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Foreword

The human population continues to grow, and the world population is predicted to reach nine billion people by the year 2050. From annual UN Food and Agriculture Organization (FAO) reports, we know that as a result of the "green revolution," based on Borlaug's cereal breeding concepts, crop production has significantly increased during the period 1950–1990, resulting in an increase in cereal production per person. However, in this century we have learned that improvement in crop production no longer keeps up with population growth. Therefore, we have to consider new concepts when discussing how to improve agricultural productivity worldwide in order to feed our growing population.

Obviously, improving fertilization and irrigation technology, as well as breeding "classical crops," does not result in the enhancement of the annual crop yield at a rate needed to meet the demand. Extending the cropping areas is also challenging, as the land in question is located in arid regions where water is scarce. Additionally, it can be calculated from FAO reports that current irrigation practices lead to annual losses of about 1.6 million ha of arable land due to salting. Current research is being aimed at stopping this loss of arable land, while at the same time encouraging the usage of low-quality water for irrigation. This ambitious goal can be reached (i) if the salt and drought resistance of our crops is significantly improved by conventional breeding methods or (ii) if already resistant species are used as new crop plants. While available literature reports only minor successes utilizing the first option, the latter method appears to generate promising results; for instance, the impressive example of the breeding of sugar beets from its salt-tolerant ancestors. It appears that, in addition to breeding success, the acceptance of new crops in society and convincing farmers to grow these new species, are among the important problems that need to be solved.

The selection of promising plant species and development of breeding concepts requires a detailed knowledge of both the physiology and anatomy of the individual plant species and easily identifiable traits to monitor and rank breeding success. While the information provided about conventional crops is incredibly detailed and widely available, finding information on potential candidates for a new crop species is much more difficult. A better understanding of strategies allowing stress-tolerant plants to thrive in a stressful environment is necessary because these traits will be used to breed resistant conventional crops. The salt-tolerance mechanism in plants was first reviewed in 1977. Since then, many reviews have followed, outlining a gradual development of knowledge about this mechanism. In the sequence of these reviews, it is documented that the investigation techniques have shifted from anatomical and physiological to molecular. It turns out that salt stress resistance is a multi-factorial trait and, therefore, salt-sensitive plants cannot be transformed into resistant ones by transferring only a few genes. Nevertheless, a gradual improvement in stress resistance is observed when adenosine triphosphate (ATP)-ase activity or trans-membrane salt transport capacity is stimulated in transgenic plants in laboratory experiments. This result is in line with the understanding that salt stress will disrupt cellular, tissue, and whole plant levels of homeostasis in water potential, as well as in trans-membrane ion distribution. This adverse effect leads to damage on metabolic (enzyme activities) and structural (membrane and cell structure and function) levels and can be observed by an inhibited growth rate or, eventually, plant death. The three principle targets of salt stress can be distinguished as such: (i) osmotic effects and selectivity of nutrient uptake at root level; (ii) salt interfering with transport processes, secondary metabolism, and growth; and (iii) saving the photosynthetic apparatus from over reduction and reactive oxygen species (ROS) production when the sugar export gets blocked.

Plant species greatly differ in their anatomical adaptations to their preferred environments. As osmotic stress is one side effect of salt stress, plants with higher water use efficiency are expected to show an improved tolerance when exposed to, at least moderate, salt concentrations. Similar observations are expected when comparing plant species differing in their root-to-shoot ratio, especially at locations where evaporation effects have led to high salt concentrations near the soil surface. Based on the previous examples, it is obvious that the analysis of plant anatomy can provide scientists with a look into potential defense mechanisms. Halophytes can be found in most plant taxa. As taxa typically differ in physiology, a huge diversity of structural and physiological adaptations to salt stress can be found among halophytes. Some desert plants avoid salt stress by growing and flowering during the rainy seasons, when salt is diluted. Other species develop succulence under salt stress, which enables these species to dilute salt inside of their vacuoles. Another common strategy is to develop bladders or salt glands and excrete the surplus salt. Overall, these features are setting different scenarios for a plant's water demand, metabolic requirement, and regulation of cell and tissue differentiation. This has to be taken into consideration when ranking plants by their salt resistance and their respective physiological response. Moreover, it can be expected that differing response patterns of gene activity will be found when the plants are under stress, though a detailed description of anatomical features has to be the basis for any further investigation into salt resistance.

The information in this book is presented in two sections, (i) general considerations and (ii) an integrative anatomical study of plant families, and followed by a conclusion. Detailed coverage on the correlation of the degree of stress resistance and anatomical modifications of the analyzed plant families is provided within the sections. In order to improve our overall crop productivity, our collective knowledge about the natural evolution of populations of plant species that have high salt stress resistance will aid in the design of future crop breeding processes, as well as when choosing halophytes for bio-remediation, revegetation, or other ecological purposes.

Hannover, Germany Yelena Churakova
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Iasi, Romania Marius-Nicusor Grigore

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Part II An Integrative Anatomical Study of Halophytes: Anatomical Structure in Different Family Species

Introduction

A UN Food and Agriculture Organization (FAO) report (*The State of Food and Agriculture*, *2007*) shows that despite unprecedented global economic growth, 1.1 billion people continue to live in extreme poverty, and more than 850 million people suffer from chronic hunger, while ecosystems are being threatened as never before.

Modern agriculture faces pressing problems, such as salinization, which is a process that is very common, but difficult to control and ameliorate. According to some projections, between 7 % (about 930 million ha) and 10 % (approximately 954 million ha) of land areas are salt affected. From these areas, about 60–100 million ha are the result of human activity. Poor irrigation, in particular, increases the salinity of agricultural land. Almost half of the world's irrigation systems are affected by salinization and waterlogging. Although irrigation systems occupy about 15 % of the global agricultural system, productivity provided by these surfaces is at least twofold higher than non-irrigated land.

In this scenario of food crisis and environmental problems, salinity and halophytes seem to act as two major key factors.

The interest in the study of halophytes is still argued by theoretical reasons, and especially in the current context of human condition, regarded as a well-defined part of the surrounding environment. Salinity has affected agriculture for millennia, having a deeply negative impact on agriculture and, most likely, being involved in the fall of some previously flourishing ancient civilizations.

Halophytes are plants able to survive in highly saline and arid conditions. Despite that halophytes and xerophytes are usually distinguished as different ecological groups, our opinion is that halophytes should be regarded as a special kind of xerophyte. In fact, in this book, halophytes are ecologically linked with saline soils that are actually affected by physiological drought.

The taxonomical diversity of halophytes is very high; they are heterogeneously distributed among plant families, and this makes their anatomical study quite difficult. In addition, halophyte adaptations represent very interesting structural strategies that help plants to cope with harsh environments; for many other species

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(glycophytes, plants living in fresh water conditions), these habitats would not be suitable for survival and reproduction.

Most likely, halophytes have been recognized from the eighteenth century; despite the huge accumulation of data about halophytes, our knowledge about these fascinating plants is still limited. Nowadays, plant sciences are dominated by molecular, biochemical, and genetic approaches that can deeply dissect many cellular mechanisms involved in salt tolerance. Nevertheless, different ways of approaching halophytes can be useful tools for obtaining a clear picture about all integrated biological levels involved in salt tolerance.

An integrative anatomy approach is proposed in this book as an expression of a tendency to deal with different structures as a whole, to correlate anatomical features with ecological, functional, adaptive, and phylogenetic implications.

This relatively new approach aims to integrate structure with function and seeks different interpretations, in order to provide various explanations (where and as possible), starting from a well identified histological structure.

An interpretation must always be made with caution and nothing is absolute assertions into exhaustive. Such claims were far from our intention, though the temptation to formulate new hypotheses where there are no others is particularly appealing.

Part I
General Considerations on Halophytes

Halophyte Definitions and Classifications

Although halophytes have certainly been recognized since the time of Goethe (ca. 1790, cf. Flowers et al. 1986), they were brought to scientific attention through the papers of Schimper (1891, 1898) and especially Warming (1895, 1897, 1906, 1909). Although halophytes have been recognized for hundreds of years, their definition remains equivocal (Flowers and Colmer 2008). There are many definitions of halophytes; some reflect the scientific background of researchers who define these plants. At the same time, we can notice an "historical" evolution regarding halophytes, taking into account the accumulated data in their biology (Grigore 2012).

Definitions of halophytes are manifold. This is explained by the following considerations (Grigore et al. 2010; Grigore 2012):

1. Halophytes are in fact a heterogeneous ecological group of plants; high salinity was not the only factor "building" the history of these plants, but several additional ecological factors also contributed to their evolution. So, describing halophytes only in relation to salinity could be reductionist. Researchers working on various aspects of halophytes adopted them unilaterally. This is, of course, natural if we think about their "professional" expertise in halophytes. It seems logical that an approach following one single criterion often leads to acceptance and internalization of a single standard definition, which scientists take into account in their research. This is one of the reasons why each author has given a specific definition of halophytes, a definition with a personal "signature" in a certain context that is preserved for several decades.
2. The concept of salinity itself, and hence the concept of saline habitats, is relative and ambiguous. The term "salinity" is not, per se, a biological one; thus, the scenario could become complicated when adopted by other natural sciences. Ecologically speaking, we think that halophytes must be considered all species that vegetate in saline habitats (Grigore 2008a, b; Grigore and Toma 2010a). This definition seems simple and accessible but only at first sight, because saline habitats are, again, imprecisely defined.

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3. As knowledge about halophytes has progressively accumulated, the directions of research have expanded and deepened accordingly. Attention was initially focused on their ecology and distribution. This quite simple interest was based mainly on intuition, allowing some correlations with morpho-anatomical adaptations. However, gradually, many aspects focusing on physiology, salt tolerance, cellular and molecular biology, or genetics were also revealed. This new context has not provided the "ideal" premise that would have led to a convergence in unifying the halophyte definitions. Moreover, it increased the number of definitions. Sometimes, in science, new discoveries deepen the older findings, and are a good opportunity to expose new challenges.
4. Another problem arises from the fact that there is a semantic field related to halophytes (especially regarding their classification). This field is made up of different terms, formulated by different authors, but sometimes these terms are synonymous with each other. Some previous terms were adopted by further researchers and, in a way, the "new" terminology does mean the halophyte semantics are clarified.
5. Not least, it must be emphasized that some difficulties exist when working in experimental conditions, where efforts are made to establish salt-tolerance thresholds. Experimental situations never completely reproduce natural conditions, where environmental factors are always variable. The intensity and variability of these factors are less predictable; in the lab, we can choose the intensity of salinity we want to test, but in the natural ecosystem, the salinity and hydric status of the soil are not constant.

In several previously published papers (Grigore 2008a, b; 2010), we dealt with some general aspects regarding the definition and classification of halophytes. These issues have been reviewed and critically discussed several times (Grigore et al. 2010; Grigore 2012).

In monographic works (Grigore et al. 2010; Grigore 2012), many existing definitions on halophytes have been collected (Table 1), suggesting that there is an "historical evolution" of the concept; moreover, semantic fields (Table 2) related to salinity and salt plants have been identified; these occur especially when translating terms from one language to another.

In the following paragraphs, several definitions and classifications about halophytes are extended.

Stocker (1928) defined halophytes as "those plants which at any stage of their life are subjected to a concentration of salt which is more than "normal" glycophytic plants can bear without dying." Glycophyte is more a convenient term for all plants that cannot grow in places where the concentration of sodium chloride (NaCl) in the soil solution is more than 0.5 %.

Chapman (1942) suggested that it must be understood that this is a purely arbitrary definition. While it may be easy to distinguish between extreme halophytes and glycophytes, it is by no means so easy to determine the class to which a plant should belong at the lower concentrations of NaCl. In addition, field observations and experimental work indicate that the boundary should be placed at about

Table 1 A survey of halophyte definitions (Grigore et al. 2010; Grigore 2012)

Definition or description related to halophytes	References	Comments
A plant containing a large quantity of common salt in its composition, and which thrives best in salty places	Crozier (1892)	Despite its earlier character, this definition is interesting because it suggests the capacity of halophytes to accumulate salt in large amounts. Nowadays, it is known that this refers to a group of halophytes accumulating salt, in contrast with those secreting it
Salt-loving plants (are in the most of their characters, strikingly similar to the xerophytes)	Barnes (1898)	Many plant ecologists consider halophytes a particular form of xerophyte (see further comments in this table)
Species of saline and alkaline soils (salt plants)	Clements (1907)	Saline and/or alkaline soils are more precise terms than other words designating saline environments
A certain amount of soluble salts must be present before halophytic vegetation is called into existence	Warming (1909)	How precise is the term "certain"?
Plants which grow where the water contains salt; the effect upon them is seen in their fleshy habit	Bower (1911)	In fact, the soil solution always contains "salt"; the issue is about concentration. Not all halophytes display fleshy tissue
Strand plants, or halophytes, living along the margin of salt water, and therefore condensed and otherwise adapted to the difficult absorption thereof	Ganong (1913)	It must discriminate that not all halophytes are strand plants; they could appear also in the inland salt marshes/areas
Halo-philous/phytes, plants of sea-coasts and salt-steppes, where the presence of salt, by checking absorption, compels a reduction of transpiration	Willis (1919)	Here it can be noticed the introduction of "physiological drought" hypothesis characterizing saline soils. This is "famous" for a certain period of plant ecology (see Grigore and Toma 2010b; Grigore and Toma 2011)
Plants which at any stage of their life are subjected to a concentration of salt, which is more than "normal" glycophytic plants can bear without dying	Stocker (1928)	The salt concept is ambiguous (see the discussions above). It is difficult to establish if the plants are constantly exposed to salt at any stage of their life cycle
Salt plants; typical halophytes; true halophytes; absolute halophytes[a]; the obligate halophytes are plants which for their normal development need certain ions of the alkali metals and halogens, and which, therefore, can exist and bear seed only in soils containing salt	Braun-Blanquet (1932)	A good definition of obligate halophytes; [a]this is the single place this term was found (!)

(continued)

Table 1 (continued)

Definition or description related to halophytes	References	Comments
Plants that grow in saline soil or in salty water are called halophytes and they are strikingly xeric	McDougall (1941)	An interesting definition stating that halophytes are a peculiar form of xerophyte (for extensive comments, see Grigore and Toma 2010b; Grigore et al. 2011)
All plants that are capable of growing in an environment where there is more than 0.5 % sodium chloride	Chapman (1942)	Chapman's comments: "its (definition) use will not imply that the species is either common or rare in such habitats nor will the term involve the assumption that a plant cannot grow under any other conditions." Salinity is a very changeable ecological factor: choosing a number for drawing a line between two different plant groups could be hazardous
Plants that can tolerate the concentrations of salts found in saline soils are termed halophytes	Oosting (1948)	
Plants tolerant of various mineral salt in the soil solution, usually sodium chloride	Lawrence (1951)	
Plants growing on salinized media	Bucur et al. (1957)	
Plant that grow exclusively on salt soil	Dansereau (1957)	"Exclusively" could also suggest that the author is actually thinking only of euhalophytes
Plants growing in saline soils	Fernald (1950)	
Salt-tolerant plants	Chapman (1960)	Neither salt nor tolerant are well defined
[. . .] the extremely saline soils which are inhabited only by specially adapted plants (halophytes); plants which habitually grow in very salty soils—halophytes, or at least *can* grow in such soils (facultative halophytes); halophytes are plants which can tolerate a considerable degree of salinity	Polunin (1960)	A good definition of euhalophytes; does growing necessarily mean reproducing?
Plants of salty or alkaline soils	Correll and Johnston (1970)	
1. Plants which grow and complete their life cycle in habitats with a high salt content. 2. Usually, the term is reserved only for plants which appear in salty habitats constantly and specifically	Waisel (1972)	1. It is very difficult to precisely say what "high salt content" represents 2. This remark suggests that the term could be applied only to euhalophytes ("true halophytes")

(continued)

Table 1 (continued)

Definition or description related to halophytes	References	Comments
Plants that can tolerate sea water, pure or diluted	Duncan (1974)	The sea water concentration it is not a universal standard, so "pure or diluted" could be regarded as quite relative adjectives
Plants of salty environments; plants adapted to live in a saline environment, be it seawater, a salt-water marsh, or a salt desert. Plants found growing under naturally saline conditions; for terrestrial plants, this means a minimum salt concentration of about 100 mM in the soil solution. Plants adapted to complete their life cycles in salinities about that of seawater	Flowers et al. (1986)	This is perhaps among the first physiological definition of halophytes
The term halophyte literally means salt plants, but is used specifically for plants that can grow in the presence of high concentrations of Na salts	Sharma and Gupta (1986)	Perhaps referring also to the character of euhalophytes
Those species for which saltmarsh is a major, and in many cases only, habitat	Adam (1990)	A good ecological definition
Plants that grow in saline conditions	Ingrouille (1992)	
Plant species with a set of ecological and physiological characteristics allowing growth and reproduction in a saline environment. *Arbitrarily* a salinity of 0.5 % NaCl in soil water should be tolerated by halophytic plants	Gorham (1995) [cited by Rozema 1996]	Some authors are aware of this arbitrariness
Halophytes are defined as those plants which grow and complete their entire life-cycle in saline habitats. Coping with salinity needs adaptations on all levels from the autecological, the tissue and cellular level to subcellular and biochemical adaptations	Breckle (1995)	"Entire" means inclusively producing seeds for assuring plant survival, colonization, and stabilization in any habitat An holistic definition
Plants that occur naturally on soils or in water too salty for the average plants are usually designated as halophytes	Dagar (1995)	
[The growth] of halophytes is optimal at relatively high levels of NaCl, a response which can be explained only in part by the role of sodium as a mineral nutrient in these species	Marschner (1995)	This is an example of an indirect definition of euhalophytes

(continued)

Table 1 (continued)

Definition or description related to halophytes	References	Comments
Halophytes are adapted to survive in a range of saline environments	Weber (1995)	
Halophyte species are those occurring in naturally saline conditions *only*	Aronson and Le Floc'h (1996)	Also suggesting the "obligate" character of (some) halophytes
The vegetation of saline habitats is designated "halophytic"	Poljakoff-Mayber and Lerner (1999)	Saline habitats are defined by these authors as those whose soils contain a high percentage of soluble salts, and one or more of these salt components is usually in excess
Salt-tolerant plants (halophytes, including salt marsh and mangrove plants) are highly evolved and specialized organisms with well-adapted morphological and physiological characteristics allowing them to proliferate in the soils possessing high salt concentrations	Khan and Duke (2001)	A good holistic definition
Plants that can grow on soils with a high salt content are termed halophytes	Fitter and Hay (2002)	
Plants that can survive in or benefit from an environment with a high level of salt (i.e., sodium chloride), as in saline soils and seawater	Mooney and Canadell (2002)	
A plant or microorganism that grows well in soils having a high salt content	Mc Graw-Hill Dictionary of Bioscience (2003)	
Halophytes are salt-resistant or salt-tolerant plants that thrive and complete their life cycles in soils or waters containing high salt concentration	Ness (2003)	
Halophytes are able to adapt faster and to tolerate extreme salinity	Schulze et al. (2005)	A deeper physiological definition
Plants that are able to grow on mildly to strongly saline soils (halobiomes). Halophytes which tolerate or endure high levels of salt are known as euhalophytes	Ingrouille and Eddie (2006)	"Mildly", "strongly", and "high levels" are terms that are not so well defined. However, these authors are among the only ones to distinguish between "halophytes and salt-tolerant plants", a very subtle but pertinent remark in the context of our previous discussions on the semantic field

(continued)

Table 1 (continued)

Definition or description related to halophytes	References	Comments
Plants that survive to reproduce in environments where the salt concentration is around 200 mM NaCl or more	Flowers and Colmer (2008)	
Halophytes grow naturally in very salty soils; they still have not lost their resistance mechanisms to salt-stress conditions	Koyro et al (2008)	
Plants of saline habitats	Holzapfel (2009)	
Plants able to complete their life cycle on saline substrates	Koyro et al (2009)	
Plants that are tolerant of excess salt	Quinn (2009)	

Table 2 Semantic field with different words related to halophytes (Grigore 2010)

Romanian	English
Halofite; plante de sărătură; plante halofile; plante iubitoare de săruri; plante de locuri sărate	Halophytes; salt-tolerant plants; salt plants; high-salinity tolerant plants; salt-loving plants; halophylous plants; halophytic plants; maritime plants

0.5 % NaCl in the soil water. However, it has been repeatedly highlighted that such definitions based on numerical data must be carefully considered; comparisons between field and laboratory results must be also made with special caution (Grigore et al. 2011; Grigore et al. 2012a, b). Chapman (1942) defines halophytes as those plants that are capable of growing in an environment where there is more than 0.5 % NaCl. Its use will not imply that the species is either common or rare in such habitats nor will the term involve the assumption that a plant cannot grow under any other conditions. The halophytes will not include plants that grow in places where the soil is characterized by an excess of a salt other than NaCl, e.g. inland areas where there is an excess of magnesium salts. The flora of such places should be distinguished from halophytes, as defined above, and the plants should be placed in another category. In the past, they have commonly been included as halophytes.

Many authors are operating with different terms when referring to halophytes, such as euhalophyte or miohalophyte. Chapman (1942) suggested that this term be restricted to those plants whose optimal growth takes place in an environment in which there is more than 0.5 % NaCl. He also stated that it is impossible to define more accurately the term "optimal growth". It is difficult to say growth to maturity because plants may flower and set seed and yet be weak or stunted. Whilst field observations may indicate whether or not growth is approaching optimum, experiment must ultimately be the decisive factor. Euhalophytes will not grow unless there is an abnormal concentration of NaCl in the habitat. This category includes species of *Salicornia, Rhizophora*, and the "submerged" halophytes, e.g. *Zostera, Cymodocea, Posidonia*.

The term miohalophyte would be applied to those plants that are to be found, either commonly or rarely, in habitats where there is more than 0.5 % NaCl; their optimal development occurs, either naturally or experimentally, in an environment where there is less than 0.5 % NaCl (Chapman 1942). The author himself admitted that, in many cases, it is difficult to know whether a species is a eu- or miohalophyte. Attention should be paid to the fact that the term miohalophyte is almost completely unknown in Romanian botanical language (for extensive and detailed discussions about this issue, see Grigore 2008a, b; 2012).

Van Eijk (1939) suggested that miohalophytes could be divided into two classes:

1. Plants that normally grow under glycophytic conditions but that nevertheless have some resistance to a concentration of more than 0.5 % NaCl. The evidence is based either upon growth in culture solutions or else upon records of occasional plants growing in a halophytic environment. This group can be termed the haloglycophytes, and then the true miohalophytes will form the second group.
2. Plants that normally grow on saline soils, but whose optimal development is under glycophytic conditions. This category includes a very large number of plants that grow around sea shores, e.g. *Aster tripolium*, *A. subulatus*, *Triglochin maritimum*, *Plantago maritima*, *P. oliganthos*.

In light of these considerations, it is most likely that the large majority of halophytes are really miohalophytes and that euhalophytes form a relatively small class. In addition, halophytes grow as well, or often even better, under glycophytic or less salinized conditions (Grigore et al. 2012b). Perhaps the great number of miohalophytes vegetate in saline environments because they are unable to compete successfully with glycophytes in non-saline areas (Chapman 1942).

Controversies regarding definition and classification of halophytes are due, inter alia, to their ecological complexity, as a distinct polymorphic group. In fact, our perception often correlates apparent and immediate "cause" to "effect", i.e. the halophyte to salinity, and vice versa, but often extra depth and insight can integrate the problem in a more complex area.

For example, we can choose the plants that vegetate on sea beaches and dunes. The question "Should they really be seen as halophytes?" is one advanced particularly by foreign researchers who also studied vegetation from these ecosystems; their studies showed that the root system of these species is often located in the freshwater phreatic layer of maritime dunes (Hill and Hanley 1914; Chapman 1937). This issue, originally released in the form of a rhetorical question (Kearney 1904), took into account other environmental factors also playing a key role in these habitats (winds that can bear salt spray, intense sunlight, overheating due to reflection of solar radiation by sand).

Kearney (1904) concluded that these plants are not generally halophytic, but rather xerophytic.

Stocker (1928) suggested that the term xero-halophyte should be reserved for plants of the salt (NaCl) desert, and that the term aero-halophyte should be reserved for plants that are subjected to salt in the form of either spray or powder. Schratz (1934), on the other hand, regarded the dunes as xero-haline in contrast to the hygro-haline habitat where there is a salt-water table. Examples of plants growing on the former are *Arenaria peploides, Psamma arenaria, Eryngium maritimum*, and on the latter any of the salt marsh plants, e.g. *Limonium vulgare, Triglochin maritimum, Spergularia marginata*.

Iversen (1936) proposed a classification that is based upon the amount of NaCl present in the soil water table; since the roots of many plants do not reach down to this depth, a more satisfactory criterion would be the percentage of $C1^{-}$ present in the soil water at the absorbing region.

Based on Iversen's classification (1936), Chapman (1942) proposed the following system, including different groups of halophytes:

Miohalophytes

1. *Glyco-mesohalophytes*. Plants that grow in habitats with a range of 0.01–1.0 % NaCl.
2. *Euryhalophytes*. Plants that grow in habitats with a range of $0.1 < 1.0$ % NaCl.

Euhalophytes

1. *Mesohalophytes*. Plants that grow in habitats with a range of 0.5–1.0 % NaCl.
2. *Meso-euhalophytes*. Plants that grow in habitats with a range of 0.5 to <1.0 % NaCl.
3. *Euhalophytes*. Plants that grow in habitats with more than 1.0 % NaCl.

The survey of classifications reviewed here and in several works (Grigore 2008a, 2008b; Grigore 2012) revealed that, in some cases, the criteria underlying a classification system is well defined (although in itself may be, however, relatively); sometimes, the criterion seems rather vague and intuitive, based on elements that are not necessarily strictly quantifiable.

However, several classifications are based on the brilliant insight of Romanian botanists: the classification by Guşuleac (1933) refers to "natural colonization of salinized areas with plants." Prodan (1939) uses the following criterion in order to classify salt plants: "the way in which plants support salt"; Ţopa (1939) chooses as a criterion "the behavior of plants in relation to salinized environments." Even so, it is surprising to see that such classification systems are "confirmed" in time by other's classifications, based on more complete and elaborate data. According to this idea, it is worth mentioning the system by Bucur et al. (1957), based on quantifiable measurable data, such as the values of salinity in the rhizosphere, in relation to plant growth (Grigore 2013).

Finally, in other situations, certain systems of classification are adapted from other authors and the language used is more or less modified.

Breckle (1995) defines halophytes as those plants that grow and complete their entire life cycle in saline habitats.

Table 3 Complexity levels of salt (NaCl) in plants and vegetation (complexity levels) (Breckle 1995)

Effective level	Example of response
Biochemical effects	Gene regulation, enzyme activities, DNA changes
Effect on membranes	Permeability, electr. potential
Effects on cell organelles	Respiration, photosynthesis, secondary compounds
Interactions with cells	Formative effects, defects
Interactions with tissues	Formative effects, altered differentiation
Interactions with intact, whole plants	Hormonal balance, mineral metabolism, water budget, adaptation and modification, growth, developmental stages
Responses of populations	Reproduction, age distribution, competitive abilities, selection
Interactions and responses in ecosystems	Salt and nutrient cycling, accumulation, mass balance, species composition, energy flow
Interactions in biomes, in the biosphere	Cycling of salt, energy flow, sedimentation, accumulation in erosion basins

However, it is very good to know and understand that coping with salinity requires changes at all levels, from the ecosystem to the plant tissue, at cellular, subcellular, and biochemical levels (Table 3). It is difficult to discuss all this in one sentence, because each level of understanding belongs to another discipline; only an interdisciplinary approach regarding salinity and its effects on each level can provide a unified picture of the adaptations in halophytes.

Breckle (1995) classified halophytes according to ecophysiological approaches, taking into account the salt uptake and fate of the salt within the plant body. Therefore, he distinguished the following:

1. Plants that are very selective with their root cell membranes and thus can exclude the great majority of NaCl from being taken up can be referred to as non-halophytes. Most plants are non-halophytes, growing in terrestrial regions with low salt concentrations in soil.
2. Plants that can withstand higher salinities without having any special adaptations, besides a very good electivity at their root membranes and in other plant tissues. They often tend to accumulate NaCl in the roots and the lower shoot parts (xylem parenchyma). These species can be nominated as pseudo-halophytes.
3. Euhalophytes are plants where a higher uptake of salts and transport to the shoot can be observed; either the leaves and/or the stems become succulent.
4. Another type of halophyte exhibits elimination of salt by special structures on the aerial organs. This elimination, called recretion,[1] is observed in a great variety of salt gland-bearing plants. These secretory structures in halophytes have been recently reviewed (Grigore and Toma 2010b).

Figure 1 is a schema of halophyte classification proposed by Breckle (1995).

[1] For further explanations regarding secretory processes in halophytes, see Grigore (2011) and Grigore and Toma (2010b).

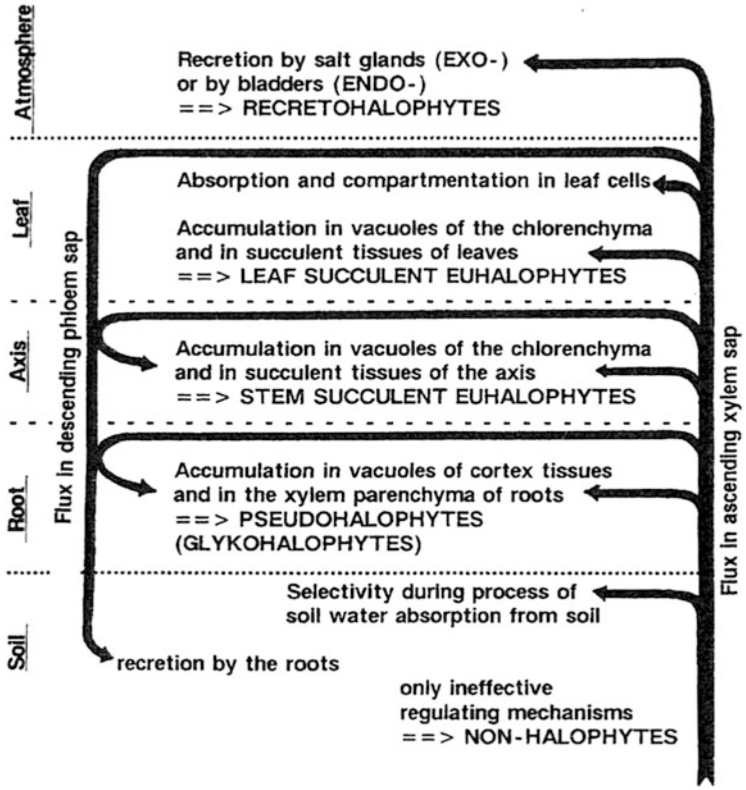

Fig. 1 Major classes of halophytes, taking into account the salt uptake, salt storage, and salt recretion (Breckle 1995)

The work of Bucur and collaborators in halophytes (1957, 1960, 1961) provided an original classification of halophytes based on their research (Grigore 2013). This research was conducted in order to establish the halophytic degree (affinity of plant species for soil salinity) in a huge number of plants naturally growing in saline areas from Jijia-Bahlui. Thus, a total of over 400 (!) salt-tolerant plants have been investigated in relation to their corresponding salinity from the rhizosphere.

For this purpose, the salinity in the rhizosphere of every found species was measured by two distinct methods, each one applied in different variants. In this way, they were able to identify the salinity threshold of each species (minimal, optimal, and maximal values). In addition, several patterns in plant behavior in terms of salinity level were clearly and logically described. Finally, based on these consistent data, a new completely original system of halophyte classifications has been proposed (Table 4).

This classification is perhaps among the most consistent and harmonious of all existing worldwide (Grigore 2013). Many classification systems are based on arbitrary criteria (see extended comments in Grigore 2008b; Grigore 2012), also

Table 4 Classification of halophytes according to Bucur et al. (1957)

Halophytes (plants vegetating in saline environments)
Euhalophytes: Halophytes strictly adapted to salinity (strictly obligated to salinity) are exclusively preferential and grow only on salinized environments, with the entire, or part of a, radicular system, both as seedlings and as mature plants
Neohalophytes: Plants able to adapt to salinity; plants adapted to the halophytic environment; they are supporting and preferential, living both on non-salinized and on salinized media, with the entire, or a part of a, radicular system
Non-halophytes (plants that do not grow in saline environments)
Plants non-adapted to salinized media, non-tolerant to high concentrations of salinity. In relation to concentrations more than 30–40 % milligrams of soluble salts, they could be tolerant and preferential

taking into consideration the numerical values chosen to describe the thresholds of salinity in which halophytes are to be included.

Moreover, with respect to other major classifications previously devised by Prodan (1939) and Ţopa (1939, 1954), a system to harmonize all these classifications has been created (Table 5).

Going deeply and having much data at their disposal, Bucur et al. proposed some hierarchies within euhalophytes (Table 6) and neohalophytes (Table 7), in respect to degree of soil salinization. These specifications are also relevant for the ecological description given by Bucur et al. (1960, 1961).

Another interesting classification of halophytes, resulting from complex research, is that provided by Pătruţ et al. (2005). They investigated the biodiversity of halophytes from Banat Plain (Câmpia Banatului), and classified halophytes according to soil reaction, humus amount, the proportion of various mineral ions in the rhizosphere, and the amount of water in the soil during the growing season. Therefore, halophytes were included in several categories:

1. Species adapted to intensely salinized biotopes with carbonate-sodic and sulphate-sodic types of salinization; these soils contain a high amount of $CaCO_3$, HCO_3^-, CO_3^{2-}, and Na^+, a strongly alkaline reaction, and low humus content. Depending on water factors, these species are grouped into two categories:

   (a) xeromesophilous species, which vegetate in biotopes that are moderately wet in spring and intensely dry in summer and autumn, such as *Camphorosma annua*, *Artemisia santonica*.

   (b) mesophilous species, which vegetate in biotopes that are intensely wet in spring and dry during summer, such as *Puccinellia distans* spp. *limosa*, *Limonium gmelini, Chamomilla recutita.*

2. Species adapted to moderately salinized habitats having carbonate-sodic and sulfate-sodic types of salinization; these soils have a high content of $CaCO_3$, HCO_3, CO_3^{2-}, and Na^+, a strongly alkaline reaction, and are rich in humus. These species occupy biotopes that are moderately to intensely wet in spring and