# SYSTEMATICS, PHYLOGENY AND GEOGRAPHY OF CULTIVATED PLANTS AND THEIR WILD RELATIVES

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# Features of the anatomical structure of leaves depending on the high-altitude growth of apricot in Dagestan

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**Background.** The adaptive changes during the distribution of *Prunus armeniaca* L. in Dagestan are important for understanding microevolution, structural and functional differentiation processes of populations along environmental gradients based on the organism's reaction norm. They can be examined by studying leaf anatomical features, having ecologically differentiating significance in natural populations with contrasting growth conditions.
**Materials and methods.** The material for the study of leaf anatomical features was taken from 7 apricot trees in 3 growing areas of Mountainous Dagestan. Comparative analysis was carried out for 42 morphological, anatomical and index parameters of the lamina and petiole.
**Results.** The anocytic structure type of the stomatal apparatus was found in all apricot samples. The differences were determined by the degree of stomata submergence depending on the cuticle's development. Trees from greater heights had more trichomes on the leaf's upper side than on its underside. Significant differences between the extreme height reference points were recorded for the number of stomata, cells of the lower epidermis, layers of the sclerenchyma, and xylem thickness. Most of the traits of the lamina decreased, and those of the petiole increased with the altitude.
**Conclusion.** The traits corresponding to the lower and upper altitude limits of *P. armeniaca* were identified on the basis of the lamina and petiole anatomical features. More xerophytic leaf traits were recorded for the altitudes of 550 m and 1900 m, and mesophytic ones for 1700 m and 1800 m. Endoderm thickness, number of endosperm layers, petiole index, and stomatal index were identified as stable indicators according to the reaction norm within the scope of altitudes: The differences were proved for more plastic traits (number of cells of the upper and lower epidermis, number of stomata, thickness of the lamina and cuticle, and the petiole's long axis diameter).

***Keywords:*** *Prunus armeniaca* L., natural cenopopulations, anatomy, lamina, petiole, altitude above sea level

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## СИСТЕМАТИКА, ФИЛОГЕНИЯ И ГЕОГРАФИЯ КУЛЬТУРНЫХ РАСТЕНИЙ И ИХ ДИКИХ РОДИЧЕЙ

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# Особенности анатомического строения листьев в зависимости от высотного произрастания абрикоса в Дагестане

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**Актуальность.** Изучение анатомических признаков листа, имеющих эколого-дифференцирующее значение в природных популяциях абрикоса (*Prunus armeniaca* L.) с контрастными условиями произрастания, позволит выявить адаптивные изменения, происходившие при распространении этого вида вдоль высотных условий Дагестана, что важно также для понимания процессов микроэволюции, структурной и функциональной дифференциации популяций вдоль средовых градиентов на основе нормы реакции организмов.
**Материал, методы и условия.** Материалом для изучения анатомических особенностей послужили листья семи деревьев абрикоса из трех мест произрастании Горного Дагестана. Сравнительный анализ проведен по 42 морфологическим, и анатомическим показателям листовой пластинки и черешка.
**Результаты.** У всех образцов абрикоса выявлен аномоцитный тип строения устьичного аппарата. Различия определялись по степени погруженности устьиц в зависимости от развитости кутикулы. Деревья с больших высот произрастания имеют значительно больше трихом на верхней стороне листа, чем его нижней стороне. Установлены достоверные различия между крайними по высоте реперными точками по количеству устьиц, клеток нижней эпидермы, слоев склеренхимы и толщине ксилемы. С высотой над уровнем моря большинство показателей признаков листовой пластинки уменьшаются, а черешка увеличиваются.
**Заключение.** По результатам сравнения анатомических признаков листа и черешка *P. armeniaca* выделены признаки, соответствующие нижнему и верхнему пределу произрастания. По совокупности признаков более ксерофитные черты листьев обнаружены на высотах 550 м и 1900 м, мезофитные – 1700 м и 1800 м. Выявлены стабильные по норме реакции в пределах высотных условий признаки: «толщина эндодермы», «число слоев эндодермы», «индекс черешка» и «устьичный индекс». У более пластичных признаков (число клеток верхней и нижней эпидермы, число устьиц, толщина листовой пластинки и кутикулы, диаметр длинной оси черешка) выявленные различия доказаны.

***Ключевые слова:*** *Prunus armeniaca* L., природные ценопопуляции, анатомия, листовая пластинка, черешок, высота над уровнем моря

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## Introduction

*Prunus armeniaca* L. (= *Armeniaca vulgaris* Lam.) is the most important cultivated fruit plant. The primary wild apricot has been found in the arid mountainous environments of Central Asia and Northeast China (Kostina, 1936; Vavilov, 1960; Zhukovsky, 1964; Vekhov et al., 1978; Avdeev, 2012; Asadulaev et al., 2020). However, apricot cultivars can suffer from a moisture deficiency stress (Genkel, 1982; Skvortsov, Kramarenko, 2007; Asadulaev et al., 2008; Starodubtseva, Dzhuraeva, 2016; Anatov et al., 2019), while under unfavorable conditions leaves lose turgor and later dry up (Gorina, 2014; Gorina et al., 2017).

In the Caucasus, the main natural apricot populations are concentrated along the river valleys of the Inner Mountainous Dagestan, at altitudes from 350 to 1500 m above mean sea level, sometimes (sporadically) along the southern slopes up to 1900 m (Asadulaev et al., 2014; Anatov, 2019). Having a significant variation in altitudinal distribution and, accordingly, significant differences in growing conditions, apricot trees should have certain structural and functional mechanisms for their leveling. Changes that provide resistance to critical environmental conditions are especially visible in the anatomical structure of vegetative organs.

Therefore, a comparative anatomical study of leaves, while making ecological characterization of woody plants, is of great importance. It is also important for the correct assessment of the adaptive potential of apricot plants growing at different altitude levels in Mountainous Dagestan, and for understanding microevolutional processes as the basis of their ecological differentiation.

For apricots of different ecogeographic groups, anatomical features of the leaf are well studied (Sokolova, 1986; Rostova, Sokolova, 1992; Sokolova, 2000). However, we are not aware of the specific features in the leaf anatomical structure of apricot trees in natural populations at different altitudes of their occurrence.

*The purpose of this work* was to identify anatomical features of the leaf that have an ecologically differentiating value along the altitude gradients in the Dagestani natural populations of apricot in order to understand microevolutional changes during the movement of this species to new territories or the selection of adapted cultivars for gardening.

## Material and methods

Three model populations differing in contrasting growth conditions along the altitudinal gradient and geographic isolation were selected in the Inner Mountainous Dagestan for the study of *P. armeniaca* anatomical features under the conditions of Mountainous Dagestan: three trees from Maydan Village, Untsukulsky District (550 m.a.s.l.); three trees from Charodinsky District between the villages of Gunukh and Murukh (1700–1800 m.a.s.l.); one tree from Gunib Village; Gunibsky District (1900 m.a.s.l.).

Live material for anatomical studies was fixed in 70% ethyl alcohol with the addition of glycerin. Temporary leaf preparations for a light microscope were made according to generally accepted techniques (Pausheva, 1974; Borisovskaya, Sokolova, 1978; Zhestyanikova, Moskaleva, 1981; Prozina, 1960; Barykina, 2004). Cross sections were made in the middle part of the blade and leaf petiole in triplicate – one middle leaf from three one-year vegetative shoots. Five leaves were separately selected from one-year shoots of medium length (25–30 cm) from each of the seven trees, starting from the first leaves at the base of the shoot, for measuring morphological parameters.

Structural elements of leaf tissues were described in accordance with the procedures developed by N. A. Aneli (1975), and Al. A. Fedorova et al. (1956).

Methods of descriptive statistics, variance, regression, discriminant and correlation analyses were used for mathematical data processing. Statistical data processing was carried out using Statistica v. 13.3.

A comparative analysis was carried out on 42 morphological and anatomical indicators and indices of the lamina and petiole (Table 1).

**Table 1. Anatomical characters of the apricot leaf and petiole used in the work**

**Таблица 1. Анатомические признаки листа и черешка абрикоса, использованные в работе**

| Characters and units / Признаки, единицы измерения | Note / Примечание |
|---|---|
| **General / Общие** | |
| Length of the lamina, cm / Длина листовой пластинки, см | L |
| Width of the lamina, cm / Ширина листовой пластинки, см | W |
| Length of the petiole, cm / Длина черешка, см | P |
| Leaf area, $cm^2$ / Площадь листа, $см^2$ | S |
| **Lamina / Листовая пластинка** | |
| Number of the upper epidermis cells per 1 $mm^2$ / Число клеток верхней эпидермы на 1 $мм^2$ | Sc1 |
| Number of the lower epidermis cells per 1 $mm^2$ / Число клеток нижней эпидермы на 1 $мм^2$ | Sc2 |
| Number of the lower epidermis stomata per 1 $mm^2$ / Число устьиц нижней эпидермы на 1 $мм^2$ | SN |
| Length of the lower epidermis stomata, μm / Длина устьиц нижней эпидермы, мкм | SL |
| Width of the lower epidermis stomata, μm / Ширина устьиц нижней эпидермы, мкм | SW |
| Thickness of the lamina, μm / Толщина листовой пластинки, мкм | LT |

**Table 1.** The end
**Таблица 1.** Окончание

| Characters and units / Признаки, единицы измерения | Note / Примечание |
|---|---|
| **Lamina / Листовая пластинка** | |
| Height of the upper epidermis cells, µm / Высота клеток верхней эпидермы, мкм | EH1 |
| Height of the lower epidermis cells, µm / Высота клеток нижней эпидермы, мкм | EH2 |
| Thickness of the upper cuticle, µm / Толщина верхней кутикулы, мкм | CT1 |
| Thickness of the lower cuticle, µm / Толщина нижней кутикулы, мкм | CT2 |
| Thickness of the palisade tissue, µm / Толщина палисадной ткани, мкм | MP |
| Thickness of the spongy tissue, µm / Толщина губчатой ткани, мкм | MS |
| Thickness of the leaf mesophyll (MP + MS), µm / Толщина мезофилла листа (MP + MS), мкм | M |
| Number of the palisade tissue layers / Число слоев палисадной ткани | MPn |
| Number of the spongy tissue layers / Число слоев губчатой ткани | MSn |
| Total number of the mesophyll layers (MPn + MSn) / Общее число слоев мезофила (MPn + MSn) | MN |
| **Petiole (abaxial side) / Черешок (абаксиальная сторона)** | |
| Thickness of the cuticle, µm / Толщина кутикулы, мкм | PC |
| Height of the epidermis, µm / Высота эпидермы, мкм | PE |
| Thickness of the collenchyma, µm / Толщина колленхимы, мкм | TC |
| Number of the collenchyma layers / Число слоев колленхимы | NC |
| Thickness of the crustal parenchyma, µm / Толщина коровой паренхимы, мкм | KT |
| Number of the parenchyma layers / Число слоев паренхимы | KN |
| Thickness of the endodermoid tissue, µm / Толщина эндодермоидной ткани, мкм | EnT |
| Number of the endodermoid tissue layers / Число слоев эндодермоидной ткани | EnN |
| Thickness of the sclerenchyma, µm / Толщина склеренхимы, мкм | BT |
| Number of the sclerenchyma layers / Число слоев склеренхимы | BN |
| Thickness of the phloem, µm / Толщина флоэмы, мкм | FT |
| Thickness of the xylem, µm / Толщина ксилемы, мкм | XT |
| Number of vessels in a modular xylem row / Число сосудов в модульном ксилемном ряду | XN |
| Radial vessel diameter, µm / Радиальный диаметр сосуда, мкм | XRd |
| Tangential vessel diameter, µm / Тангентальный диаметр сосуда, мкм | XTd |
| Perimedullary zone thickness, µm / Толщина перимедуллярной зоны, мкм | PZt |
| Number of the perimedullary zone layers / Число слоев перимедуллярной зоны | PZn |
| Cross-sectional tangential diameter, µm / Тангентальный диаметр поперечного сечения, мкм | OL |
| Cross-sectional radial diameter, µm / Радиальный диаметр поперечного сечения, мкм | OS |
| **Indices / Индексы** | |
| Petiole index (OL/OS) / Индекс черешка (OL/OS) | InP |
| Palisade index (MP/MS) / Индекс палисадности (MP/MS) | InM |
| Stomatal index (SL/SW) / Устьичный индекс (SL/SW) | InS |

## Results

Apricot trees from all growth levels (550, 1700, 1800, and 1900 m) had typical dorsoventral leaves with various combinations of xeromorphic features. The outlines of the surface projection of the cell walls of the upper epidermis were rectilinear, those of the lower epidermis were curved. The cells of the upper epidermis were larger than those of the lower epidermis.

The thickness of the cuticle of the upper and lower epidermis increased with altitudes above sea level. We attribute this feature to an increase in solar insolation and evaporation with rising altitudes. It is believed that when the stomata are open, the loss of water through the cuticle is insignificant, but when the stomata are closed, cuticular transpiration becomes important in the water regime of the plant (Kosulina, 1993).

Apricot leaves are hypostomatic, with anomocytic stomata, and scaphoid guard cells. The size of the stomata on the abaxial epidermis of the lamina varied slightly in different trees, but their number per 1 mm$^2$ increased with higher altitudes from 373.4 in the Maydan sample to 708.7 in the Gunib sample. In addition to an increase in solar radiation, this may also be due to a decrease in air density at high altitudes and the need to ensure the process of optimal respiration by increasing the number of stomata.

The structure of the stomatal apparatus, indicators of the number and size of stomata are considered ecological characters and one of the mechanisms of plant adaptation to water deficit (Sorokopudov et al., 2014). At the same time, according to some opinions, xeromorphic leaves are characterized by smaller, numerous stomata; according to others, on the contrary, the low frequency of stomata in combination with their large sizes contributes to more effective control of water loss (Sokolova, 2000).

The degree of immersion of stomata into the epidermis varied in different trees, depending on the cuticle's degree of development. Predominating in the sample from the Gunukh locality were stomata located on the same level with the epidermal cells. We can assume that the location of the stomata relative to the surface of the epidermis is associated with the intensity of transpiration; the deeper the stomata are immersed, the less is water evaporation. It follows from this assumption that the evaporation rate is probably higher in the leaves of the Gunukh sample than in the other two samples. The reasons may be a higher moisture supply in Charodinsky District, compared to the Gunib Plateau and the conditions of Untsukulsky District, as well as the possible cultigenic origin of this sample. The issue deserves a more detailed further study.

The presence of numerous (708.7 pcs. per 1 mm$^2$) and relatively small (27.7 μm long) submerged stomata on the lamina of the Gunib sample suggests the dependence of this character's parameters on the ecological conditions in its growth sites (the southern microslope, and the highest altitude above sea level – 1900 m – cause high evaporation, insolation, and temperature drops). This sample of all studied can be recognized as the most xeromorphic.

Another equally important trait is the presence of trichomes. Most researchers consider trichomes a xeromorphic trait. It is believed that trichomes are able to protect the mesophyll from overheating when the stomata are closed (Maksimov, 1931). However, in the works dedicated to the study of the role of trichomes in the regulation processes of the plant water regime, unambiguous results have not been obtained; in the period of leaf growth, on the contrary, trichomes can expand the evaporating surface (Esau, 1980; Sokolova, 2000).

In apricot trees from medium-altitude heights (Gunukh, Murukh, and Gunib), unicellular trichomes have a conical shape and are present on the upper side of the leaf (Figure 1). But the Gunib sample (1900 m) has them on the lower sides of the leaf and petiole as well. Trichomes are short on the adaxial side of the petiole, and long on the abaxial side. The presence of pubescence on the leaves of the Gunib sample confirms the opinion that this feature is related to the intensity of solar insolation. In trees from a lower growth altitude (550 m), trichomes are found only on the petiole, both on the abaxial and adaxial sides.

The characteristics of the average values for leaves from different growing areas are presented below (Table 2). Larger leaves were taken from the altitudes of 1700 and 1800 m (with the highest moisture supply), and smaller ones from the altitude of 1900 m (the southern microslope, and the highest evaporation rate).

E. A. Sokolova (2000) believes that apricot cultivars with a dense mesophyll structure exhibit the greatest drought resistance; the lamina is thicker than 230 μm, the number of mesophyll layers is more than 6, and the palisade coefficient is above the average. In our study, the first and third samples from Maydan had the highest leaf thickness, while the thinnest were observed at Gunib. The number of mesophyll layers in all samples was more than 6; the highest values were recorded for the first sample from Murukh and Gunib. The second and third samples from Maydan, and the sample from Gunib had high values of the palisade index (InM).

The resulting data attest to the existence of differences in values for the same characters under similar growing conditions. Based on this, the values of each character cannot be interpreted from the point of view of their informativeness for assessing the stability and adaptability of a sample. In addition, such xeromorphic traits as small cells and a high number of stomata may indicate the insufficiency of nutrients, exposure to low or high temperatures, etc. (Vasilevskaya, 1954). However, according to the sum of traits, it can be assumed that the trees from Maydan and Gunib are more drought-resistant than the trees from Charodinsky District. We associate this with the difference in climatic conditions of the two districts. Charodinsky District belongs to the High Mountainous Dagestan with higher moisture content; accordingly, there will be more mesomorphic traits than under the conditions of a moisture deficit in the Inner Mountainous Dagestan (especially the samples from Maydan).

One-way analysis of variance – the factor "interindividual differences" (df = 6) was used – helped to assess the differences among all the registered trees. The analysis of the data showed that the studied trees significantly differed among themselves in most of the leaf characteristics (Table 3). The greatest differences were found for the following characters: the number of the upper epidermis cells, number of stomata, tangential diameter of the petiole's cross section, radial diameter of the petiole's cross section, thickness of the cuticle, and number of the palisade tissue layers. Insignificant differences were observed for the characters: thickness of the lower cuticle", thickness of the crustal parenchyma (in the leaf), and the number of parenchyma layers (in the petiole).

An analysis of variance, taking into account the places of growth (Untsukulsky, Charodinsky, and Gunibsky Districts), was carried out to determine the effect size of environmental factors. The results showed a decrease in significance of the values of some features and identified ecologically dependent traits. A number of characters (the number of stomata, "thickness of the cuticle, tangential diameter of the petiole's cross

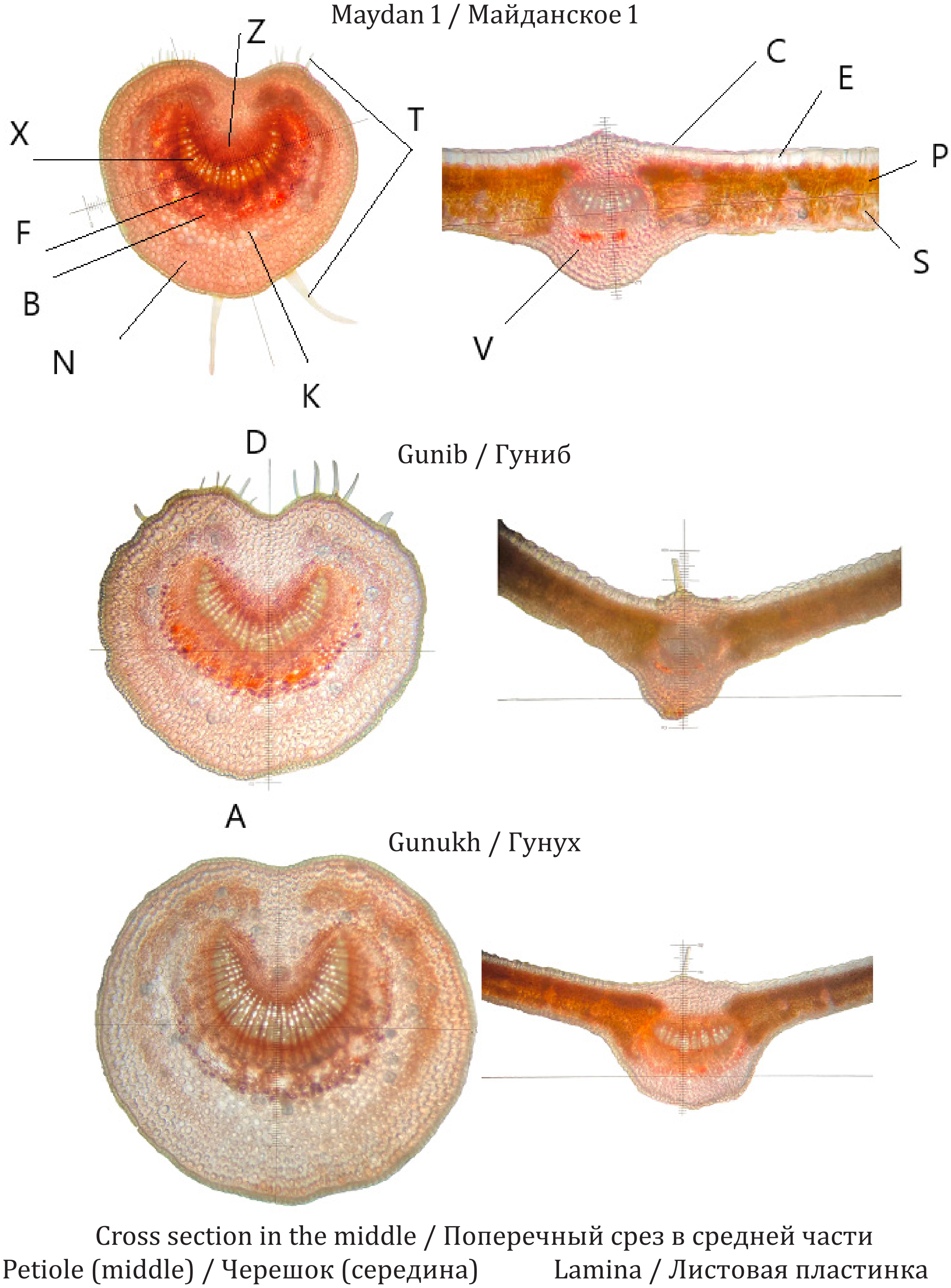


**Fig. 1. Cross sections of apricot petioles and laminae from natural populations of Dagestan (resolution 10 × 10)**
Note: T – trichomes; C – cuticle; E – epidermis; P – palisade tissue; S – spongy tissue; V – vascular fibrous bundle; X – xylem; F – phloem; B – sclerenchyma; N – collenchyma; K – crustal parenchyma; Z – perimedular zone; A – abaxial side; D – adaxial side

**Рис. 1. Поперечные срезы черешков и листовой пластинки абрикоса из природных популяций Дагестана (разрешение 10 × 10)**
Примечание: T – трихомы; C – кутикула; E – эпидерма; P – палисадная ткань; S – губчатая ткань; V – сосудисто-волокнистый пучок; X – ксилема; F – флоэма; B – склеренхима; N – колленхима; K – коровая паренхима; Z – перимедулярная зона; A – абаксиальная сторона; D – адаксиальная сторона

**Table 2.** Comparative characteristics of apricot trees according to average values
**Таблица 2.** Сравнительная характеристика деревьев абрикоса по средним значениям

| Characters / Признаки | Maydan / Майданское | | | Gunukh / Гунух | Murukh / Мурух | | Gunib / Гуниб |
|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | | 1 | 2 | 3 |
| L | 4.5 ± 0.29 | 5.4 ± 0.13 | 5.2 ± 0.07 | 7.2 ± 0.66 | 6.9 ± 0.25 | 6.2 ± 0.26 | 4.6 ± 0.43 |
| W | 3.9 ± 0.43 | 4.3 ± 0.09 | 4.4 ± 0.07 | 4.9 ± 0.30 | 4.6 ± 0.22 | 5.2 ± 0.35 | 3.7 ± 0.15 |
| P | 1.8 ± 0.19 | 3.3 ± 0.23 | 2.3 ± 0.03 | 3.0 ± 0.30 | 2.6 ± 0.29 | 2.9 ± 0.10 | 1. 9± 0.21 |
| S | 12.8 ± 2.17 | 15.4 ± 0.68 | 14.6 ± 0.45 | 23.8 ± 3.48 | 20.8 ± 1.25 | 22.8 ± 2.49 | 11.4 ± 1.27 |
| Sc1 | 765.7 ± 33.78 | 1078.1 ± 34.77 | 1260.9 ± 33.65 | 998.1 ± 49.82 | 742.9 ± 33.47 | 640.1 ± 20.29 | 860.8 ± 24.54 |
| Sc2 | 3017.1 ± 104.96 | 3059.0 ± 92.28 | 3173.3 ± 82.47 | 3858.9 ± 138.60 | 3710.5 ± 119.28 | 3580.9 ± 57.32 | 3874.3 ± 108.02 |
| SN | 373.4 ± 16,56 | 419.0 ± 15.40 | 438.0 ± 14.36 | 529.5 ± 28.71 | 544.6 ± 17.54 | 559.9 ± 19.54 | 708.7 ± 28.84 |
| SL | 31.0 ± 0.54 | 31.8 ± 0.88 | 30.5 ± 0.63 | 28.7 ± 0.88 | 33.3 ± 0.78 | 30.1 ± 0.72 | 27.7 ± 0.69 |
| SW | 23.3 ± 0.44 | 24.6 ± 0.51 | 25.3 ± 0.47 | 23.3 ± 0.62 | 24.1 ± 0.53 | 22.8 ± 0.51 | 21.5 ± 0.44 |
| LT | 242.3 ± 6.45 | 212.5 ± 3.76 | 236.6 ± 4.73 | 206.8 ± 9.42 | 226.5 ± 4.35 | 206.5 ± 4.23 | 174.2 ± 0.90 |
| EH1 | 43.6 ± 1.88 | 39.4 ± 1.63 | 39.1 ± 1.19 | 33.6 ± 1.12 | 41.3 ± 1.32 | 43.3 ± 1.39 | 35.0 ± 0.85 |
| EH2 | 21.0 ± 0.90 | 19.5 ± 0.74 | 18.8 ± 0.67 | 16.4 ± 0.48 | 16.0 ± 0.54 | 17.6 ± 0.58 | 15.3 ± 0,31 |
| CT1 | 1.5 ± 0.13 | 1.,5 ± 0.13 | 1.7 ± 0.13 | 1.9 ± 0.07 | 1.6 ± 0.13 | 1.8 ± 0.11 | 1.9 ± 0.12 |
| CT2 | 1.2 ± 0.11 | 1.5 ± 0.13 | 1.3 ± 0.12 | 1.5 ± 0.13 | 1.5 ± 0.13 | 1.6 ± 0.13 | 1.5 ± 0.13 |
| MP | 68.1 ± 3.40 | 65.9 ± 2.18 | 75.3 ± 1.96 | 59.9 ± 4.00 | 63.6 ± 2.04 | 56,7±1,95 | 52.7 ± 1.05 |
| MS | 103.4 ± 3.17 | 81.9 ± 3.43 | 98.7 ± 3.48 | 91.6 ± 5.27 | 100.1 ± 2.46 | 83.4 ± 2.40 | 65.5 ± 1.51 |
| M | 171.4 ± 5.56 | 147.8 ± 3.48 | 174.0 ± 4.30 | 151.6 ± 8.38 | 163.6 ± 3.68 | 140.2 ± 3.17 | 118.2 ± 1.50 |
| MPn | 2.5 ± 0.13 | 2.2 ± 0.11 | 2.7 ± 0.12 | 2.0 ± 0.00 | 3.2 ± 0.11 | 2.3 ± 0.13 | 3.3 ± 0.13 |
| MSn | 5.3 ± 0.21 | 4.1 ± 0.19 | 5.0 ± 0.24 | 4.7 ± 0.29 | 5.9 ± 0.21 | 5.5 ± 0.13 | 4.7 ± 0.12 |
| MN | 7.8 ± 0.24 | 6.3 ± 0.16 | 7.7 ± 0.28 | 6.7 ± 0.29 | 9.1 ± 0.24 | 7.8 ± 0.22 | 8.1 ± 0.15 |
| PC | 5.0 ± 0.00 | 5.0 ± 0.00 | 5.0 ± 0.00 | 5.0 ± 0.00 | 5.0 ± 0.00 | 5.0 ± 0.00 | 6.5 ± 0.33 |
| PE | 21.5 ± 0.94 | 20.3 ± 0.64 | 22.8 ± 0.48 | 20.8 ± 0.76 | 23.0 ± 0.50 | 26.0 ± 0.72 | 23.0 ± 0.74 |

**Table 2.** The end
**Таблица 2.** Окончание

| Characters / Признаки | Maydan / Майданское | | | Gunukh / Гунух | Murukh / Мурух | | Gunib / Гуниб |
|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | | 1 | 2 | 3 |
| TC | 114.3 ± 5.07 | 160.5 ± 7.15 | 128.5 ± 2.89 | 132.7 ± 5.61 | 139.2 ± 4.97 | 138.5 ± 5.86 | 119.2 ± 4.14 |
| NC | 3.7 ± 0.27 | 5.5 ± 0.26 | 4.5 ± 0.13 | 4.5 ± 0.19 | 5.0 ± 0.00 | 4.9 ± 0.09 | 4.0 ± 0.17 |
| KT | 122.2 ± 2.60 | 114.5 ± 4.00 | 121.0 ± 2.02 | 117.7 ± 3.96 | 110.7 ± 5.07 | 117.2 ± 3.30 | 117.2 ± 4.45 |
| KN | 4.8 ± 0.24 | 5.1 ± 0.15 | 4.5 ± 0.13 | 5.0 ± 0.14 | 4.5 ± 0.13 | 4.7 ± 0.12 | 4.9 ± 0.19 |
| EnT | 56.0 ± 4.86 | 28.7 ± 3.01 | 26.0 ± 1.72 | 30.2 ± 1.96 | 34.8 ± 2.22 | 27.2 ± 2.01 | 33.3 ± 3.04 |
| EnN | 2.0 ± 0.14 | 1.3 ± 0.12 | 1.1 ± 0.09 | 1.2 ± 0.11 | 1.3 ± 0.13 | 1.3 ± 0.12 | 1.5 ± 0.13 |
| BT | 65.5 ± 4.22 | 65.2 ± 3.21 | 64.8 ± 2.17 | 68.0 ± 2.77 | 81.5 ± 1.72 | 74.2 ± 1.74 | 69.8 ± 3.14 |
| BN | 5.9 ± 0.35 | 6.5 ± 0.22 | 6.8 ± 0.17 | 6.9 ± 0.36 | 8.0 ± 0.28 | 8.3 ± 0.23 | 8.0 ± 0.41 |
| FT | 65.8 ± 3.69 | 56.3 ± 2.40 | 58.0 ± 1.81 | 78.8 ± 5.67 | 78.5 ± 2.32 | 74.5 ± 1.64 | 67.0 ± 3.31 |
| XT | 83.7 ± 6.71 | 82.3 ± 3.27 | 94.5 ± 2.86 | 103.0 ± 3.78 | 116.3 ± 6.53 | 110.5 ± 2.92 | 102.3 ± 1.90 |
| XN | 5.0 ± 0.48 | 4.6 ± 0.16 | 5.6 ± 0.16 | 5.5 ± 0.27 | 6.4 ± 0.13 | 5.3 ± 0.16 | 5.6 ± 0.21 |
| XRd | 20.8 ± 1.21 | 23.5 ± 0.76 | 21.3 ± 0.73 | 26.8 ± 1.10 | 26.3 ± 1.03 | 23.7 ± 0.54 | 19.3 ± 1.45 |
| XTd | 14.0 ± 0.48 | 15.2 ± 0.52 | 15.5 ± 0.27 | 16.5 ± 0.53 | 18.0 ± 0.92 | 16.2 ± 0.33 | 17.3 ± 1.08 |
| PZt | 68.8 ± 3.42 | 60.8 ± 2.69 | 75.2 ± 3.03 | 74.3 ± 3.25 | 79.2 ± 2.46 | 77.5 ± 1.95 | 77.3 ± 2.70 |
| PZn | 6.3 ± 0.34 | 6.5 ± 0.32 | 6.9 ± 0.32 | 8.1 ± 0.27 | 8.0 ± 0.29 | 8.7 ± 0.12 | 6.7 ± 0.27 |
| OL | 1159.3 ± 34.04 | 1302.0 ± 13.77 | 1262.0 ± 13.95 | 1310.7 ± 41.71 | 1461.3 ± 19.17 | 1392.0 ±2 6.84 | 1070.7 ± 10.80 |
| OS | 924.0 ± 32.57 | 1136.7 ± 22.88 | 1151.3 ± 8.44 | 1121.3 ± 45.32 | 1270.0 ± 22.06 | 1180.7 ± 26.54 | 917.3 ± 2.06 |
| InP | 1.26 ± 0.019 | 1.15 ± 0.020 | 1.10 ± 0.013 | 1.18 ± 0.014 | 1.15 ± 0.010 | 1.18 ± 0.013 | 1.17 ± 0.012 |
| InM | 0.66 ± 0.032 | 0.83 ± 0.056 | 0.78 ± 0.031 | 0.66 ± 0.035 | 0.64 ± 0.021 | 0.69 ± 0.028 | 0.81 ± 0.029 |
| InS | 1.34 ± 0.025 | 1.30 ± 0.040 | 1.21 ± 0.020 | 1.24 ± 0.032 | 1.39 ± 0.045 | 1.32 ± 0.033 | 1.29 ± 0.029 |

Note: here and hereinafter, the symbols used are taken from Table 1
Примечание: здесь и далее условные обозначения приводятся из таблицы 1

**Table 3.** Results of the one-way ANOVA and regression analyses, and of Tukey's test for apricot leaf characters in natural populations of Mountainous Dagestan

**Таблица 3.** Результаты однофакторного дисперсионного, регрессионного анализов и критерия Тьюки по признакам листа абрикоса в природных популяциях Горного Дагестана

| Characters / Признаки | Interindividual differences / Межиндивидуальные различия df = 6 | | | Differences in the place of growth / Различия по месту произрастания df = 2 | | | Tukey's test / Критерий Тьюки | | |
|---|---|---|---|---|---|---|---|---|---|
| | $h_1^2$, % | $r_1^2$, % | $r_{1xy}$ | $h_2^2$, % | $r_2^2$, % | $r_{2xy}$ | U/CH | U/G | G/CH |
| Sc1 | 71.4*** | 22.9*** | –0.48*** | 22.6*** | 20.6*** | -0.45*** | *** | – | – |
| Sc2 | 44.7*** | 40.8*** | 0.64*** | 42.0*** | 41.9*** | 0.65*** | *** | *** | – |
| SN | 63.8*** | 48.5*** | 0.70*** | 61.6*** | 50.2*** | 0.71*** | *** | *** | *** |
| SL | 27.8*** | – | – | 11.9** | 4.3* | –0.21* | – | * | * |
| SW | 26.8*** | 11.7*** | –0.34*** | 18.1*** | 12.5*** | –0.35*** | – | *** | * |
| LT | 52.4*** | 23.0*** | –0.48*** | 39.8*** | 25.0*** | –0.50*** | ** | *** | *** |
| EH1 | 32.6*** | – | – | 8.9** | 4.6* | –0.21* | – | * | – |
| EH2 | 40.2*** | 32.4*** | –0.57*** | 34.0*** | 33.2*** | –0.58*** | *** | *** | – |
| CT1 | 11,8* | 6.2* | 0.25* | 7,4* | 6.8* | 0.26* | – | * | – |
| CT2 | – | – | – | – | – | – | – | – | – |
| MP | 35.0*** | 24.6*** | –0.50*** | 27.6*** | 25.3*** | –0.50*** | *** | *** | – |
| MS | 50.0*** | 9.2** | –0.30** | 31.5*** | 10.4*** | –0.32*** | – | *** | *** |
| M | 51.0*** | 19.3*** | –0.44*** | 35.6*** | 20.7*** | –0.46*** | * | *** | *** |
| MPn | 55.8*** | 6.1* | 0.25* | 22.5*** | 6.0* | 0.24* | – | *** | *** |
| MSn | 33.9*** | 3.9* | 0.20* | 8.6* | – | – | * | – | – |
| MN | 49.3*** | 7.9** | 0.28** | 6.8* | 6.7* | 0,26* | – | * | – |
| PC | 56.3*** | 9.8** | 0.31** | 56.3*** | 11.6*** | 0.34*** | – | *** | *** |
| PE | 30.8*** | 7.6** | 0.28** | 6.9* | 6.5* | 0.26* | * | – | – |
| TC | 33.9*** | – | – | 5.9* | – | – | * | – | – |
| NC | 39.7*** | – | – | 9.1** | – | – | – | – | * |
| KT | – | – | – | – | – | – | – | – | – |
| KN | – | – | – | – | – | – | – | – | – |
| EnT | 44.2*** | – | – | – | – | – | – | – | – |
| EnN | 26.8*** | – | – | – | – | – | – | – | – |
| BT | 22.1*** | 11.6*** | 0.34*** | 13.1*** | 10.3*** | 0.32*** | *** | – | – |
| BN | 36.7*** | 27.1*** | 0.52*** | 25.8*** | 25.8*** | 0.51*** | *** | ** | – |
| FT | 33.0*** | 21.9*** | 0.47*** | 28.9*** | 21.2*** | 0.46*** | *** | – | – |
| XT | 34.8*** | 26.7*** | 0.52*** | 28.5*** | 25,3*** | 0.50*** | *** | * | – |
| XN | 23.2*** | 8.6** | 0.29** | 8.6** | 8.1** | 0.28** | ** | – | – |
| XRd | 31.8*** | 3.7* | 0.19* | 25.2*** | – | – | *** | – | *** |
| XTd | 20.9*** | 15.0*** | 0.39*** | 14.9*** | 14.8*** | 0.39*** | ** | * | – |
| PZt | 24.1*** | 13.2*** | 0.36*** | 12.9*** | 12.8*** | 0.36*** | ** | – | – |
| PZn | 40.2*** | 19.2*** | 0.44*** | 36.0*** | 17.6*** | 0.42*** | *** | – | *** |

**Table 3.** The end

**Таблица 3.** Окончание

| Characters / Признаки | Interindividual differences / Межиндивидуальные различия df = 6 | | | Differences in the place of growth / Различия по месту произрастания df = 2 | | | Tukey's test / Критерий Тьюки | | |
|---|---|---|---|---|---|---|---|---|---|
| | $h_1^2$, % | $r_1^2$, % | $r_{1xy}$ | $h_2^2$, % | $r_2^2$, % | $r_{2xy}$ | U/CH | U/G | G/CH |
| OL | 62.7*** | – | – | 49.5*** | – | – | *** | *** | *** |
| OS | 60.3*** | – | – | 35.1*** | – | – | *** | ** | *** |
| InP | 41.5*** | – | – | – | – | – | – | – | – |
| InM | 24.6*** | – | – | 14.1*** | – | – | ** | – | ** |
| InS | 17.5** | – | – | – | – | – | – | – | – |

Note: CH – Charodinsky District; U – Untsukulsky District; G – Gunibsky District; $h_1^2$ – components of variance according to the factor “interindividual differences”; $h_2^2$ – components of dispersion according to the factor “place of growth”; $r_1^2$ and $r_2^2$ – coefficients of determination of the corresponding factors; $r_{1xy}$ and $r_{2xy}$ – correlation coefficients between the altitude and the studied character; * – *P* < 0.05, ** – *P* < 0.01, *** – *P* < 0.001 – confidence levels; a dash means no significant difference

Примечание: CH – чародинские; U – унцукульские; G – гунибские; $h_1^2$ – компоненты дисперсии по фактору «межиндивидуальные различия»; $h_2^2$ – компоненты дисперсии по фактору «место произрастания»; $r_1^2$ и $r_2^2$ – коэффициенты детерминации соответствующих факторов; $r_{1xy}$ и $r_{2xy}$ – коэффициенты корреляции между высотой над уровнем моря и изучаемым признаком; * – P < 0,05, ** – P < 0,01, *** – P < 0,001 – уровни достоверности; прочерк означает отсутствие достоверных различий

section, and number of the upper epidermis cells) showed the greatest dependence on growing conditions. The thickness of the endoderm, number of the endoderm layers, index of the petiole axis, and stomatal index depended somewhat less on the growing conditions.

A post-hoc analysis based on the analysis of variance (df = 2) revealed that the studied populations differed well in most of the average values (Table 3). When the growth sites were compared in pairs according to Tukey's criterion, higher isolation of the Maydan samples from the rest was noticeable, and the differences from the Gunib ones were greater in the lamina indicators, and from those from Charodinsky District in the petiole. For five characters (the number of stomata of the lower epidermis, thickness of the lamina, thickness of the mesophyll, and tangential and radial diameters of the petiole's cross section), the differences were significant between all compared pairs, most of which were associated with the morphological dimensions of the leaf, while the rest were unreliable.

The data of the regression analysis for interindividual differences and for the difference in conditions of the growth sites showed approximately the same results. At the same time, the linear effect of the altitude above sea level on interpopulation differentiation was statistically significant in many ways. Insignificant differences between the components of dispersion and determination ($h^2$ и $r^2$) were found for the indicators associated with the lamina, and less often with the petiole. For example, for the character “number of the lower epidermis cells”, the effect of factor $h_2^2$, % (42.0%) was due to interindividual differentiation, i.e., ecological growth conditions, while its linear impact ($r_2^2$, %) was equal to 41.9%. Based on this dependence, the effect size of the influence of the factor “altitude of the growth site” (Δr) in the total variability can be expressed by the formula:

$$\Delta r = \frac{r^2}{h^2}\,100\%$$

Accordingly, Δr for this indicator will be 0,419*100% / 0,420 = 99,8%, i.e., only 0.2% of the total variability of this character is caused by non-linear effects.

Correlation coefficient $r_{xy}$ displayed noticeable positive correlations of the altitude above sea level with the following characters: the number of stomata, number of the lower epidermis cells, number of the sclerenchyma layers, and thickness of the xylem, and negative correlations with the characters: the number of the upper epidermis cells, thickness of the lamina, height of the lower epidermis cells, and thickness of the palisade tissue. The indices of most lamina characteristics decreased with the altitude above sea level, and those of the petiole increased.

It can be concluded that the traits of xerophilicity gradually increased in natural apricot populations with the altitude above sea level.

Such a manifestation of the aggregate of indicators can be associated both with changes in the genotype and with purely functional changes within the normal range. In addition, the reason for arid conditions may be an increase in the evaporation of moisture on the southern slopes with the same amount of precipitation.

The discriminant analysis conducted with step-by-step inclusion at F ≥ 5.00 identified 11 most differentiating features (Table 4). The rest of the characters turned out to be of little information. The most discriminating function was observed in the following characters: the number of the upper epidermis cells, number of the lower epidermis stomata, thickness of the cuticle, number of the palisade tissue layers, and thickness of the endoderm.

Figure 2 shows the location of objects in the space of two canonical roots based on the results of the discriminant analysis. The first discriminant function (cor. 1) accounts for 54.4% of the explained variance, the second (cor. 2) for 19.6%.

The location pattern of the objects suggests that along the first axis they are located according to the change in the numbers of the upper epidermis cells and the lower epidermis stomata, and the thickness of the cuticle of the petiole and lamina. The scatter of indicators and the location of samples along the second axis reflect the diversity in the endoderm thickness and petiole index. The genotype from Gunib is separated according to the first function and Maydan 1 according to the second. Maydan 3 is also highly different, but with an admixture of Maydan 2.

**Table 4.** Results of the step-by-step analysis with inclusion by the grouping variable – trees (7 gr.)

**Таблица 4.** Итоги пошагового анализа с включением по группирующей переменной – деревья (7 гр.)

| Step / Шаг | Characters / Признаки | F incl. / Вкл. | *p*-level / Уровень | Lambda / Лямбда | F-values / Критерий | *p*-level / Уровень |
|---|---|---|---|---|---|---|
| 1 | Sc1 | 40.782 | 0.000000 | 0.285970 | 40.782 | 0.000000 |
| 2 | SN | 26.378 | 0.000000 | 0.108666 | 32.876 | 0.000000 |
| 3 | PC | 16.402 | 0.000000 | 0.053660 | 27.395 | 0.000000 |
| 4 | MPn | 13.075 | 0.000000 | 0.029390 | 24.233 | 0.000000 |
| 5 | EnT | 11.009 | 0.000000 | 0.017260 | 22.162 | 0.000000 |
| 6 | LT | 9.696 | 0.000000 | 0.010618 | 20.731 | 0.000000 |
| 7 | FT | 8.840 | 0.000000 | 0.006735 | 19.719 | 0.000000 |
| 8 | NC | 8.348 | 0.000000 | 0.004344 | 19.017 | 0.000000 |
| 9 | InP | 7.939 | 0.000001 | 0.002841 | 18.524 | 0.000000 |
| 10 | PZn | 6.977 | 0.000004 | 0.001932 | 18.038 | 0.000000 |
| 11 | PE | 5.877 | 0.000034 | 0.001379 | 17.496 | 0.000000 |

Note: there are 11 variables in the model; and 23 not in the model; n = 105

Примечание: переменных в модели – 11; не в модели – 23; n = 105

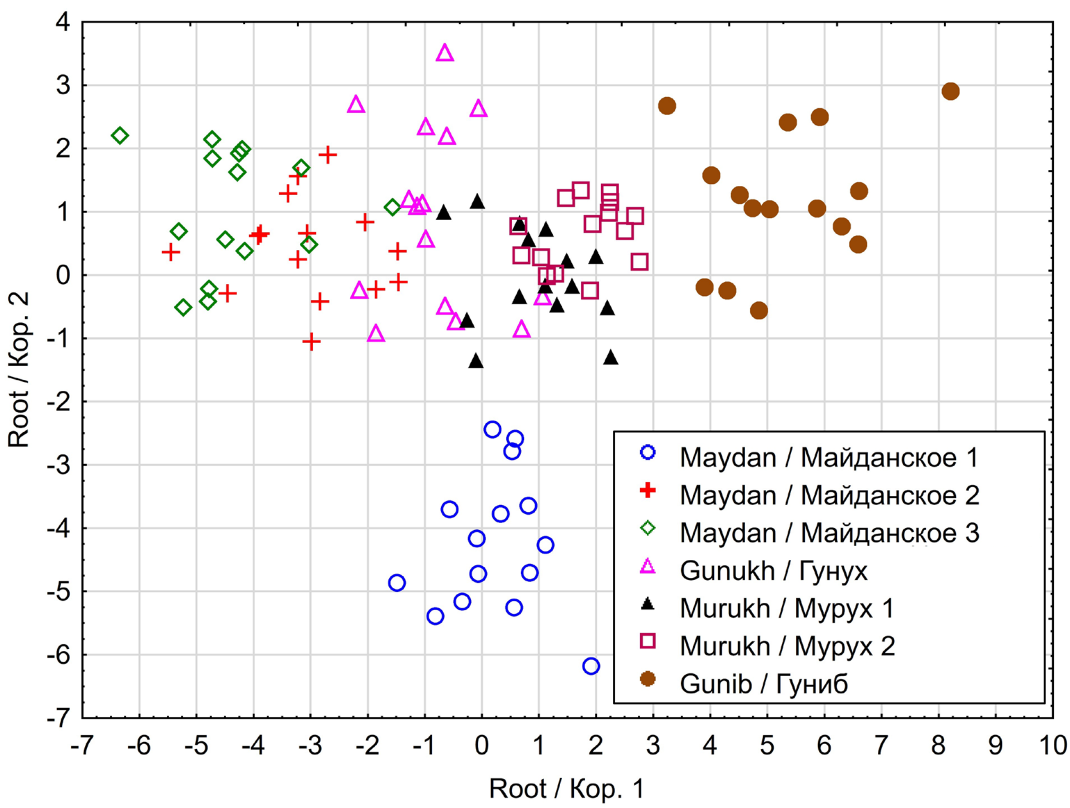


**Fig. 2.** Scattering graph of objects in the space of two canonical roots according to the leaf anatomical characters

**Рис. 2.** График рассеивания объектов в пространстве двух канонических корней по анатомическим признакам листа

### Conclusion

Within the general range of *P. armeniaca* in Dagestan, the selected reference points correspond to the lower and upper limits of distribution (with more critical growth conditions) and the central part of the range (with optimal conditions). In this case, the anatomical characters selected for the assessment of adaptive characteristics are grouped according to the parameters of the morphogenetic response to complex growing conditions.

The determinants of the studied genotypes turned out to be as follows: the thickness of the lower cuticle, thickness of the crustal parenchyma, and number of the parenchyma layers. The following characters appeared less informative within the studied altitude conditions: the "thickness of the endoderm", "number of the endoderm layers", "petiole index", and "stomatal index". Their values did not show significant differences in the reaction rate. Other features ("number of cells of the upper epidermis", "number of cells of the lower epidermis", "number of stomata", "thickness of the lamina", "thickness of the cuticle", "tangential diameter of the petiole's cross section") showed significant differences, which could be due to two reasons: a narrow limit of their reaction rate, or a wide range of exposure to one of the abiotic factors (light, temperature, humidity, etc.), or their combined action that goes beyond their ecological optimum.

The altitude as a complex factor in Mountainous Dagestan can exert the greatest effect on the variability of parameters of such apricot leaf features as the area and thickness of the lamina. We associate a decrease in the parameters of these characters with the accelerated implementation of the stages of morphogenesis of vegetative organs in connection with a reduction in the total growing season with the altitudes of growth sites, and, therefore, they are highly adaptive.

The leaves of the Gunib sample (1900 m) were characterized by the greatest xeromorphism. They have a multi-layered dense small-celled mesophyll, with a relatively thin lamina. The small-celled lower epidermis, a large number of stomata, and the total set of traits indicates an earlier stoppage of the leaf in growth.

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