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Ecological Features of the Leaf Structure and Plastid Apparatus of Far East Araliaceae Species

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Abstract—The structure of assimilative tissues of several Araliaceae species that grow in the Russian Far East is studied. Considering the specifics of the area, life forms, and quantitative leaf anatomy, a comparative description of their adaptivity relative to light and water modes is given.

Keywords: Russian Far East, Araliaceae, life form, adaptation, mesophyll structure, quantitative leaf anatomy
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Comparative studies of plant morphology and anatomy allow one to assess the main ways and regularities of their adaptation to certain living conditions. According to T.K. Goryshina [1], these studies should regard species of closely related taxons or species of one taxon. Historically, these surveys have involved species of one sort [2–5], and works in which species are considered that belong to one family are not very numerous [6–7]. Araliaceae, particularly its Far East representatives, are perfect objects for these investigations. One distinctive feature of species belonging to this family that grow in the moderate zone of the northern hemisphere is their attraction to near-pelagian territories; in addition, all the Far East species of this family are considered medicinal and biologically active. The family is an ancient relict and many of its species are classified as threatened or endangered.

Information about the anatomy of vegetative organs of *Aralia continentalis* Kitag. is given in work by I.S. Andreeva [8]; a comparative anatomical leaf characteristic of *Panax* L. species is given by I.V. Grushnitskiy et al. in [2]. These works mainly provide a comparative description of coating leaf tissues, structure of fibrous bundles, and secretory ducts. The characteristics of the leaf mesostructure of *Panax ginseng* C. A. Mey. are given in works by Yu.N. Zhuravlev and O.L. Burundukova et al. [9, 10]. In a work by Chinese researchers [11], the influence of different illumination intensities on the leaf mesostructure of *P. ginseng* is shown. No information about the leaf mesostructure of other Far East species belonging to this family is available in the literature. This article is based on data obtained by the authors during studies of the structure of the assimilative leaf apparatus of the Araliaceae species growing in the Russian Far East.

MATERIALS AND METHODS

The objects of research were Araliceae species growing in the Russian Far East.

Kalopanax septemlobus (Thunb.) Koidz. (seven-blade kalopanax) is a high tree belonging to the first layer. The species is included in the Red Book of the Russian Soviet Federative Socialist Republic (RSFSR) [12]; it grows in mixed and broad-leaved forests, light forests, on forest edges, in river valleys, and along mountain slopes.

Aralia elata (Mid.) Seem. (Japanese angelica tree) is a short pachycaul tree found in cedar silver–fir–broad-leaved, mixed, and lime–oak forests; on forest edges; in river valleys; and along mountain slopes.

Aralia cordata Thunb. is a redivive included in the Red Book of the RSFSR [12]. It grows in mixed and coniferous forests, on forest edges, in brakes, and in herb meadows.

Aralia continentalis Kitag. (continental aralia) is a redivive included in the Red Book of the RSFSR [12]. It grows in fir tree, broad-leaved, and oak forests, on mountain slopes, in dusky ravines, and in spring valleys.

Eleutherococcus senticosus (Rupr. et Maxim.) Maxim. (spiny eleuterococcus) is a shrub and one of the typical species of underwood in mixed and coniferous forests; it grows on mountain slopes and in river valleys.

Eleutherococcus sessiflorus (Rupr. et Maxim.) S. Y. Hu (sessile-flowered eleuterococcus) is a shrub growing in groups or as single plants in broad-leaved and coniferous–broad-leaved forests, on forest edges, and in brakes.

Oplopanax elatus (Nakai) Nakai (devil's-club) is an undershrub included in the Red Book of the RSFSR [12]. It grows in small groups on rock screes and plac-

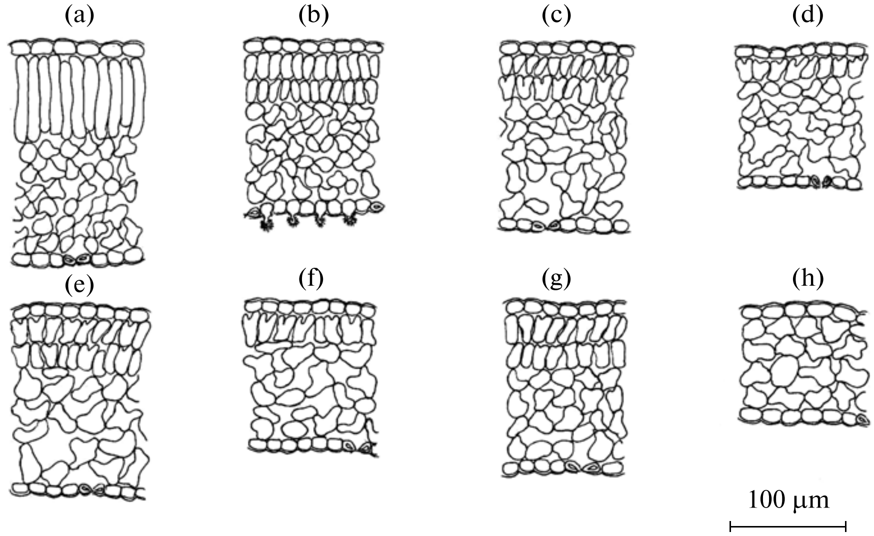

Fig. 1. Structural arrangement of soft-leaf mesophyll tissues in the Araliceae species that grow in the Russian Far East: (a) *Kalopanax septemlobus*, (b) *Aralia elata*, (c) *Eleutherococcus senticosus*, (d) *Eleutherococcus sessiliflorus*, (e) *Oplopanax elatus*, (f) *Aralia continentalis*, (g) *Aralia cordata*, and (h) *Panax ginseng*.

ers; in spruce–fir, fir, and mixed forests; and sometimes along springs.

Panax gingseng C. A. Mey. is a redivive included in the Red Book of the RSFSR [12]. It grows in groups or as single plants in broad-leaved and coniferous broad-leaved forests.

The sample leaves were gathered in the Upper Ussuri station, the arboretum of the montane taiga station, and the Botanic Garden Institute of the Far East Branch of the Russian Academy of Sciences.

To calculate the indexes of quantitative leaf anatomy, available methods were used as guidelines [1, 13]. The studies concerned adult leaves of the middle layer that had been picked from 3–10 representatives of each species. The diagrams of anatomic drawings were made with the help of a PA-4 drawing device. The number of chloroplasts in a cell and the number of cells per unit of leaf area were analyzed for palisade and spongy tissues separately, for which a material was fixed in a 3.5% glutaraldehyde solution in a phosphate buffer (pH 7). The number of cells per 1 cm^2 of leaf area was calculated after macerating the tissues in a 50% solution of KOH during heating; the number of chloroplasts per cell was calculated after macerating the tissues in a 5% solution of chromium oxide in 1 N HCI during heating to 60–80°C. According to the requirements of the procedure for calculating leaf thickness and the number of chloroplasts per cell, the number of measurements was 15 and 30, respectively. The number of cells in the macerates (to calculate the number of cell per 1 cm^2 of leaf area) was calculated with 20-fold repeatability in 90 squares of a Goryaev camera. The stomata were studied with the imprint method [14]. The number of stomata in the visibility range of a light microscope with a known area was calculated for each sample with 20-fold repeatability. The number of measurements of the length of closing stomata cells was 30 for each sampling. Epiderm molds were photographed in an oil immersion system under an Axioskop-40 microscope with the help of an Axio-Cam HRc inbuilt camera (Zeiss, Germany). The measurements were partially performed on temporary preparations with the help of Axio Vision 4.8.3. The volume and area of complex-shaped mesophyll cells were calculated using the method proposed by Yu.A. Khrolenko and O.L. Burundukova in [15].

The final results were statistically processed in Statistica 8.0.

RESULTS AND DISCUSSION

During studies of the leaf mesostructure of the representatives of Araliaceae at tissue and cell levels, both heliomorphic and sciomorphic features were discovered. The features had different degrees of manifestation. All the species had hypostomatic leaves, their air pores were above or at the same level as epidermis surface, and the spongy mesophyll consisted of amoeba-like cells. Structural features typical of each species were detected relative to the illumination mode of the areas. One distinctive feature of the leaf mesophyll in *A. continentalis*, *A. cordata*, *O. elatus*, *E. sessiflorus*, and *E. senticosus* is the existence of column palmate (from the word *palm*) cells. The arrangement of these cells is typical of column tissue, but they also have constrictions on their ends (Fig. 1). These cells can be cut in two and even in three. It is possible that they compensate to a certain extent the inability of typical column cells in the focusing of weak and diffused light. All five species represent the underwood of mixed and

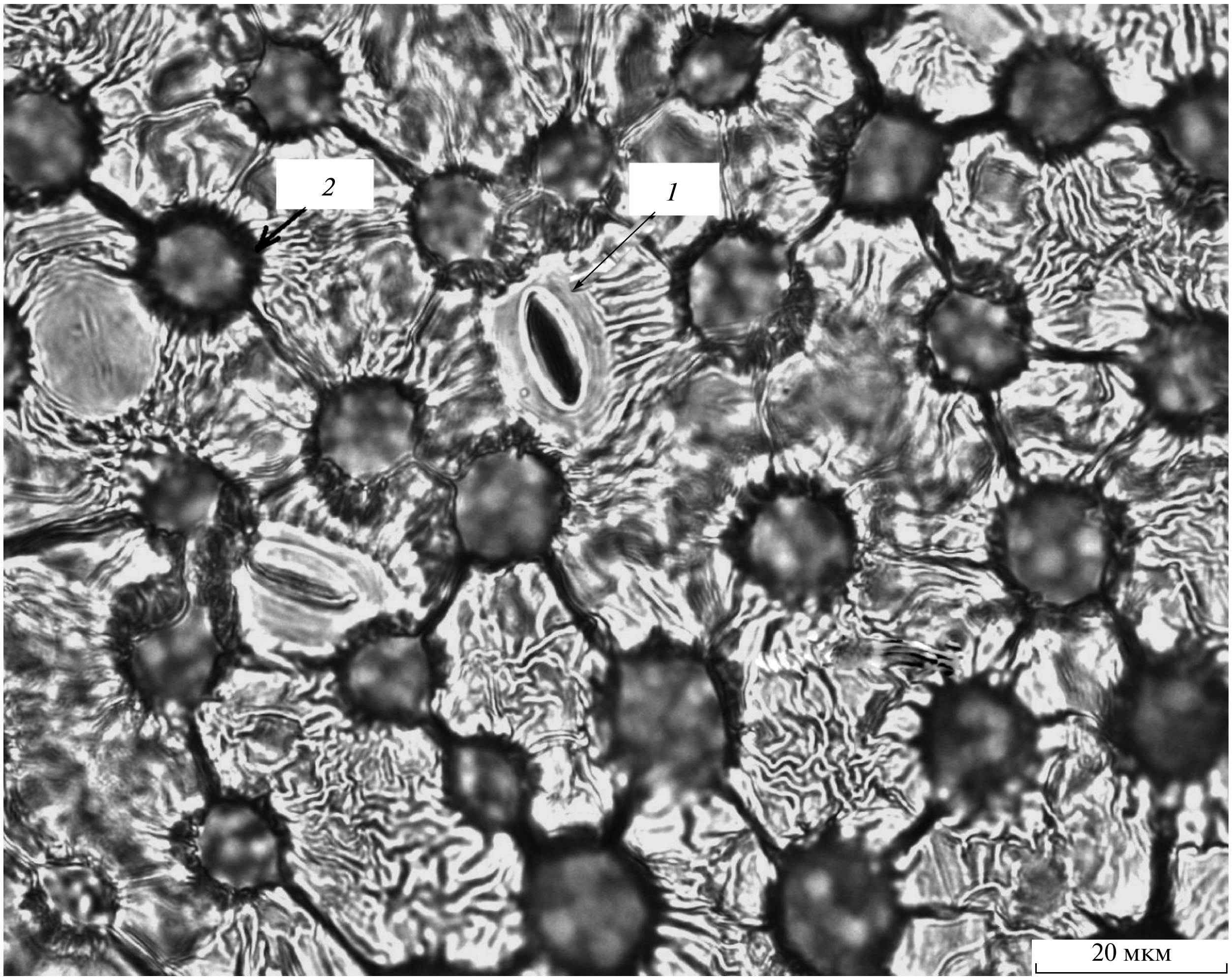

Fig. 2. Epiderm of the bottom part of a leaf of *Aralia elata*: (*1*) stomata and (*2*) trichome.

coniferous forests, and the illumination in this area is lower than in the upper layer. It is known that pear-shaped cells, the external walls of which look like lenses, and palmate cells can concentrate weak illumination and transfer it to chloroplasts [16, 17]. That is why these cells are a better fit for absorbing diffused light. Since the leaf mesophyll in *P. ginseng* is not differentiated in spongy and palisade tissue (homogeneous type of mesophyll), this species comes to the forefront in terms of a number of sciomorphic features compared with other species of the family (Fig. 1).

Heliomorphism shows up as well in the leaf anatomy of the studied species. However, for *P. ginseng*, all the species have dorsoventral mesophyll with 1–2 layers of palisade parenchyma. A clear division of mesophyll into palisade and spongy tissue is typical of *A. elata* and *K. septemlobus*. Palisade parenchyma occupies 1–2 layers and is represented with typical column cells; concurrently, the column cells of *K. septemlobus* are more prolate (their height is 6–7 times as large as their width), which increases the total plate thickness (see Fig. 1). Thus light-demanding species (*A. elata* and *K. septemlobus*) are clearly distinguished. The former species grows in open areas along glades and high-voltage lines. The height of trees belonging to the latter species reaches 20–27 and even 30 m and enters the upper canopy.

Unfortunately, it is difficult to divide adaptive plant features into typically heliomorphic and xeromorphic, because they usually overlap each other. Adaptation to a lack of humidity is expressed most clearly in *A. elata*, which greatly differs from other species of the family in terms of the structure of the epiderm of the axial leaf surface (Fig. 1). The typical attributes of this species are very fine downiness and the presence of trichomes (special emergences that protect the leaf). The epiderm cells look very much like polygons in the corners of which hairs grow, the cuticula is folded, and the folds converge radially to the basis of the hairs (Fig. 2). It is considered that trichomes can prevent mesophyll from overheating [18], but it seems that the leaf downiness in *A. elata* offers protection from other factors as well. Compared with other species, *A. elata* had the lowest leaf vulnerability under the influence of mod-

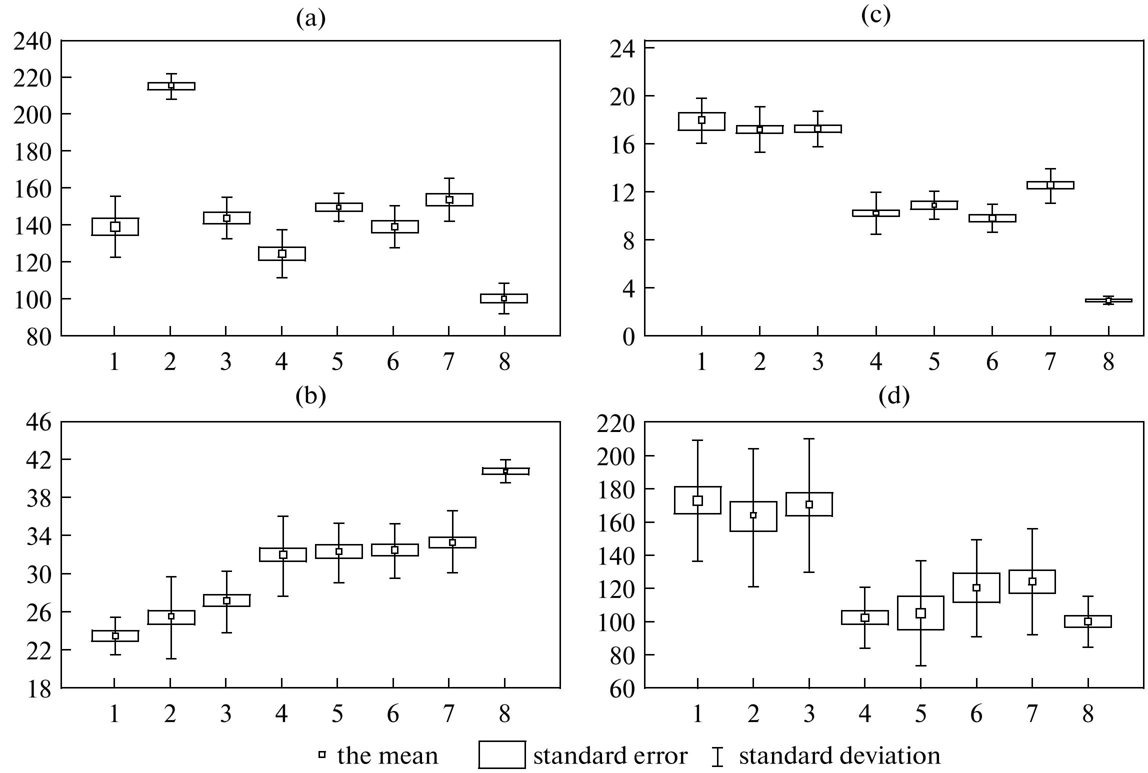

Fig. 3. Quantitative anatomy and thickness of leaves of Far East Araliaceae species. The signs along the base line are as follows: (1) Aralia elata, (2) Kalopanax septemlobus, (3) Eleutherococcus senticosus, (4) Eleutherococcus sessiliflorus, (5) Oplopanax elatus, (6) Aralia continentalis, (7) Aralia cordata, and (8) *Panax ginseng*. The signs along the ordinate are as follows: (a) leaf-plate thickness, μm; (b) stomata length, μm; (c) the number of stomata per 1 cm^2, thou pieces; and (d) number of cells per 1 cm^2, thou pieces.

eled acid precipitation [19]. The leaves of *A. elata* and *K. septemlobus* differ from other Far East aralia plants in their smaller cells and mesophyll of more densely arranged cells (Fig. 1).

An analysis of the quantitative anatomy of leaf mesophyll will yield more information about and define more exactly those tendencies that were discovered in the morphological description of leaf anatomy. The negative correlation between the frequency of arrangement and the length of stomata known from literary sources [20] was discovered during the comparison of Aralia species (Fig. 3). For instance, while the stomata of leaves of *A. elata* are the smallest (23.4 μm), they have the maximal density per leaf (18000/cm^2). On the contrary, leaves of *P. ginseng* have the largest stomata (41 μm) but the lowest stomata density (2900/cm^2). In terms of leaf-plate thickness, the species are classified as follows: *K. septemlobus* appeared to have the thickest leaves and *P. ginseng* turned out to have the thinnest leaves (Fig. 3). The thickness of leaves of the other species is 110–160 μm. As for the number of cells per unit of leaf area, the species were divided in two large groups: the first included *A. elata*, *K. septemlobus*, and *E. senticosus* (162000–172000 cells per cm^2) and the second included *P. ginseng*, *A. continentalis*, *A. cordata*, *O. elatus*, and *E. sessiflorus* (82000–123000 cells per cm^2). A similar tendency toward variation is observed in plastid leaf filling (table). The maximal and close to maximal numbers of chloroplasts per 1 cm^2 of leaf area were registered in *A. elata*, *K. septemlobus*, and *E. sentocosus*; the minimal numbers were observed in *P. ginseng* and *E. sessiliflorus.* The sizes of spongy cells are given in the table: *P. ginseng*, *O. elatus*, and *A. continentalis* have the largest cells and *A. elata* has the smallest cells.

In terms of humidity, all the species should be classified as *mesophytic* plants, as is indicated by their leaf structure: the mesophyll cells are very large and, consequently, strongly watered. For reference, the volume of spongy cells of *Pentaphylloides mandshurica* (Maxim.), a typical xerophyte, is 200 μm^3, and for *Arisaems japonicum* Blume, which is a typical plant for shaded areas, this index is 18300 μm^3 [21]. According to G. Ostrogradskiy [22], *O. elatus* is related, in terms of damping, to hygromesophytes of dark coniferous forests of the southern part of Sikhote Alin. It is interesting that *Oplopanax* Miq. is the only representative of tropical araliaceae plants populating the moderate zone that has no vaxular tracheids in wood [23]. At the same time, the author reckons that vascular tracheids function as an additional conducting system that is the means of adapting to life in places with a periodical

Volume of cells of spongy leaf tissue and quantitative indicators of the plastid apparatus of the Araliceae species that grow in the Russian Far East

Species	Cell volume, 10^3 μm^3	Number of chloroplasts		Plastids per 1 cm^2 of leaf area, mln
		in column cells, pcs	in spongy cells, pcs	P + SP
Aralia elata	4.5 ± 0.3	28.3 ± 0.9	36.4 ± 1.4	5.6 ± 0.4
Kalopanax septemlobus	9.1 ± 0.6	45.1 ± 2.2	34.9 ± 1.9	6.5 ± 0.6
Eleutherococcus senticosus	9.4 ± 0.4	36.0 ± 1.1	39.9 ± 0.9	6.5 ± 0.4
Eleutherococcus sessiliflorus	8.8 ± 0.9	32.3 ± 1.2	37.2 ± 1.2	3.5 ± 0.3
Oplopanax elatus	19.9 ± 0.1	36.7 ± 1.3	39.9 ± 1.9	4.1 ± 0.5
Aralia continentalis	13.6 ± 0.8	34.5 ± 2.7	35.4 ± 1.1	4.2 ± 0.4
Aralia cordata	7.7 ± 0.5	34.8 ± 0.9	40.7 ± 1.1	4.7 ± 0.4
Panax ginseng	29.8 ± 0.9	–	44.8 ± 1.9	3.6 ± 0.3

Note: (P + SP) sum for palisade and spongy tissues; (–) the absence of palisade cells.

water deficit. It seems that, among all araliaceae trees and shrubs, *O. elatus* is the least adapted to a moderate climate. This drawback is compensated for by the tendency of the plant to grow in high montane areas with excessive humidity, frequent fog, and limitations to photosythetic active radiation, which allows it to avoid competition. This possibly explains why this plant is so rare. As early as in the beginning of the past century, when there was no great anthropogenic pressure on this drug plant, A.A. Bulavkina [24] called it "a plant twice as rare."

The tendency toward changeability among quantitative indicators of leaf anatomy is largely explained by the fact that the species of the family belong to different life forms. In the line trees (*K. septemlobus*, *A. elata*), shrubs (*O. elatus*, *E. sessiliflorus*, *E. senticosus*), and herbs (*A. continentalis*, *A. cordata*, *P. ginseng*), the number of stomata, cells, and chloroplasts per unit of leaf area decreases and the closing stomata cells and mesophyll cells increase in size. It should be noted that this tendency does not cover each mesostructural feature. It is easy to see that, in terms of quantitative indicators of leaf anatomy, *E. senticosus* stands equal to the arboreous species of the family. The leaf mesophyll of this shrub is differentiated, and in most cases it has only one layer of palisade parenchyme and a transitional layer of palmate cells and spongy mesophyll of 4–5 layers (Fig. 1). According to literary data, *E. senticosus* is very flexible relative to illumination; it resists deep shading well, but can also grow in fully illuminated open areas [25]. In works by E.D. Solodukhin [26] and T.A. Komarova [27], it is shown that *A. elata* and *E. senticosus* make up part of the new growth on cut-over and burnt lands, where they often form impervious brushwood. It is seen that plants of different life forms can belong to one ecological group and vice versa: plants that belong to one life form can belong to different ecological groups.

In addition to the fact that *Araliaceae* species belong to different life forms, they also have different karyotypes. For instance, *A. elata* and *A. cordata* are diploids ($2n = 24$) and *A. continentalis* is a tetraploid ($2n = 48$) [28, 29]. It is well known that diploid species have more stomata per unit of leaf area and smaller epidermic and mesophyll cells than tetraploid species [30]. That is why, despite the fact that *A. continentalis* and *A. cordata* are redivives, they have different quantitative indicators of leaf mesophyll. This is observed especially clearly in the number of stomata per 1 cm^2 of leaf area (Fig. 3) and the volume of spongy cells (Table).

Mesophytic plants of different life forms differ in degree of density of mesophyll cells. Compared to herbaceous plants, arboreous plants have a denser distribution of phototrophic tissues that consist of many small cells [31]. *A. elata* and *K. septemlobus* have small cells and many cells per unit of leaf area (table). According to literary sources, these two species have highly specialized wood (ring-porous with vascular tracheids), and in the moderate zone this level of specialization acquires an adaptive significance for tropical representatives of the family in question [23]. The structure of the leaf mesophyll of these trees gives them broad environmental adaptivity. For instance, among all Araliaceae species that grow in the Russian Far East, *K. septemlobus* occupies the most extensive area [32].

P. ginseng has the finest leaves, no palisade mesophyll tissue, the lowest number of layers of mesophyll, the largest mesophyll cells, the smallest number of stomata per 1 cm^2, and the largest stomata. I.V. Grushvitskii [2, 33] pointed out that the genus *Panax* stands very much apart in the family. *Panax* and *Stilbocarpa* are the only genuses in the Araliceae family that are represented solely by herbaceous plants [34]. Most Araliceae species have alternate leaf arrangements;

opposite leaf arrangement is observed only among the *Cleirodendron*, *Eremopanax*, and *Arthrophyllum* genuses; and verticillate leaf arrangement is a feature observed only in the *Panax* genus [35]. The underground emergence of seedlings is typical only of *Panax* species. In accordance with the performed comparison, the structure of leaf mesophyll was also a feature that made *P. ginseng* sharply different from other species of the family, including even those of its representatives that are redivives as well.

The results match the notions about the adaptive abilities of plants and, particularly, the fact that species with dorsoventral mesophyll have a broad ecological amplitude. On the contrary, species with homogeneous and isolateral mesophyll are considered narrowly defined [36, 37].

CONCLUSIONS

As a result of a comparative analysis of the leaf mesostructure of Far East representatives of the Araliaceae family, the specifics of the anatomic leaf structure relative to ecology and life forms of the species was identified. The ranking of the species according to the parameters of leaf mesostructure displays natural changes in ecological characteristics: the abatement of heliomorphic and intensification of sciomorphic features (*A. elata*—*P. ginseng*). The extreme species in the line are narrowly specialized, preferring high and low illumination, respectively. The species in between are more ecologically flexible, which should be taken into account in the introduction, reintroduction, and plantation cultivation of these rare relict and medicinal species.

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