

HISTO-ANATOMICAL STRATEGIES OF *CHENOPODIACEAE* HALOPHYTES: ADAPTIVE, ECOLOGICAL AND EVOLUTIONARY IMPLICATIONS

MARIUS-NICUȘOR GRIGORE, CONSTANTIN TOMA

Faculty of Biology

Al. I. Cuza University, Jassy

Bd. Carol I, 20 A, 700505

ROMANIA

marisgrigorepsyche@yahoo.com, ctoma@uaic.ro

Abstract: The authors of the present study have investigated six halophyte species from *Chenopodiaceae* family. These species have been harvested from different saline habitats. Some interesting and intriguing features such as successive cambia phenomenon, succulence, salt hairs, tracheids, fleshy tissues and peculiar foliar anatomy structures have been noticed. These aspects are discussed in relation to their ecological, adaptive and evolutionary significance.

Key words: - adaptation, lignin, C₄ plants, Kranz anatomy, photosynthesis, strategy, evolution

1 Introduction

Chenopodiaceae is one of the most interesting families with respect to having species with a large diversity in the structure of the carbon assimilating organs with different types of photosynthesis [83].

Generally, halophytes face a two-fold problem: they must tolerate the high salt concentrations of their habitats and they must absorb water from a soil solution that has a low water potential [43].

Any histo-anatomical feature must be considered theoretically and hypothetically as an adaptive feature. It should be asserted that each one of them has the same importance or relevance in proving that a plant belongs to a certain ecological group.

The adaptive and evolutionary process has taken place over the long and shaping influence of the environmental agents. The high salinity of soils and the soil's moisture has a major impact on halophytes' anatomical structures and has formative effects. Their cumulated action has accompanied the halophytes evolution through time, as an active and dynamic component of the evolutionary "adventure" [26].

2 Materials and Method

In the present study, the following taxa: *Atriplex tatarica* L., *Petrosimonia oppositifolia*

(Pallas) Simonkai, *Salicornia europaea* L., *Suaeda maritima* (L.) Dumort, *Bassia hirsuta* (L.) Asch. and *Camphorosma annua* Pall., belonging to the *Chenopodiaceae* family have been selected. All these six taxa have been harvested from saline soils in Moldavia (Romania). The material was fixed and preserved in ethylic alcohol (70°) for subsequent histo-anatomical investigations.

The sectioning of the vegetative organs was made using a botanical razor and a microtome. The cross sections thus obtained have been subsequently subjected to the "classical" stages of any histo-anatomical experiment: javelization with sodium hypochlorite for 20-30 min., washing with acetic water and running water and then colouring.

The colouring was done using two different compounds: 1. iodine green (for 1 min.) followed by washing in ethylic alcohol (90°) bath; 2. red carmine alauinate (for 20 min.) followed by washing with water. The cross-sections were finally fixed in glycerol-gelatine.

The permanent preparations obtained have been photographed on a NOVEX (Holland) photonic microscope using a Canon photo digital camera.

3 Results and discussions

All investigated species, except for the species *Bassia hirsuta*, presented the successive

cambia phenomenon that occurred in the axial vegetative organs (root and stem). Some authors [30]; [49]; [21] consider this phenomenon a structural anomaly. Successive cambia occur in bands or strands of secondary phloem and secondary xylem (vascular increments), which are embedded in a background of parenchyma or fibers (conjunctive tissue) [9]. This phenomenon consists shortly of the following succession of histological events: the typical, general structure is generated by a normal cambium that generally produces a few secondary phloemic and xylemic vessels. Afterwards, on behalf of the pericycle, an additional (supernumerary) cambium is born, this one providing a ring of fundamental parenchyma, where the vascular bundles are placed circularly, with the phloem outside and the xylem inside. Each abnormal cambium is born after that from the phloemic parenchyma produced by the former cambium [44]. Nevertheless, one should say it does not exist a strictly general plan to explain the formation and the functioning of the successive cambia. Moreover, even the language used by different authors is not unitary, but they often use imprecise and vague terms, that can make heavier the understanding of the phenomenon. For example, some authors have referred to successive cambia under the vague terms “anomalous secondary thickening” or “included phloem.” But the secondary phloem of successive cambia is not included within wood at all [71]. As Carlquist also reveals [9], the maintenance of such terms may have been furthered by those who are involved with wood identification and who therefore want simple terms. The tendency to use such a term as “included phloem” probably indicates a desire to consider the background tissue of plants with successive cambia as “wood”. This background tissue, although often woody in texture, is not wood in the ordinary sense. Wood anatomists, who have worked in detail with plants affected by successive cambia, have used the term “conjunctive tissue” for the background of fibers and/or parenchyma, in which vascular increments are embedded.

Successive cambia are known in 34 families of dicotyledons, as Carlquist estimated (2001), cit. from Carlquist [9].

Our investigations have revealed that in *Petrosimonia oppositifolia*, the phenomenon is manifesting in the root (Fig. 1) at all the three analyzed levels, as well in the stem (Fig. 2), mainly in its inferior and median third.

The successive cambia phenomenon is also present in the *Atriplex tatarica* root (fig.3).

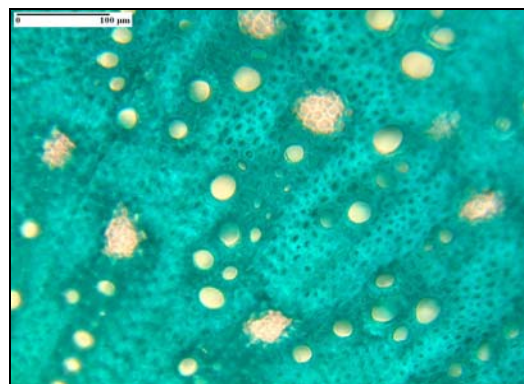


Fig.1. Cross sections through the root of *Petrosimonia oppositifolia*

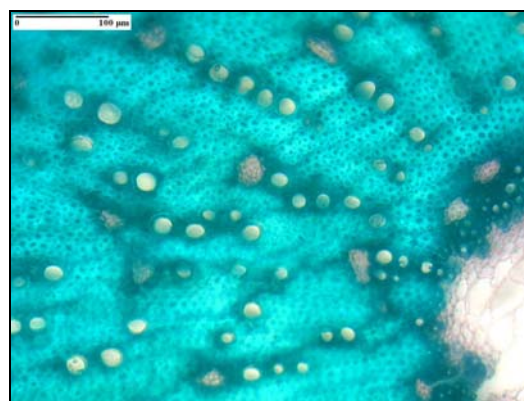


Fig. 2. Cross sections through the stem of *Petrosimonia oppositifolia*

Two such additional cambia are formed and active in its inferior third.

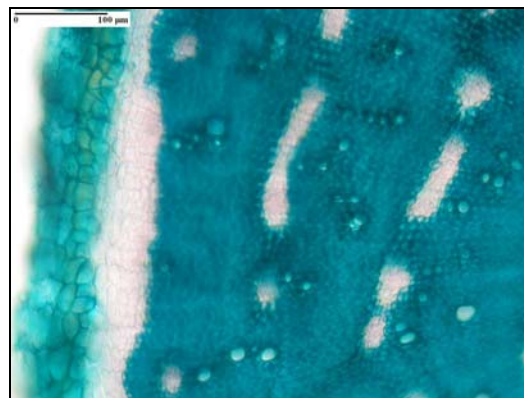


Fig. 3. Cross sections through the root of *Atriplex tatarica*;

In *Salicornia europaea* the successive cambia phenomenon affects both the root (Fig.4) and stem's non-articulated part.

In the root of *Suaeda maritima* (Fig. 5) the activity of the additional cambia results in 5 rings of conductive tissues, each of them being mainly

occupied by the libriform, that contains a few irregularly-arranged vessels inside, as well as numerous phloemic islands, separated by a cellulosic or a weakly-lignified parenchyma. The phloemic islands are neither equidistant nor equal.

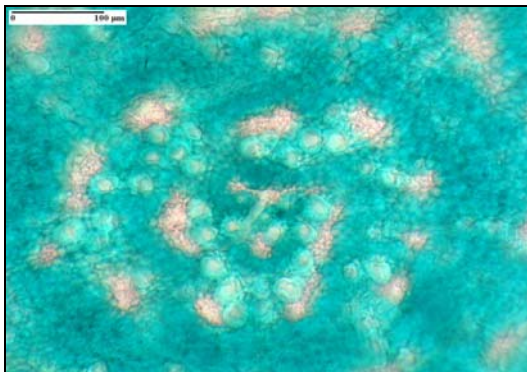


Fig. 4. Cross sections through the root of *Salicornia europaea*

In the structure of *Camphorosma annua*'s root function an amount of 2-3 successive cambia, resulting an adequate number of xylemic and phloemic rings, the xylemic ones much thicker and strongly lignified (Fig. 6). The libriform makes discontinuous springs in the center area of the organ (Fig. 7).

On the entire depth of root, but mainly inside the external xylemic rings, the libriform fibers have extremely thick and acutely lignified walls. The secondary structure can be recognized from the great number of vessels per surface unity and also the libriform elements between them, with medium-thick and slight lignified walls.

As for the structure of stem, we revealed a successive cambium only at the base. From its activity resulted a relatively thick xylemic ring and another one, thinner, phloemic. In the xylemic ring, the vessels are rare, and at the periphery of the phloemic ring, are occurred more sclerenchymatic fiber strings, very thin, with medium-thick and slight lignified walls (Fig. 8).

Also, at other species of *Chenopodiaceae* we investigated, for example *Atriplex littoralis* L. or *Atriplex prostrata* Boucher ex D. C. only the base of the stem is affected by successive cambia phenomenon [26]. The rest of the stem remains with the normal, characteristic structure.

In the central cylinder of the axial organs we evidenced a considerable amount of libriform that has thick lignified walls. The massive lignifications present in the root's central cylinder of the species affected by successive cambia may be induced by the soil's excessive salinity [5]. Kozłowski [45]

underlines that salinity raises the amount of fibers productions. Considering the complex adaptations of plants, each species possibly reacts through metabolic changes. The lignin can be viewed as a metabolically answer which may also increase the cell walls' resistance at osmotic high pressure in order to exceed the osmotic pressure of soil solution.



Fig.5. Cross sections through the root of *Suaeda maritima*

However, the relatively high contribution played by lignin in the structure of halophytes should be cautiously viewed as the relation between the lignin and the salinity is not always highly conclusive. Thus, in some sorts of rice (salt-sensitive and salt-resistant) a high value of salinity (40 mM NaCl) increases the lignin content [68]. In the same context, histochemical observations at salt-tolerant wheat confirms a more intense lignification in the root cells of the salt-tolerant species compared to the sensitive species, under the effect of NaCl [36]. On the other hand we should mention the fact that a high salinity might reduce the lignin content in the internodes of *Suaeda maritima* [27]. At *Atriplex prostrata*, grown in 0,5 and 1,0 % NaCl the lignified area in the third and fourth internodes decreased in comparison with plants from 0,0 % NaCl [86].

Moreover, very interesting correlations can be made between lignin, extensin and increased salinity conditions. It is generally noticed, as in *Atriplex prostrata* [86], that extensin increased in plants grown under increasingly saline conditions. This way, in the first and second internodes, plants from 2, 0% NaCl had the highest level of extensin in the vascular tissue, cortex, epidermis and pith. The level of extensin in the vascular tissue was enhanced as the salinity increased in the third internode, and the level of extension increased in the vascular tissue as well as in the pith at high salinity in the fourth internode.

As one can observe, there was more soluble extensin in the younger (the first and the second internodes) than older internodes (the third and fourth internodes) [86].

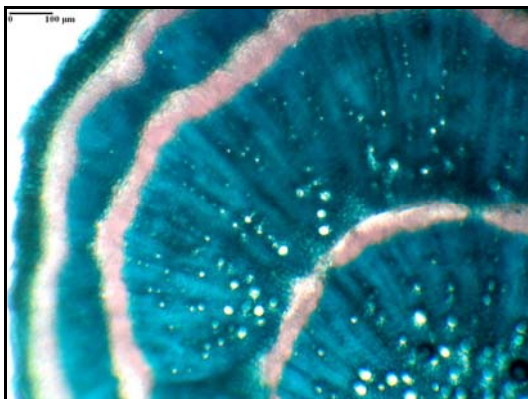


Fig. 6. Cross sections through the root of *Camphorosma annua*

This is because extension molecules tend to cross-link with each other with other wall components after secretion into the wall [70]. In addition, extensin is found to be closely associated with lignin deposition and may provide mechanical support in cells subjected to compression or torsional stress, brought about by vascular growth or transport of vascular fluids [77]; [47].

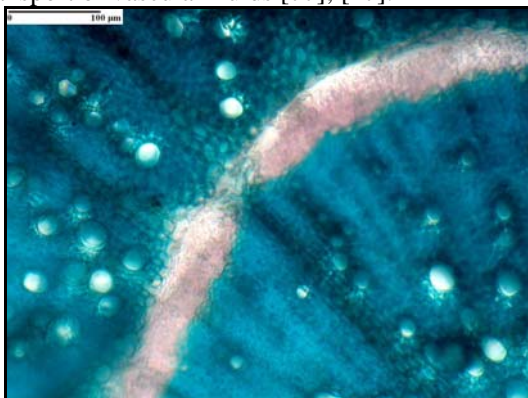


Fig. 7. Cross sections through the root of *Camphorosma annua*

Both lignin and extension serve to strengthen the cell wall. Lignin is generally localized in xylem whereas extensin is found mostly in phloem [93]; [70]. It has been noticed that in the older internodes, where phloem and xylem are well developed, an increase of extensin is not observed in pith but in vascular tissue. In addition, the area of lignification (xylem) was reduced, but the area of phloem was increased under salinity conditions. This can be correlated with the fact that some organic solutes are synthesized to maintain turgor potential under saline

conditions so that phloem tissue is specifically developed to translocate these organic solutes. Extensin becomes abundant overall in the stem but lignin content declines. These data imply that the extensin may replace lignin to strengthen the cells walls of plants under salt stress conditions. As we know, lignin is an important component in the secondary cell wall, while extension is more commonly found in the primary cell wall.



Fig. 8. Cross sections through the stem of *Camphorosma annua*

A general observation to be made is that salinity may increase lignification at root level, while it decreases it at stem level. In our opinion, phylogenetically and ontogenetically this situation may be correlated with the position and the part played by the root in the life of plants. As a matter of fact the root represents the organ most exposed to soil salinity. At root level there should exist – at least hypothetically – mechanisms capable of controlling the penetration of the salt water and its retention in this organ. The existence of certain well-established mechanisms such as the well-developed endodermis capable of controlling the penetration and subsequent distribution of the salt has been actually demonstrated [18]; [23]; [54]; [66]. Some authors [80]; [72]; [89] suppose that the active transport mechanism resides either in endodermis or in the xylem parenchyma. All these represent only few examples that prove the special part played by the root in the life of plants exposed to a high salinity.

In our opinion, the lignin might confer resistance to the cell walls. This resistance is also involved in supporting and counteracting the high osmotic pressure which the halophytes have to face at the level of the rhizosphere. This makes the root the most important interface between the plant and the hypersaline medium. Not accidentally the lignification is not so pronounced at stem level, at least in the superior parts [25]; [26]. It's widely

accepted that the young tissues are more sensitive to salts [84].

The ecological significance of successive cambia phenomenon is still obscure. As we showed elsewhere [26] this interesting phenomenon of halophytes could be related to the formative environmental factors. In order to explain this phenomenon we should consider certain mechanisms that adjust the salt content: the second dilution of salt through growing [24], the salt retaining in root and stem [6]; [16]; [33]; [34] and the re-transportation of salts into the root and their elimination through environment [91]; [12]. At least the mechanism of salt retaining in root and stem may be related to the internal large surface of the organ in case we consider the high ability to retain the saline water in the root and the stem.

Unfortunately, the halophytes represent a highly heterogenous ecological group, and different species present a great diversity regarding the habitats, the halophilic rank or the way they respond to the environmental factors. Because of this, the interpretations and the extrapolations from one species to another have to be made prudently, even if we have to accept the idea of a convergence, probably induced by the same factor, the salinity of the soil.

Nevertheless, we can accept the idea that the alternation of vascular increments with parenchyma provided by the successive cambial mode of construction offers an ideal histological plan for storage and retrieval of photosynthates and water [9]. It is a known fact that the roots of *Beta* [2], another representative of the family *Chenopodiaceae*, and *Mirabilis* [50] have thin cylindrical vascular increments spaced from each other by relatively wide zones of parenchyma. Sugar is stored abundantly in roots of *Beta*, starch in those of *Mirabilis*. This seems clearly correlated with adaptation to photosynthate storage and retrieval rather than water storage.

On the other hand, the cork from the external part of the root could delay the water absorption. Thus, the salts penetrate hardly through the root, but once they get there they spread within this enlarged surface. The water distribution to the rest of the plant might literally “be delayed”. The enlargement of the root surface confers a larger dispersion place for salts where they are diluted and finally less harmful to the plant.

Biosemiotically the root exercises a “protective” role on the rest of plant organs by its temporary retention and/or deposition of salts. The flowering is partially favoured by restricting salt penetration in the rest of the plant as long as the

flowering is a very salt sensitive phase in a plant’s ontogenetic development [84].

As for us, we believe that this sort of phenomenon, complex and sometimes difficult to understand, cannot be approached but in a complex form. Subsequent researches should establish the differences in quality and/or quantity that might appear the species of *Chenopodiaceae*, harvested from saline soils as much as from nonsaline ones. In the future, the histo-anatomic investigation of a greater amount of halophytes from this family, belonging to Romanian flora, will enable us to do some statistic analyses, to establish some clearer correlations between this phenomenon and the ecological factors.

The succulence is another major strategy of halophytes. The succulence is represented by a water storage tissue evidenced in the upper third of the *Petrosimonia oppositifolia* stem and in the structure of its foliar limb. The water storage tissue of stem (Fig.9) is formed by very large cells with meatus among them while in the structure of the foliar limb (Fig. 10) its fundamental mass is represented by a water storage parenchyma formed by very large cells with relatively thin walls and meatus among them. It has also been identified in the structure of the fleshy tissues of *Salicornia europaea* (Fig.11) and in the structure of the foliar limb of *Suaeda maritima* (Fig. 12). The characteristic water storage parenchyma provides the succulence of *S. europaea* plants.



Fig. 9. Cross sections through the stem of *Petrosimonia oppositifolia*

A few considerations on this phenomenon have to be made. The succulence is generally viewed as one of the main factors involved in the plant tolerance to salts. Besides other adaptive characteristics, such as reduction of the foliar surface, thick leaves, a higher plasticity of the cell walls, a reduced numbers of stomata on unit of surface, it represents one of the features best defining in halophytes [65]; [73]; [54].



Fig. 10. Cross sections through the foliar limb of *Petrosimonia oppositifolia*

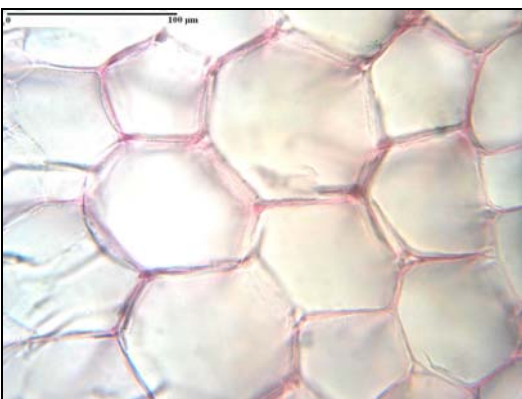


Fig. 11. Cross sections through the foliar limb of *Salicornia europaea*

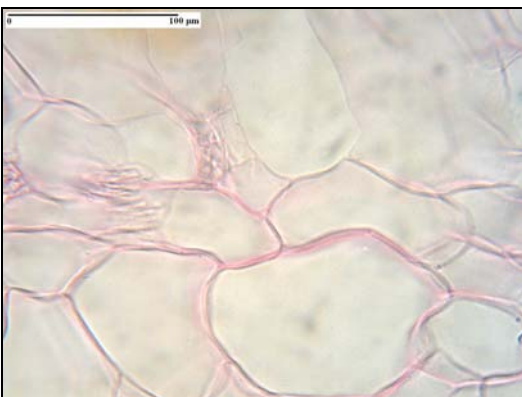


Fig. 12. Cross sections through the foliar limb of *Suaeda maritima*

As a matter of fact the presence of succulence, the reduction of the foliar surface, the protecting hairs that occur in both desert plants and halophytes represent the basis that permitted Schimper to elaborate his theory on “physiological drought.” Actually the high salinity causes severe internal water deficit and plants affected by this stress type may sometimes develop xeromorphic

structures [84]. The succulence can be expressed in direction of increase in cell size, decrease in extension growth, reduction in surface area per volume tissue. Halophytes accumulate therefore big amounts of salts through their shoots and show the highest degree of succulence. Succulence exercises a dilution effect upon the salts accumulated in plants, upon the toxic ions from the cells, thus permitting the plant to cope with higher salt amounts [84]. On the other side, succulence may cause disadvantages to the plant as it is capable of a concomitant reduction in the concentration of the calcium and potassium ions present in the salt-affected tissues, which may therefore increase the toxicity effect of other ions in the cells. It is known that the Na and Cl ions are viewed as aggressive osmolytes for plants’ cells because of their low ionic diameter and of their high hydration capacity [67], while the resistance to salts depends, at least partially, on plant’s capacity of mobilizing energy for Na elimination off the cells and also for K accumulation [84]. This way the two-sided character of succulence might be better grasped.

However, it’s obvious that the succulence represents a major strategy of halophytes, in their permanent “negotiation” with soil’s increased salinity. Consequently, salinity may be viewed as the converging modeling factor that induces succulence to various groups of halophytes. The halophytes secreting salts (“crynohalophytes”) possess another major strategy as long as they maintain a low salt content in their tissues and they generally evidence no succulence.

But differences in structure are well known between plants of dry saline habitats and of wet ones. Consequently, two types of succulent halophytes are described as succulent mesomorphs and succulent xeromorphs on the basis of their water relationships [90]. The first type correspond to the hygro-halophytes (*S. europaea*), the second, to the xero-halophytes (*P. oppositifolia*). At hygro-halophytes all leaf cells, including epidermal cells, are succulent and the number of stomata per unit area is low. The xeromorphs subjected to the water stress are characterized by succulent and large mesophyll cells.

The xero-halophytes are additionally characterized by a highly developed lignified vascular system (the case of *P. oppositifolia*). Therefore the ecological significance of succulence may be correlated with the local environmental factors. Thus, *Petrosimonia oppositifolia* has been harvested from dry saline soils; it might be classified as a xero-halophyte which could explain the necessary presence of some water storage

tissues. *Salicornia europaea* and *Suaeda maritima* are hygro-halophytes that have been harvested from wet, sandy, sometimes and colmatated saline soils. The presence of succulence and the above-discussed dilution effect contribute to maintaining cellular turgescence that is also responsible for plant's erected stature. This should be closely correlated to the rudimentary and weakly developed mechanical tissues of this plant species. "As long as turgescence is no longer assured by the absence of water, the plant inevitably dies" [55] (with reference to *Salicornia*). That's why this species grows in intensely saline, chlorurated and wet media. A closed microecological chain is practically involved here. The chlorurated salinity of the soil induces succulence which assures both the dilution of the toxic ions and the maintenance of the osmotic pressure of turgescence. This ensures the absorption of the sap in the plant and its erected position. The plant may die in the absence of the water from the soils because of salts' accumulation in the cells which induces a lethal effect or because of losing reversibly or not the erect stature. This means that not only the salts' balance but also the hydric balance should be carefully considered. Consequently, *Salicornia europaea* appears to be a hydrophilic and medium-to-intensely halophytic plant that grows in flooded plains with humic gley soils that are wet inside and less wet towards the surface [8]. It has almost the same ecological requirements as *Suaeda maritima*. Both of them are species that form chloruric association of plants [76]. In this respect it has been assumed that *S. europaea* has a lacustrine origin [76] as it vegetates very well in the vicinity of the sea where it naturally finds the necessary and the indispensable living conditions such as humidity and salty water. The capital importance of water for *Salicornia* is more obvious when taking into account the fact that in most cases seeds' germination occurs in the presence of rainfall water in which, according to the same author, the salts are much diluted.

The formative capacity of salts upon plants should also be mentioned. It is know that sodium chloride was found to be the most efficient salt in promoting succulence [81] at *S. herbacea*. So chloride rather than sodium played the major role in its induction. Similar conclusions were reached by other authors [39]; [85]; [92]; [75]; [29]; [74]; [48]. Therefore, the degree of succulence in halophytes varies with external salinity and the succulence is the expression of the increased size of individual cells. For example, studies on *Atriplex hastata* indicate that succulence is due to increased ion uptake [7].

Another interesting structure has been evidenced in *Salicornia* at the level of the palisadic tissue. It's about several saculiform tracheoidioblasts that are as high as the thickness of the palisadic tissue and evidence some peculiar thickened areas (Fig. 13 and Fig. 14). They have also been evidenced in *S. virginica* [3], *S. fruticosa* [11], *S. australis* [13], *S. europaea* [41] and *Arthrocnemum glaucum* [20].



Fig. 13. Tracheids in foliar limb of *Salicornia europaea*

Such peculiar structures have been defined by Chermezon [11] as "les grandes cellules spiralées". This author cited Duval-Jouve who also evidenced them and granted them an aquiferous role. Mangin (1882) cited by Chermezon [11] considered that they have a supporting role, once they have no contacts with the stomata. Warming (1902), cited by the same author, speculate that they play the role of aquiferous tracheids. Cooke [13] believed that they have an aquiferous role, while Keshavarzi and Zare [41] stated that they intervene in water's transport towards the peripheral tissues. Their contribution to the hydric equilibrium has been also supported by Anderson [3].



Fig.14. Tracheids in foliar limb of *Salicornia europaea*

Our opinion is that these structural elements cannot be viewed as salt glands because *Salicornia europaea* is not a “cryohalophyte” species and possesses different mechanisms for salt’s regulation. According to the definition given by Fahn [19]: “the salt glands are either specialized epidermic cells or specialized trichomes, known as playing an active role in the secretion of mineral salt solutions”. Thus they cannot be considered, *stricto sensu*, as glands. It is true that this situation may be available for *Arthrocnemum fruticosum*, where “the vessel-like tracheoid idioblasts” are connected with the epidermis. Moreover, it was suggested that these structures play a role in the uptake of dew by the stomata [62]. The analysis of our cross-sections showed that they are not in direct contact with the epidermis, the stomata or any other formations involved in salt secretion. Anyways, these “sclereids”, as Waisel [84] defined them, seem to attain larger sizes in plants grown under saline conditions than in those grown on medium free of sodium chloride.

Salicornia is a controversial genus and no agreement has still been found as the nature of its fleshy tissues. Some researchers [14]; [28]; [35] regarded fleshy tissues as being foliar in origin, whereas others [20]; [17] considered them to be derived from stem cortex. Our investigations support the hypothesis that histo-anatomically these fleshy tissues have a foliar nature because of their peculiar epidermis and of their characteristic palisade tissue. Our researches also support De Fraigne’s [14] observations according to which this fleshy cortex has a foliar origin, derived from decurrent growth. This is based on the following facts: similarity of the tissue of the fleshy cortex to that of the leaves; venation of the cortex derived from the anastomosing lateral branches of the leaf strands; shedding of the assimilatory cortex in the fall as a result of suberization of inner layers of cells; similarity in the development of the cotyledons and hypocotyl to that of the subsequent leaves and internodes.

Duval-Jouve [15] held that the cortex originated from decurrent growth of the leaves. His point of view was based on the anatomical structure and the phenomena of shedding of the cortex.

Some authors as Dangeard (1887) and Monteil (1906), cited by De Fraigne [14] working on species of *Salicornia* and *Arthrocnemum*, assumed the fleshy cortex to represent the fused sheaths of the opposite leaves.

Keller [40] claims that in *Salicornia* sp. the cortex originated from the fusion and adnation of the leaves to the stem. His conclusions are based on

the study of some anomalies, i.e., seedlings with 3 cotyledons and unifoliate nodes or asymmetrical arrangement of the internodal fleshy cortex in some plants which grew in his plots.

Leysle [46] states that in *Anabasis aphylla* the cortex is derived from the fusion of the opposite leaves. His point of view is supported by the following: (1) In the seedling of *A. aphylla*, the lowest nodes, adjacent to the cotyledons, have quite prominent leaves, while in those more distant the leaves are gradually reduced. Leysle speculated this by an indicative of foliar fusion. (2) From the free leaf tips to the base of the internodal cortex, similar palisade and water storage tissues occur. (3) The different leaf lengths in various species of *Anabasis* are regarded by him as being a result of foliar fusion.

In fact, the authors previously mentioned, that sustain the foliar origin of these fleshy tissues, are based, generally, on the following elements: similarity of the anatomical structure, especially of the assimilatory tissues, in the cortex and leaves; the gradual decrease of the free portions of the leaves in seedlings of *Anabasis aphylla*; the fact that the decurrent growth is a vascular supply to the cortex which is derived from the lateral branches of the leaf strands.

Fahn and Arzee [20] consider these prove as relative and unconvincing. They suggest that the fleshy tissue external to the central cylinder of these succulent plants to be regarded as true cortex.

According to other authors [10] it is possible that succulents such as *Allenrolfea*, *Halocnemum* or *Salicornia* discard portions of their fleshy cortex together with their leaves, thus releasing large quantities of salts from plants.

The structures of the foliar limb and the vesicular salt secreting hairs have been evidenced on the limb’s internal side in *Atriplex tatarica* (Fig. 15).

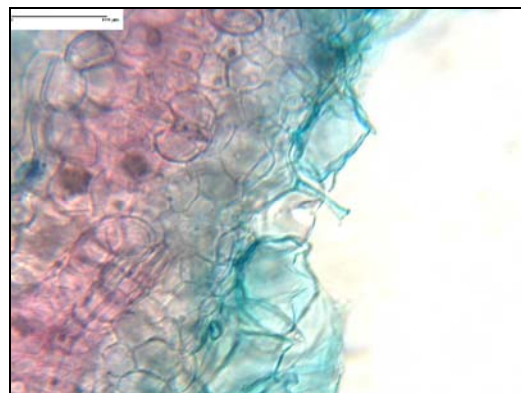


Fig. 15. Cross sections through the foliar limb of *Atriplex tatarica*

The vesicular salt secreting hairs are formed by a pedicle („stalk cell”) and a globular part („bladder”) that actually accumulates the salts for their subsequent elimination. At the level of the „vesicle” the salt concentration is undoubtedly higher than that recorded at the level of the mesophyll cells [52]; [84]; [4]; [1]. The accumulation of these salts in the upper part of the hair involves the destruction of the vesicle and subsequently the deposition of salts on the leaf surface and their removal.

The presence of salt secreting hairs represents actually the second great strategy of halophytes and it usually occurs in halophytes that have no mechanisms of internal regulation of salt dilution.

Some peculiar features have been evidenced at the level of the foliar limb. They refer to the distribution and parts played by some tissues and are closely related to a certain functional anatomy. These tissues are arranged concentrically with respect to vascular tissues in C_4 shoots, a structural pattern known as Kranz anatomy.

Kranz anatomy provides one of the best examples of the intimate connection between plant form and function and represents a suite of structural characters that have evolved repeatedly from C_3 ancestors [63]; [64]. This internal configuration physically partitions the biochemical events of the C_4 pathway into two main phases. In the first phase, atmospheric CO_2 is initially assimilated into C_4 acids by PCA (photosynthetic carbon assimilative or outer mesophyll) – tissue – specific phosphoenolpyruvate carboxylase. In the second phase, these acids diffuse into the PCR (photosynthetic carbon reductive or inner bundle sheath) compartment, where they are decarboxylated, and the released CO_2 is re-fixed by PCR- tissue-specific Rubisco.

Actually this biphasic C_4 system enhances CO_2 levels around Rubisco, suppressing photorespiration and improving plant carbon balance [37].

Three subtypes of the C_4 biochemical pathway are defined, based on the leading C_4 acid decarboxylase that liberates CO_2 from C_4 acids in the PCR compartment: NADP-malic enzyme (NADP-ME), NAD-malic enzyme (NAD-ME), and phosphoenolpyruvate carboxikinase (PEP-CK) [37]. These three subtypes occur in grasses. In contrast to C_4 grasses, only NADP-ME and NAD-ME subtypes are present in eudicots.

Thus, the structure of the *Atriplex tatarica* limb reminds of what the literature in the field generically calls atriplicoid type [32]; [53] which

consists in vascular bundles surrounded, in most cases, each, by a parenchymatous sheath, formed of large, elongated, radiary-arranged Kranz cells (Fig. 16).

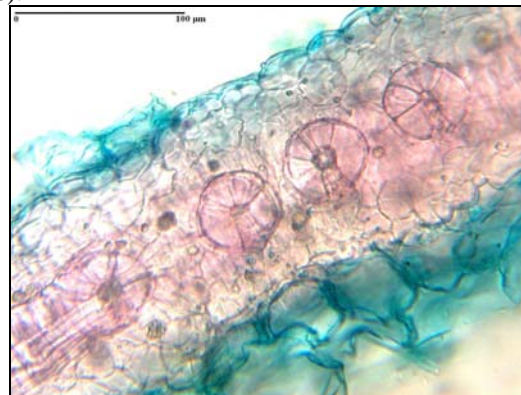


Fig. 16. Cross sections through the foliar limb of *Atriplex tatarica*

This particular type of structure, owing its name to Moser [51], is related to the sort of photosynthetic activity developed. The phenomenon is present in several *Atriplex* species, where the veins are surrounded by a sheath of cubic cells, containing chloroplasts with a diameter larger than of the other cells forming the mesophyll [84]. This type of structure has been evidenced in *Atriplex lampa* [61] and *A. buchananii* [79]. As we already settled, there is a close connection between the C_4 photosynthetic path and this type of anatomy [31].

A very recent study [53], which includes a total of 33 C_4 species and 21 closely related C_3 species, has proved that atriplicoid anatomy is the most common and has arisen independently in 21 (of a total of 32) known C_4 eudicot lineages, providing a striking example of extensive evolution convergence. C_4 eudicots lineages with atriplicoid Kranz anatomy are either NADP-ME or NAD-ME biochemical subtypes. The appearance of atriplicoid type anatomy in numerous lineages of C_4 eudicots reflects, in part, the prevalence of laminate leaves in C_3 ancestral taxa.

In *Petrosimonia oppositifolia* the foliar limb has also a special structure formed by epidermis, unilayered palisadic tissue with very low cells (PCA tissue). Its internal side contains a layer of assimilatory isodiametric cells (PCR tissue). Both layers of tissues are slightly discontinuous and define the anatomical kochioid type [32] [53] [22] (Fig. 17). Such an arrangement of tissues is very similar to the salsoloid type [22]; [57]; [83]; [32]; [60]; [53] where the two tissues tend to form continuous layers. We believe that it is necessary to maintain these features continuous, on more cross-sections, at a certain species, because the two types can be

confused, if it proves that this feature of continuity/discontinuity varies at the same species. Very interesting is the fact that this peculiar structure of the foliar limb occurs also in the upper third of the stem, although discontinuously (Fig. 9). The second species of *Petrosimonia* present in the Romanian flora, *P. triandra*, investigated by the authors (unpublished data) does not have this structure in the stem. Instead, the structure of the foliar limb is very similar with the one from *P. oppositifolia*; they can be integrated in the same anatomic type (Fig. 18, unpublished data).



Fig. 17. Cross sections through the foliar limb of *Petrosimonia oppositifolia*



Fig. 18. Cross sections through the foliar limb of *Petrosimonia triandra*

At *Camphorosma annua*, the interior architecture of both tissues (PCA and PCR) also defines the same anatomical type, the kochioid one. Furthermore, there is a well-differenced hypodermis and a water storage tissue formed by large cells (Fig. 19).

The kochioid type occurs also in *Zygophyllum simplex* (*Zygophyllaceae*) [82], an annual C_4 halophyte with cylindrical succulent leaves [42]. This species is biochemically C_4 NAD-ME, while the C_4 chenopods with the kochioid type are specific to the NADP-ME subtype [58]. Thus,

C_4 eudicots from two distantly related families have converged on this unique form of Kranz anatomy, yet have evolved different biochemical paths of C_4 photosynthesis [53].



Fig. 19. Cross sections through the foliar limb of *Camphorosma annua*

As we already mentioned there are many variations within the „Kranz anatomy” structure.

Apparently the presence of a layer of chlorenchymatic cells in the vicinity of the vascular bundles is not absolutely necessary for defining a plant as belonging to the C_4 photosynthetic type [69]. Immunological, ultrastructural and biochemical studies have evidenced the relation between these anatomical dispositions and the photosynthetic mechanisms. It is known that a significant part of plant evolution has been the development of mechanisms for inhibiting photorespiration by concentrating CO_2 around Rubisco [38]. Crassulacean acid metabolism (CAM) concentrates CO_2 around Rubisco through the use of dual carboxylation pathways, first by CO_2 fixation with phosphoenolpyruvate carboxylase (PEPCase) and secondarily by Rubisco. C_4 photosynthesis is a second major mechanism for concentrating CO_2 . C_4 plants also exhibit a double carboxylation, but these steps are rather separated spatially in different tissues of the leaf. PEPCase fixation of CO_2 occurs in the outer mesophyll, and malate (or aspartate) is transported to a special sheath of thick-walled chlorophyllous cells, known as the bundle sheath cells, where these organic acid carriers are decarboxylated and CO_2 is concentrated around Rubisco [38]. More than that, the implications of such anatomical structures are much more profound than may seem at first sight, as they might be involved in some stages of the C_4 type plants' evolution; it has been assumed that the evolution of C_4 type plants became possible only after the initiation of an intense activity of the Rubisco enzyme in this bundle sheath. The following steps would have assumed thickening of these bundle

sheath cells, thus preventing the loss of glycin-decarboxylase and other modifications of foliar anatomy, along with restriction of the Rubisco enzyme to these bundle sheath cells [38]. For example the investigations made in some C_4 salsoloid type species from *Chenopodiaceae* showed that there was a very strong labeling for Rubisco in bundle sheath cells with little or no labeling in mesophyll cells [83].

Extremely interesting is the fact that all these anatomic and biochemical „acquisitions” have conferred a natural evolutionary and ecological advantage of these plants. It is generally known that many of the C_4 type plants are linked to habitats conferring quite severe living conditions, for example, deserts or saline soils. Different studies proved that the C_4 plants show higher tolerances to drought, high temperature, high irradiance and salinity. For example many C_4 plants were identified during the investigations conducted in saline meadows of northeastern China. Many of the C_4 species identified were C_4 halophytes [87]. This means that these plants have a greater capacity to tolerate saline stress in the region. Another study showed that 50 species with C_4 photosynthesis were found in deserts of China [88]. This is another example that shows the adaptability of these plants to the severe living conditions.

In the vegetation of Mongolia C_4 *Chenopodiaceae* species make up 45 % of the total chenopods and are very important ecologically in saline areas and in cold arid deserts [59]. Here species with a salsoloid type of Kranz anatomy were the plants most resistant to ecological stress and conditions in highly arid Gobian deserts. Most of the annual C_4 chenopods species were halophytes succulent and occurred in saline and arid environments in steppe and desert regions.

For many of these species, the key to adaptation is the ability to maintain their growing process at high values of temperature and aridity, while the C_4 type plants are latent, which reduce the competition for water. The photosynthetic ratios of the C_4 type plants are not higher than those of the C_3 type plants, although the efficiency of water's utilization is higher [38].

Nevertheless, it must be mentioned that the anatomical type had no predictive value for the biochemical subtype. Correlations can be obviously established between the internal architecture of the foliar limb and the photosynthetic type or the biochemical subtype, but these should not be regarded as having an absolute value. It is more likely our intention to have an integrative anatomical view. The histo-anatomical

investigations should always be completed with biochemical and physiological data.

Our subsequent researches will firstly establish, through repetitions and different methods, if these anatomical features (like the two types of chlorenchyma tissues) have a constant character and not an alternative one.

The anatomic structures of the foliar limb of *Suaeda maritima* (Fig. 20) and of the succulent tissues of *Salicornia europaea* correspond apparently to the anatomic type defined as “sympegmoid” which derives from the name of the *Sympegma* [60].

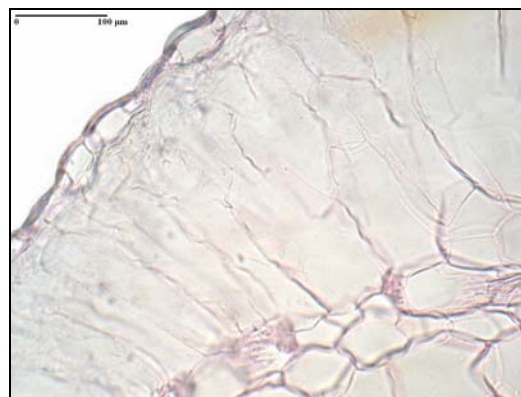


Fig. 20. Cross sections through the foliar limb of *Suaeda maritima*

It consists of peripheric, palisadic cells with small fascicles inside that come in contact with them and of the central fascicle included in the water storage parenchyma.

At *Bassia hirsuta*, the crossing sections through the foliar limb bring a palisadic tissue, bi- or tri-layered, which occupies the biggest part of the section and have a layer of large, water storage cells on their periphery. The limb's succulence is granted by both tissues' presence (Fig. 21).



Fig. 21. Cross sections through the foliar limb of *Bassia hirsuta*

4 Conclusions

All species investigated possess well-established mechanisms that permit them to face the harsh living conditions (soil's excessive salinity, aridity). Thus, at the level of the foliar limb *Atriplex tatarica* evidences vesicular hairs for salts' excretion which appears as an important strategy common to other halophytes. All taxa studied in the present paper, except for *Bassia hirsuta*, present the successive cambia phenomenon at the level of the axial vegetative organs. Many authors consider this phenomenon a structural anomaly which occurs frequently within the *Chenopodiaceae* family [25]; [26]. It might also have a possible evolutionary and ecological significance.

Another important adaptive phenomenon is the succulence which has already been evidenced in *Suaeda maritima*, *Salicornia europaea*, *Camphorosma annua*, *Bassia hirsuta* and *Petrosimonia oppositifolia*. It plays a leading part in salts' dilution of the above mentioned species.

The presence of some tracheoidioblasts in the structure of the succulent tissues of *Salicornia europaea* has been also evidenced. They are possibly involved in the maintenance and dynamics of water inside the plant.

At the same time all species analyzed presented some specific and interesting arrangements of foliar tissues. For example, the atriplicoid type Kranz anatomy was found in *Atriplex tatarica*, the kochioid type anatomy was evidenced in *Petrosimonia oppositifolia* and *Camphorosma annua* while the "sympegmoid" structure was identified in *Suaeda maritima* and *Salicornia europaea*. All these structural features are related to a certain functionality of the photosynthetic apparatus and seem to have had significant evolutionary and ecological implications.

The anatomical characteristics of the analyzed plants may be correlated with the peculiarities of the environment in which the plants grow. Therefore, *Petrosimonia oppositifolia*, *Suaeda maritima* and *Salicornia europaea* are halophytes well adapted to the high salinity of soils and correspond to the category of "obligatory halophytes" [8]; [56]; [78].

Atriplex tatarica seems to have a larger ecological spectrum because it is not strictly related to intense salinity. It has been defined as a "crynohalophyte" because of its (secretory) vesicular hairs. This species may also be considered a nitrophyle plant taking into account the fact that it has been harvested in the vicinity of some possibly nitrogen sources (manure, vegetal rest).

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