Tyualoy River. Birch crooked forest. The upper forest line
2,480	North	The upper reach of the Sharo-Argun River. The vicinity of the Kachu Pass (side ridge). Rhododendron-birch forest. The upper forest line

Sections for quantitative anatomical analysis have been prepared using the Reichert freezing microtome (Austria) in 3 projections: transverse, tangential and radial. Xylotomic descriptions have been performed in accordance with generally accepted methods [18, 19, 35].

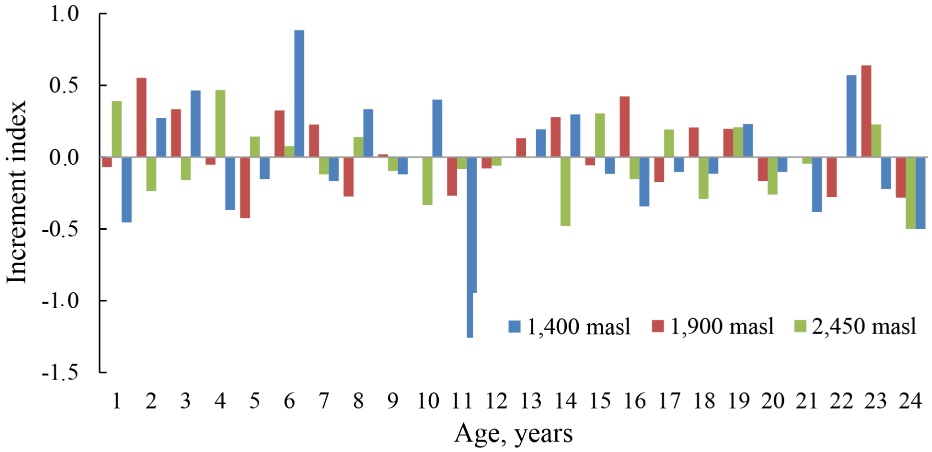
The following parameters have been studied: the width of the annual ring, the number of vessels per unit area in spring and summerwood, the diameter of the vessels and the thickness of their walls, the number of axial parenchyma cells per unit area and the number of rays per a millimeter of tangential section (total, single-rowed and two- or three-rowed), the layering (height in cells) and the linear height of the rays in μm. The terminology of the International Association of Wood Anatomists (IAWA) has been used [34].

The obtained data has been processed using the methods of correlation, factor and variance analysis, etc. [7, 13, 16, 17, 26, 27]. The findings are significant at a 5 % significance level.

Results and Discussion

In the secondary xylem of woody plants (coniferous and dicotyledonous angiosperms), the most responsive element to any change in the environment is the width of the annual ring [14, 24, 25, 30]. The vast majority of the obtained tree-ring chronologies show a significant sensitivity to annual climate changes (sensitivity coefficient from 0.319 to 0.586). The exceptions concern individual series of radial increment in samples collected from a maximum altitude of more than 2,000 m. Spatial analysis of the synchronicity of tree ring fluctuations along the mountain ash stem radius failed to reveal any significant correlation between the chronologies at different altitudes. It has revealed a tendency towards increasing restrictions on the freedom of fluctuations in increment with altitude, which has been demonstrated by the dynamics of the increment index (see Figure). The range of scatter of values by module has been: 2.14 for the altitude of 1,400 masl, 1.06 for 1,900 masl and 0.97 for 2,450 masl.

It has been previously noted that the fluctuation in the width of annual rings demonstrate a certain inertia due to the physiological mechanisms of the formation of increment and its structural elements [1, 21]. The obtained chronologies show the presence of a connection between the current year increment and the previous period. The autocorrelation values with a one-year lag (r_1) for the original tree-ring chronologies vary in the range from 0.234 to 0.821 (the correlation ratio spreads from weak to high). In this case, we can only talk about the trend of a correlation ratio (r_1) increase with the increase in altitude above sea level. The evaluation the autocorrelation function with a time lag of more than one year has allowed us to judge the presence of pronounced cyclical fluctuations of varying intensity. Due to the insignificant length of the considered mountain ash increment series, the maximum time lag has been taken to be 7 years ($r_2 ... r_7$). In our case, for both individual and aggregated increment series, no clear markers of the presence of short-period increment cycles have been identified based on the habitat altitude, since the first-order autocorrelation coefficient turned out to be the highest.



The dynamics of mountain ash increment index change at different altitudes

At high altitudes (of 2,450 to 2,480 masl), narrower rings are more common; their boundaries are difficult to distinguish, since the summerwood is very thin-walled and fairly narrow. A sharp narrowing of annual rings in some years is observed in plants even in lower levels of habitats. At the upper forest line, individual or group rings are often wedged out, in which case multiple or “false” rings are formed.

By analyzing the variability of the width of annual rings in a single time series, we are essentially considering the dynamics of xylem production by the elementary unit of cambium. In this case, when comparing different radii, endogenous variability intervenes with the increment dynamics. The value of this indicator fluctuates on average from 38 to 42 %. With the deterioration of soil and hydrological conditions, using the example of gymnosperms of the taiga zone, a narrowing of the radial increment values range has been noted. Trees become no longer capable of fully materializing their abilities [23]. In our example, no significant differences have been found in the magnitude of endogenous variability in diameter increment depending on altitude above sea level. An excess of the value of individual variability within individual locations over the level of geographic variability has been noted, which seems logical [22].

Many researchers have found out that woody plants most often respond to any negative external influence in a non-specific manner, by developing narrow annual rings [3, 15, 20, 31, 32]. The narrowing of the increments and the reduction of the vascular pores in response to a more adverse environment (Table 2), in our case expressed through an increase in altitude above sea level, should have led to a reduction in the water-transporting tissue volume. However, at the same time, we observe in a separate part a significant (when comparing a successive series of lower altitudes: 1,400–2,450; 2,480 and 1,900–2,450; 2,480) an increase in the number of vessels per 1 mm^2. The total number of vessels per unit area in mountain ash wood varies more at the upper habitat limit: 17–22 % at altitudes up to 1,900 masl and 24–28 % at an altitude of 2,450 masl.

Table 2

The size of the vessel pores in spring- and summerwood of *Sorbus aucuparia* (*M* ± *m*)

Altitude, masl	Annual ring width, mm	Vessel pores			
		Springwood		Summerwood	
		Quantity, pcs/mm^2	Tangential diameter, μm	Quantity, pcs/mm^2	Tangential diameter, μm
1,400	0.87 ± 0.07	293 ± 23	35.0 ± 1.75	172 ± 18	25.7 ± 1.25
1,900	0.73 ± 0.06	380 ± 26	32.4 ± 1.54	252 ± 22	27.8 ± 1.26
2,450	0.58 ± 0.05	664 ± 26	22.8 ± 1.08	259 ± 22	20.5 ± 0.90
2,480	0.59 ± 0.05	597 ± 35	22.8 ± 1.15	299 ± 24	19.1 ± 0.84

The density and diameter of the vessels are directly related to the rate of water supply to the crown and, undoubtedly, the relationship between the number of vessels and the narrowing of their diameters is the most logical response for maintaining the total area of water-transporting routes and the normal water supply.

With an increase in the habitat altitude, the parenchymal elements, in contrast to the water-transporting ones, experience only minor changes. No significant values have been found in the dynamics of numerical parameters and linear dimensions of individual axial and radial parenchyma elements.

The axial parenchyma is very labile. Its volume can vary greatly both within a one annual ring and over the stem in height and radius. In our study, no patterns of distribution of axial parenchyma depending on the age of the plant have been found in *Sorbus aucuparia* wood. Within one annual increment, the axial parenchyma cells can show different distribution patterns: most often they are concentrated in the summerwood zone, but can be evenly scattered throughout the annual ring (diffuse parenchyma) or form narrow strips of up to 4 cells at the outer increment border (terminal parenchyma).

With an increase in the habitat altitude, an increase in the density of axial parenchyma cells is noted in mountain-ash wood: 255±31 at 1,400 masl; 417±28 at 1,900 masl; 527±39 at 2,450 masl; 591±33 at 2,480 masl ($t_{act} > t_{table}$ (2.04) when comparing data at 1,400–1,900; 2,450; 2,480 and 1,900–2,450; 2,480). The range of variability at different altitudes varies from 18 to 39 %. The magnitude of variability of the considered parameter does not correlate with the volume of parenchyma in the annual ring.

Radial rays make up a significant part of the parenchyma volume. There are no clearly defined patterns in their distribution and quantity. The number and ratio of differently rowed rays remain to a certain extent constant values (Table 3). In different habitats at different altitudes above sea level, the content and ratio of differently rowed rays in wood is not the same. There is a tendency for the density of rays to increase by 1 mm with an increase in altitude above sea level (the actual Student's t-test values do not exceed t_{table} of 2.04), with the variability at different altitudes from 26 to 30 %. Given a conditionally constant average value of two and three-rowed rays, the number of single-rowed rays increases by 2 times with the ascent into the mountains. And while at altitudes of 1,400 and 1,900 masl, two-rowed rays prevail over single-rowed ones, at extreme altitudes single-rowed rays prevail. Thus, the ratio of the considered groups of rays by rows, when moving towards the upper habitat limit, tends towards the range of 1.0 to 1.1.

Table 3

The average values of the radial parenchyma parameters of *Sorbus aucuparia*

Altitude, masl	Number of rays, pcs/mm				Ray height, mm			
					Single-rowed		Two-, Three-rowed	
	total	single-rowed	two-, three-rowed	ratio	Layering, n-cells	Linear height, mm	Layering, n-cells	Linear height, mm
1,400	8.5 ± 0.6	3.2	5.3	0.60	5.4 ± 0.4	95.6 ± 13.0	11.4 ± 1.0	178.6 ± 23.1
1,900	10.2 ± 0.8	3.7	6.5	0.57	5.3 ± 0.4	94.2 ± 12.2	11.3 ± 1.1	175.3 ± 25.2
2,450	10.0 ± 0.8	4.9	5.1	0.96	5.7 ± 0.4	96.5 ± 12.6	12.0 ± 1.3	165.5 ± 21.6
2,480	10.7 ± 0.9	5.6	5.1	1.10	4.5 ± 0.4	100.9 ± 16.1	11.6 ± 1.1	200.8 ± 28.9

The layering of rays (height in cells) is a highly variable parameter, yet showing sufficient stability in rays of a specific row number, and thus, can be used as an additional parameter in comparative anatomical studies [33]. In our material, no significant changes in layering at different altitudes from 1,400 to 2,480 masl have been detected. In single-rowed rays, the layering averages 4–6 cells (maximum 14), and in two- and three-rowed rays, the average is 10–13 cells (maximum 33).

The linear height of single-rowed rays fluctuates within the range of 22 to 255 μm, and for two- and three-rowed rays, from 40 to 563 μm. Table 3 shows the average values of the linear size of the rays by altitude. The differences in the average ray height between the individuals of the same habitat are more pronounced than those between the individuals from different locations at different altitudes above sea level. No significant changes in this parameter have been noted with an increase in the habitat altitude (correlation (r) 0.284 ± 0.041; t_r = 1.57).

Thus, the ray linear dimensions depend more on the height of the ray-composing cells than on the layering. For example, the measurement results show that in depressed individuals at the upper habitat limits, the rays, especially the single-rowed ones, contain higher cells. In this case, the correlation ratio is represented by values of $r = 0.892 \pm 0.053$ with the measurement reliability of $t_r = 10.44$.

The specific volume of single-rowed and two- or three-rowed rays in mountain-ash wood is 10 and 12 %, respectively. The studied material showed that in the definitive xylem, two- and three-rowed rays most often occupy a larger volume. In samples taken from the upper habitat limits, the volume of single-rowed rays and their number are higher than in mountain ash wood from lower altitudes. No noticeable difference has been found in the volume of wider rays due to changes in the environmental factor under consideration.

A comparative anatomical analysis of the mountain ash wood taken from different altitudes above sea level indicates that any changes in it with increasing altitude are mainly quantitative in nature. The relationship between the characteristics of water-transporting, mechanical and storage elements is the closer the harsher the living conditions.

Table 4

The correlation (*r*) between the total number of rays and variously-rowed rays in the wood of *Sorbus aucuparia*

Altitude, masl	Quantity of rays	Single-rowed	Two-, three-rowed
1,400	Total	+0.632 ± 0.146	+0.557 ± 0.157
	Single-rowed	–	–0.284 ± 0.181
1,900	Total	+0.623 ± 0.148	+0.217 ± 0.184
	Single-rowed	–	–0.601 ± 0.151
2,450	Total	+0.459 ± 0.168	+0.388 ± 0.174
	Single-rowed	–	–0.644 ± 0.145
2,480	Total	+0.700 ± 0.135	+0.374 ± 0.175
	Single-rowed	–	–0.516 ± 0.162

The total density of rays at different heights depends more on the number of single-rowed than two- or three-rowed rays (Table 4). A comparison of the same annual increments of water-transporting elements (vessels) and storage elements (axial parenchyma cells) has not revealed any correlation them: springwood $r = 0.306 \pm 0.180$; $t_r = 1.70 < t_{table}$; summerwood $r = -0.091 \pm 0.162$; $t_r = 0.56$.

Conclusion

The results of the study of the adaptation of *Sorbus aucuparia* wood to various, including pessimal, habitat conditions due to the altitude above sea level in the mountains of the North Caucasus have shown that:

1. The basic response of mountain ash to the ascent in the mountains and the decrease in growth power, as well as to greater transpiration intensity, is a decrease in the size of the plant and narrowing of the annual increment of the stem in diameter. At the same time, the wood itself experiences a number of quantitative changes that are mainly aimed at optimizing the water-transporting function. With increasing altitude, as water supply conditions become more stringent, maintaining normal water balance is achieved by narrowing the vessel diameters and increasing their number per unit area. The increase in the total area of the pores occurs due to an increase in the

number of narrow, single vessels. The anatomical changes quantitatively established during the study are adaptive in nature.

2. In the storage parenchyma of wood, an increase in the density and linear dimensions of the rays has been observed. The volume of the radial parenchyma with a relatively constant average layering value occurs due to an increase in the height of the ray-composing cells.

From the above, it can be concluded that sufficient water balance and enrichment of *Sorbus aucuparia* wood with the living axial and radial parenchyma cells increases the viability and plasticity of the entire organism, covers the energy costs of reparative processes, and also stimulates the possibility of vegetative reproduction in conditions unfavourable for seed regeneration. A significant range of fluctuations in the quantitative characteristics of mountain ash wood elements increases its adaptive capabilities, helping it to occupy a variety of ecological niches in nature, as evidenced by the wide distribution area of this species.

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