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Bioecological features of lowbush blueberry, *Vaccinium angustifolium* Aiton in the Moscow Region, Russia

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ABSTRACT

The results of a study on the bioecological characteristics of lowbush blueberry (*Vaccinium angustifolium* Aiton) cultivars (Lakomka, Neya, Pomorochka) under the introduction conditions of the R.I. Schroeder Arboretum (Moscow, Russia) are presented. Anatomical analysis revealed that plant leaves not only exhibited an increase in the linear size of chlorenchyma cells, but also a change in the ratio of spongy and columnar mesophyll. An increase in the palisade coefficient and stomatal index of leaves of *V. angustifolium* varieties was recorded from 2023 to 2025, indicating an elevation in the photosynthetic activity of plants and their adaptation to the light and heat conditions of the Moscow Region, Russia. The highest value of stomatal index of leaves in 2025 (Ui = 32.08) was noted for the Pomorochka cultivar, while the lowest value (Ui = 27.20) for the Neya cultivar. The low coefficient of variation of the studied anatomical parameters of leaves of cultivar plants in 2025 indicates stabilization of the morphometric characteristics of leaves under the conditions of introduction. The assessment of the yield of varieties showed that in 2025 the Pomorochka cultivar had the highest yield (5.58 kg/bush), while the Neya cultivar the lowest (4.16 kg/bush). The Neya cultivar had the highest berry weight (1.28 g), while the Pomorochka cultivar the lowest (1.12 g). The low coefficient of variation for the yield and fruit weight of *V. angustifolium* cultivars in 2025 indicates stabilization of economically valuable traits under the conditions of introduction in the Moscow Region, Russia. *V. angustifolium* cultivars showed fairly good winter hardiness. The survival of plants after the winter of 2023-2024 and 2024-2025 was 100%. The experiment noted partial freezing of annual shoots in the studied *V. angustifolium* cultivars (freezing severity 1–2). The Pomorochka cultivar proved to be the most winter-hardy under the experimental conditions over the entire observation period, as the plants exhibited the lowest percentage of damaged annual shoots and buds. The least winter-hardy of all the studied varieties was the Neya cultivar, which exhibited the highest degree of damage to the above-ground parts of the plants over the entire observation period.

Key words: *Vaccinium angustifolium*, Anatomical and diagnostic features, leaf, Stomatal index, Palisade ratio, Winter hardiness, Productivity
Article type: Review Article.

INTRODUCTION

Lowbush blueberry, *Vaccinium angustifolium* Aiton belongs to the family Ericaceae Juss., and subfamily Vaccinioideae Arn. The species is native to eastern and central Canada (from Manitoba to Newfoundland), the northeastern part of United States, south to the Great Smoky Mountains, and west to the Great Lakes region. Lowbush blueberry naturally grows in coniferous (primarily spruce) and, less commonly, deciduous forests, on mountain slopes, on the edges of raised bogs, and in the undergrowth of sparse stands, forming fairly dense thickets on light, acidic soils (Flora of North America 2009). The plants are characterized by high winter hardiness and are able to withstand temperature drops to –34…–40 °C (Cappiello & Dunham 1994), which potentially expands the regions for growing this crop. *V. angustifolium* fruits contain various minerals, vitamins, fatty acids, and dietary fiber, as well as a wide variety of bioactive compounds, including phenolic compounds. The bioactive

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substances in blueberries exert a protective effect against chronic human diseases, including cardiovascular disease, cancer, Alzheimer's disease, and others (Ly *et al.* 2018; Miller *et al.* 2019; Wood *et al.* 2019). Due to the high nutritional and medicinal value of *V. angustifolium* berries, there is currently a sharp increase in demand for products from this valuable crop. This necessitates the expansion of lowbush blueberry cultivation areas across Russia to provide the population with local berry products. When introducing economically valuable plants, in addition to studying its phenology, biomorphology, and ontogenesis, it is extremely important to establish the morphological and anatomical characteristics of the introduced plants (Cheryatova 2021). Changes in plants at the anatomical level can serve as the basis for analyzing the structural and morphological adaptations of species in response to changing growing conditions. Scientists have found that the leaf is the most flexible plant organ to changing environmental conditions (Cheryatova & Arnautova 2021). Many authors have noted changes in the anatomy of introduced plant leaves due to changes in the temperature regime of the area (Bacelar *et al.* 2004; Oberbauer *et al.* 2007). Low temperature is one of the most important limiting factors determining plant introduction (Hartikainen *et al.* 2009). It has been established that plant photosynthesis increases by elevating leaf temperature until the temperature reaches an optimum (Sharp *et al.* 2013). Therefore, when introducing plants to warmer regions, a positive effect of temperature on photosynthetic activity can be confidently expected, which will be reflected in the change in the stomatal index of plants (Welker *et al.* 2004). The issue of changes in the anatomical characteristics of leaves of introduced plants has been widely covered in the literature (Natali *et al.* 2011). It was found that long-term responses of species to temperature changes can cause a shift in the optimal temperature for leaf photosynthesis, which stimulates photosynthesis at the new growing temperature and often leads to changes in the leaf at the anatomical level (Natali *et al.* 2014). Plants growing in a cool region can also increase the activity of enzymes associated with photosynthesis to adapt to warming, thereby increasing photosynthesis (Berry & Björkman 1980). Among the anatomical traits of leaves, the structure of the columnar mesophyll is an important characteristic for assessing plant photosynthesis. Scientists have found that the thickness of the columnar mesophyll positively correlates with the rate of photosynthesis (Yamori *et al.* 2014). It is also important to note that photosynthesis is relatively sensitive to environmental factors such as temperature, light, and water balance (Hernández-Fuentes *et al.* 2015). Therefore, the activity of photosynthetic enzymes naturally increases by elevating temperature, which stimulates the process of photosynthesis itself and, accordingly, can contribute to changes in plant leaf anatomy. Scientists note that plants respond to warming by increasing the overall thickness of leaves and epidermis, as well as the ratio of columnar to spongy mesophyll (Schollert *et al.* 2017; Schollert *et al.* 2018). A higher ratio of columnar to spongy mesophyll in leaves promotes a more compact arrangement of cells, which improves CO_2 uptake and, consequently, helps sustain higher rates of plant photosynthesis (Carroll *et al.* 2017). It should also be emphasized that, under warming conditions, maintaining water balance becomes extremely important for plants, so it is no coincidence that many authors have documented thickening of epidermal cells as a response by species (Chartzoulakis *et al.* 2000). However, the magnitude and direction of photosynthetic responses of introduced plants to warming can vary significantly depending on the species and its geographic origin. Therefore, knowledge of species-specific plant responses (including anatomical ones) to climate change can help better understand species adaptations and develop agronomic measures for their cultivation. International scientific literature lacks comprehensive information on the anatomical structure of narrow-leaved blueberry leaves, particularly regarding the stomatal index and descriptions of petiolar anatomy. An important component in evaluating introduced berry plants in central Russia is their winter hardiness (Gudovskikh *et al.* 2021). Winter hardiness is a key indicator of a variety's suitability for cultivation under specific climatic conditions. Berry crops cultivated in central Russia face markedly different environmental conditions between summer and winter. Since higher plants are sessile, they have evolved various strategies to adapt to these changes in light, temperature, moisture, and other environmental factors. Perennial berry plants spend the early winter in a state of deep dormancy, during which they become unresponsive to environmental changes. During winter dormancy, all physiological and biochemical processes in perennial plants cease. With the onset of warm spring weather, perennial plants gradually emerge from winter dormancy, eventually causing budding and bud break. During the spring regeneration period, vegetative growth resumes with the formation of new shoots. This cycle of growth and dormancy is central to the ability of perennial plants to adapt to growing at different latitudes and altitudes. It has been established that the further north or the higher the altitude at which berry plants grow, the earlier in the season the species enter the growth cessation stage and the later they bud break in the spring (Kostamo *et al.* 2018). Moreover, recent years have seen global climate change, which in turn is beginning to have a profound impact on the annual growth cycle of many plants (Estrada Jimenez, 2006). For example, the early spring observed in recent years in central Russia, leading to abnormally high temperatures in March, may cause earlier spring growth and bud break in perennial plants. In connection with the above, it becomes obvious that comprehensive bioecological studies of introduced plants are needed. Currently, the scientific literature contains numerous results of morphological, anatomical, and biochemical studies of flowers and fruits of representatives of the genus *Vaccinium* (Schollert *et al.* 2015; Del Bo' *et al.* 2016; Yang *et al.* 2021; Zhu *et al.* 2024). Today, extensive introduction studies of the genus *Vaccinium* are being conducted in various regions of Russia (Makarov *et al.* 2021; Sungurova *et al.* 2025). Scientists are evaluating the biomorphological and bioecological characteristics of *Vaccinium* representatives for the purpose of further breeding work (Makarov *et al.* 2024, 2025). Since there is currently no information on the anatomical adaptation of *V. angustifolium* to changing agroclimatic growing conditions, this work is relevant and timely, especially in connection with the expansion of regions where this valuable berry crop is cultivated. The aim of the research is to study bioecological features of lowbush blueberry, *Vaccinium angustifolium* Aiton under conditions of introduction in the Moscow Region, Russia.

MATERIALS AND METHODS

The research was conducted at the Russian State Agrarian University – Moscow Timiryazev Agricultural Academy in 2023-2025. The objects of study are freshly picked shoots, leaves and fruits from 4-5-year-old narrow-leaf blueberry, *Vaccinium angustifolium* Ait. plants of Russian-bred cultivars (Lakomka, Neya, Pomorochka) growing on the territory of the Arboretum named after R.I. Schroeder, Russian State Agrarian University – Moscow Timiryazev Agricultural Academy (northwestern part of Moscow, Russian Federation). Lakomka (authors – G.V. Tyak, and S.S. Makarov) – a mid-season cultivar selected among seedlings from open pollination of the Putte cultivar; Neya (authors – V.A. Makeev, G.Yu. Makeeva, and S.S. Makarov) – a mid-season cultivar selected among seedlings from partially controlled crossing (♀ Northblue cultivar × ♂ pollen mixture of *V. angustifolium* forms); Pomorochka (authors – G.V. Tyak, and S.S. Makarov) selected among seedlings from open pollination of the Putte cultivar (Makeeva *et al.* 2023). The variety testing plot of blueberry is located on a total area of 0.2 ha (N 55.8292°, E 37.5451°), with a flat relief. The plants were planted in trenches (50 cm wide and 40 cm deep) filled with high-moor peat (pH 2.9-3.4). The distance between rows is 2.0 m, the distance between plants in a row is 1.5 m. A drip irrigation system was used. The climate in research region is moderately continental. Weather conditions during the planting period were favorable. For the period 2023–2024, the average perennial long-term data (for 1961–1990; Kobysheva *et al.* 2001) were exceeded by 2.4 °C in average monthly temperature and by 248 mm in precipitation during the active growing season (Table 1). A feature of the winter periods of 2023–2024 and 2024–2025 was the large amount of precipitation, which exceeded the average long-term value by 177.7 mm and 163.4 mm, respectively. Spring in 2024 was characterized by a sharp change in weather, from temperatures above +20 °C in the 2nd–3rd ten-day periods of April to a sharp cold snap to –7 °C in the 1st ten-day period of May; July was consistently hot, with daytime temperatures of at least +28 °C. Plant material was collected in July during the mass fruiting phase. Ten well-formed leaves were selected from the midsection of one-year-old shoots on five plants. Anatomical characteristics of the leaves were studied in accordance with the requirements of the State Pharmacopoeia of the Russian Federation (2008). For anatomical analysis, temporary microscope slides of transverse and longitudinal sections of plant leaves were prepared. Lignification processes in plant parts were detected using a phloroglucinol reagent with concentrated hydrochloric acid (HCl). The sections were cleared with glycerol diluted with water (1:1). The microscope slides were examined using a Carl Zeiss Primo Star microscope (Carl Zeiss, Germany). Microphotography was performed using a Canon Digital IXUS 105 digital camera (Canon, Japan). Linear measurements of leaf anatomical structures were performed using a Euromex EWF10×/22mm eyepiece micrometer (Euromex Microscopen, Netherlands) in 10 replicates.

Based on the data obtained, parameters such as the stomatal index and palisade coefficient were calculated.

The palisade ratio was calculated using formula (1):

$$K = \frac{S_{pal}}{S_{pal}+S_{spon}} \times 100\%, \quad \textbf{(1)}$$

where: S_{pal}, S_{spon} are the areas of the cross-sections of the plate occupied by the cells of the columnar and spongy mesophyll, respectively.

The stomatal index was calculated using formula (2):

$$Ui = \frac{2N_{stom}}{2N_{stom}+2N_{cell\_low}} \times 100\%, \quad \textbf{(2)}$$

where: N_{stom} – is the number of stomata per 1 mm^2 of the lower epidermal surface; N_{cell_low} – is the number of principal cells of the lower epidermis per 1 mm^2. The biomorphological analysis and winter hardiness assessment of plants were carried out according to the Program and methods of variety study of fruit, berry and nut crops (Sedov & Ogoltsova 1999). The degree of freezing of annual shoots was noted by each bush and assessed in points on a 6-point scale: 0 points – no freezing is observed; 1 point - very slight freezing of the ends of annual growths (no more than ¼ of length); 2 points – more severe freezing of annual growths, complete freezing of individual shoots and single older shoots is possible; 3 points – freezing of 2-year-old wood and individual perennial shoots; 4 points – freezing of most of the perennial shoots; 5 points - complete freezing of the aboveground part. The degree of freezing of flower buds was determined during the period of their swelling according to a 4-point scale: 0 points – no freezing observed; 1 point – slight (up to 10% of buds frozen); 2 points – moderate (up to 30% of buds frozen); 3 points – severe (more than 30% of buds frozen). Statistical processing of the data was carried out using standard mathematical and statistical methods (Dospekhov 2011) using Microsoft Office Excel 2019 and StatSoft Statistica v10 software.

Table 1. Meteorological conditions on the territory of the R.I. Schroeder Arboretum (Moscow, Russia) during 2023-2025.

Year	Month											
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
Average monthly air temperature (°C)												
2023	–4.7	–4.1	1.4	9.9	12.8	16.9	18.5	19.8	15.3	5.4	0.7	–4.4
2024	–10.0	–4.4	2.0	11.0	12.9	20.1	22.4	19.2	18.0	7.9	1.6	–2.1
2025	0.1	–4.6	4.3	9.0	13.5	17.1	21.8	17.2	No data			
Average perennial	–9.3	–7.7	–2.2	–5.8	13.1	16.6	18.2	16.4	11.0	5.1	–1.2	–6.1
Average monthly precipitation (mm)												
2023	35.7	42.7	64.9	37.7	33.3	78.2	151.2	39.7	10.4	114.9	87.9	83.8
2024	49.9	60.7	9.4	46.5	36.0	166.3	92.2	34.4	10.6	77.3	74.6	54.9
2025	41.1	8.8	31.0	53.5	72.0	89.5	183.8	88.9	No data			
Average perennial	11.0	8.0	8.0	9.0	8.0	11.0	12.0	10.0	11.0	10.0	12.0	12.0
Snow depth, cm												
2023	28.3	34.3	29.7	-	-	-	-	-	-	-	4.0	25.0
2024	27.3	50.6	34.9	-	0.1	-	-	-	-	0.1	1.63	10.0
2025	2.5	2.1	0.6	1.9	0.2	-	-	-	No data			
Average perennial	24.0	35.0	29.0	2.0	-	-	-	-	-	-	4.0	12.0

RESULTS AND DISCUSSION

A morphological and anatomical analysis of the structure of *V. angustifolium* revealed the following. The stems of annual shoots of the narrow-leaved blueberry are green, sparsely covered with short, simple, unicellular hairs. Perennial stems of the plant, on which the periderm is located, are brown. The cross-sectional shape of the annual stem of the narrow-leaved blueberry is elliptical with two symmetrically located ribs. It is important to note that the stem shape of blueberry shoots becomes cylindrical by increasing age. The *V. angustifolium* stem is characterized by a non-fascicular (solid) type of anatomical structure (Fig. 1).

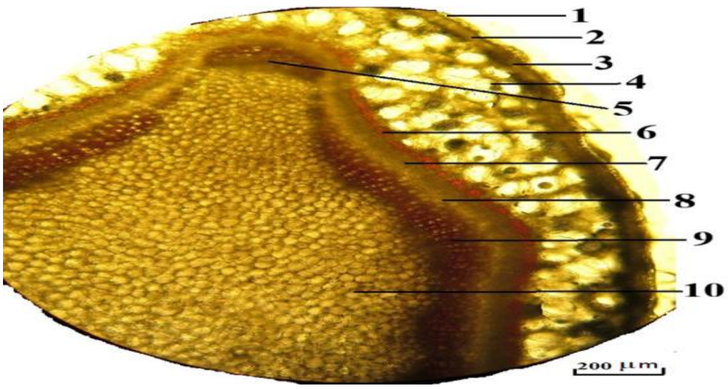
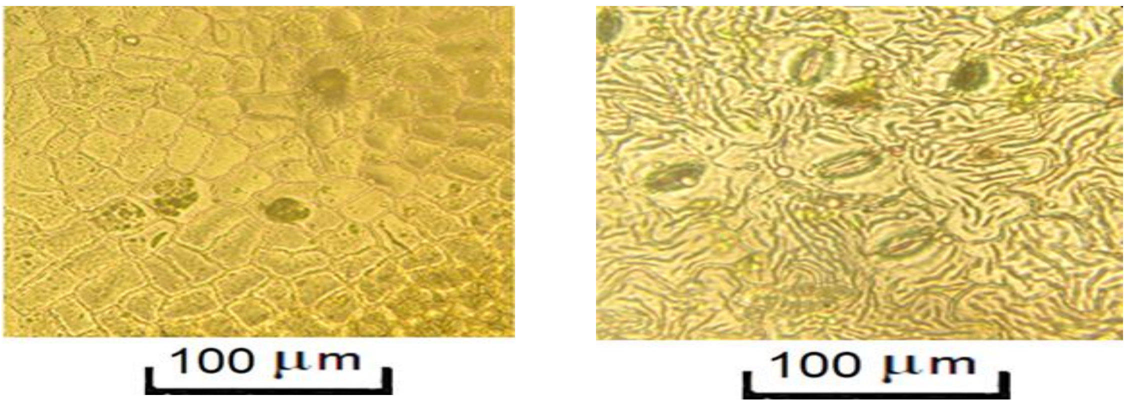


Fig. 1. Fragment of a cross-section of *Vaccinium angustifolium* stem: 1 – epidermis with cuticle; 2 – primary cortex; 3 – collenchyma of the primary cortex; 4 – chlorenchyma of the primary cortex; 5 – multilayered xylem in the rib of the stem; 6 – sclerenchyma of the pericycle; 7 – phloem of the central cylinder; 8 – cambium; 9 – xylem of the central cylinder; 10 – parenchyma of the pith.

The following anatomical and topographical zones can be distinguished in *V. angustifolium* stem: integumentary tissue, primary cortex, central cylinder, and pith. The outer surface of the stem is covered with a single-layered epidermis with a cuticle and sparse single-celled simple trichomes (hairs). Beneath the stem epidermis lies a broad primary cortex, the outer layer of which is represented by 4-5-layered collenchyma. The collenchyma is followed by multi-layered chlorenchyma, which, due to the formation of large intercellular spaces, takes on the appearance of aerenchyma. The central cylinder of the stem begins with a two- to three-layered sclerenchyma of the pericycle, followed by vascular tissues arranged in a closed ring. Histological elements of xylem and phloem form nested cylinders in the cross-section of the narrow-leaved blueberry stem. The cambial zone is clearly visible in the stem. The main internal portion of the stem is occupied by pith parenchyma, which serves as a nutrient reserve. It should be noted that pith parenchyma cells tend to be larger in the central portion. *V. angustifolium* leaves are simple, petiolate, lanceolate, and weakly pubescent with simple, unicellular trichomes. The length of leaves on annual shoots varied widely depending on their ordinal number, from 4.5 to 5.6 cm; the width, from 1.5 to 2.1 cm. The leaf color is dark green on the upper side, and light green on the underside, due to more pronounced pubescence. The greatest number of hairs is found along the main vein, the edge of the leaf blade, and the petiole. The cells of the single-layered upper epidermis are characterized by straight cell walls with clearly visible pore canals. The cells of the lower epidermis of the leaf have more sinuous wall outlines compared to the cell walls of the upper epidermis (Fig. 2).

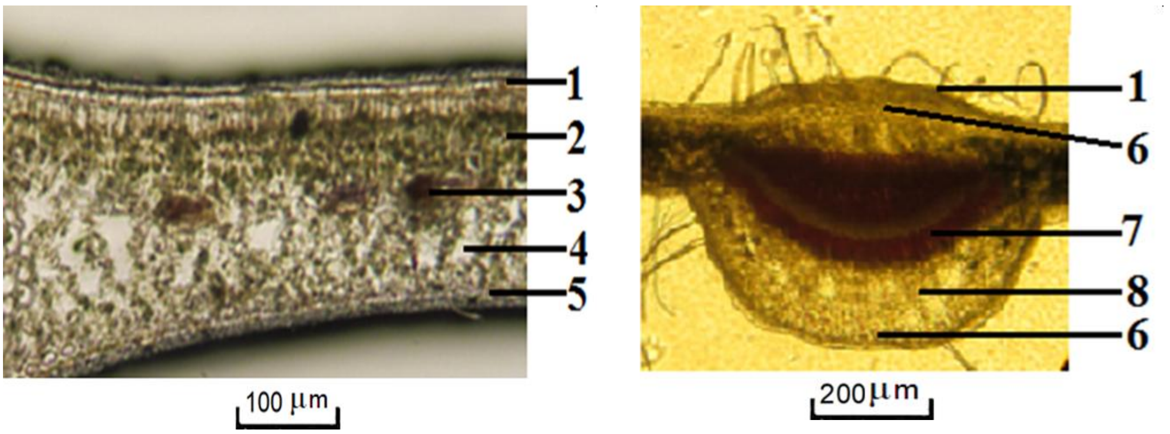


a b

Fig. 2. Structure of the epidermis of *Vaccinium angustifolium* leaf blade (paradermal section):
a – upper epidermis; b – lower epidermis.

V. angustifolium leaf blade is hypostomatic, with stomata found only on the lower epidermis. The mosaic distribution of stomata on the leaf blade is particularly noteworthy. The stomatal apparatus of *V. angustifolium* leaves is paracytic, with subsidiary cells arranged parallel to the guard cells and the stomatal slit (Fig. 2b). The guard cells of the stomata have an elongated kidney-shaped outline. The leaves of *V. angustifolium* are dorsoventral. The columnar mesophyll consists of rectangular-elongated cells; the spongy mesophyll is characterized by oval-shaped cells with distinct intercellular spaces (Fig. 3). The venation of *V. angustifolium* leaf is pinnate. The vascular bundle of the main vein is closed, collateral, oval-elongated, and surrounded by a multilayered sclerenchymatous sheath (Fig. 3b). The lateral veins of the leaf blade were characterized by smaller, closed collateral bundles. The blade received exceptional mechanical strength from multi-row strands of angular collenchyma located beneath the upper and lower epidermis of the leaf along the main vein. Crystalline inclusions in the form of druses (star-shaped crystals) of calcium oxalate were found in the mesophyll of *V. angustifolium* leaves (Fig. 4). The druses were quite large, often occupying more than 50% of the cell's volume. They were more numerous in the spongy mesophyll of the blade. The results of a detailed analysis of the biometric parameters of *V. angustifolium* leaves are presented in Table 2. The data in Table 1 show that over the years of observation, leaf biometric parameters of all studied *V. angustifolium* cultivars showed a general increase, which may indicate the plants' adaptation to the dry summer of the observation period. An increase in the thickness of the lower epidermal cells with the cuticle and the overall thickness of the columnar mesophyll of the leaf blade were also noted. *V. angustifolium* leaves had not only an increase in the linear size of chlorenchyma cells but also a change in the ratio of spongy to columnar mesophyll in favor of an increase in the latter. Thus, an elevation in the palisade coefficient and stomatal index of *V. angustifolium* cultivars leaves from 2023 to 2025 indicates an upraise in the photosynthetic activity of plants and its adaptation to the light and heat conditions of the Moscow Region, Russia.

It was found that the efficiency of plant photosynthetic activity also increased due to a consistent elevation in the number of stomata per 1 mm^2 of leaf surface. The highest stomatal index of leaves in 2025 was noted for the Pomorochka cultivar (Ui = 32.08), while the lowest index for the Neya cultivar (Ui = 27.2). The low coefficient of variation (Cv, %) of the studied anatomical parameters of the leaves of plant varieties in 2025 indicates stabilization of the morphometric anatomical parameters of the leaves under the conditions of the introduction of the R.I. Schroeder Arboretum. However, it should be noted that the stomatal index and leaf palisade ratio of *V. angustifolium* remain at a relatively low level compared to other systematic groups of mesotrophic plants in central Russia. Since the palisade ratio (index) is the most informative parameter, also determining plant resistance to drought, the increase in this parameter in the experiment further demonstrates the adaptability of narrow-leaved blueberry to the rather dry summer observation period of 2023-2025. The highest leaf palisade ratio in 2025 is observed for the Pomorochka cultivar (K = 39.50), while the lowest index during this observation period for the Neya cultivar (K = 37.43). In recent years, studying petiole anatomy has become especially important in the study of introduced plants. Petiole anatomy differs from leaf anatomy in that it undergoes the fewest anatomical changes due to the plants' unique adaptation to new growing conditions. Therefore, data on petiole anatomy of plants (including *V. angustifolium*) can be reliably used when incorporating the anatomical analysis of introduced plants. *V. angustifolium* petiole is densely covered by simple, soft, unicellular hairs. The semicylindrical petiole contains a large, closed collateral bundle in the central region, the wiry tissues of which (primary xylem and phloem) are arranged in a semicircular sector in cross section (Fig. 5).



a b

Fig. 3. Anatomical structure of *Vaccinium angustifolium* leaf blade: a – mesophyll in a cross-section of a leaf; b – a cross-section of a leaf blade in the area of main vein; 1 – upper epidermis; 2 – columnar mesophyll; 3 – closed collateral bundle of the lateral vein; 4 – spongy mesophyll; 5 – lower epidermis; 6 – angular collenchyma; 7 – closed collateral bundle of the main vein; 8 – spongy mesophyll with large intercellular spaces.

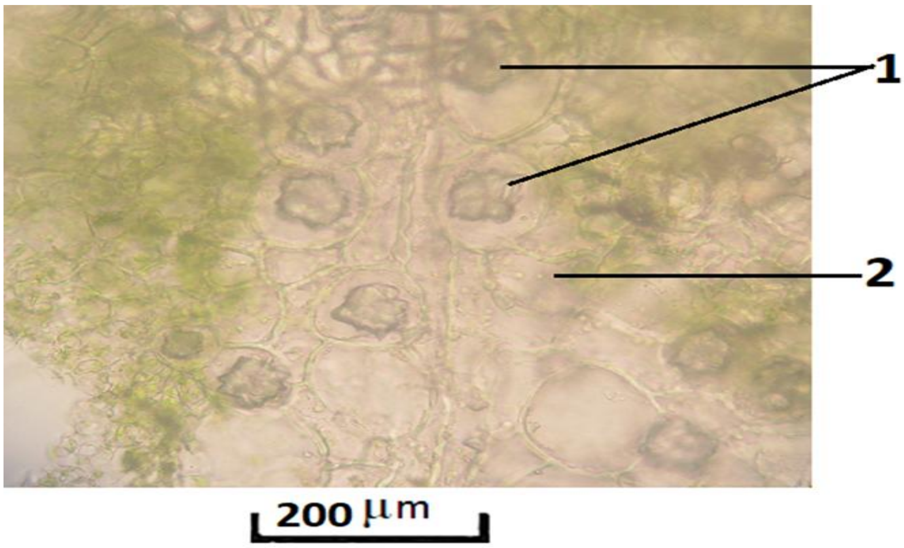


Fig. 4. Crystalline inclusions in the mesophyll of the leaf blade of *Vaccinium angustifolium*:
1 – calcium oxalate druses; 2 – spongy mesophyll cells.

Table 2. Biometric parameters of *Vaccinium angustifolium* leaf.

Biometric indicator	**Value**					
	2023		**2024**		**2025**	
	M±m_M	**Cv (%)**	**M±m_M**	**Cv (%)**	**M±m_M**	**Cv (%)**
Lakomka						
Leaf blade thickness (μm)	168.80 ± 2.29	15.46	172.50 ± 3.87	14.27	180.80 ± 4.22	12.85
Total thickness of columnar mesophyll of leaf blade (μm)	64.30 ± 2.11	12.58	66.80 ± 2.53	11.25	72.50 ± 2.15	10.34
Total thickness of spongy mesophyll of leaf blade (μm)	105.20 ± 2.24	11.25	108.40 ± 2.65	8.31	110.50 ± 2.58	8.02
Thickness of outer layer of columnar mesophyll cells (μm)	30.10 ± 0.43	7.34	32.54 ± 0.62	6.56	38.41 ± 0.75	5.92
Diameter of spongy mesophyll cells (μm)	7.13 ± 0.15	10.12	7.42 ± 0.17	9.23	7.86 ± 0.12	8.16
Thickness of upper epidermis with cuticle (μm)	14.80 ± 0.42	13.34	15.30 ± 0.52	11.25	16.00 ± 0.54	11.04
Height of upper epidermis cells, μm	13.5 ± 0.33	9.28	14.80 ± 0.49	8.06	15.30 ± 0.56	7.85
Cross-sectional size of upper epidermis cells (μm)	24.60 ± 0.65	12.85	25.70 ± 0.80	11.62	27.50 ± 0.97	10.03
Thickness of lower epidermis with cuticle (μm)	11.0 ± 0.38	9.07	11.90 ± 0.46	8.67	12.50 ± 0.49	8.32
Height of lower epidermis cells (μm)	10.4 ± 0.35	7.34	11.70 ± 0.44	6.59	12.40 ± 0.50	6.12
Cross-sectional size of lower epidermis cells (μm)	20.30 ± 0.49	11.49	21.40 ± 0.62	10.35	22.00 ± 0.75	9.61
Palisade ratio (K), %	31.5 ± 1.49	11.67	34.90 ± 1.53	11.15	38.50 ± 1.78	9.66
Number of stomata per 1 mm_2 of leaf surface (pcs.)	96.55 ± 5.25	13.36	108.42 ± 4.89	12.84	115.25 ± 4.66	9.75
Stomatal index (Ui; %)	25.70 ± 0.85	10.05	26.30 ± 0.75	9.46	29.20 ± 0.69	9.18
Neya						
Leaf blade thickness (μm)	156.30 ± 2.15	12.37	168.24 ± 3.52	13.28	177.25 ± 3.91	11.85
Total thickness of columnar mesophyll of leaf blade (μm)	61.24 ± 2.09	11.46	64.57 ± 2.13	10.75	70.32 ± 2.05	10.14
Total thickness of spongy mesophyll of leaf blade (μm)	101.15 ± 2.18	11.52	106.23 ± 2.44	9.86	108.43 ± 2.15	9.27
Thickness of outer layer of columnar mesophyll cells (μm)	29.85 ± 0.37	8.16	30.36 ± 0.59	7.95	36.52 ± 0.58	6.12
Diameter of spongy mesophyll cells (μm)	6.95 ± 0.12	11.03	7.08 ± 0.15	10.45	7.34 ± 0.11	9.42
Thickness of upper epidermis with cuticle (μm)	13.87 ± 0.35	11.15	14.23 ± 0.49	12.06	15.41 ± 0.48	10.57
Height of upper epidermis cells (μm)	12.8 ± 0.27	8.65	13.96 ± 0.43	9.12	14.49 ± 0.43	8.24
Cross-sectional size of upper epidermis cells (μm)	23.71 ± 0.58	13.15	24.68 ± 0.73	12.37	26.35 ± 0.87	9.95
Thickness of lower epidermis with cuticle (μm)	10.42 ± 0.39	10.12	11.15 ± 0.473	9.85	11.74 ± 0.497	9.83
Height of lower epidermis cells (μm)	9.85 ± 0.45	9.35	11.04 ± 0.39	7.73	11.76 ± 0.47	8.54
Cross-sectional size of lower epidermis cells (μm)	19.23 ± 0.41	12.03	20.56 ± 0.71	11.75	21.13 ± 0.82	11.15
Palisade ratio (K; %)	30.5 ± 1.52	12.37	33.48 ± 1.65	13.09	37.43 ± 1.82	11.58
Number of stomata per 1 mm_2 of leaf surface (pcs.)	95.49 ± 6.15	14.03	106.25 ± 5.32	12.96	113.88 ± 5.37	12.95
Stomatal index (Ui; %)	23.55 ± 0.75	9.56	25.12 ± 0.65	10.08	27.20 ± 0.71	9.87
Pomorochka						
Leaf blade thickness (μm)	175.93 ± 3.72	14.35	180.05 ± 4.26	13.84	183.95 ± 4.77	10.27
Total thickness of columnar mesophyll of leaf blade (μm)	66.15 ± 2.71	12.05	68.72 ± 2.88	10.93	75.42 ± 2.55	9.66
Total thickness of spongy mesophyll of leaf blade (μm)	108.22 ± 3.01	10.43	110.16 ± 2.98	9.54	117.12 ± 3.86	10.27
Thickness of outer layer of columnar mesophyll cells (μm)	33.06 ± 0.52	9.26	35.43 ± 0.72	8.96	41.12 ± 0.98	7.85
Diameter of spongy mesophyll cells (μm)	7.84 ± 0.18	11.23	8.15 ± 0.22	10.46	9.75 ± 0.16	9.03
Thickness of upper epidermis with cuticle (μm)	15.56 ± 0.62	12.87	16.94 ± 0.58	11.95	17.67 ± 0.49	10.14
Height of upper epidermis cells (μm)	14.16 ± 0.37	10.41	15.88 ± 0.54	10.02	16.86 ± 0.61	9.93
Cross-sectional size of upper epidermis cells (μm)	25.70 ± 0.75	14.25	26.99 ± 0.83	12.37	29.95 ± 0.93	9.86
Thickness of lower epidermis with cuticle (μm)	11.75 ± 0.421	10.38	12.84 ± 0.523	10.19	13.68 ± 0.497	8.55
Height of lower epidermis cells (μm)	11.41 ± 0.42	9.26	12.34 ± 0.51	9.03	13.54 ± 0.55	7.69
Cross-sectional size of lower epidermis cells (μm)	21.45 ± 0.52	12.17	22.68 ± 0.74	11.12	23.02 ± 0.81	9.88
Palisade ratio (K; %)	32.3 ± 1.53	12.05	35.75 ± 1.67	11.93	39.50 ± 1.78	9.52
Number of stomata per 1 mm_2 of leaf surface (pcs.)	102.95 ± 7.57	14.55	110.56 ± 6.32	13.07	116.15 ± 5.18	8.95
Stomatal index (Ui; %)	27.15 ± 0.75	9.26	29.63 ± 0.64	8.93	32.08 ± 0.58	7.95

On the phloem side of the vascular bundle, a clearly visible sclerenchyma was observed, enhancing the mechanical function of the petiole. The petiole's resistance to bending was ensured by the angular collenchyma of its cortex. Notably, the number of angular collenchyma layers in the petiole depended on its location. The number of collenchyma layers varied from three to eight, increasing along the ribs of the petiole. The largest internal space of the petiole was occupied by the ground parenchyma, whose cells contained a few chloroplasts. *V. angustifolium* fruit is a syncarpous, five-locular, multi-seeded berry. The fruit is spherical berry, slightly flattened at the top (Fig. 6). The berry size ranged from 1.2 to 1.8 cm in diameter. *V. angustifolium* fruits have a sweet, slightly tart flavor. Blueberry sap is colored due to the high concentration of anthocyanins. The berry is covered externally by a single-layer epidermis with a cuticle. The epicuticular wax (wax coating) of the berry epidermis is quite dense, giving blueberries their characteristic whitish waxy coating. The epidermis (berry skin) is the exocarp (outer layer of the pericarp) of the berry. The meso- and endocarp in blueberries are not clearly differentiated and represent the berry's storage parenchyma, which accumulates nutrients and biologically active compounds. The color of narrow-leaved blueberries depended on the level of morphological maturity and the level of anthocyanin accumulation (Fig. 7). *V. angustifolium* fruits have ripened unevenly, resulting in uneven fruit coloration within the same shoots of the plant and even within the same cluster. Fruits ranged in color from light green (unripe fruits), reddish-burgundy, blue, and even dark blue. Fruits reached morphological maturity with dark blue skin and a matte surface. The number of matured and full-bodied seeds per fruit ranged from 7 to 15 pcs. *V. angustifolium* plant yield was assessed as part of the ongoing primary introduction trials (Table 3). A study of the yield of cultivar plants revealed that its productivity increased from 2023 to 2025 due to the increasing age of the plants. A comprehensive assessment of the yield of *V. angustifolium* cultivars revealed that in 2025, the Pomorochka cultivar had the highest yield (5.58 kg/bush), while the Neya cultivar the lowest (4.16 kg/bush).

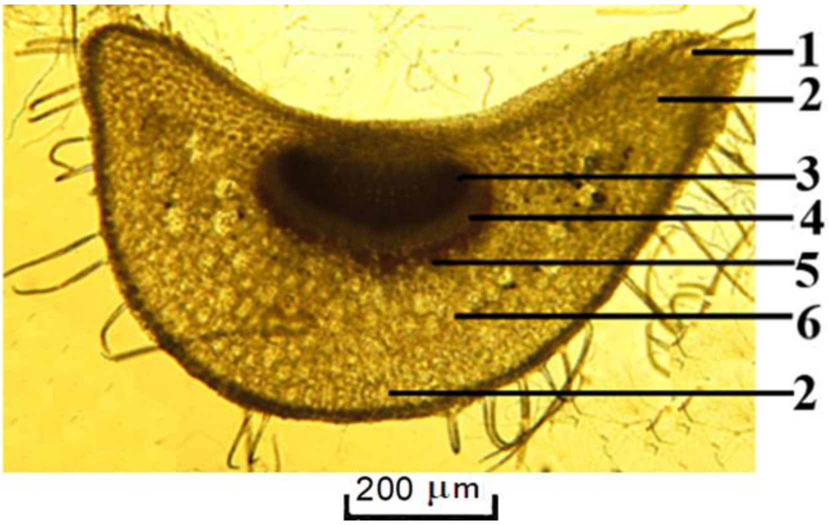


Fig. 5. Anatomical structure of the cross-section of *Vaccinium angustifolium* leaf petiole:
1 – epidermis with trichomes; 2 – angular collenchyma; 3 – primary xylem of collateral bundle;
4 – primary phloem of collateral bundle; 5 – sclerenchyma fibers; 6 – main parenchyma of cortex.

Fig. 6. Appearance of *Vaccinium angustifolium* fruits.

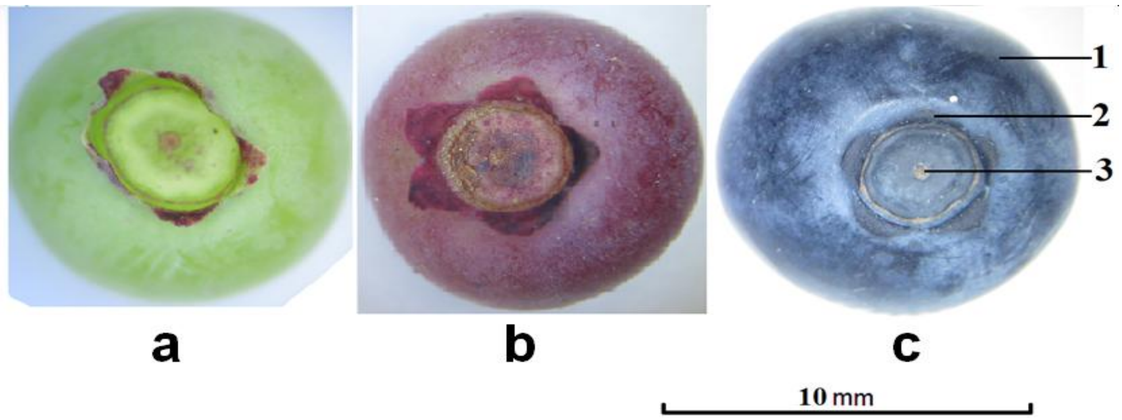


Fig. 7. *Vaccinium angustifolium* fruit maturity: a – unripe; b– beginning of ripening; c– morphologically ripe;
1 – pericarp (epiderm with a waxy coating); 2 – remains of calyx; 3 – scar from style of flower pistil.

Neya cultivar plants had the highest berry weight (1.28 g), while the Pomorochka cultivar the lowest (1.12 g). However, due to its overall high yield, the Pomorochka cultivar performed very well under the introduction conditions. The low coefficient of variation for yield and fruit weight of *V. angustifolium* cultivars in 2025 indicates stabilization of economically valuable traits under the introduction conditions of the Moscow Region, Russia.

Table 3. Productivity of *Vaccinium angustifolium* cultivars in the conditions of the R.I. Schroeder Arboretum (Moscow), 2023–2025

Cultivar	**Yield (kg/bush)**		**Fruit weight (g)**	
	$M \pm m_M$	Cv (%)	$M \pm m_M$	Cv (%)
		2023		
Lakomka	5.86 ± 0.16	13.1	1.18 ± 0.14	10.8
Neya	3.78 ± 0.10	14.5	1.22 ± 0.12	9.7
Pomorochka	5.32 ± 0.18	15.9	1.07 ± 0.12	13.6
		2024		
Lakomka	6.05 ± 0.15	11.4	1.21 ± 0.12	7.9
Neya	4.12 ± 0.12	14.3	1.25 ± 0.11	10.2
Pomorochka	5.49 ± 0.16	15.2	1.10 ± 0.16	11.4
		2025		
Lakomka	6.35 ± 0.14	10.2	1.24 ± 0.13	8.5
Neya	4.16 ± 0.11	11.7	1.28 ± 0.12	9.4
Pomorochka	5.58 ± 0.13	13.5	1.12 ± 0.15	9.8

The results of the winter hardiness assessment of *V. angustifolium* cultivars on the variety testing plot are presented in Table 4.

Table 4. Winter hardiness of *Vaccinium angustifolium* cultivars in the conditions of Moscow for the 2023-2024 and 2024-2025 winter seasons.

Cultivar	**Proportion of damaged annual shoots (%)**	**Proportion of damaged flower buds (%)**	**Severity of damage (points)**
		2023-2024	
Lakomka	9	8	1
Neya	11	10	2
Pomorochka	7	10	1
		2024-2025	
Lakomka	7	6	1
Neya	8	8	1
Pomorochka	5	7	1

V. angustifolium cultivars demonstrated relatively good winter hardiness in the experimental conditions of the Arboretum. No plant losses were observed during the entire observation period. Plant survival after the winters of 2023-2024 and 2024-2025 was 100%. Partial freezing of annual shoots was observed in the studied narrow-leaved blueberry varieties (freezing severity of 1-2 points). The highest degree of shoot freezing during the winter of 2023-2024 was observed for the Neya cultivar. The Pomorochka cultivar proved to be the most winter-hardy under the experimental conditions over the entire observation period, as the plants exhibited the lowest percentage of damaged annual shoots and flower buds. Thus, the Neya cultivar had a least winter-hardy, since plants exhibited the highest degree of damage to the above-ground parts of plants over the entire observation period.

CONCLUSIONS

The adaptive capacity of introduced plants depends largely on the structure of the leaf blade. The stomatal apparatus, as well as other elements of the *V. angustifolium* epidermis, can play a decisive role in the plant's resistance to various stress factors, including changes in climatic conditions. This anatomical study of the leaves of narrow-leaved blueberry cultivars provides an insight into the ecological nature of this species and the degree of adaptation of cultivars to changing environmental conditions. The response of *V. angustifolium* cultivars to Moscow conditions was manifested by changes in mesophyll structure and the number of stomata per unit leaf area. During adaptation, the plants showed a gradual increase in the thickness of the columnar mesophyll layer, as well as an elevation in its proportion in the total leaf blade thickness, as clearly indicated by an upraise in the palisade index. The increase in the palisade ratio may indicate the adaptation of narrow-leaf blueberry to more intense light in the open, well-lit experimental plot of the R.I. Schroeder Arboretum, as the columnar palisade mesophyll more efficiently absorbs light for photosynthesis. It also indicates the adaptability of *V. angustifolium* to the relatively dry summer periods of 2023-2025. Over the entire observation period, a consistent pattern of *V. angustifolium* leaf structure changes was observed across the climatic gradient of the Moscow Region and the agrometeorological conditions of the introduction site. Plants exhibited increases in overall leaf thickness, upper and lower epidermis, columnar and spongy mesophyll, a shift in the ratio of spongy to columnar mesophyll toward an elevation in the proportion of the latter, and an upraise in stomatal density and size. Based on an analysis of extensive factual data, it can be concluded that the main structural changes in *V. angustifolium* leaves following introduction to the Moscow region include increases in leaf blade thickness, palisade index, and stomatal index. It was established that *V. angustifolium* simultaneously undergoes both photosynthetic adaptation to changing climatic conditions in the introduction region and adaptive changes in leaf anatomy. As a result of the conducted research, the main anatomical and diagnostic features of *V. angustifolium* leaves were established, which can be used to compile anatomical atlases of cultivated plants, identify and evaluate the authenticity of raw materials of plant leaves, assess the adaptive potential of introduced plants, and also serve as a theoretical basis for the development of methods for the introduction of berry crops. Over the years of research, the Pomorochka cultivar has demonstrated the highest yield, while the Neya cultivar the lowest. The Neya cultivar has the highest fruit weight, while the Pomorochka cultivar the lowest. A comprehensive approach to *V. angustifolium* cultivars testing and yield assessment allows us to recommend the commercial cultivation of these plants in the Moscow Region, Russia. Over the entire observation period, a consistent pattern of leaf structure changes in narrow-leaved blueberries was observed across the climatic gradient of the Moscow Region and the agrometeorological conditions of the introduction area. Plants exhibited increases in overall leaf thickness, upper and lower epidermis, columnar and spongy mesophyll, a shift in the spongy-to-columnar mesophyll ratio toward an upraise in the proportion of the latter, and also an elevation in stomatal density and size. Based on an analysis of extensive factual research data, it can be concluded that the main structural changes in the leaves of *V. angustifolium* cultivars introduced to the Moscow Region include increases in leaf blade thickness, palisade index, and stomatal index. It was established that *V. angustifolium* cultivars simultaneously undergo both photosynthetic adaptation to changing climatic conditions in the introduction region and adaptive alterations in leaf anatomy. Based on the winter hardiness assessment of *V. angustifolium* for the 2023–2024 and 2024–2025 winter periods, the studied cultivars can be considered sufficiently suitable for cultivation in Center of European part of Russia and, based on this indicator, can be used as sources and donors of economically valuable traits. The winter period of 2024–2025 was the most favorable for overwintering for all studied cultivars. Notably, in the context of introduction, especially when cultivating perennial berry crops, the most important task is assessing their winter hardiness and yield. By applying agricultural practices and managing plant morphogenesis in cultivation, it is possible to increase their frost resistance, winter hardiness, and productivity. However, the success of this task will directly depend on our understanding of the species-specific responses and bioecological characteristics of plants.

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