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ADAPTIVE MORPHO-ANATOMICAL CHARACTERISTICS OF LEAVES AND CONES IN *JUNIPERUS SERAVSCHANICA* KOM.: STUDIES OF POLYPHENOLIC PARENCHYMA CELLS, SECRETORY TISSUES, SCLEREIDS AND TRACHEIDS

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Running title: *Rezanejad et al. ……… Morpho-anatomical characteristics of* J. seravschanica

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Conifers are long-lived species that cope with multiple abiotic and biotic stresses. To defend themselves, they have evolved a wide array of morphological, anatomical and chemical traits. Morpho-anatomical traits of *Juniperus seravschanica*, particularly in male and female cones, have not been studied. Thus, in this survey, these structures were studied to investigate the adaptative traits. The species is frost- and drought-tolerant and grows at a 2200-3800 m altitude on normal, chalky, calcareous, rocky, and mountainous outcrops with other species or as pure patches. The seedlings and young plant leaves were small and needle-like, while the main leaves of adult plants were scale-like and overlapping; there was a conspicuous resin gland (duct) in the outer surface of scale-like leaves secreting a white and sticky resinous substance, particularly in damaged leaves. The epidermis was thick with thicker outer walls and sunken stomata; the hypodermis showed 1-3 layers of lignified cells with a narrow lumen. The palisade parenchyma was observed on both sides. Sclereids, phenolic- and starchy cells were observed in leaves, particularly scale-like ones. Male cones were small with overlapping and decussate scales, in which resin glands (ducts) and phenolic cells were also observed. Similarly, female cones had overlapping and decussate scales converting to fleshy, berry-like, and bluish appearance during development. They revealed the presence of several resin glands, a thick epidermis, phenolic cells in young cones, and numerous sclereid cells in mature cones. Tracheids were narrow in leaves and cones. The features such as high sclerophylly, resin glands, phenolic cells, narrow tracheids, sunken stomata, increasing thickness of the epidermis, cuticle, hypodermis, as well as the presence of palisade parenchyma on both sides enable the species to survive in hard conditions.

Keywords: conifer, hypodermis, resin gland, sclerophylly, stress, tracheids

INTRODUCTION

The genus *Juniperus* (Cupressaceae), with 75 species, is the second most diverse genus of all conifers after *Pinus*. It is a genus of evergreen shrubs or trees occurring from sea level to above 3000 m above sea level. Junipers are slow-growing and long-lived trees that sometimes live up to 2000 years or more (Adams, 2008; Pirani et al., 2011; Rezanejad et al., 2022).

Most of the species of the genus *Juniperus* are important in both ecological and economic terms. The genus is divided into three sections: the *Caryocedrus* section has one species, the *Juniperus* section has 14 species, and the *Sabina* section has 60 species. The junipers distributed in Kerman province were originally thought to be populations of *J. polycarpos* K. Koch, but have recently been confirmed to be the Zeravschan juniper, *Juniperus seravschanica* Kom. from the section *Sabina* (Farhat et al., 2019; Hojjati et al., 2018). The *J. seravschanica* has a wide distribution in the southeast of Iran (Kerman province). It grows from Kazakhstan to Iran, and the population in Oman is the isolated southernmost population of this species (Adams et al., 2014).

Longevity is one of the key traits of conifers for both the whole plants and their organs such as leaves. The leaf life span in the Chilean *Araucaria araucana* (Molina) K. Koch is 25 years. During their long-life times, they are exposed to different biotic and abiotic stresses. Their capacity has been attributed to decay resistance in the wood and the presence of resin canals, which protects them against severe conditions (Brodribb et al., 2012).

It has been cited that conifers, especially the Cupressaceae, Podocarpaceae, and Pinaceae are highly successful against hard conditions, especially freezing. Cupressaceae has generated a fascinating comparison with two other families because it reveals a panglobal distribution. Further, it can also survive in very dry areas, where the efficient capacity of water uptake in angiosperms is restricted by ordinary exposure to intense water stress (Brodribb et al., 2012).

A secretory structure that produces a secretion within or on a plant, can be simple or elaborate. Different types of secretory structures are observed in plants including glandular trichomes, extrafloral nectaries, secretory idioblasts, secretory canals, cavities, and reservoirs.

The secretory cells and tissues produce different chemical compounds with various beneficial functions. These secretory structures produce mucilage, terpenoids, tannins, and phenolic compounds used as medicines. Further, these compounds may be involved in water retention by leaves, protection against UV radiation, hot and cold temperatures, and plant defense mechanisms (Crang et al., 2018; Fortuna-Perez et al., 2021). It has been stated that plants, including different crops, remobilize their starch to release energy, sugars, and derived metabolites to reduce stress. This process increases plant fitness and productivity under extreme environmental conditions (Thalmann and Santelia, 2017).

The secretory structures of conifers produce oleoresin that results in physical and chemical defense against different herbivores and pathogens. The oleoresin is a complex mixture of terpenes, including monoterpenes, sesquiterpenes, and diterpenes, with the latter usually occurring as diterpene resin acids. These compounds are accumulated constitutively in different structures of conifers such as resin cells, resin blisters, resin glands, or resin ducts (Fahn, 1979). In addition, conifers respond to biotic and abiotic stresses by the inducible resin duct formation in different organs. Resin duct and resin glands generally consist of an extracellular lumen lined with epithelial cells secreting terpene (Kshatriya et al., 2018).

Plants synthesize different phenolic compounds (flavonoids, phenolic acids, tannins, and lignins) to cope with constantly changing environments and to survive in various stressful conditions. The accumulation of phenolic compounds is regarded as a distinctive trait of plants against different stresses. These compounds not only help plants to defend themselves but are also known to influence animals and humans consuming these plant products (Naikoo et al., 2019).

It has been reported that tropical and mountainous plants have higher levels of flavonoids than temperate plants. Cold stress induces production of phenolic compounds into the cell wall as the deposition of suberin or lignin. This wall thickening increases plant resistance against freezing stress. Further, the induction of cell wall thickening could decrease cell collapse during freezing-induced dehydration and mechanical stress and consequently increases the resistance against plant freezing (Naikoo et al., 2019).

The study of different idioblasts helps our understanding of plant defensive capacity. These structures, including sclerenchyma, polyphenolic parenchyma cells (PP cells) as well as resin ducts and their protective mechanisms have been studied in the secondary phloem of some conifers (Krekling et al., 2000). However, information on these idioblasts and secretory systems in female cones is lacking. In addition, there is no data on these structures in cones and leaves of *Juniperus seravschanica*. Therefore, the purpose of this study was to examine the histology and spatial distribution of polyphenolic parenchyma cells, the secretory tissues, sclereids, and tracheids in cones and leaves of *Juniperus seravschanica*. Morphological traits confirming adaptive strategies were studied as well. Such information is needed in ecological and physiological investigations.

MATERIALS AND METHODS

Cotyledon, needle- and scale-like leaves were collected from *Juniperus seravschanica* plants growing in the Sarduiyeh region (Jiroft county, Kerman province, Iran). Sections were then taken by hand using a razor blade and stained with double staining by carmine- methyl green and safranin- fast green. Intracellular starch granules were stained with Lugol’s solution. Some sections were studied without staining for detection of their contents, particularly phenolic cells.

The cone anatomy was studied from serial sections using the classical paraffin technique and subsequent hematoxylin and Eosin staining. Female and male cones were fixed in FAA (100 ml FAA = 90 ml 70% ethanol + 5 ml acetic acid 96% + 5 ml formaldehyde solution 37%). Then, they were dehydrated in a graded alcohol series. The samples went through a gradual histo clear solution change up to 100% histo clear and then were embedded in paraffin. The samples were sectioned at 10 μm thickness with a rotary microtome, stained with hematoxylin and eosin and examined by light microscopy (Dörken et al., 2017; Rezanejad, 2008). Thick sections of female cones were studied by sectioning microscopy without staining. Freshly collected material was photographed for morphological studies.

RESULTS

Juniperus seravschanica grows at a 2200-3800 m altitude and is drought- and frost-tolerant. It grows in some mountainous areas where the minimum temperature reaches -30°C. The species is distributed in various soils such as normal, chalky, calcareous, rocky, and mountainous outcrops (Fig. 1). Usually, the species can grow with other plant species (Fig. 1a-e), but in some zones it forms pure patches (Fig. 1f, g).

J. seravschanica has two types of leaves: seedlings, young plants and some twigs of older trees have needle-like to narrowly oblong leaves. The main leaves on adult plants are overlapping and scale-like. The leaves of young plants are arranged in whorls of three, but scale-like leaves have opposite-decussate arrangements. Two cotyledon leaves are seen as linear to oblong (Fig. 2).

The species is dioecious; male and female cones grow on separate plants. Male cones, which are small and solitary, mature and shed annually (Fig. 3). Female cones are solitary and their scales (bract/seed scale complex, but for simplicity, we here use the term cone scale when referring to this entire complex) are gathered during development and ripening, forming fleshy and berry-like cones in the second year (Fig. 2d and Fig. 3).

We observed several characteristics related to morphological and anatomical traits that may protect the species against biotic and abiotic stresses (Figs. 2-4): leaves were small, needle-like, or overlapping scale-like (Figs. 2- 4). In addition, there is a conspicuous more or less oval gland in the outer (lower) surface of every scale-like leaf (Fig. 4a). These glands frequently, particularly in the fall or in damaged leaves (drying and degenerating), secrete a sticky resinous substance, which dries into a white material (Fig. 4).

Anatomical and cellular studies of different leaves (cotyledon, needle- and scale-like leaves) showed both similarities and differences. They have important adaptive tools for the success of the species in different adverse habitats. The studies of cotyledon leaves showed that the epidermal cells with thickened walls and hypodermal lignified cells were observed during the first to second development month of young seedlings. In this developmental stage, the hypodermal layer was not continuous, but its continuity in the leaf margin was obvious. These cells contained phenolic compounds conferring orange coloration to the hypodermis. The palisade parenchyma is observed in both the adaxial side and the abaxial side. The spongy parenchyma is loose and uncompacted. However, no resin duct was observed in these leaves (Fig. 5).

Needle- and scale-like leaves showed more differentiated protective characteristics compared with cotyledon leaves (Figs. 6, 7): the epidermis was thick with thicker outer periclinal walls because of cuticle formation (Fig. 6a-d and Fig. 7a-h); the stomata were sunken (Fig. 7g). The hypodermis showed two or three layers of lignified cells, with very thick walls and a narrow lumen. The hypodermis layer, which was just under the epidermis, was continuous, while the other layers did not present this characteristic (Fig. 6b and Fig. 7g, h). The mesophyll was composed of both palisade and spongy parenchyma; the palisade parenchyma was present beneath the epidermis in both the upper and lower side of the leaves, forming the main part of the mesophyll. The spongy parenchyma was compact with small intercellular spaces. A resin gland (duct) was observed in each scale- and needle-like leaf, occupying 30–50% of the total leaf volume. A high degree of sclerophylly was observed in the leaf mesophyll (Fig. 6a-d and Fig. 7a-f). The presence of numerous starch cells stained with Lugol's solution was detected as dark color (Fig. 7e). Tracheids with narrow conduits were observed compactly (Fig. 7a).

Male cones appeared on the top of current-year branches. They were present for a short period and fell as soon as they had shed their pollen. They were small and had decussate scales (bracts or sporophylls) surrounding and protecting pollen sacs. In addition, male cone scales had resin glands and phenolic compounds. High levels of phenolic compounds are responsible for the yellowish to brownish color of male cones and their scales. These structures were seen in scale-like leaves of male cones, the cone axis, and the stalks connecting the scales to the cone axis as well as in pollen sacs in both young and mature cones (Fig. 8a-i).

Like male cones, female cones appeared at the top of short shoots of current-year branches. They showed adaptive strategies against different damages. The scales forming the female cones showed a decussate arrangement protecting the ovules (seeds) placed on them. The scales were foliage-like and became peltate and fused after pollination and during expansion and development, giving female cones a berry-like and dark blue color appearance (Fig. 9a-c). The presence of numerous resin glands and their exudates was observed by sectioning microscopy (Fig. 9d-f).

Anatomical sections prepared using a microtome and hands-free sections of female cones revealed the presence of a thick epidermis with abundant phenolic content and a thick cuticular layer, narrow and compact tracheids, numerous resin glands, and a lot of phenolic and sclereid cells (Figs. 10, 11). The comparison of young (immature) and ripe cones showed that the amount of phenolic compounds was high in young cones, giving them yellowish-brown color (Fig. 10a-f). However, the phenolic cells and other parenchyma cells were differentiated into lignified cells (sclereid cells) during ripening, so that sclereid cells were found abundantly scattered in berry-like cones (mature cones) (Fig. 11a-f).

DISCUSSION

Activation of different mechanisms of plants at various structural, chemical, and functional levels resulted in overcoming stressful conditions. These mechanisms depend on the nature of stress, its duration, and severity. The major trait determining plant stress tolerance is concerned with the leaf, which is the main site of gaseous exchange, photosynthesis, and metabolic activities. In addition, leaves are the most exposed organs of the plant. Morphological and anatomical changes in the leaf structure are therefore interpreted as adaptations to specific environments. Environmental conditions and nutrients are the main factors regulating these leaf features (Chelli-Chaabouni, 2014; Fahn and Cutler, 1992; Rivera et al., 2017; Tian et al., 2016).

The morphological, anatomical, and biochemical features, considered to be stress-tolerant traits in many species of junipers exposed to various biotic and abiotic forms of stress, include increasing thickness of leaf epidermis and its cuticle, reducing the epidermal cell size and tracheid size, increasing sclerophylly, accumulating starch, decreasing leaf size as well as increasing secondary metabolite levels (antioxidant) such as phenolics, terpenoids, resins, tannins, alkaloids, etc. (Chelli-Chaabouni, 2014; Kshatriya et al., 2018; Lata et al., 2021; Naikoo et al., 2019; Osakabe et al., 2011; Tian et al., 2016). The anatomical features of scale-like leaves of four species of *Juniperus* (*J. deppeana*, *J. monosperma*, *J. scopulorum* and *J. osteosperma*) collected in Arizona showed that they are generally similar in structure but vary in structural details. *J. monosperma* and *J. deppeana* usually represent the extremes in variations of these adaptive characteristics. *J. osteosperma* is usually intermediate between these two species, with Rocky Mountain juniper (*J. scopulorum)* usually being similar to alligator juniper (*J. deppeana*) (Johnsen, 1963). The study showed that the leaves are characterized by a multiple epidermis including compact layers or bands of fiber-like cells on the abaxial side, sunken stomata, mesophyll divided into palisade and spongy parenchyma, a single resin gland near the leaf base in the mesophyll on the abaxial side (Johnsen, 1963). The mentioned results were also observed in *J. seravschanica*; however, in the present study two surface layers were observed. Anatomical characteristics of the leaves of three species of *Juniperus* (*J. drupacea*, *J. communis* and *J. oxycedrus*) distributed in Turkey showed that, similar to our study, the palisade parenchyma is usually located on both upper and lower surfaces (Güvenç et al., 2011). According to this study, in *J. drupacea*, secretory canals are present in the spongy parenchyma but in two other species they were observed in the palisade parenchyma. Similarly, in this study, resin glands were seen in the palisade parenchyma in both needle- and scale-like leaves. Multivariate analysis of 13 populations of different varieties of *J. communis* and *J. deltoides* from the Balkan peninsula showed that the level of anatomical differentiation of these taxa was conditioned partially by phylogenetic association of individual taxa, and partially by ecological conditions of the habitat. The results of the analysis showed that anatomical characteristics of needle- and primary structures of the stem of these species have taxonomic significance at the species and infraspecies levels (Lakušić and Lakušić, 2011).

These adaptive features were observed in the leaves and cones of *J. seravschanica* too. The species was found at a 2200-3800 m altitude, in stony and shallow soils of mountainous regions of southeastern Iran (Kerman province) with cold winters and dry summers. These adaptive characteristics result in plant protection and survival in the face of winter frost, water and drought stress, rocky slopes, shallow soils, and herbivores. However, these adaptive and defensive traits were more obvious in scale-like leaves compared with cotyledon and needle-like ones. Therefore, the species can have the essential potential for reforestation, especially in areas with harsh environments.

Stresses such as water deficit, high light intensity, and nitrogen deficiency are the main factors causing a lower ratio of leaf surface to volume showing xeromorphic features. In many species, the presence of a thick epidermis or multiple layers of wax reduces light absorption causing formation of two to three layers of the palisade parenchyma. The multiple-layer formation of the palisade parenchyma probably leads to better efficiency in the use of photosynthetic light (Rotondi et al., 2003). It has been reported that the presence of specialized cell types such as sclereid cells, phenolic cells, or resin glands in severe environments, protects the mesophyll cells against excess radiation or herbivores and reduces the evaporation rate (Crang et al., 2018; Fahn and Cutler, 1992; Fortuna-Perez et al., 2021). Tian et al. (2016) reported that with increasing altitude, the ratio of the palisade parenchyma to the mesophyll parenchyma increased (Tian et al., 2016). Similarly, in the present study that sampling was done from a high altitude (2930 m above sea level), and the thickness of the palisade tissue was higher than of the spongy one. Therefore, a higher palisade-leaf mesophyll thickness ratio in high altitudes may enhance the photosynthetic capacity during a short growing season. Overall, these relationships between anatomical traits show the plant’s adaptation to changing environmental conditions by regulating the ratios of the leaf anatomical structure (Tian et al., 2016).

Phenolic cells were observed in the leaf epidermis of seedlings, male and female cones. There was a conspicuous resin gland in the outer (lower) surface of every scale-like leaf secreting a sticky resinous substance that dries into a white material, particularly in the fall or in damaged leaves showing defensive functions. In female cones, the presence of abundant resin glands was also observed. Studies on *Juniperus communis* L. have shown that its foliage is rich in secondary substances, particularly terpenoids and phenolics (Stark and Martz, 2018). Phenolic compounds act as a screen inside the epidermal cell layer to defend plants from different damages and by adjusting the antioxidant systems at both the cell and whole organism level, thereby intercepting mutagenesis and cell death by dimerization of thymine units in the DNA, and possible photo destruction of coenzymes NAD or NADP (Naikoo et al., 2019).

During female cone development, phenolic cells were differentiated into sclereid cells so that they constituted the main part of berry-like cones. Therefore, an increase in the leaf thickness and sclerophylly in both leaves and female cones was observed with increasing age. In accordance with the results of this study, Chelli-Chaabouni (2014) reported that at a seedling stage, plants may produce defensive compounds to resist stress conditions, but during maturation, the biochemical protective strategy decreases progressively while many protective structural changes (greater leaf thickness, higher lignin and fiber content) occur. The increase of plant sclerophylly with age has been suggested as the result of natural selection based on the energy reallocation according to the cost/benefit ratio (Chelli-Chaabouni, 2014). Given that *J. seravschanica* is evergreen and its female cones take two or three years to ripen, both leaves and female cones need to invest more defensive traits because of the high risk of exposition to biotic and abiotic stressors during their lifespan. However, there is no published study on *J. seravschanica* phenolic compounds and resin ducts that function as a physical constitutive defense as they exist in a tree prior to stressors, and as an inducible defense that produces higher levels in response to stresses. Experimental evidence from pines and other conifers indicates that resin defense characteristics such as flow rates and chemistry are heritable genetic traits, and thus subject to selection from insects, pathogens, and environmental factors (Ferrenberg et al., 2014).

Scale-like leaves showed more supporting traits compared to needle leaves including a thicker hypodermis and more sclereids. Similarly, the studies of heterophylly in *J. sabina* L. showed that scale-like leaves are better able to conserve water for storage and survival in harsh environmental conditions (Zhang et al., 2019). Therefore, scale-like leaves are more successful than needle leaves in dry and cold habitats. Studies on juvenile and adult foliage of *J. occidentalis* Hook. showed that needles, due to the higher levels of photosynthetic rate and lower costs of construction, increase plant establishment and early growth, whereas scale-like leaves reveal more tolerance against stress (Zhang et al., 2019).

Tracheids in leaves and berry-like cones of *J. seravschanica* had a small lumen. The species is highly resistant to frost, growing in some areas where the minimum temperature reaches -30^{o}C. This trait of tracheids can prevent frost- or drought-induced embolism. It has been reported that conifers tracheids enable slow but safe water transport and increase resistance against drought and freezing-induced embolism. These characteristics of conifers can help their survival and dominance in hard conditions (Song et al., 2022). In addition, studies have shown that junipers are potentially better adapted to stressors compared with taller plants containing wider tracheids, such as pines. Therefore, junipers may experience a higher chance against xylem embolism (Camarero et al., 2021).

In conclusion, this study demonstrated morphological and anatomical traits of *J. seravschanica* growing in harsh environmental conditions that has ecological and economic importance. The results showed that it is very resistant against different stresses, growing in some areas where the minimum temperature reaches -30^{o}C, the height is 3800 meters above sea level, and in some years, there is no rain in the summer. The features such as high sclerophylly, resin glands, phenolic cells, narrow tracheids, sunken stomata, increasing thickness of epidermal cells, cuticle, hypodermis, and palisade parenchyma enable the species to survive and adapt to the surrounding environment with extreme conditions. These characteristics were more obvious in scale-like leaves than needle-like leaves as well as in female cones than male ones.

AUTHORS’ CONTRIBUTION

F.R. study conception, design, supervision and led the research project; F.R., F.G.H. and F.B. investigation, visualization and collected data and samples in the field; F.R. and F.G.H. writing original draft, review and editing. All authors read and approved the final manuscript. The authors declare no conflict of interest.

The datasets produced in this study are available from the corresponding author, (F.R), upon reasonable request.

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FIGURES:

Fig. 1. Distribution of *Juniperus seravschanica* in different zones. (**a**-**e**) Growing with other species, (**f**,**g**) distributed as pure patches in rocky and mountainous zones.

Fig. 2. Needle-, scale-like and cotyledon leaves of *J. seravschanica*. (**a**-**c**) Needle-like leaves with acute apex in seedling (**a**) and juvenile plants (**b**,**c**). Cotyledon leaves are linear (**d**,**e**). Scale-like leaves of adult plants, unripe female cones have scale-like leaves too. Cl – cotyledon leaves, Sl – scale-like leaves, Nl – needle leaves, Fc – female cone.

Fig. 3. Female and male branches of *J. seravschanica*. (**a**,**b**) The unripe and ripe cones (berries) respectively, (**c**) male cones.

Fig. 4. Morphological traits of leaves of *J. seravschanica*, leaves are small, scale-like and overlapping (**a**-**f**). Resin glands are observed in the lower half of each leaf (**a**), their secretions are seen as white and sticky resinous patches on leaves (shoots) (**a**-**f**). Rg – resin gland.

Fig. 5. (**a**-**d**) Anatomical traits of cotyledon leaves of *J. seravschanica* for its protection against different damages; epidermis with thickened walls, discontinuous and thickened hypodermal cells with phenolic compounds (orange color) and palisade parenchyma (in adaxial and abaxial side) are observed in cotyledon leaves of young seedlings. The continuity of hypodermis was only seen in the leaf margin. E – epidermis, H – hypodermal cells, Pp – palisade parenchyma, Vb – vascular bundle.

Fig. 6. (**a-d**) Cross-section of anatomical traits of needle-like leaves of *J. seravschanica* showing their protection against different damages. Leaves showed various characteristics related to their adaptations for controlling and maximizing the success including epidermis with thickened walls, thickened hypodermal cells, the presence of palisade parenchyma in both levels, large resin glands and sclereid cells. E – epidermis, H – hypodermal cells, Pp – palisade parenchyma, Sc – sclereid cells, Rg – resin gland.

Fig. 7. (**a-h**) Anatomical traits of scale-like leaves of *J. seravschanica* showing their protection against different damages. Leaves showed various characteristics related to their adaptations for controlling and maximizing the success including epidermis with thickened walls, thickened hypodermal cells, the presence of palisade parenchyma in both levels, large resin glands and intracellular starch granules stained with Lugol’s solution were observed as dark color. E – epidermis, H – hypodermal cells, Pp – palisade parenchyma, Sc – sclereid cells, Rg – resin gland, St – stoma, S – starch, Vb – vascular bundle, T – tracheids.

Fig. 8. (**a-i**) Morphology and anatomy of male cones in *J. seravschanica* showing adaptive features. Small size, yellowish color, the overlapping and decussate arrangement of cone scales are apparent (**a-c**). Cross section of male cones and their scales showed the presence of resin glands in cone scales (**d**,**e**,**h**,**i**) as well as phenolic compounds (yellow to brown in color) in cone scales (**d-i**), cone axes (**i**) and stalks (**h**,**i**). In **g**, young cone and in **h** and **i**, mature cones are observed. Mcs – male cone scale, E – epidermis, Pt – phenolic tissue, Pc – phenolic cells, Rg – resin gland, Rg – resin gland, Ca – cone axis, S – stalk, Ps – pollen sacs

Fig. 9. (**a-h**) Morphological and anatomical traits of female cones of *J. seravschanica* showing their adaptive strategies against different damages. The cones showed different adaptive traits such as the overlapping and decussate arrangement of the scales in young female cones, gathering of fes (bracts) and their fusing during ripening (**a-c**). Thick sections studied using sectioning microscopy revealed the presence of numerous resin glands and their exudates in both young (**d**,**e**) and ripen (**f-h**) cones. Urc – unripen cone, Rc – ripen cone, Rg – resin gland, Re – resin exudate.

Fig. 10. (**a-f**) Cross section of young female cones of *J. seravschanica* showing the abundance of phenolic cells (observed yellowish-brown in color), resin glands (**a-f**) and thick epidermis with phenolic content and thick cuticle (**f**). During development, the walls of phenolic cells are lignified but they still contain phenolic content (**d**). Pc – phenolic cells, Rg – resin gland, Sc – developing sclereid cells.

Fig. 11. (**a-f**) Cross section of mature female cones of *J. seravschanica*. The presence of numerous resin glands (**a**,**b**), thick epidermis (**b**) and sclereid cells with different shapes (**a-f**) is visible. Vb – vascular bundle, T – tracheids, Rg – resin gland, Sc – sclereid cells.

Figure 1

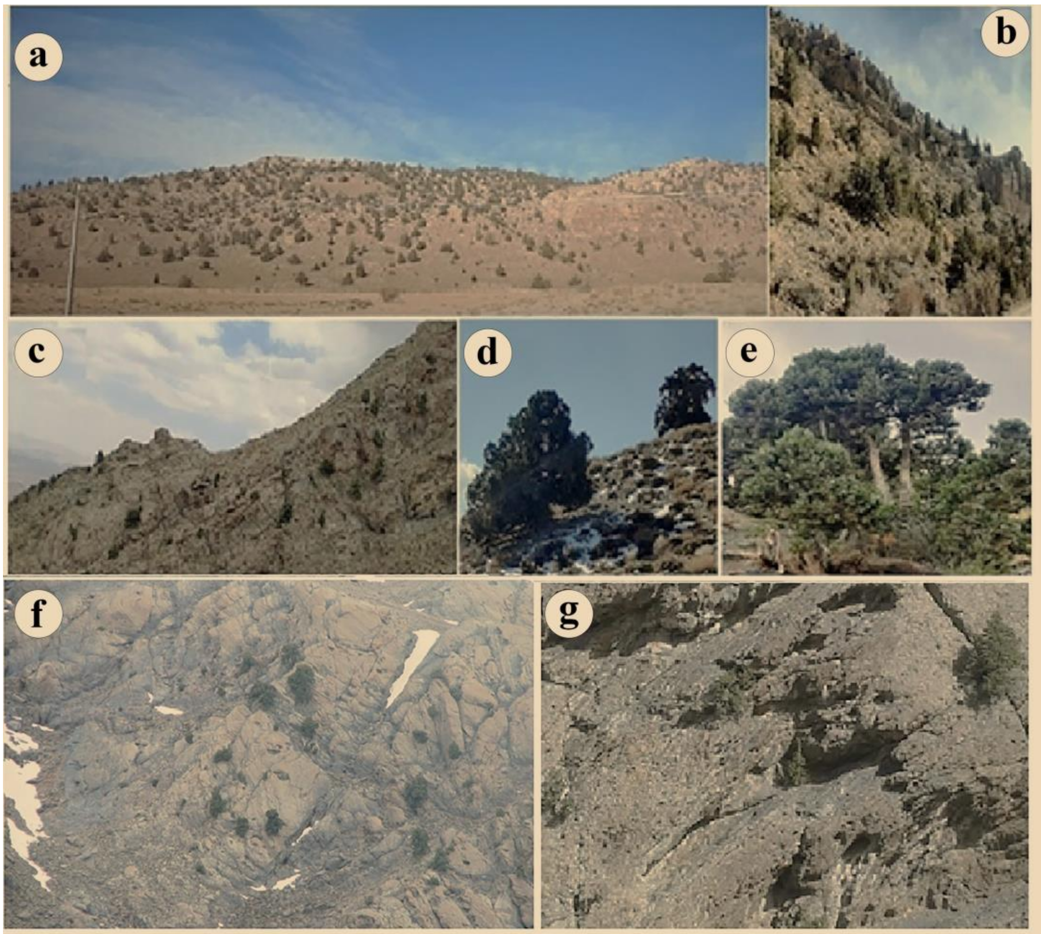
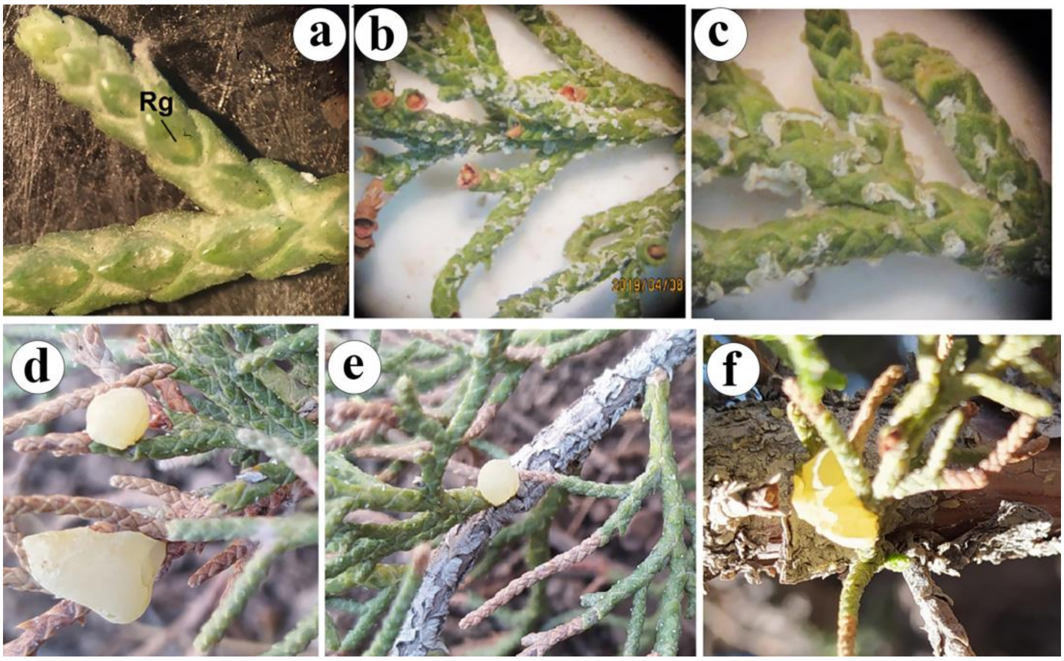


Figure 2

Figure 3

Figure 4



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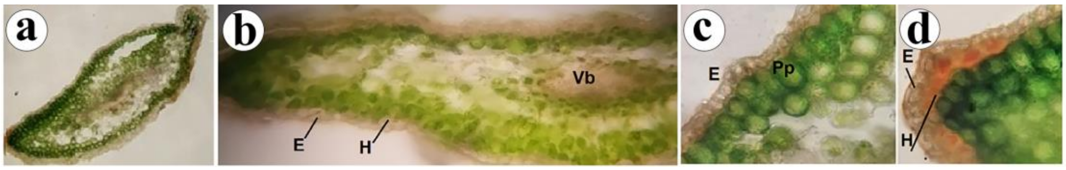

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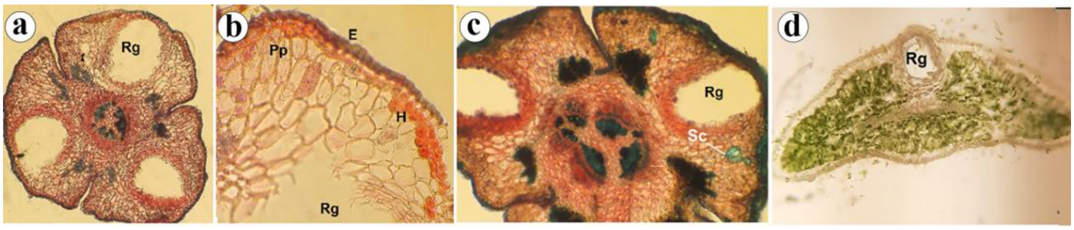

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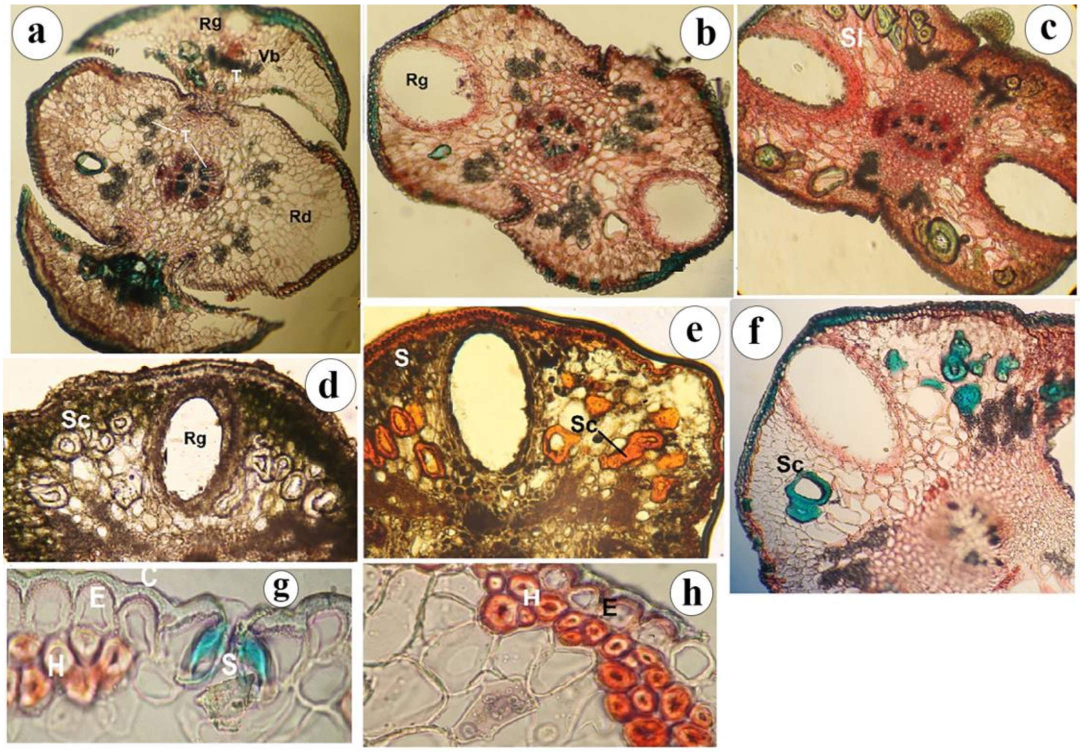

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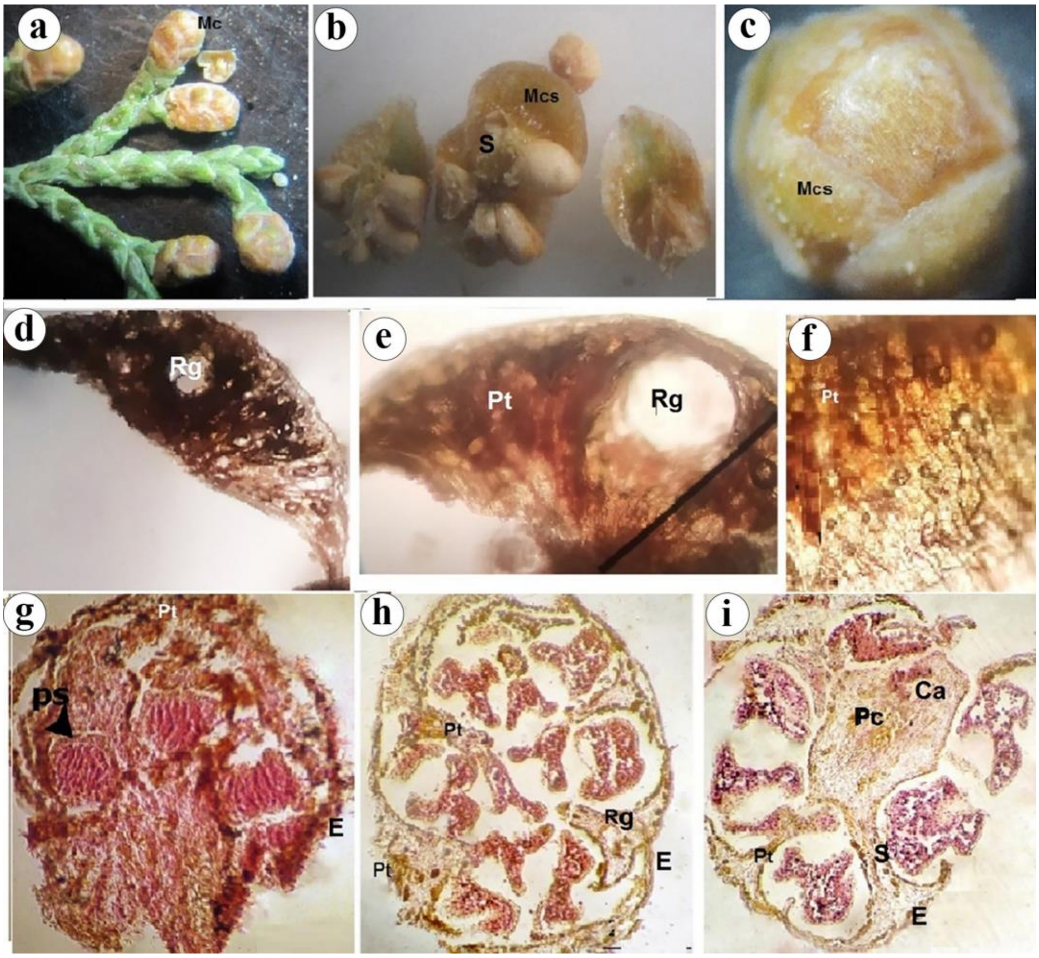
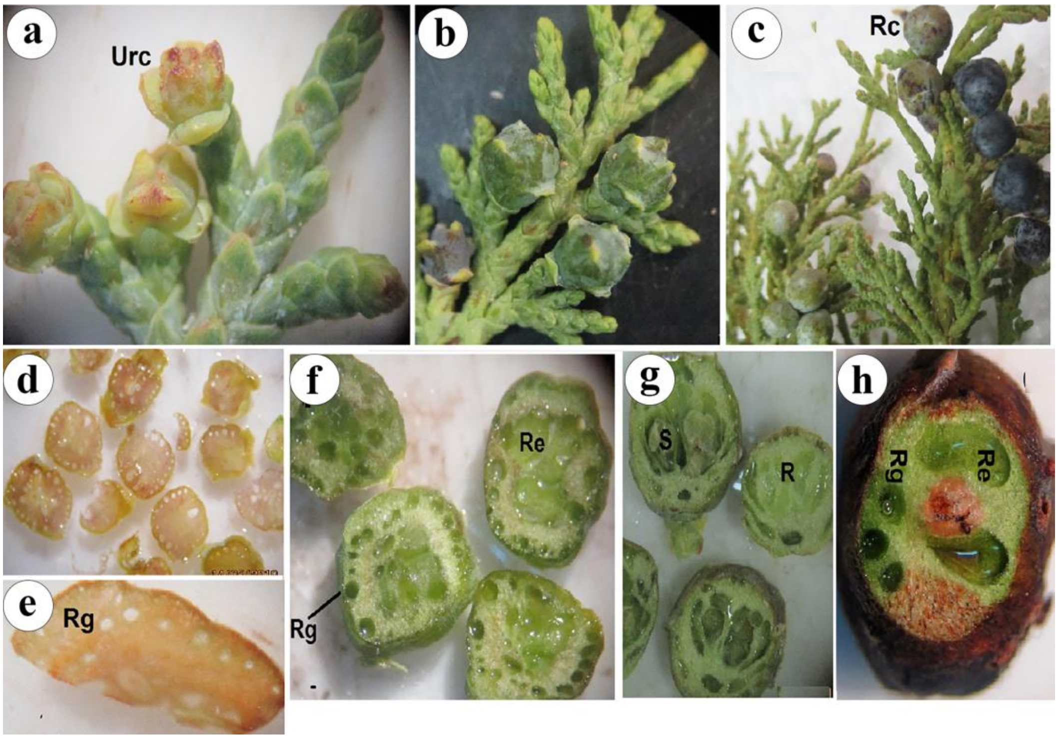


Figure 9



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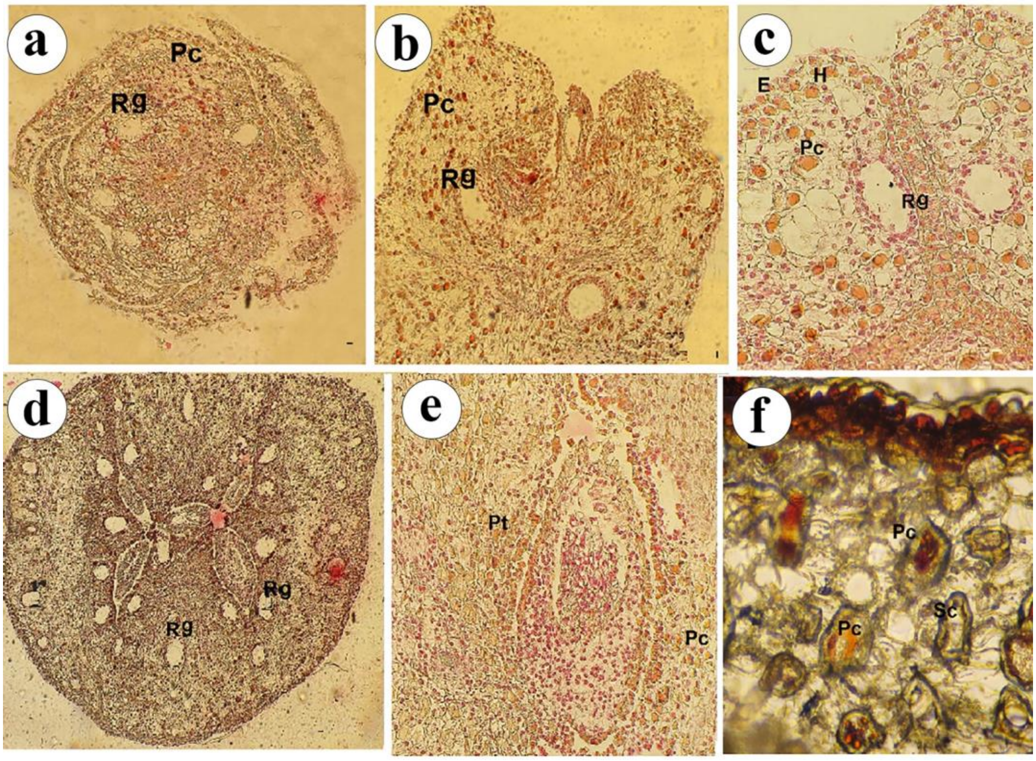

Figure 11